

Effects of linear anthropogenic corridors on insect pollinator movement and diversity, and
understory shrub fruit production in the boreal forest of northeastern Alberta

by

Connor Jacob Nelson

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Abstract

Fragmentation of habitats is a primary concern in the conservation of global biodiversity.

Anthropogenic linear disturbances, such as roads, trails, and power lines, are a major source of habitat fragmentation worldwide. In Alberta's boreal forest, a common, pervasive type of disturbance is seismic lines. These long, narrow, clear-cut corridors criss-cross the landscape at densities of up to 50 km/km² dissecting and fragmenting mature forest environments with early seral ones. Seismic lines are known to affect a wide variety of organisms, such as creating movement barriers for some birds, acting as dispersal corridors for invasive plants, and directing the movement of bears, caribou, wolves, and butterflies. Seismic lines have also been found to increase fruit production for a common understory shrub, *Vaccinium myrtilloides*, the velvet leaf blueberry. Little is known about the mechanism and specifically how it relates to pollination by insects. In this thesis, I investigate the effects of seismic lines on understory shrub reproduction, with a specific focus on pollination and the behaviour of insect pollinators.

First, I assessed how seismic lines affect fruit production of understory shrubs, including *V. myrtilloides*, and tested whether insect pollination explains these responses. Specifically, I collected data on fruit production and flower visitation by insect pollinators at 12 replicated xeric forest sites, each with a 30 m transect on a seismic line and adjacent forest interior to compare fruit and flower visitations. I found that *V. myrtilloides* fruit production and pollinator visits on seismic lines were both 3-times higher compared to nearby forest interiors. I also found that pollinator richness was significantly related with fruit production, suggesting that insect pollination is a key mechanism for the observed increase in fruit production on seismic lines.

Second, I investigated how the abundance, diversity, and movement of bees, an important group of insect pollinators, responded to the presence of seismic lines. Specifically, I compared pan

trap samples placed on seismic lines to those placed in the interior forest and found that bees were 3-times more abundant and 1.5-times more diverse on seismic lines. I also used directional malaise traps to assess if bees preferentially travelled along seismic lines. I found that bees travelled 3-times more frequently along seismic lines and likely use them as travel corridors, potentially expanding their foraging range and thereby increasing interactions between previously isolated plant-pollinator communities.

These results suggest that seismic lines affect the movement and behaviour of insect pollinators and change the way they provide pollination services. They also broaden our understanding of how organisms respond to linear anthropogenic corridors with important implications in the conservation of both pollinator and understory plant species in the boreal forest.

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Chapter 1 – Forest fragmentation, corridors, and pollination

Anthropogenic habitat loss is considered a major threat to biodiversity (Millenium Ecosystem Assessment, 2005). Habitat fragmentation, a process that breaks continuous natural habitats into smaller, more isolated patches (Fahrig, 2003), frequently accompanies habitat loss and has been identified as an area of primary concern for the function and biodiversity of ecosystems (Fletcher et al., 2018; Haddad et al., 2015; Krauss et al., 2010). The overall effects of fragmentation on biodiversity are contested among experts (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018). Responses are highly variable among species, with many responding positively to some forms of fragmentation (Fahrig, 2017; Fahrig et al., 2019; Riva et al., 2018a; Townsend & Levey, 2005; Winfree et al., 2011) and many responding negatively (Dabros et al., 2017; Fletcher et al., 2018; Haddad et al., 2014; Potts et al., 2010; St. Clair et al., 1998).

Fragmentation is known to drastically affect an ecosystem's connectivity – the flow of organisms and ecological processes (Taylor et al., 1999). Organisms rely on a well-connected ecosystem to disperse, forage, and migrate, and there is a movement in the field of conservation towards practises that restore connectivity (Krosby et al., 2010). This has led to the study of ecological corridors, which are often used to increase connectivity between habitat patches (Gustafsson & Hansson, 1997). Whether they are highway crossings for wildlife (McDonald & St. Clair, 2004) or cut blocks through mature forest (Haddad, 1999), corridors have been shown to facilitate movement and connectivity in a wide range of organisms (Bayne et al., 2005; Boscolo et al., 2017; James & Stuart-Smith, 2000; Latham et al., 2011; Riva et al., 2018b; Roberts et al., 2018; Suárez-Esteban et al., 2013; Tigner et al., 2014; Townsend & Levey, 2005). This increased connectivity, though usually considered a positive effect, can also have negative effects.

Increased connectivity can facilitate interactions between communities that were isolated under natural conditions, causing them to function more like a single community. This can cause taxonomic homogenization among plant-pollinator communities and make them more vulnerable to disturbances such as disease (Haddad et al., 2014; Keith et al., 2009; Leibold et al., 2004). Thus, it is important to study the responses of species to specific types of disturbances in specific ecosystems to better inform conservation at smaller, regional scales.

As the world's third largest producer of crude oil, fossil fuel extraction is a major industry in Canada (Government of Canada, 2020). Indeed, 97% of the country's oil is located in oil sands, which often require open pit mines to extract the oil with all of the native habitat removed (Government of Canada, 2020; Northrup & Wittemyer, 2013). However, most of these oil sand reserves are located deeper than economically feasible to extract through open pit mining, requiring instead "in situ" extraction methods (Government of Canada, 2020; Northrup & Wittemyer, 2013). These methods do not remove as much habitat as open pit mining, but they still cause widespread habitat disturbance due to the seismic assessments necessary to locate underground reserves, creating linear anthropogenic corridors, locally known as seismic lines (Lee & Boutin, 2006; Rosa et al., 2017; Van Rensen et al., 2015) and in some places exploratory and extraction well pads and road infrastructure. Seismic lines, however, represent the largest in situ footprint and the one with the greatest effect on forest fragmentation.

Seismic lines are long, narrow, anthropogenic corridors created during seismic assessments, where woody vegetation is removed in order to transport industrial equipment (Lee & Boutin, 2006; Pattison et al., 2016; Van Rensen et al., 2015). In Alberta, conventional seismic lines are generally 6 – 10 m wide, with an average density of 5 km/km², but densities can reach up to 20 km/km² in some regions (Lee & Boutin, 2006). Although the industry transitioned to "low

impact” seismic lines in the late 1990’s and early 2000’s, there are still hundreds of thousands kilometers of conventional seismic lines remaining across the boreal forest (Dabros et al., 2018). Many seismic lines have remained undisturbed since they were initially created. This results in the natural regeneration of early seral forests on seismic lines (Filicetti & Nielsen, 2018; Finnegan et al., 2018). However, this regeneration is highly variable between ecosites, with dry, upland sites regenerating twice as fast after fire as nearby interiors (Filicetti & Nielsen, 2018), while many seismic lines in wet areas fail to show any significant signs of regeneration even after 50 years (Van Rensen et al., 2015). The linear removal of woody vegetation also creates a unique landscape structure, making it easier for a wide range of organisms to move. Several species preferentially move along seismic lines, including black bears (Tigner et al., 2014), caribou (James & Stuart-Smith, 2000; Tattersall et al., 2020), wolves (Latham et al., 2011), birds (St. Clair et al., 1998), butterflies (Riva et al., 2018b), and invasive plants (Roberts et al., 2018).

Recently, seismic lines have also been found to increase the fruit production of *Vaccinium myrtilloides*, the velvet leaf blueberry (Dawe et al., 2017). This is a dominant species in dry, upland boreal forests in Alberta, especially in recently post-burned sites, that is culturally significant to the region’s Indigenous Peoples (Hart & Chen, 2008; Kuhnlein & Turner, 1992; Macdonald, 2007; Turner & Cocksedge, 2001). Previous research has shown that fruit production in this species is positively correlated with canopy openness (Moola & Mallik, 1998; Nielsen et al., 2020), but the precise mechanism(s) that drive this correlation are currently unknown. Although increased sunlight exposure is a likely contributor (Moola & Mallik, 1998), studies on *V. myrtilloides* and other members of the genus have shown that pollination by insects is of importance to its reproductive success, partially due to its self incompatibility (Fournier et

al., 2020; Moisan-Deserres et al., 2014). It is currently not known how seismic lines affect insect pollination.

Pollination by animals is a vital ecosystem service in terrestrial ecosystems and is important in maintaining flowering plant diversity (Allsopp et al., 2008). Over 85% of flowering plants rely on some form of animal mediated pollination for effective sexual reproduction (Ollerton et al., 2011). This holds true for the boreal forest, despite the apparent dominance of wind-pollinated plants. Many understory shrubs in the boreal forest, such as *V. myrtilloides*, rely on insect pollination to effectively reproduce (Allsopp et al., 2008; Barrett & Helenurm, 1987; Kevan et al., 1993). Declines in insect pollinators, especially bees, have been reported worldwide (Burkle et al., 2013; Goulson et al., 2008; Potts et al., 2010), with habitat fragmentation often identified as one of the drivers of these losses (Goulson et al., 2008; Potts et al., 2010; Winfree et al., 2009). Given the irreplaceable ecosystem service provided by insect pollinators, it is of great interest to understand how they respond to specific types of fragmentation.

In this thesis, I investigate how linear anthropogenic corridors (seismic lines) affect insect pollinator abundance and diversity, and understory pollination. In Chapter 2, I assess how flower visitation by insect pollinators is affected by seismic lines, and whether these differences can explain variation in understory shrub fruit production. In Chapter 3, I test the affect of seismic lines on the abundance, diversity, community composition and movement of bees, an important group of insect pollinators.

Chapter 2 - Insect pollinator richness explains increased fruit production in an ericaceous shrub on linear anthropogenic corridors

Abstract

Anthropogenic linear disturbances are a major contributor to habitat dissection and fragmentation. The boreal forest of western Canada is highly fragmented due to frequent wildfires and industrial development. Seismic lines, narrow anthropogenic linear corridors, are a common type of anthropogenic linear disturbance in western boreal forests of Canada. Seismic lines have been shown to direct the movement of animal species, accelerate the spread of invasive plant species, and increase the fruit production of some shrub species. It is currently unclear how the various abiotic and biotic changes on seismic lines interact to affect the understory shrub community. Here, I investigated whether increases in insect pollination explain increases in fruit production on seismic lines in common boreal shrubs. Specifically, I hand-net sampled pollinator visitation (abundance and richness) on flowers and tracked fruit production between paired transects on seismic lines and adjacent forest interiors at 12 replicated sites in northeast Alberta, Canada. *Vaccinium myrtilloides*, the most abundant species, had significantly higher fruit production on seismic lines compared to adjacent forest interiors, and pollinator rarefied species richness explained this variation, even when accounting for flower abundance and vigour. These results identify one mechanism by which a common boreal shrub species responds to linear anthropogenic corridors in the boreal forest.

Introduction

Anthropogenic corridors are a pervasive type of environmental disturbance that take many forms, such as roads, trails, power lines, or industrial cut lines. These corridors dissect and fragment the landscape, reducing habitat patch size for many species, and increasing the prevalence of habitat edges (Forman et al., 2003; Forman & Alexander, 1998; Laurance et al., 2009; Pardini et al., 2005). Seismic lines are a type of linear anthropogenic corridor created by industrial fossil fuel exploration and are a common type of disturbance in the boreal forests of northeastern Alberta, Canada, with densities up to 50 km/km² in some regions (Lee & Boutin, 2006). These cut lines have a wide variety of effects, including acting as a habitat barrier that ovenbirds are less likely to cross (Bayne et al., 2005), increasing butterfly abundance and diversity (Riva et al., 2018a), and serving as travel corridors for wolves, caribou (James & Stuart-Smith, 2000), black bears (Tigner et al., 2014), butterflies (Riva et al., 2018b), and invasive plants (Roberts et al., 2018). Seismic lines also positively affect the fruit production and vigour of the shrub *Vaccinium myrtilloides*, the velvet leaf blueberry (Dawe et al., 2017). Although abiotic conditions on seismic lines may be favourable for understory shrubs (Stern et al., 2018), such as higher canopy openness resulting in higher energy available for both shrub growth and fruit production, Dawe et al. (2017) found an increase in *V. myrtilloides* fruit production on seismic lines over and above its increase in vigour. This suggests the possible presence of a biotic factor enhancing fruit production of shrubs on seismic lines. Here I test the hypothesis that this increase in fruit production is related to flower visitations by insect pollinators.

Despite the fossil fuel industry's transition from wider, conventional seismic lines to narrow, "low-impact" lines in the mid-1990s (Dabros et al., 2018), many of these legacy conventional

lines have not fully recovered, with less canopy cover than the adjacent forest (Van Rensen et al., 2015). This results in higher sunlight exposure, temperature, wind speeds, and soil temperature on seismic lines (Dabros et al., 2017; Stern et al., 2018). Increased light levels are known to improve plant growth and fruit production in *Vaccinium* species (Faison et al., 2014; Moola & Mallik, 1998; Nielsen et al., 2020). However, there are other factors that may be improving fruit production of shrubs on seismic lines relative to adjacent interior forests. Insect pollinators have been found to preferentially visit flowers along anthropogenic corridors in other forested landscapes (Tewksbury et al., 2002; Townsend & Levey, 2005). There is evidence that this holds true for seismic lines, at least for some pollinating insects, as butterflies preferentially travel along seismic lines in Alberta's boreal forest (Riva et al., 2018b). Additionally, both bees (Winfrey et al., 2007) and butterflies (Riva et al., 2018a) show a preference for some disturbed areas in temperate and boreal forests. Given the direct link between insect pollination (especially by bees) and fruit production in *Vaccinium* species (Usui et al., 2005), an increased visitation rate of insect pollinators could be contributing to increases in fruit production on seismic lines relative to intact forest.

Given the importance of understory fruit production to indigenous peoples and certain wildlife, it is of interest to understand the mechanisms by which seismic lines increase fruit production (Gottesfeld, 1994; Kuhnlein & Turner, 1992). The objectives of this study were to investigate: 1) If fruit production of common boreal shrubs is higher on seismic lines compared to nearby interior forests; 2) If flower visitation by insect pollinators explains variation in shrub fruit production. Although I targeted all shrubs, *V. myrtilloides* and *R. acicularis* were the only ones that were sufficiently abundant to examine and are therefore the two of focus here.

Methods

Study Area and Site Selection

I 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 6-12 m in width, crisscrossing the landscape in a grid pattern at densities averaging at least 1.5 km/km² (Lee & 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 & Nielsen, 2018).

I 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 (Figure 2.1A). 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 clear-cuts, 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. At each site I established 10 circular quadrats 1 m in radius along each transect. I placed quadrats systematically 3 m apart along the length of the transect, and randomly 0-3 m on either side of the transect (Figure 2.1B).

Understory Plant and Pollinator Sampling

To assess the effect of seismic lines on fruit production of common understory shrubs, I collected data at each site on the abundance of fruit and flowers on shrubs for both the seismic line and interior forest. Although *V. myrtilloides*, as the most abundant shrub species, was the main focus of this study, I also collected data on other woody shrubs. I counted the number of fruit and flowers of each species in various phenophases (flower buds, flowers, unripe fruit, ripe fruit) in each quadrat continuously throughout the season. In many plots, shrub density was prohibitively high, so I estimated the total number of reproductive bodies in the 1-m radius quadrat by counting the fruit and flowers within three sub-samples of 1% cover of each species. I averaged these sub-samples to estimate the number of fruit and flowers per-percent cover of each species. I multiplied these values by percent cover estimates of the quadrat to get an estimate of the total number of fruit and flowers of each species in each quadrat. If a single plot contained multiple phenophases, I completed this process for each phenophase individually. I report the total fruit and flower values for each transect. With then quadrats per transect, these values represent a sampling area of approximately 31.4 m².

I used fruit production as a metric for reproductive success. I defined fruit production as the highest number of fruits, ripe or unripe, counted for a plant species in a quadrat on any single site visit. This definition is comparable with Dawe et al. (2017), who measured fruit production as the number of fruits on a plant after fruit set but before full ripening.

To assess the effect of seismic lines on flower visitation, I sampled pollinators using hand netting of insects on flowers. An assistant and I walked along each transect for 20 minutes, catching any insect that landed on a flower within 4 m of the transect, for a total sampling area of 240 m². I recorded plant species at the time of capture. The insect species was identified to the species

level using taxonomic keys, and where no keys existed, to morphospecies. I identified all bees (Superfamily Apoidea), J. Acorn identified all Lepidoptera and Coleoptera species, B. Wingert identified all Diptera species, J. Glasier identified all Formicidae species, and I. Jimenez identified all remaining Hymenoptera species. All visiting insects were considered potential pollinators and are referred to hereinafter as “pollinators”. Although other methods have been developed to more accurately identify effective pollination, such as single visit pollen deposition, they are prohibitively time consuming, and would not have allowed replication across sites (King et al., 2013). For these reasons, I selected visitation as the most appropriate pollination metric, as has been done in similar studies (e.g. Grindeland et al., 2005; Herrera, 1989; Lopezaraiza-Mikel et al., 2007).

I visited each of the 24 transects (12 pairs) 10-15 times throughout the season, for a total of 300 unique visits between May 9 - August 10, 2019. I collected data on fruit and flower abundance and pollinator visitation during each visit, but did not collect pollinators on rainy days, as they have been shown to change their foraging behaviours during rain (Vicens & Bosch, 2000). I always visited sites between the hours of 09:00 and 17:00. Although exact timing can differ, daytime pollinators tend to be most active within these hours, and restricting the timing of sampling is standard for pollinators (Ballantyne et al., 2017; Forup et al., 2008; Lefebvre et al., 2014; Riva et al., 2020).

At the end of the season (July 24-28), I also collected data on understory shrub abundance, diversity, and canopy openness. I identified and measured the abundance of all shrubs. I counted all plants with stems inside the 1-m radius quadrat to measure the abundance of each species. Totals are reported for each transect, with a total sampling area of approximately 31.4 m². For all shrub species, I measured the maximum height in each quadrat as a proxy for vigour since it has

been shown to be a useful proxy elsewhere (Dawe et al., 2017). I also measured canopy openness using a spherical densiometer, held at breast height, in three locations along each transect: one at each end and once in the center, averaging the values for a single transect-level value.

I calculated species diversity for shrubs, as well as flowers and pollinators, for all species at the transect level using rarefied species richness and Shannon's Hill number. Rarefied species richness, as opposed to raw richness, accounts for sample size when comparing the number of species between sites. 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. It is the number of equally abundant species necessary to produce the observed value of diversity (Hill, 1973; Oksanen et al., 2019).

Statistical Analysis

To address my first question, as to how seismic lines affect fruit production, and also to test the effects of seismic line on pollinator visitation, and other variables potentially related to fruit production, I ran a generalized linear mixed model (GLMM) for each shrub species with fruit production as the response variable. In the end, I only had enough data for statistical analysis on two shrub species: *Vaccinium myrtilloides* and *Rosa acicularis*. Treatment type (seismic line vs. interior forest) was included as a fixed explanatory effect and site was included as a random effect. Next, I used pollinator abundance, pollinator rarefied richness, and pollinator Shannon's Hill number as response variables. I created separate sets of models for each shrub species and a set of models for total pollinator abundance and diversity observed on all flower species. I also created models with flower abundance as the response variable for each shrub species, as well as

models for total flower abundance, rarefied richness, and Shannon's Hill number for all flower species as response variables. For each shrub species, I also created models with abundance and vigour as response variables. Finally, I created a model with canopy openness as the response variable.

I also visualized the effect of seismic lines on pollinator species composition using a Nonmetric Multidimension Scaling (NMDS) analysis using a Bray-Curtis distance estimation matrix (McArdle & Anderson, 2001). I also used permutational multivariate analyses of variance (PerMANOVA) using both Bray-Curtis (which considers species relative abundances) and Jaccard (which considers only species' presences/absences) distance estimation to test the dissimilarity of seismic line and interior pollinator communities. I included treatment type, flower abundance, canopy openness, study site, and an interaction between flower abundance and treatment type as predictor variables in both analyses.

To address my second question on whether the variation in fruit production can be explained by flower visitation, I created another GLMM for each shrub species. I used fruit production as the response variable, site as a random effect, and flower abundance, vigour, canopy openness, pollinator abundance, and pollinator rarefied richness as fixed explanatory effects. I chose pollinator richness over pollinator Shannon's Hill number as the diversity metric so that rare pollinator species were given more weight, as some plant species require fewer visits for equally effective pollination (Madjidian et al., 2008). I also included all two-way interactions between canopy openness, flower abundance, and pollinator abundance, as well as the interaction between canopy openness and pollinator rarefied richness, and the interaction between flower abundance and pollinator rarefied richness.

To better understand how these explanatory variables affect one another, I created several more GLMMs. One had pollinator abundance for all flower species as the response variable and total flower abundance, canopy openness, and flower rarefied richness as fixed effects. I also created a model that used the same fixed effects, but had pollinator rarefied richness as the response variable, and another that used pollinator Shannon's Hill number as the response variable, but used flower Shannon's Hill number as a fixed effect instead of flower rarefied richness. I replicated these three models again, instead using pollinator abundance, rarefied richness, and Shannon's Hill number of pollinators only on each shrub species as explanatory variables. These models serve to clarify how other variables may be affecting fruit production indirectly by increasing flower visitation. For each shrub species, I created another model with flower abundance as the response variable and canopy openness and vigour as explanatory variables. Finally, for each shrub species, I created a model with shrub vigour as the response variable and canopy openness as the explanatory variable. All of these models had site as a random effect.

For every GLMM, I simplified the fixed effects structure of the models 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 decreased the deviance of the model based on an analysis of variance (Crawley, 2005). I interpreted the results of the final models after this selection process. Given the high number of models used in this analysis (27), I applied a Dunn-Šidák correction to maintain Type I error at 0.05. Therefore, when interpreting the final models, I only considered p-values less than 0.00189 as significant.

I initially fit each model to either a Poisson or Gaussian distribution, based on the expected distributions of the data (e.g. count data was expected to be Poisson distributed). I tested each

final model that used a Poisson distribution for overdispersion. If I found they were overdispersed, I refitted the initial model to a negative binomial distribution, did the model simplification process again, and tested the new model for overdispersion. For models that were initially fit to a Gaussian distribution, I used a Shapiro-Wilk test on the residuals of the final model to test for normality. I also inspected a fitted value versus residuals plot to confirm the assumption of homogeneity of variances. I transformed models that did not pass one or both tests and retested the new models for the assumptions of normality and homogeneity of variances of residuals.

I calculated two different R^2 values for each final model. 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, 2020; Nakagawa et al., 2017). Reporting both metrics allows a more complete understanding of what conclusions can be drawn from the models. 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., 2019), *glmmTMB* (Magnusson et al., 2020), *MuMIn* (Bartoń, 2020), *ecodist* (Goslee & Urban, 2007), *DHARMA* (Hartig, 2018), and *RVAideMemoire* (Herve, 2019).

Results

I counted a total of 1886 individual shrubs on seismic lines and 2510 individuals from in the interior forest. All were one of five shrub species: *Vaccinium myrtilloides*, *Rosa acicularis*, *Prunus pensylvanica*, *Rubus idaeus*, or *Rhododendron groenlandicum*. *R. groenlandicum*, *P. pensylvanica*, and *R. idaeus* were observed at too few sites to analyze at the species-level. I

captured a total of 158 flower-visiting pollinators (120 on seismic lines, 38 in the interior forest) of 41 species (Appendix A).

Forest canopy on seismic lines was more than twice as open ($43.86\% \pm 3.71$) than in forest interiors ($16.81\% \pm 3.43$, $p < 0.001$, Table 2.1). When considering all flowering plant species, total flower abundance per transect (in a 31.4 m^2 sampling area) was over 2.5-times higher on seismic lines (1833.92 ± 396.62) compared to interior forests (680.35 ± 196.86 , $p < 0.001$, Appendix B). Flower rarefied richness was over 1.5-times higher on seismic lines (9.91 ± 1.08) compared to forest interiors (5.75 ± 0.83 , $p < 0.001$), and Shannon's Hill Number was approximately 1.2-times higher but was not significantly different with Dunn-Šidák correction (1.16 ± 0.09 on seismic lines, 0.92 ± 0.08 in forest interiors, $p = 0.038$, Figure 2.2, Table 2.1). Pollinator abundance at all flower species was nearly 5-times higher on seismic lines (25.66 ± 3.53) compared to forest interiors (5.41 ± 2.18 , $p < 0.001$, Figure 2.3). Pollinator rarefied richness was over 2.5-times higher on seismic lines (13.67 ± 1.75 on seismic lines vs. 3.50 ± 1.50 in forest interiors, $p < 0.001$), as was pollinator Shannon's Hill number (11.22 ± 1.48 on seismic lines vs. 3.08 ± 1.36 in forest interiors, $p < 0.001$, Figure 2.3, Table 2.1).

The NMDS of pollinator diversity showed that seismic line transects had a more similar composition of species to each other (tighter clustering of points) than the interior forest transects, despite no major separation in species composition between the two treatment types (Figure 2.3). The perMANOVA of pollinator species composition showed that treatment type had a significant effect using both the Jaccard ($R^2 = 0.08$, $p < 0.001$) and Bray-Curtis ($R^2 = 0.10$, $p < 0.001$) distance estimators (Table 2.2), indicating that seismic lines affected both pollinator species occurrence and relative abundances.

Total *V. myrtilloides* stem abundance per transect (in a 31.4 m² area) was lower on seismic lines (137 ± 19) as compared to interior forests (192 ± 37), but this difference was not significant ($p = 0.171$, Figure 2.4, Table 2.3). However, the total number of *V. myrtilloides* flowers per transect was more than twice as high on seismic lines (664 ± 169) than forest interiors, but again this difference was not significant with Dunn–Šidák correction (231 ± 85, $p = 0.017$). Analysis revealed that flower abundance was significantly, positively associated with shrub vigour ($p < 0.001$). *V. myrtilloides* tended to be more vigorous on seismic lines (28 cm ± 2) than interior forests (22 ± 1, $p = 0.014$), but this difference was not significant with Dunn–Šidák correction, nor was it significantly explained by canopy openness. Fruit production of *V. myrtilloides* was 3-times as high on seismic line transects (731 ± 187) compared to interior forest transects (202 ± 55, $p = 0.001$). *V. myrtilloides* pollinator abundance was more than 3-times higher on seismic lines (2.5 ± 0.8) compared to nearby forest interiors (0.6 ± 0.3, $p < 0.001$). Pollinator rarefied richness for *V. myrtilloides* was also higher on seismic lines (1.7 ± 0.5 on seismic lines vs. 0.5 ± 0.2 in forest interiors, $p = 0.009$), as was pollinator Shannon’s Hill number, but neither of these differences were significant with Dunn–Šidák corrections (1.6 ± 0.5 on seismic lines vs. 0.5 ± 0.2 in forest interiors, $p = 0.012$, Figure 2.5, Table 2.3). Analysis revealed that these trends were primarily driven by canopy openness that inevitably relate to the presence of seismic lines (Table 2.3).

In a model for *V. myrtilloides* fruit production, vigour, flower abundance, and pollinator richness were all significantly, positively associated with fruit production. In addition, the interactions between flower abundance and pollinator abundance, as well as flower abundance and pollinator richness, were significantly, positively associated with fruit production (Table 2.3). No variables for *R. acicularis* were significantly different on seismic lines compared to interior forests (Table

2.4, Figure 2.6). Despite relatively high total pollinator visits (92) compared to *V. myrtilloides* (27), total estimated *R. acicularis* flower abundance was low (122) compared to *V. myrtilloides* (10743), as was total shrub abundance (328 for *R. acicularis*, 3964 for *V. myrtilloides*). Thus, the insignificant results for *R. acicularis* may be indicative of insufficient sample size rather than evidence for the absence of trends, so these results will not be interpreted further.

Discussion

I found that *V. myrtilloides* fruit production significantly increased on seismic lines, over and above the shrub's increase in both vigour and flower production on seismic lines. This increase in fruit production was better explained by the higher pollinator species richness on seismic lines than by either the higher pollinator abundance or higher canopy openness on seismic lines. Thus, my study confirms the result reported by Dawe et al. (2017) for *V. myrtilloides* and provides strong evidence that one of the mechanisms for the increase in fruit production on seismic lines is increased pollination by insects. I was not able to reach conclusions for additional boreal shrub species due to their much lower prevalence and abundance in this ecosystem, but *R. acicularis* showed the same trend of higher fruit production on seismic lines, despite trending toward lower vigour on seismic lines, and appeared to be far more attractive to pollinators than *V. myrtilloides*.

Pollinator rarefied richness remained as a significant explanatory variable for *V. myrtilloides* fruit production after model selection, even when canopy openness, flower abundance, and vigour were also in the model, suggesting insect pollination has an additive effect on fruit production independent of any correlation with these variables. There was also a significant interaction between flower abundance and pollinator richness, suggesting that when there were more species of pollinators, there was a stronger correlation between fruit production and flower

abundance. This was also true for the interaction between flower abundance and pollinator abundance.

Although pollinator visitation is not a perfect metric for effective pollination (King et al., 2013), the fact that pollinator richness was significantly, positively related with shrub fruit production nonetheless suggests that it is a relevant factor in increasing shrub reproduction on seismic lines. This is consistent with studies that show that increased pollinator species diversity is generally associated with lower pollen limitation (Albrecht et al., 2012; Gómez et al., 2007; T. M. Knight et al., 2005). Although there is evidence that this relationship may plateau, and further increases in pollinator diversity may not be positively correlated with reproductive success (Albrecht et al., 2012), it seems unlikely that *V. myrtilloides* would reach this threshold given the relatively low pollinator richness for this species (16) compared to similar studies (e.g. Albrecht et al., 2012; Gómez et al., 2007; Lázaro & Totland, 2010; Lopezaraiza-Mikel et al., 2007).

There are very few studies on *V. myrtilloides* pollination, but studies in other *Vaccinium* species have found that bees in the genera *Bombus* and *Andrena* are the most effective pollinators of these shrubs due to their ability to sonicate (also known as “buzz pollination”), even though *Vaccinium* tends to attract a highly diverse set of pollinators (Cane et al., 1985; De Luca & Vallejo-Marín, 2013; Javorek et al., 2002). Appendix A shows that *Bombus* and *Andrena* visited *V. myrtilloides* flowers less often relative to other taxa (e.g. *Osmia*, Vespidae) and visited flowers more frequently on seismic lines than forest interiors. Thus, it is possible that the observed higher pollinator richness represented more visits from effective pollinator species, while pollinator abundance was primarily driven by taxa known to be less effective pollinators of *Vaccinium* (Pinilla-Gallego & Isaacs, 2018). This would explain why pollinator rarefied richness

was significantly, positively associated with *V. myrtilloides* fruit set while pollinator abundance was not.

The increased pollinator abundance, pollinator rarefied richness, and pollinator Shannon's Hill number on seismic lines also suggests that insect pollinators are changing their behaviour in response to seismic lines, a result that is supported by the current literature on insect responses to anthropogenic corridors in general (Haddad et al., 2003; Tewksbury et al., 2002; Townsend & Levey, 2005) and on seismic lines specifically (Riva et al., 2018a, 2018b). This topic is investigated further in Chapter 3 of this thesis.

Although canopy openness was not significant in the model for *V. myrtilloides* fruit production, nor did it significantly affect pollinator abundance or diversity, there is evidence that it is correlated with overall insect pollinator abundance and diversity (Boscolo et al., 2017; Taki et al., 2013; Townsend & Levey, 2005; Winfree et al., 2007, 2011; also see Chapter 3).

Additionally, other studies have found that canopy openness is significantly, positively linked with *V. myrtilloides* fruit production (Dawe et al., 2017; Moola & Mallik, 1998; Nielsen et al., 2020). Additionally, my analysis indicates that canopy openness does not significantly increase shrub vigour, but there may still be an effect of sunlight on shrub growth. The metric used for vigour, though an important predictor of fruit production (Dawe et al., 2017; Pitelka et al., 1980), may not effectively capture the effect of sunlight on plant growth and overall health. It is well established that increased sunlight exposure improves shrub growth (Denslow et al., 1990; Montané et al., 2016; Moola & Mallik, 1998), thus it is likely that increased fruit production associated with shrub vigour is partially mediated by increased sunlight availability on seismic lines. Thus, it seems likely that the metrics included in this study (vigour, flower abundance,

pollinator visitation) collectively act as mechanisms for the known relationship between canopy openness and *V. myrtilloides* fruit production.

What is still unclear is the effect of seismic lines, via flower visitation or sunlight, on overall reproductive success of *V. myrtilloides*. Though the shrubs are likely using the additional sunlight resources from seismic lines to produce more flowers, which eventually turn into more fruit, they may abort any unripe fruit if lacking the energy for full development (Bos et al., 2007). Increased sunlight exposure and pollination can also increase seed production, rather than just increasing fruit production, which the method used here would not have detected. I also did not find a significantly higher abundance of *V. myrtilloides* on seismic lines, which would be expected if this species was more reproductively successful on these corridors. Future studies should investigate metrics, such as total seed set, to gather a more complete understanding of how forest gaps affect the life cycle and reproduction of *V. myrtilloides* and other understory shrubs.

In conclusion, the increased fruit production in *V. myrtilloides* on seismic lines reported by Dawe et al. (2017) is positively related with pollinator richness, which was higher on seismic lines than in interior forests. These conclusions contribute to the growing understanding of the mechanisms by which anthropogenic corridors and forest landscape structure affect shrub reproduction.

Future studies should use alternative methods of quantifying effective pollination in this ecosystem, such as single visit pollen deposition (SVPD; King et al., 2013), to better understand the role of insect pollination in shrub reproduction on seismic lines. Although SVPD values have been calculated for this species in other systems (Stephens, 2012), changes in this metric between treatments may help clarify the mechanism for the effects reported here. Additionally,

future work should investigate other metrics of shrub reproductive success and test these for other shrub species.

Tables

Table 2.1. Final model structure for GLMMs showing how response variables for all flowering plants varied in response to treatments. “Coef.” describes the estimated treatment effect of seismic lines (1) relative to forest interiors (0) from the GLMM. Site was included as a random effect in all models and treatment was the only fixed effect. Significant p-values (< 0.00189) are bolded.

| Variable | Coef. | S.E. | p | Marginal R² | Conditional R² |
|----------------------------------|--------------|-------------|----------------|-------------------------------|----------------------------------|
| Canopy openness | 27.056 | 3.048 | < 0.001 | 0.461 | 0.584 |
| Flower abundance | 1.340 | 0.376 | < 0.001 | 0.244 | 0.557 |
| Flower rarefied richness | 4.166 | 0.840 | < 0.001 | 0.307 | 0.713 |
| Flower Shannon’s Hill number | 0.237 | 0.114 | 0.038 | 0.145 | 0.226 |
| Pollinator abundance | 1.556 | 0.136 | < 0.001 | 0.632 | 0.934 |
| Pollinator rarefied richness | 1.362 | 0.179 | < 0.001 | 0.573 | 0.854 |
| Pollinator Shannon’s Hill number | 1.291 | 0.186 | < 0.001 | 0.553 | 0.808 |

Table 2.2. Results of the perMANOVA on pollinator species composition. Significant p-values (< 0.00189) are bolded.

| Variable | df | SS | MS | F | R² | p |
|--|-----------|-----------|-----------|----------|----------------------|----------------|
| <i>a. Bray-Curtis distance estimator</i> | | | | | | |
| Treatment type | 1 | 0.79 | 0.79 | 2.10 | 0.10 | < 0.001 |
| Flower abundance | 1 | 0.45 | 0.45 | 1.20 | 0.06 | 0.22 |
| Canopy openness | 1 | 0.44 | 0.44 | 1.16 | 0.06 | 0.26 |
| Site | 1 | 0.30 | 0.30 | 0.80 | 0.04 | 0.78 |
| Treatment type:Flower abundance | 1 | 0.42 | 0.42 | 1.10 | 0.05 | 0.33 |
| Residuals | 14 | 5.30 | 0.38 | | 0.69 | |
| Total | 19 | 7.70 | | | 1.00 | |
| <i>b. Jaccard distance estimator</i> | | | | | | |
| Treatment type | 1 | 0.68 | 0.68 | 1.60 | 0.08 | < 0.001 |
| Flower abundance | 1 | 0.47 | 0.47 | 1.10 | 0.06 | 0.26 |
| Canopy openness | 1 | 0.48 | 0.48 | 1.12 | 0.06 | 0.22 |
| Site | 1 | 0.37 | 0.37 | 0.86 | 0.04 | 0.80 |
| Treatment type:Flower abundance | 1 | 0.45 | 0.45 | 1.05 | 0.05 | 0.34 |
| Residuals | 14 | 5.97 | 0.43 | | 0.71 | |
| Total | 19 | 8.42 | | | 1.00 | |

Table 2.3. Final model structure for GLMMs illustrating how response variables for just *V. myrtilloides* differed in response to treatments and other explanatory variables. For section “a”, full models included only treatment type. “Coef.” describes the estimated effect of seismic lines (1) relative to forest interiors (0) from the GLMM. For section “b”, all variables from the full model are listed, except for interactions between canopy openness and pollinator abundance, and canopy openness and pollinator richness. For section “c”, canopy openness, vigour, and flower abundance were included as fixed effects where they were not response variables. Site was included as a random effect in all models. Significant p-values (< 0.00189) are bolded. Models with “N/A” values had no significant variables remaining after model selection.

| Response variable | Explanatory variables | Coef. | S.E. | p | Marginal R ² | Conditional R ² |
|----------------------------------|------------------------------|-------|-------------------|-------------------|-------------------------|----------------------------|
| <i>a. Treatment type models</i> | | | | | | |
| Abundance | Treatment type | N/A | N/A | N/A | N/A | N/A |
| Flower abundance | Treatment type | 1.289 | 0.542 | 0.017 | 0.118 | 0.520 |
| Fruit production | Treatment type | 1.354 | 0.439 | 0.001 | 0.157 | 0.620 |
| Pollinator abundance | Treatment type | 1.455 | 0.419 | < 0.001 | 0.264 | 0.564 |
| Pollinator rarefied richness | Treatment type | 1.204 | 0.465 | 0.009 | 0.166 | 0.354 |
| Pollinator Shannon’s Hill number | Treatment type | 1.168 | 0.467 | 0.012 | 0.159 | 0.319 |
| Vigour | Treatment type | 6.141 | 2.512 | 0.014 | 0.201 | 0.226 |
| <i>b. Fruit production model</i> | | | | | | |
| Flower abundance | Vigour | 0.158 | 0.041 | < 0.001 | 0.359 | 0.579 |
| Fruit production | Canopy openness | 0.003 | 0.001 | 0.283 | 0.573 | 0.925 |
| | Flower abundance | 0.001 | < 0.001 | < 0.001 | | |
| | Pollinator abundance | 0.351 | 0.113 | 0.002 | | |
| | Pollinator rarefied richness | 0.647 | 0.158 | < 0.001 | | |
| | Vigour | 0.081 | 0.008 | < 0.001 | | |

| | | | | | | |
|------------------------------------|---------------------------------------|---------|---------|----------------|-------|-------|
| | Flower abundance:Canopy openness | < 0.001 | < 0.001 | 0.026 | | |
| | Flower abundance:Pollinator abundance | 0.002 | < 0.001 | < 0.001 | | |
| | Flower abundance:Pollinator richness | 0.003 | < 0.001 | < 0.001 | | |
| <i>c. Other mechanistic models</i> | | | | | | |
| Flower abundance | Vigour | 0.158 | 0.041 | < 0.001 | 0.359 | 0.579 |
| Pollinator abundance | Canopy openness | 0.036 | 0.013 | 0.005 | 0.215 | 0.561 |
| Pollinator rarefied richness | Canopy openness | 0.027 | 0.013 | 0.039 | 0.114 | 0.320 |
| Pollinator Shannon's Hill number | Canopy openness | 0.026 | 0.013 | 0.047 | 0.105 | 0.281 |
| Vigour | N/A | N/A | N/A | N/A | N/A | N/A |

Table 2.4. Final model structure for GLMMs showing how various response variables related to *Rosa acicularis* differed in response to listed explanatory variables. For treatment, “Coef.” describes the estimated effect of seismic lines (1) relative to forest interiors (0) from the GLMM. Site was included as a random effect in all models. Significant p-values (< 0.00189) are bolded. Models with “N/A” values had no significant variables remaining after model selection.

| Response variable | Explanatory variables | Coef. | S.E. | p | Marginal R² | Conditional R² |
|----------------------------------|------------------------------|--------------|-------------|----------|-------------------------------|----------------------------------|
| Vigour | N/A | N/A | N/A | N/A | N/A | N/A |
| Abundance | N/A | N/A | N/A | N/A | N/A | N/A |
| Flower Abundance | N/A | N/A | N/A | N/A | N/A | N/A |
| Pollinator Abundance | Treatment Type | 0.817 | 0.258 | 0.002 | 0.058 | 0.939 |
| Pollinator Rarefied Richness | Treatment Type | 0.776 | 0.353 | 0.028 | 0.081 | 0.705 |
| Pollinator Shannon’s Hill Number | Treatment Type | 0.933 | 0.392 | 0.174 | 0.122 | 0.569 |
| Fruit Production | N/A | N/A | N/A | N/A | N/A | N/A |

Figures

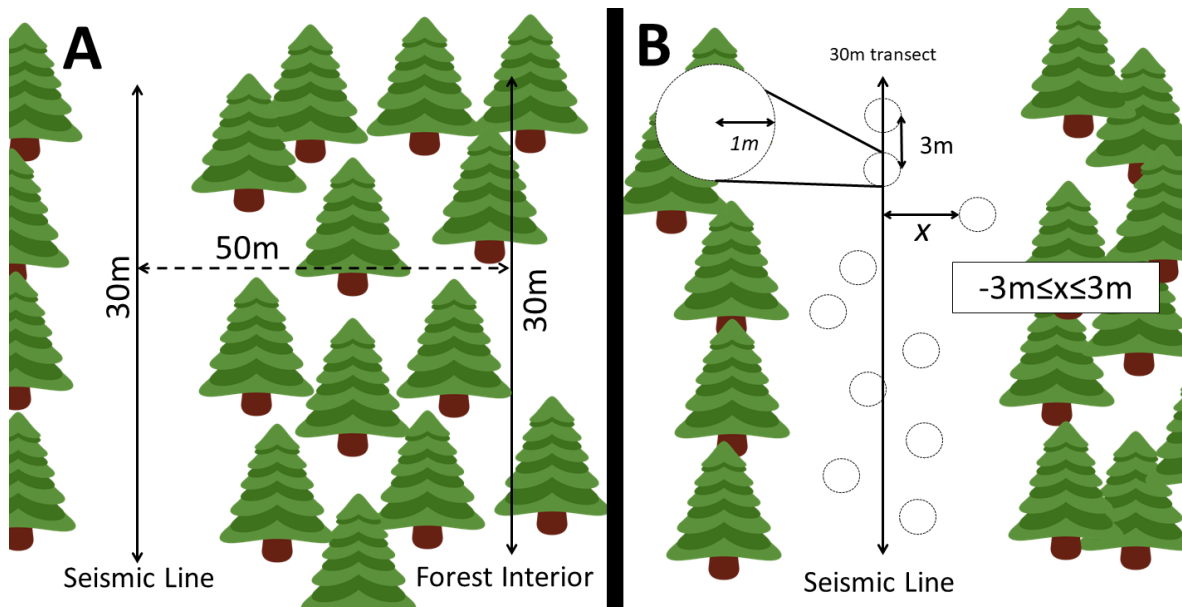


Figure 2.1. A) Orientation and spacing of the paired transects at each site. B) An example of sub-sample quadrats at a single transect. Images not to scale.

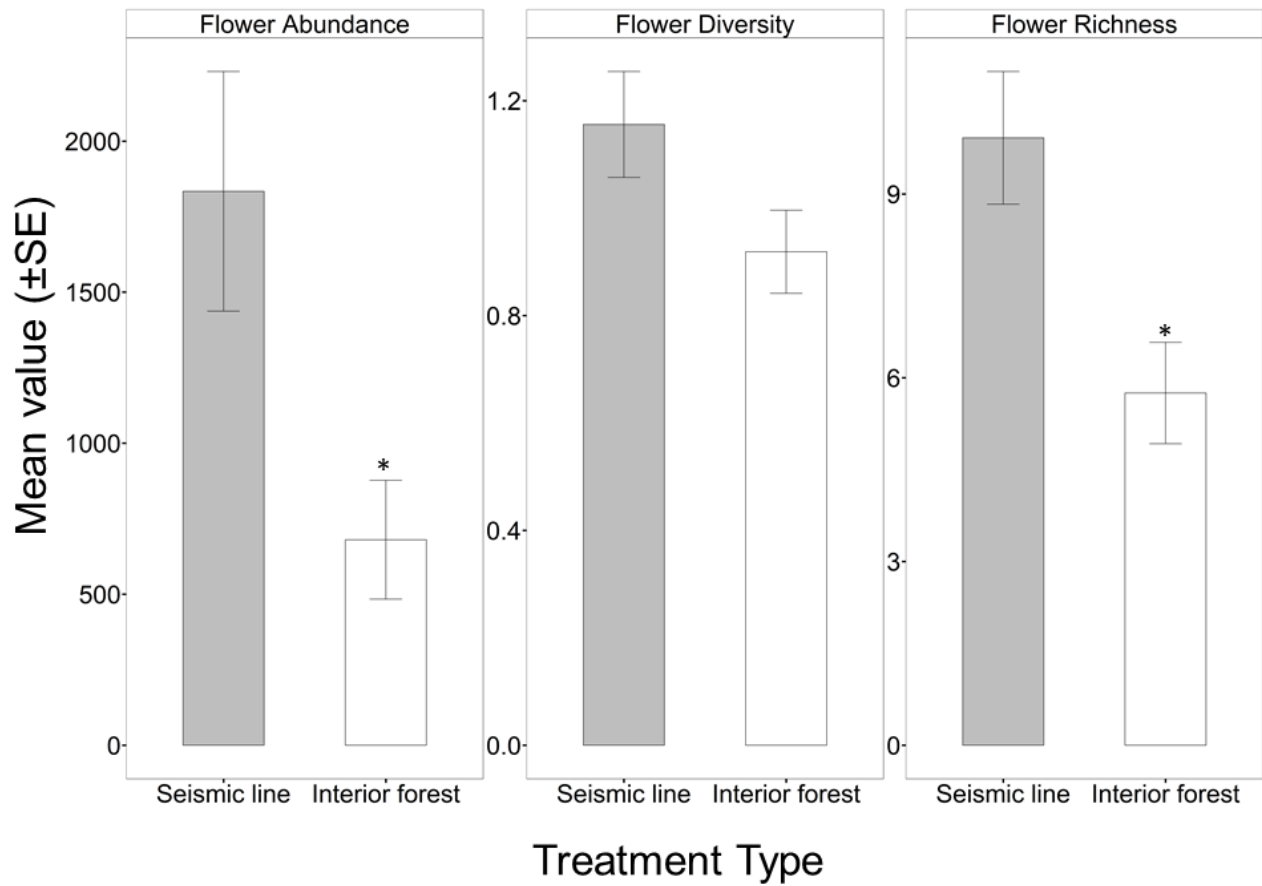


Figure 2.2. Mean values of flower abundance, diversity (Shannon’s Hill number), and rarefied richness for all species on seismic lines and interior forests. Interior forest bars with an asterisk indicate a significant difference ($p < 0.00189$) from the corresponding seismic line bar.

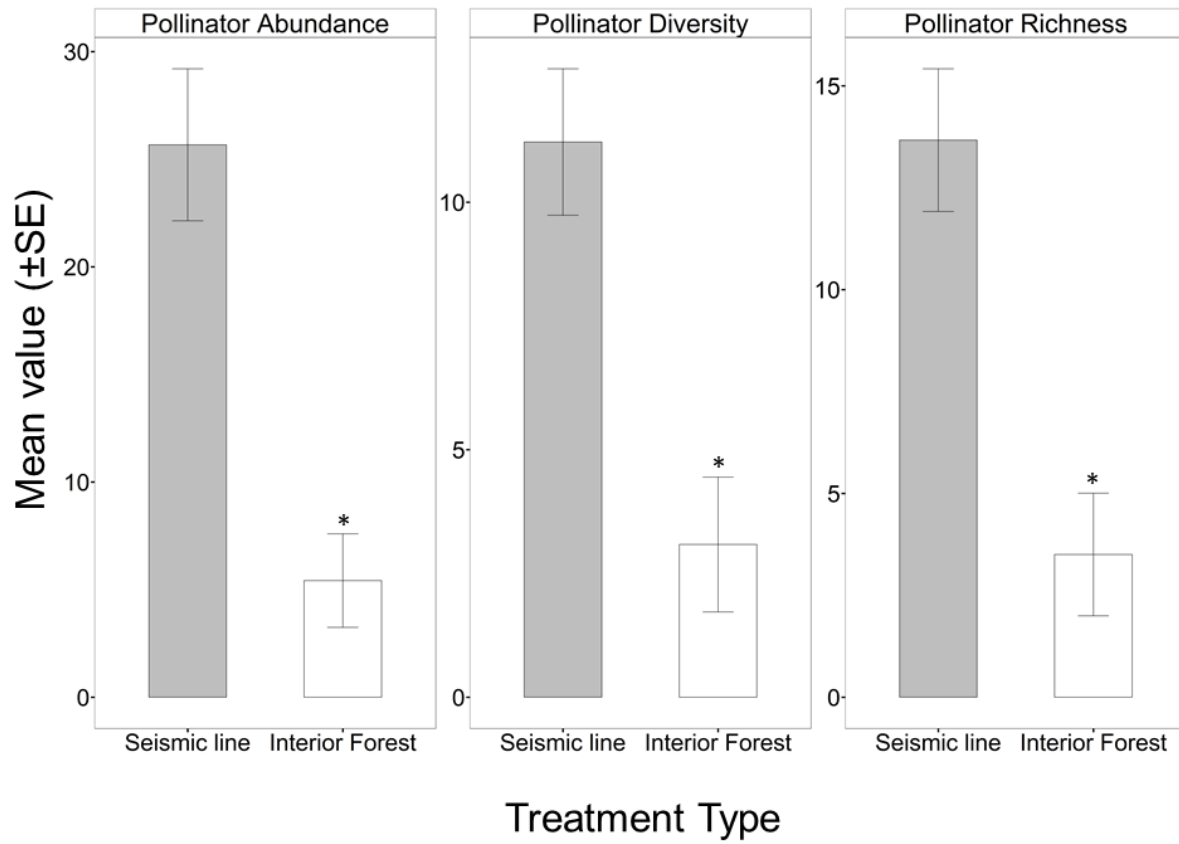


Figure 2.3. Mean values of flower pollinator abundance, diversity (Shannon’s Hill number), and rarefied richness for all flower species on seismic lines and interior forests. Interior forest bars with an asterisk indicate a significant difference ($p < 0.00189$) from the corresponding seismic line bar.

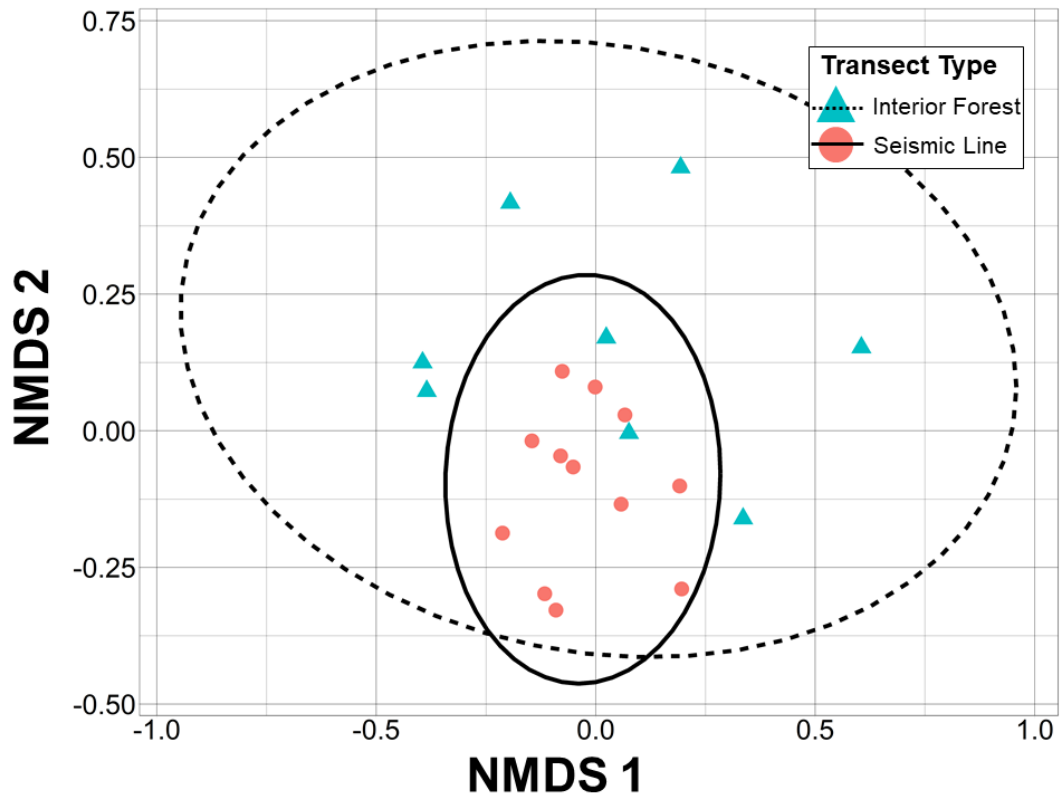


Figure 2.4. NMDS of pollinator species composition. Blue triangles represent interior forest and red circles represent seismic lines. The solid and dotted ellipses represent the distributions of seismic line and interior forest transects, respectively. Sites with no pollinator observations are not shown.

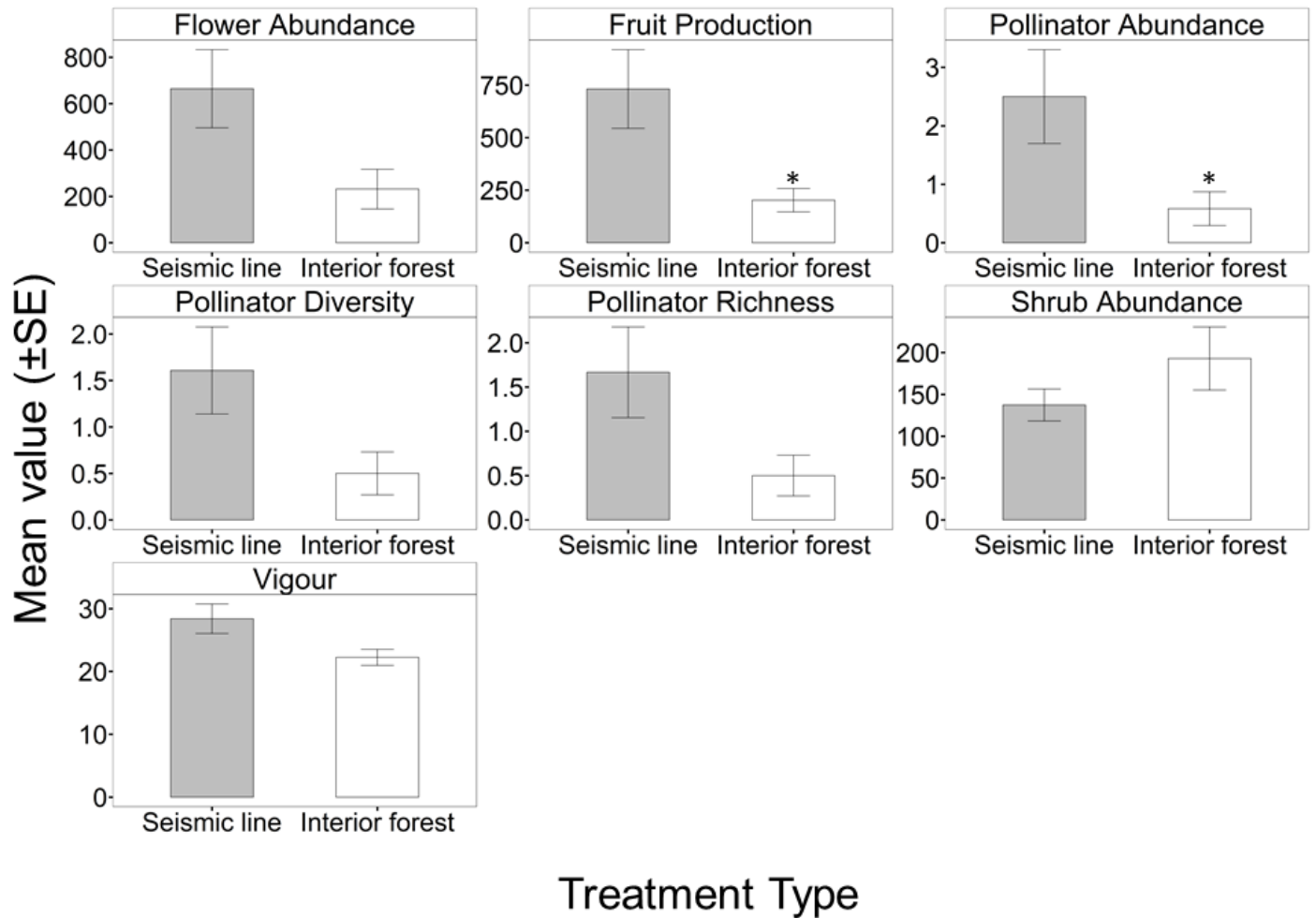


Figure 2.5. Mean values of *Vaccinium myrtilloides* flower abundance, fruit production, shrub abundance (per 31.4 m²), vigour (height in cm), pollinator abundance, diversity (Shannon's Hill number) and rarefied richness (per 240 m²) on seismic lines and interior forests. Interior forest bars with an asterisk indicate a significant difference ($p < 0.00189$) from the corresponding seismic line bar.

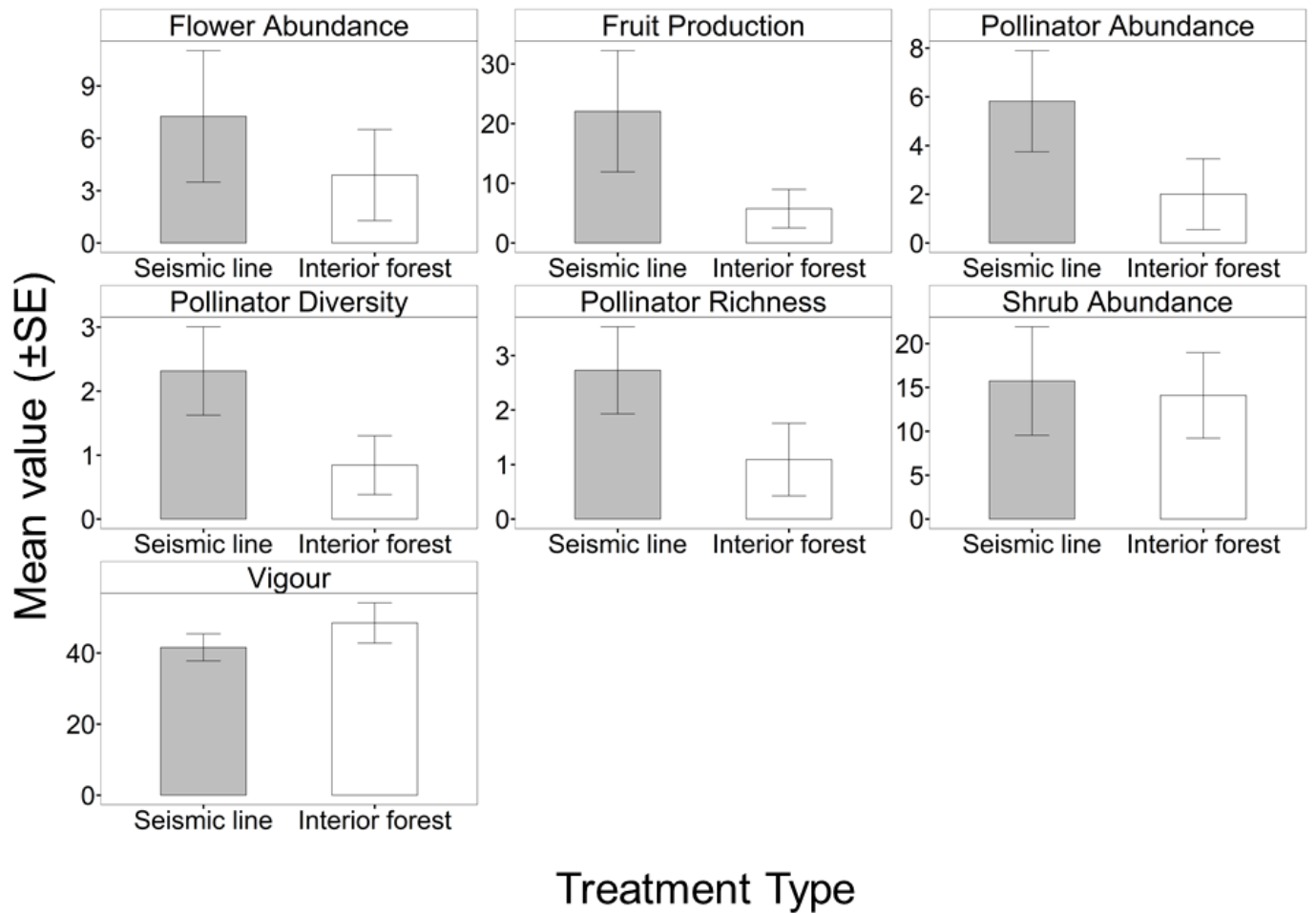


Figure 2.6. Mean values of *Rosa acicularis* flower abundance, fruit production, shrub abundance (per 31.4m²), vigour, pollinator abundance, diversity (Shannon’s Hill number) and rarefied richness (per 240 m²) on seismic lines and interior forests. No pairs of bars were significantly different from one another ($p > 0.00189$).

Chapter 3 - Narrow anthropogenic linear corridors increase the abundance, diversity, and movement of bees in boreal forests

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.

Introduction

Habitat fragmentation is a major concern for many ecosystems (Fahrig, 2003; Haddad et al., 2015), including boreal forests (Schindler & 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 & 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 (Figure 3.1; 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 & 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 & Kouki, 2015). Given evidence for increased understory plant productivity on seismic lines (Dawe et al., 2017; Riva, Pinzon, 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 & 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 & 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 & 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 metacommunity structure of bees (Aguilar et al., 2006; Roland & 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.

Methods

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 6-12 m in width, crisscrossing the landscape in a grid pattern at densities averaging at least 1.5 km/km² (Lee & 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 & 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.

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, 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 406 hours; however, total sampling effort across the season was identical at all sites. 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).

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 2 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 hours 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 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 & 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 held at breast height. 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).

Statistical analysis

To assess the effect of seismic lines on bee abundance and diversity, we created three generalized 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 & 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 & 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. Flower abundance and diversity were measured along each transect

several times 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 flower abundance. This was done in ten 1-m radius quadrats for each 30-m transect and averaged for the transect (see Chapter 2).

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 & 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., 2019), glmmTMB (Magnusson et al., 2020), MuMIn (Bartoń & Barton, 2020), ecodist (Goslee & Urban, 2007), DHARMA (Hartig, 2018), and RVAideMemoire (Herve, 2019).

Results

Bee abundance and diversity

We collected and identified a total of 4,836 bees of 62 species from 305 pan trap samples, with a total of 39,687 hours of trapping time between all samples (Appendix C). We collected and identified 777 bees of 48 species from 260 malaise trap samples, with a total of 34,243 hours of trapping time between all samples (Appendix D).

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 , $p < 0.001$, Appendix B). 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 , $p = 0.013$, Figure 3.2, Table 3.1).

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 , $p = 0.949$, Figure 3.3, Table 3.1).

Species composition between seismic lines and the forest interior was 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 3.2). 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 (Figure 3.4).

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 (Figure 3.5A, 3.5D, Table 3.3). Bee abundance ($p = 0.002$) and rarefied richness ($p < 0.001$) were also positively associated with flower rarefied richness (Figure 3.5C, 3.5E). Bee abundance also significantly decreased with increased flower abundance ($p = 0.028$, Figure 3.5B, Table 3.3). 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 3.4). See Appendix E for a summary of key relationships.

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 Figure 3.6) 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.

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, whether considering just species presence/absence or species relative abundances. When considering canopy openness, flower abundance, and flower rarefied richness and removing treatment type largely relating to canopy structure, 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 bee abundance was higher on seismic lines and these effects 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. 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.

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 & Rehan, 2020; Rodríguez & 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 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 & 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 (Cartar et al., 2019). However, changes in bee abundance appear to also respond 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 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 nesting habitats. In a temperate forest in Indiana, USA, the diversity of bees was positively associated with the presence of increased nesting materials (Grundel et al., 2010), 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 & 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 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 & Willmer, 1997). Temperature can also affect bee foraging, as the temperature for optimal foraging activity varies between species (Rader et al., 2013). Thus, increased temperature and woody debris on anthropogenic linear corridors could be improving nesting conditions and creating a preferred thermal habitat for bees.

The malaise traps caught more bees, and a more diverse community of bees, on seismic lines compared to interior forests, and travelling along seismic lines as opposed to across them. The interaction between these variables was significant for bee rarefied richness and Shannon's Hill number, while bee abundance demonstrated additive effects. Post hoc analysis showed that malaise traps on seismic lines oriented to catch bees flying along the corridor had a significantly higher abundance, rarefied richness, and Shannon's Hill number than any other combination of treatment type and orientation. This suggests that 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 & 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 & 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 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. Finally, species-level trends in bee responses, as well as responses by other pollinator taxa, should be a topic of future research.

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.

Tables

Table 3.1. 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). “ β ” 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 | β | S.E. | p | Marginal R² | Conditional R² |
|------------------------------|---------------------------|-------------|----------------|-------------------------------|----------------------------------|
| Bee abundance | + 226.320 | 32.071 | < 0.001 | 0.520 | 0.520 |
| Bee rarefied richness | + 10.583 | 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 | + 989.610 | 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 |

Table 3.2. 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 | R² | p |
|--|-----------|-----------|-----------|----------|----------------------|-------------------|
| <i>a. Bray-Curtis distance estimator</i> | | | | | | |
| 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 | |
| <i>b. Jaccard distance estimator</i> | | | | | | |
| 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 | |

Table 3.3. Final model structure for GLMMs (Gaussian distribution) showing how bee abundance and diversity varies with canopy openness, flower abundance, and flower diversity.

“ β ” 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 | β | S.E. | p | Marginal R² | Conditional R² |
|--------------------------|------------------------------|---------------------------|-------------|----------------|-------------------------------|----------------------------------|
| Abundance | | | | | 0.712 | 0.712 |
| | Canopy openness | 6.333 | 1.033 | < 0.001 | | |
| | Flower abundance | - 0.060 | 0.027 | 0.028 | | |
| | Flower rarefied richness | 23.120 | 1.033 | 0.002 | | |
| Rarefied richness | | | | | 0.766 | 0.766 |
| | Canopy openness | 0.244 | 0.040 | < 0.001 | | |
| | Flower richness | 0.789 | 0.191 | < 0.001 | | |
| Shannon’s Hill number | | | | | N/A | N/A |
| | None | N/A | N/A | N/A | | |

Table 3.4. 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 | R² | p |
|--|-----------|-----------|-----------|----------|----------------------|-------------------|
| <i>a. Bray-Curtis distance estimator</i> | | | | | | |
| 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 | |
| <i>b. Jaccard distance estimator</i> | | | | | | |
| 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 | |

Table 3.5. 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, “ β ” describes the estimated effect of seismic lines (1) relative to forest interiors (0) from the GLMM. For orientation, “ β ” 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 | β | S.E. | p | Marginal R ² | Conditional R ² |
|-----------------------|----------------------------|----------|-------|----------------|-------------------------|----------------------------|
| Abundance | | | | | 0.435 | 0.713 |
| | Treatment type | + 1.047 | 0.236 | < 0.001 | | |
| | Orientation | + 0.712 | 0.236 | 0.003 | | |
| Rarefied richness | | | | | 0.513 | 0.683 |
| | Treatment type | + 3.200 | 2.844 | 0.261 | | |
| | Orientation | + 11.000 | 2.844 | < 0.001 | | |
| | Treatment type:Orientation | + 9.400 | 4.022 | 0.019 | | |
| Shannon’s Hill number | | | | | 0.594 | 0.626 |
| | Treatment type | + 1.632 | 1.646 | 0.321 | | |
| | Orientation | + 6.367 | 1.646 | < 0.001 | | |
| | Treatment type:Orientation | + 5.772 | 2.328 | 0.013 | | |

Figures



Figure 3.1. 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 to 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.

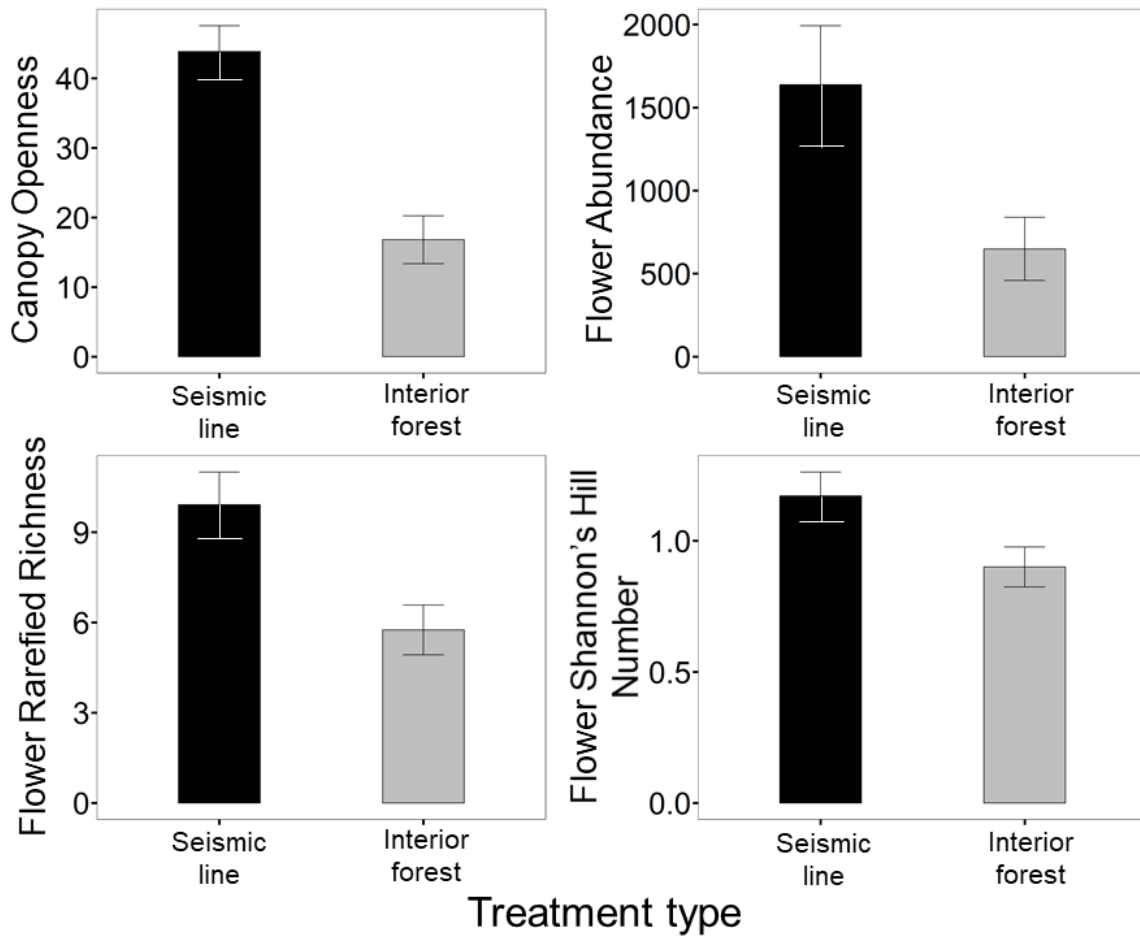


Figure 3.2. Mean and standard error of canopy openness, flower abundance, flower rarefied richness, and flower Shannon's Hill number on seismic lines compared to forest interiors. All metrics are significantly different between seismic lines and interior forests ($p < 0.05$).

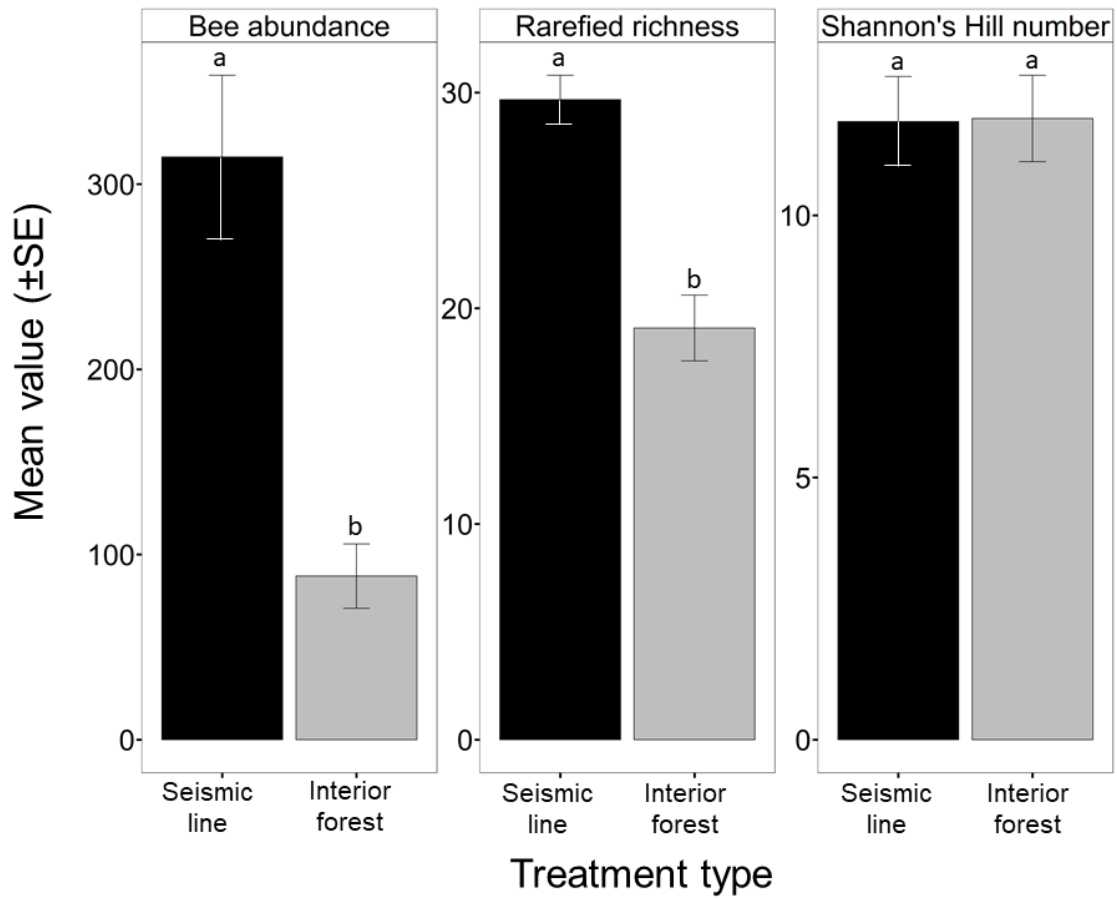


Figure 3.3. Means and standard error of abundance, rarefied richness, and Shannon's Hill number of bees caught in pan traps on seismic lines and in the interior forest. Different letters indicate a significant effect of treatment type on each metric ($p < 0.05$).

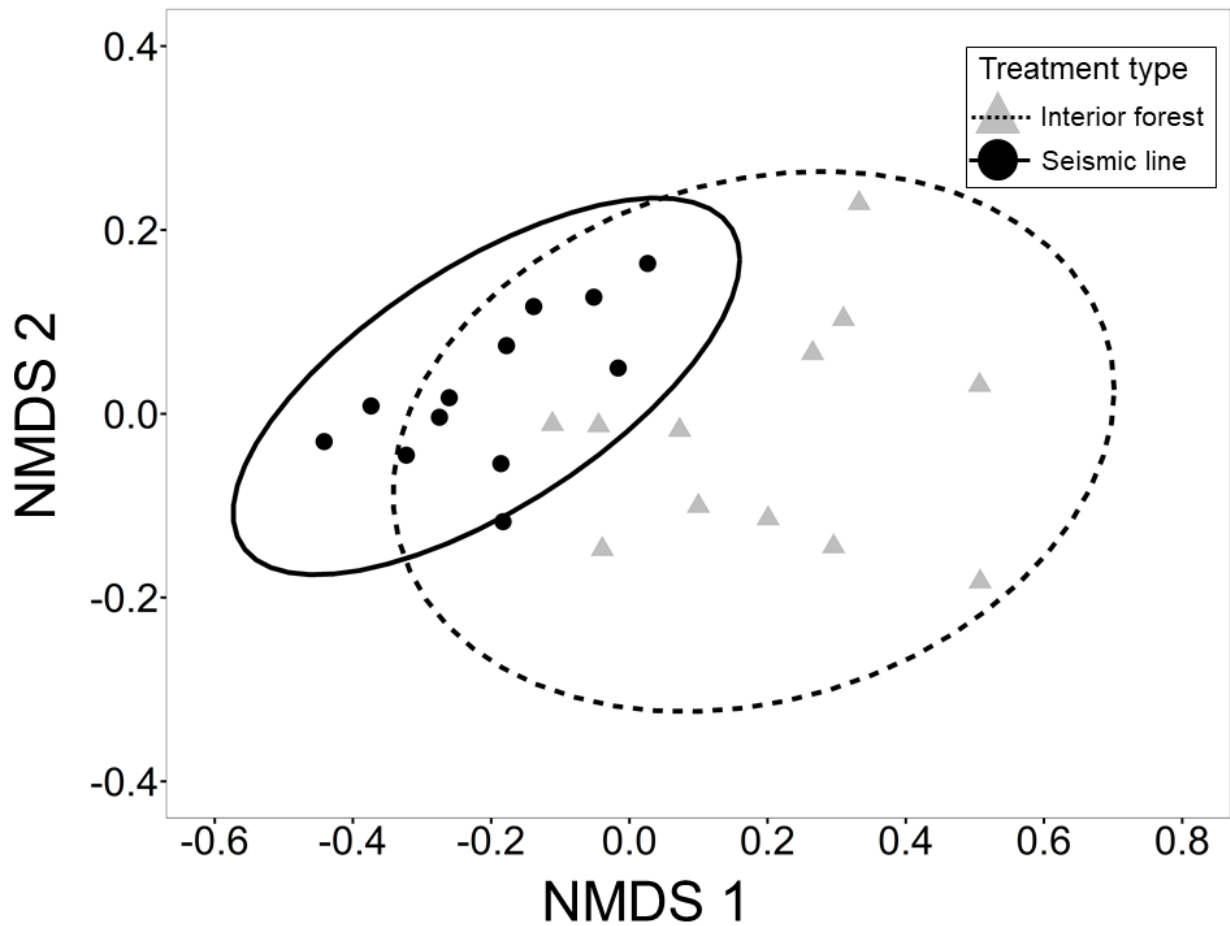


Figure 3.4. NMDS of species composition for bees caught in pan traps using Bray-Curtis distance estimation. Grey triangles represent transects from the interior forest and black circles represent transects from seismic lines. The solid and dotted ellipses represent the distributions of seismic line and interior forest transects, respectively. Stress = 0.098.

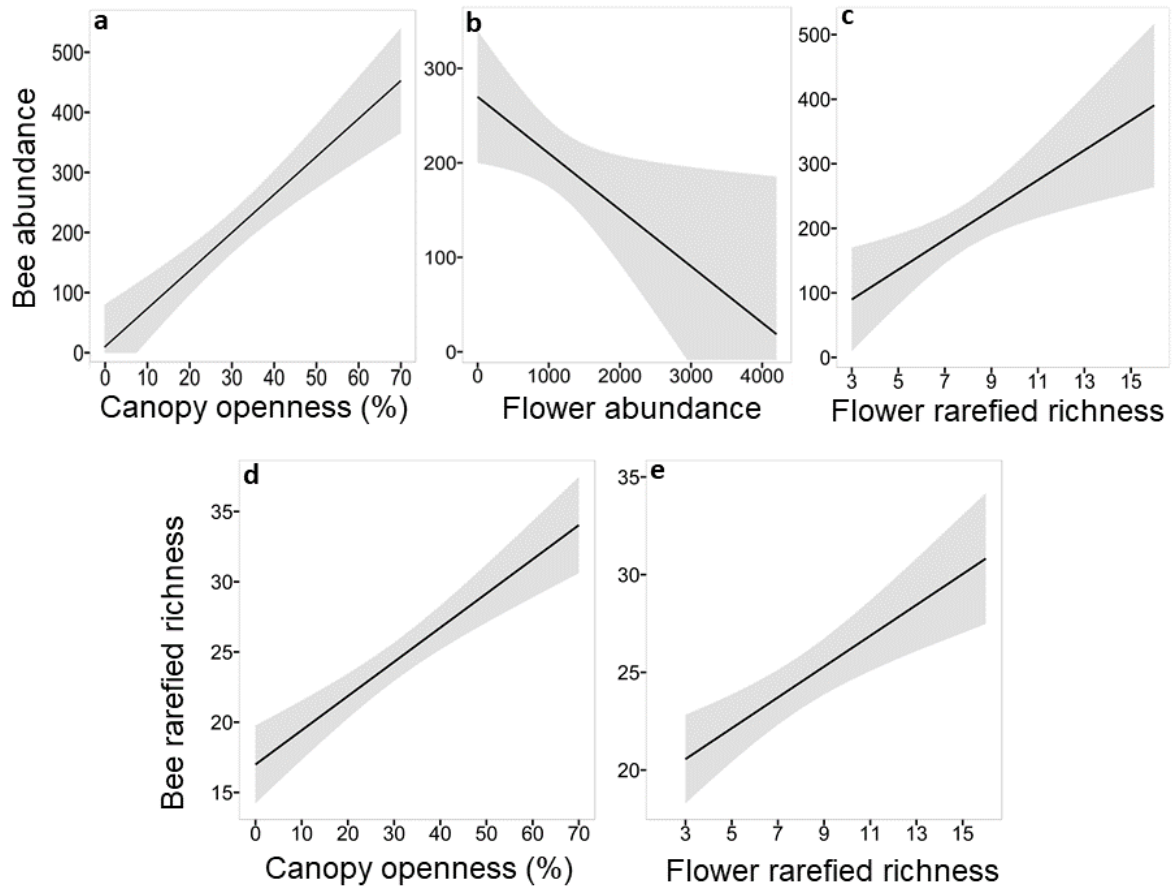


Figure 3.5. Marginal plots showing the effects of explanatory variables (canopy openness, flower abundance, flower rarefied richness) on the predicted values response variables they significantly ($p < 0.05$) affected (bee abundance and rarefied richness), with all other variables held at their means (see Table 3.3). The black lines represent the predicted relationships and the grey bars represent a 95% confidence interval.

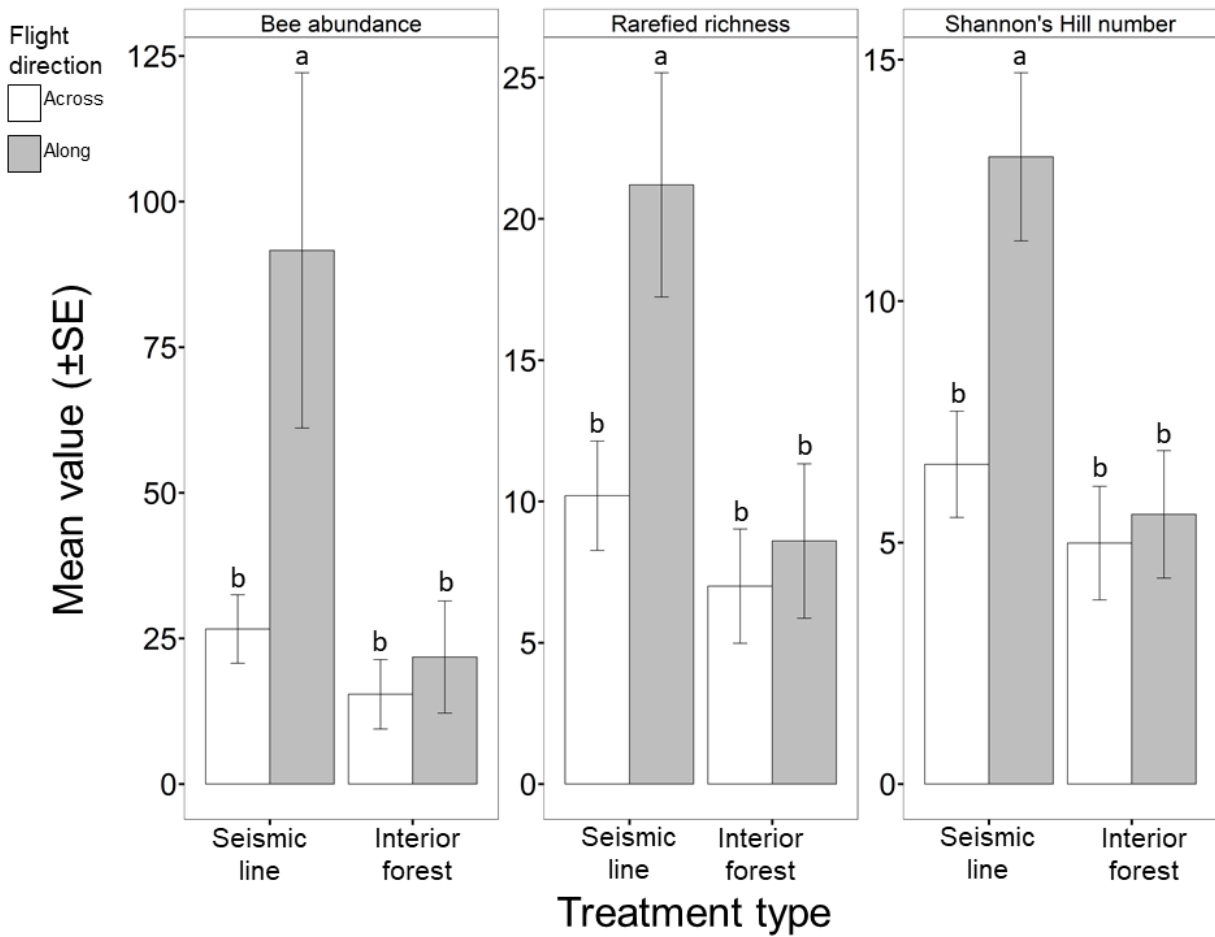


Figure 3.6. Means and standard error of abundance, rarefied richness, and Shannon's Hill number of bees caught in malaise traps testing bee movement. Bar shading indicates flight direction relative to the seismic line. Different letters for each response variable indicate a significant difference ($p < 0.05$) from a Tukey pairwise comparison.

Chapter 4 - Summary and Conclusions

Anthropogenic habitat fragmentation is a major concern in the conservation of global biodiversity (Haddad et al., 2015; Krauss et al., 2010; Millenium Ecosystem Assessment, 2005). Understanding how organisms respond to various types of fragmentation is vital to informing the conservation of species and habitats. Anthropogenic linear corridors represent a common form of fragmentation in Alberta, where seismic lines criss-cross much of the boreal forest (Lee & Boutin, 2006; Pattison et al., 2016). Although research has been conducted on the responses of several species to these corridors (e.g. Bayne et al. 2005; Tigner et al. 2014; Dawe et al. 2017; Riva et al. 2020), no study has investigated how seismic lines affect insect pollination, an irreplaceable ecosystem service that is vital in conserving both plant and invertebrate communities (Allsopp et al., 2008; Ollerton et al., 2011). Here, I have presented two approaches to assessing the affect of seismic lines on insect pollination: one from the perspective of a flowering shrub species and one from the perspective of bee communities.

In Chapter 2, I evaluated the effect of seismic lines on pollinator visitation and fruit production of *Vaccinium myrtilloides*, the velvet leaf blueberry. I found that *V. myrtilloides* received 3-times more flower visits by insects on seismic lines than in the nearby interior forest. I also found that *V. myrtilloides* fruit production was 3-times higher on seismic lines and showed that insect pollinator richness, vigour, and flower abundance are likely mechanisms for this pattern. There were also significant interactions between flower abundance and pollinator rarefied richness, as well as flower abundance and pollinator abundance, suggesting that increased visitation from a diverse community of insect pollinators resulted in a closer correlation between flower abundance and fruit production. When considering the relative abundances of pollinator species from Appendix A, it is likely that these interactions represent increased visitation by more

effective, but less abundant, pollinator groups such as *Bombus* and *Andrena*, as opposed to groups known to be relatively ineffective pollinators, such as *Osmia* and Vespidae, which visited *V. myrtilloides* in high abundances (Cane et al., 1985; Javorek et al., 2002; Pinilla-Gallego & Isaacs, 2018). Although the increased canopy openness on seismic lines was not significant in my model for fruit production, the results of this chapter offer specific mechanisms for the known link between canopy openness and *V. myrtilloides* fruit production (Dawe et al., 2017; Moola & Mallik, 1998; Nielsen et al., 2020).

In Chapter 3, I assessed the effect of seismic lines on the abundance, diversity, community composition, and movement of bees, an important group of insect pollinators. I found that bees were 3-times more abundant and 1.5-times more diverse on seismic lines. These results mirror the findings from pollinator visitation analyses in Chapter 2. They also align with the body of literature demonstrating that bees prefer early successional and moderately disturbed habitat as compared to mature forests (Odanaka & Rehan, 2020; Rodríguez & Kouki, 2015, 2017; Townsend & Levey, 2005; Winfree et al., 2007, 2009). I found that this trend was significantly explained by flower rarefied richness, suggesting that a diverse community of flowers on seismic lines attracts a greater abundance and diversity of bees, which is unsurprising given how important floral resources are to bee communities (Gathmann & Tschardt, 2002; Westerfelt et al., 2018).

This chapter also showed that bees travelled 3-times more frequently along seismic lines than across them. Given the evidence that other invertebrates respond similarly to seismic lines (Riva et al., 2018b) and that pollen transfer increases along similar linear anthropogenic corridors (Townsend & Levey, 2005), these results were expected, but have not before been directly demonstrated for a whole community of bees. When considered in tandem, results of these

chapters clearly demonstrate that seismic lines alter the abundance, diversity, and behaviour of insect pollinator communities, which subsequently affects the pollination services provided to at least one species of understory shrub. These results provide insight into mechanisms responsible for findings from previous work on seismic lines and boreal shrubs (Dawe et al., 2017; Nielsen et al., 2020; Riva et al., 2020) and add to a growing body of literature on responses to anthropogenic linear corridors.

In addition to increasing connectivity of bee populations and communities across the boreal forest, seismic lines may be drawing insect pollinators out of interior forests. Unless seismic lines are increasing the total number of pollinators on the landscape, it is likely that pollinators are preferentially foraging on seismic lines and neglecting forest interiors. If this is the case, shrub species that are dominant on seismic lines, such as *V. myrtilloides*, will receive a greater share of pollinator resources than on a typical boreal landscape. This hypothesis is further supported by the PerMANOVA results from both chapters, showing that insect pollinator communities are significantly different on seismic lines. If a subset of pollinator species is responding to seismic lines, pollinating a subset of shrub species, then these disturbances may be homogenizing plant-pollinator communities in the boreal forest. This effect is especially concerning if specialist pollinator species, which make up approximately 20% of species in the region (Sheffield et al., 2014), are responding to changes in spatial distribution of the plants species they rely on. Significant changes in the relative abundances of generalist and specialist pollinators may affect the stability and niche partitioning of plant-pollinator networks in the region, making them more susceptible to disease and extirpation, in addition to contributing to homogenization. This is partly due to the fact that a high abundance of generalist pollinators in a

pollination network tends to have a stabilizing effect (Valdovinos et al., 2016; Zografou et al., 2020).

The conservation implications and restoration of seismic lines is an active area of research that varies greatly based on ecosite and microclimate conditions. For example, regeneration of trees and understory plants alike is relatively slow in peatlands (Filicetti & Nielsen, 2020; Lee & Boutin, 2006; Van Rensen et al., 2015), but dry, upland, regions like the one studied in this thesis have been shown to regenerate quickly post-fire (Filicetti & Nielsen, 2018). The results presented here confirm the previously established pattern that, at dry, upland, Jack Pine dominated sites, *V. myrtilloides* reproduction is improved on seismic lines (Dawe et al., 2017). Given the cultural and economic significance of this shrub species to the region's Indigenous Peoples (Gottesfeld, 1994; Kuhnlein & Turner, 1992), restoration action that may further disturb the understory shrub community, such as mounding (Echiverri et al., 2020), may prevent *V. myrtilloides* from further benefitting from seismic lines. Although seismic lines may disproportionately benefit habitat generalists, such as *V. myrtilloides* (Moola & Mallik, 1998), thereby affecting understory community composition (Zhang et al., 2014), these effects are likely to decrease in severity after natural regeneration (Filicetti & Nielsen, 2018).

Conservation of bees and other insect pollinators is often challenging, especially in boreal Canada as there is little available data on occurrence or abundance for bees in this region (Sheffield et al., 2014). However, I did collect members of two species in pan traps that are listed as Threatened or Special Concern under the Species at Risk Act: *Bombus suckleyi* and *Bombus terricola* (Government of Canada, 2019). The results of this thesis indicate that bees, including these species, are more abundant on seismic lines and preferentially forage on the corridors; however, there was also evidence that seismic lines affect insect pollinator community

composition and may have homogenizing effects. Thus, it is likely that seismic lines are not equally beneficial for all bee species. Until future research is able to clarify species-level effects of pollinator visitation on seismic lines, as well as the potential impacts on meta-community connectivity, we cannot conclude whether seismic lines are beneficial overall to bee community health, despite increases in bee abundance and diversity. From the perspective of bee community conservation, as with *V. myrtilloides*, it seems most advisable to allow natural regeneration to take its course on seismic lines in this region.

Future research in this area should seek to broaden the results presented here to other flowering plant species, other pollinator taxa, and other ecosite types in Alberta's boreal forest. Although there were not significant results for *R. acicularis*, the overall trends in the data were consistent with *V. myrtilloides*, suggesting that effects may be detected with more extensive sampling.

Future work could also investigate species-specific plant-pollinator relationships to determine if the fruit production pattern in *V. myrtilloides* is driven by only a few groups of effective pollinators, as suggested in Chapter 2. In addition, metrics besides flower visitation and fruit production could be used to better understand the relationship between pollination and overall shrub reproductive success on seismic lines. Future studies should also expand on the conclusions made here about bee movement along seismic lines to broader spatial scales. It is still unclear whether bees are using these linear corridors for foraging (local movements), dispersal (long-distance movements), or both. The answer to this question would be a major step towards understanding the consequences of seismic lines for plant-pollinator metacommunity connectivity and stability.

Overall, the results presented in this thesis provide the first insight into how insect pollinator communities and understory shrub pollination respond to seismic lines, contributing to the

growing body literature on anthropogenic linear corridors. These corridors increased the abundance and diversity of bees and, subsequently, the fruit production of an important ericaceous shrub, showing that even narrow strips of early successional habitat can serve as refugia for species (see also Riva et al. 2020 for similar fire refugia effects). The corridors also facilitated bee movement, expanding the potential applications of anthropogenic corridors in increasing connectivity between fragmented habitat patches in disturbed landscapes.

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Appendices

Appendix A

Table A.1: Flower pollinator species abundances by treatment type and plant species. Morphospecies are listed as “[Genus] spp.”

| Order | Family | Genus | Species | Seismic Line | Interior Forest | R. acicularis | V. myrtilloides |
|-------------|--------------|-----------------------|-----------------------|--------------|-----------------|---------------|-----------------|
| Coleoptera | Buprestidae | <i>Anthaxia</i> | <i>inornata</i> | 5 | 9 | 14 | 0 |
| Coleoptera | Byturidae | <i>Byturus</i> | <i>unicolor</i> | 3 | 0 | 3 | 0 |
| Coleoptera | Cerambycidae | <i>Acmaeops</i> | <i>proteus</i> | 1 | 0 | 1 | 0 |
| Coleoptera | Cerambycidae | <i>Gnathacmaeops</i> | <i>pratensis</i> | 25 | 11 | 35 | 0 |
| Coleoptera | Cerambycidae | <i>Judolia</i> | <i>montivagans</i> | 1 | 0 | 1 | 0 |
| Coleoptera | Cerambycidae | <i>Lepturobosca</i> | <i>chrysocoma</i> | 3 | 0 | 3 | 0 |
| Coleoptera | Cerambycidae | <i>Trachysida</i> | <i>aspera</i> | 0 | 1 | 1 | 0 |
| Coleoptera | Scarabaeidae | <i>Trichiotinus</i> | <i>assimilis</i> | 1 | 0 | 1 | 0 |
| Diptera | Syrphidae | <i>Chalcosyrphus</i> | <i>interruptus</i> | 1 | 0 | 1 | 0 |
| Diptera | Syrphidae | <i>Chalcosyrphus</i> | <i>xylotomima</i> | 0 | 1 | 1 | 0 |
| Diptera | Syrphidae | <i>Eristalis</i> | <i>obscura</i> | 1 | 0 | 1 | 0 |
| Diptera | Syrphidae | <i>Helophilus</i> | <i>hybridus</i> | 0 | 1 | 0 | 1 |
| Diptera | Syrphidae | <i>Orthonevra</i> | <i>pulchella</i> | 0 | 1 | 1 | 0 |
| Diptera | Syrphidae | <i>Platycheirus</i> | <i>scambus</i> | 0 | 1 | 0 | 1 |
| Diptera | Syrphidae | <i>Sphaerophoria</i> | <i>cranbrookensis</i> | 1 | 0 | 0 | 1 |
| Diptera | Syrphidae | <i>Sphaerophoria</i> | spp. 3 | 1 | 0 | 1 | 0 |
| Diptera | Tachinidae | <i>Ptilodexia</i> | <i>rufipennis</i> | 2 | 0 | 0 | 0 |
| Hymenoptera | Vespidae | <i>Dolichovespula</i> | <i>norvegicoides</i> | 1 | 0 | 0 | 1 |
| Hymenoptera | Vespidae | <i>Eumenes</i> | <i>crucifera</i> | 1 | 0 | 0 | 1 |
| Hymenoptera | Vespidae | <i>Euodynerus</i> | <i>foraminatus</i> | 1 | 0 | 0 | 0 |
| Hymenoptera | Vespidae | <i>Symmorphus</i> | <i>albomarginatus</i> | 2 | 0 | 0 | 0 |
| Hymenoptera | Andrenidae | <i>Andrena</i> | <i>thaspiae</i> | 3 | 1 | 2 | 2 |
| Hymenoptera | Andrenidae | <i>Andrena</i> | <i>vicina</i> | 3 | 1 | 3 | 1 |
| Hymenoptera | Apidae | <i>Anthophora</i> | <i>bomboides</i> | 1 | 0 | 1 | 0 |
| Hymenoptera | Apidae | <i>Bombus</i> | <i>frigidus</i> | 4 | 0 | 0 | 1 |
| Hymenoptera | Apidae | <i>Bombus</i> | <i>sandersoni</i> | 1 | 0 | 0 | 0 |
| Hymenoptera | Apidae | <i>Bombus</i> | <i>ternarius</i> | 9 | 3 | 12 | 0 |
| Hymenoptera | Apidae | <i>Bombus</i> | <i>vagans</i> | 8 | 0 | 0 | 2 |
| Hymenoptera | Apidae | <i>Melissodes</i> | <i>coreopsis</i> | 1 | 0 | 0 | 1 |
| Hymenoptera | Colletidae | <i>Hylaeus</i> | <i>annulatus</i> | 2 | 0 | 2 | 0 |
| Hymenoptera | Colletidae | <i>Hylaeus</i> | <i>basalis</i> | 1 | 1 | 2 | 0 |
| Hymenoptera | Halictidae | <i>Lasioglossum</i> | <i>abundipunctum</i> | 1 | 1 | 2 | 0 |
| Hymenoptera | Halictidae | <i>Lasioglossum</i> | <i>pavoninum</i> | 1 | 0 | 1 | 0 |
| Hymenoptera | Megachilidae | <i>Hoplitis</i> | <i>albifrons</i> | 1 | 0 | 1 | 0 |

| | | | | | | | |
|-------------|--------------|-----------------------|----------------------|---|---|---|---|
| Hymenoptera | Megachilidae | <i>Megachile</i> | <i>lapponica</i> | 0 | 1 | 0 | 1 |
| Hymenoptera | Megachilidae | <i>Osmia</i> | spp 4 | 1 | 0 | 0 | 1 |
| Hymenoptera | Megachilidae | <i>Osmia</i> | <i>proxima</i> | 8 | 0 | 2 | 6 |
| Hymenoptera | Vespidae | <i>Dolichovespula</i> | <i>arenaria</i> | 0 | 2 | 0 | 2 |
| Hymenoptera | Vespidae | <i>Dolichovespula</i> | <i>norvegicoides</i> | 1 | 0 | 0 | 1 |
| Hymenoptera | Vespidae | <i>Vespula</i> | <i>acadica</i> | 2 | 0 | 0 | 2 |
| Hymenoptera | Vespidae | <i>Vespula</i> | <i>vulgaris</i> | 0 | 1 | 0 | 1 |
| Lepidoptera | Lycaenidae | <i>Callophrys</i> | <i>niphon</i> | 1 | 0 | 0 | 1 |

Appendix B

Table B.1: 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 | 12005 |
| Asparagales | Orchidaceae | <i>Cypripedium</i> | <i>acaule</i> | 1 | 0 | 1 |
| Asterales | Asteraceae | <i>Aster</i> | spp. | 19 | 0 | 19 |
| Asterales | Asteraceae | <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 | 10598 |
| 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 | | | | 21369 | 7976 | 29345 |

Appendix C

Table C.1: 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>thaspis</i> | 11 | 4 | 15 |
| Andrenidae | <i>Andrena</i> | <i>vicina</i> | 4 | 1 | 5 |
| Andrenidae | <i>Andrena</i> | <i>vincina</i> | 24 | 16 | 40 |
| 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>Melssodes</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> | 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> | 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>paraforbesii</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> | spp. 1 | 6 | 1 | 7 |
| Halictidae | <i>Sphecodes</i> | spp. 2 | 3 | 0 | 3 |
| Halictidae | <i>Sphecodes</i> | spp. 3 | 4 | 1 | 5 |
| Megachilidae | <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> | spp. 1 | 20 | 8 | 28 |
| Megachilidae | <i>Osmia</i> | spp. 2 | 5 | 1 | 6 |
| Megachilidae | <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 D

Table D.1: 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> | 4 | 0 | 4 |
| Andrenidae | <i>Andrena</i> | <i>vincina</i> | 14 | 2 | 16 |
| 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>Melssodes</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> | spp. 1 | 7 | 0 | 7 |
| Halictidae | <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> | spp. 1 | 0 | 1 | 1 |
| Megachilidae | <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 E

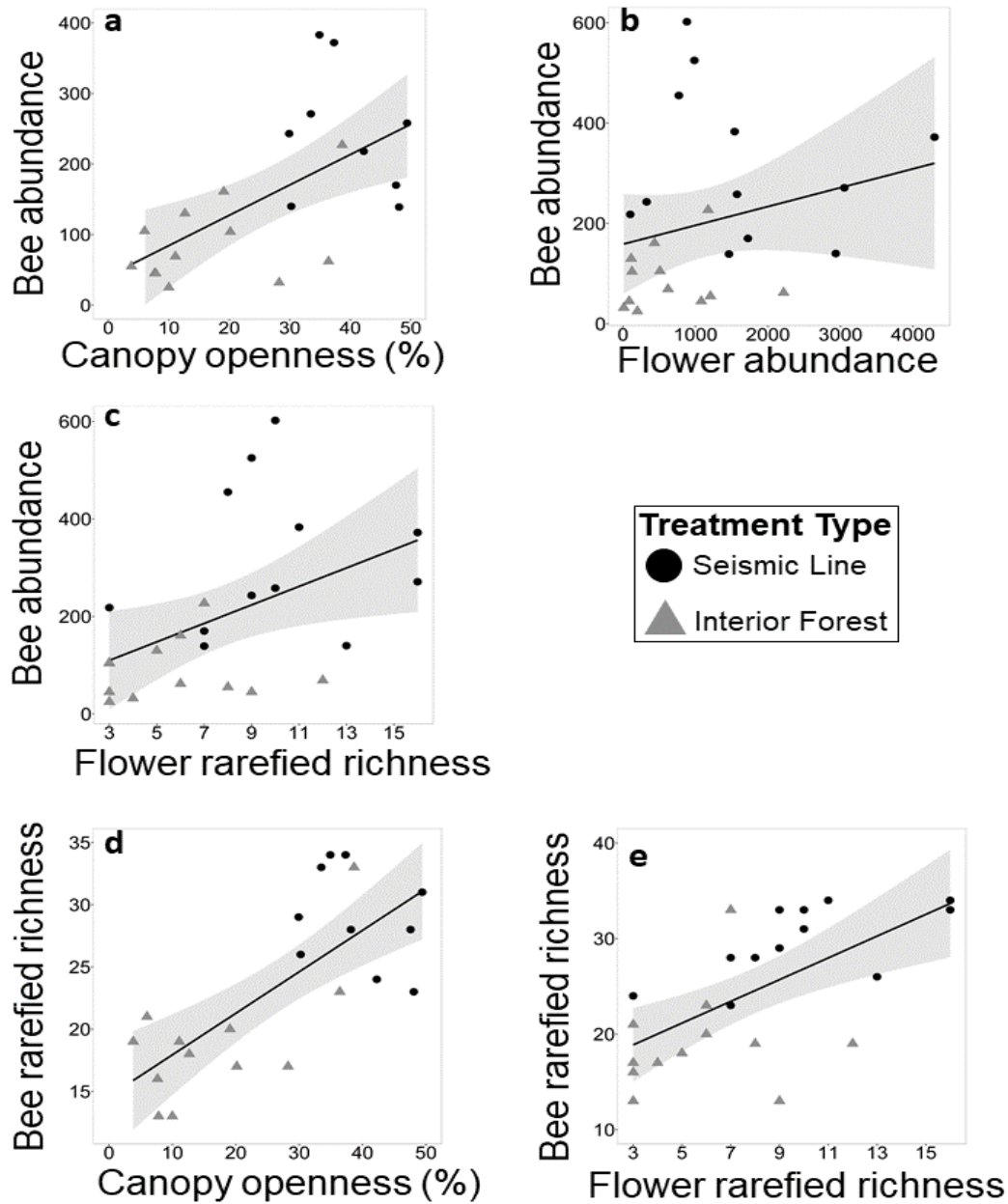


Figure E.1: Scatter plots showing the relationship between key explanatory variables (canopy openness, flower abundance, flower rarefied richness) and either bee abundance or rarefied richness. Grey bars represent a 95% confidence interval of a linear regression.