Small Restoration, Big Impacts: How Habitat Influences Native Pollinators in Intensive Agricultural Landscapes

by

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ABSTRACT

SMALL RESTORATION, BIG IMPACTS: HOW HABITAT INFLUENCES NATIVE POLLINATORS IN INTENSIVE AGRICULTURAL LANDSCAPES

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This study examined the impact of small-scale restoration of tallgrass prairie on native bee community composition on farms in Southern Ontario, Canada. Three farms with various crops (corn (*Zea*), Saskatoon berries (*Amelanchier alnifolia*), squash, pumpkin, zucchini, melon (*Curcurbitaceae*), soybeans (*Glycine*), and green beans (*Phaseolus*)) were surveyed in the summer of 2013. Availability of nesting and foraging habitat for bees was estimated and a combination of pan-trapping and sweep netting was used to capture specimens on 40 plots per farm. Results were analysed using ordination-based techniques in R, and indicated that prairie provides a diverse floral resource on which a complex and abundant array of bees forage. Restored habitat accounted for 33% of the total richness and 72% of the total abundance of native bees. This demonstrates that even small-scale restoration (~10% of each farm) may have an impact on the ability of farms in southern Ontario to support native bees.

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THESIS OVERVIEW

Intensive and widespread agricultural land management faces a ‘pollination paradox’ – the industry may need to increasingly depend on native pollinators for crop production, while at the same time farming-related activities are destroying the habitat (food resources, nesting) needed to support them, through cultivation, spraying, and the fostering of exotic weeds that may be unfriendly to pollinators. This habitat destruction is now occurring at an accelerating pace, given the explosion in food prices globally and the increasing cultivation of marginal habitats known to support pollinator populations in intensively managed agricultural landscapes (Wright and Wimberly 2013).

My research examines some aspects of this issue in an intensively farmed region of southwestern Ontario (the ‘sand plains’ region of Norfolk County, see Figure 1), by exploring how habitat diversity on farms - a function of past and ongoing land management - affects diversity, distribution, and abundance of native pollinators. To date, several questions regarding pollinator-declines in agricultural landscapes remain unclear. These include uncertainties over (i) which types of habitat on contemporary landscapes support compositionally complex and abundant native pollinator communities (e.g., oldfields, ditches, nearby forest remnants, crop fields); (ii) the life histories of those remaining species (are ground-nesting bees rarer than expected due to an absence of suitable nesting sites? Are specialists rarer than generalists?); (iii) whether food or nesting resources play a greater role in structuring pollinator communities?; (iv) whether habitat type even matters to remnant pollinator populations or are their food and nesting needs easily meet in areas of marginal farm land and crop fields?; (v) Or, conversely, does native pollinator diversity increase in restored resource-rich habitat such as forb-rich tallgrass prairie?; And (vi) might there be potential ‘spill-over’ effects of restored habitat on crop production in adjacent fields?

Survey-based approaches combined with spatial modelling were used to test various aspects of these questions on a collection of farms in Norfolk County, Ontario. This approach was carried out with two main objectives: (i) to estimate habitat quality within and among farms, and (ii) to quantify variation in the abundance and diversity of pollinator functional groups among habitat types including restored prairie. I test the hypothesis that the diversity and trophic complexity of pollinator communities are associated with increased floral availability and nesting sites in restored areas. As well, my spatial analyses allowed me to quantify the distribution of bees including possible ‘spill-over’ effects from one habitat type into another? (e.g., if native pollinators are concentrated in certain habitat types, how far from these habitats can these effects be detected?).

These results will help quantify the impacts of the restoration of tallgrass prairie on pollinator diversity and how habitat could influence pollination success on agricultural landscapes. The OMAFRA-funded work was conducted in close collaboration with ALUS (Agricultural Land-use and Services), a non-governmental farmer-led organization of 158 farms in Norfolk County interested in combining conventional agricultural practices with multi-value land management including biodiversity protection and enhanced ecosystem services (pollinator diversity, carbon sequestration in soils). Many ALUS farms have begun restoring prairie over the last half-decade but the functional significance for pollinators is still being tested (e.g., some work by CanPolin: http://www.uoguelph.ca/canpolin/Publications/pubs.html). My collaboration with ALUS will help connect the theoretical components of my research on habitat-pollinator dynamics with on-the-ground applied land management.

INTRODUCTION

In the wake of dwindling honey bee populations, as a result of colony collapse disorder, agricultural products that rely on bee pollination may have to increasingly rely on native bee populations. The explicit cause of colony collapse disorder remains unresolved, but it is hypothesized to be a result of pathogens and parasites (Varroa mites) in combination with developmental stress caused by pesticides (Cox-Foster et al. 2007, Duan et al. 2008, Potts et al. 2010, Smith et al. 2014, Staveley et al. 2013, vanEngelsdorp et al. 2009, vanEngelsdorp and Meixner 2010, Winfree et al. 2009). Many agricultural crops in Canada rely on pollination services, of which native pollinators can either provide all or a proportion of these services, depending on the crop species, the location and the use of honey bees or other managed bee species. There is evidence, although limited, that native bees can provide all of the pollination that certain crops require, even in the absence of managed honeybees (Garibaldi et al. 2013). Globally, 35% of food directly consumed by humans is derived from crops that benefit from flower visitation by insects (Klein 2007). We also depend indirectly on visitation to forage crops used in the dairy and meat industries, such as alfalfa and clover (Delapane and Mayer 2000) and soybeans (Chiari et al. 2005). Native bees, with over 4000 species in North America, are diverse in terms of foraging and nesting habitat requirements, with species varying in terms of tongue length (allowing them to forage for nectar on a limited set of plant species) and preferred nesting substrate (varying from ground to cavity to tunnel-nesting). [Note: insects other than native bees can also influence pollination but their contributions are relatively small compared to bees, typically because they do not visit inflorescences in patterns that result in maximum pollen deposition or they do not carry high pollen loads on their bodies (Bischoff et al. 2013, Fishbein and Venable 1996, Horsburgh et al. 2011, Mayfield et al. 2001, Stone, 1996, Zych et al. 2013) – I will only dealing with native bees in my study]. Agricultural intensification is thought to have reduced the availability of habitat for many native bee species due to activities such as the farming of monocultures, tillage practices, burning, and the application of herbicides and pesticides (Goulson et al. 2008, Kearns et al. 1998, Kevan and Viana 2003, Schuler et al. 2005, Steffan-Dewenter and Westphal 2008, Winfree 2010).

Two main characteristics of vegetation are needed to support diverse, functional pollinator communities. The first deals with foraging resources (pollen and nectar), while the second deals with nesting resources. Both types of resources are vital, in order to sustain pollinator populations over the course of their life cycle. The availability of floral resources throughout the growing season are essential to support a variety of pollinators with diverse life histories, which is problematic in intensively cropped systems where floral resources (e.g. canola) may be abundant but only available for a small period. It is therefore important, that habitats somewhere else in the landscape have reproductive phenological diversity (i.e., flowers available at all times of the growing season), otherwise, pollinator populations may not be sustained. For example, in German organic fields with higher flower cover and higher diversity of flowering plants, bee diversity was higher compared to conventional farms (Holzschuh et al. 2007). Similarly in Indonesia, pollination rates in coffee plants increased with increasing spatial heterogeneity (in terms of the timing and availability of floral resources) in coffee flowers (Tylianakis et al. 2008).

It is critical to determine how phenological diversity in flowering in crops, weeds and native plants affects populations of pollinators, and their resulting contributions to pollination ecosystem services (Kremen et al. 2007). A wide range of morphological characteristics in flowering plants (including shape, nectar) is also important to support species of pollinators that may differ in size and tongue length. Potts (2006) found that energy availability and diversity in nectar resources were key habitat characters responsible for structuring bee communities. Additionally, the presence, richness, and percent cover of attractive plants may work to increase temporal stability in the frequency of pollinator visitation, and thus sustain effective pollination and plant reproduction (Ebeling et al. 2008). This has been experimentally confirmed to a degree by Ghazoul (2006), who determined that pollination facilitation occurs among co-flowering plants with morphologically distinct flowers. Several mechanisms were suggested to explain this occurrence, including resource complementarity (for species that obtain pollen and nectar from separate plant species that co-flower), sampling effects (discussed later on), and positive facilitative interactions between pollinator species (Ghazoul 2006).

Lastly, it is imperative that the availability of nesting substrate be diverse, as wild bees possess a range of nesting strategies, including ground, tunnel, cavity, and hive nesting as defined in Table 11 (Packer et al. 2007, The Xerces Society 2011). Land management practices such as tilling can have significant indirect negative effects on pollination, since some highly effective species such as squash bees are ground-nesters, and thus depend on the availability of undisturbed soil to create their nests (Schuler et al. 2005). Undisturbed but open soil is a relatively uncommon feature of modern-day agricultural landscapes, suggesting that ground-nesting species may be selected against relative to species with other strategies. Anecdotal data from both local farmers and from recent prairie restoration in southwestern Ontario suggest that tilled and unplanted bare soil in late spring can be rapidly colonized by high densities of ground -nesting insects, although the identities of these insects are unclear (unpublished data, Andrew MacDougall). Species respond differently to various soil conditions resulting from land management practices and more abundant and diverse bee communities have been found with nesting sites in farms that contain patches of natural habitat nearby (Kim et al. 2006).

According to some field studies, species richness of both plants and pollinators may lead to increased stability (i.e. temporarily and spatially consistent pollen deposition) of pollination ecosystem services. Differential responses of species to disturbances (i.e., different species tolerating different forms of land management, meaning there are always pollinators present) may potentially act as a buffer to the provisioning of pollination ecosystem services across land use gradients (Elmqvist et al. 2003). Species may also respond differently to increases in land use (for example, some are able to fly further distances to forage), which could also dampen the negative effects of agricultural intensification on pollinators (Winfree and Kremen 2008). Field studies of pumpkins and both lowland and highland coffee beans indicate that species richness of bees may be more important than total bee abundance in explaining differences in pollination ecosystem services (Klein et al. 2003, Klein et al. 2008, Delaplane and Mayer 2000, Hoehn et al. 2008). Another field study of coffee plants indicated that adequate pollination was only received when plants were closest to forest fragments, where rich bee communities were present (Ricketts 2004). On watermelon farms, only those with low intensity land management practices and rich bee communities received sufficient pollination services (Kremen 2004). In a Venezuelan study, agricultural intensification (specifically, habitat loss) was correlated with decreasing richness and abundance of pollinators (Larsen et al. 2005).

A critical question that has been the target of considerable research over the last 20 years including in Canada and Ontario specifically (e.g. http://pollinator.ca/canpolin/index.html) is "how are these changes in pollinator communities and the provisioning of pollination ecosystem services unfolding in agricultural landscapes"? One uncertainty is the role that so-called marginal farmland may play in the life-histories of pollinators. Marginal lands may be defined as all land in agricultural landscapes that is not intensively managed, or can be intensively managed but requires unusually high amounts of resource inputs (e.g., irrigation, fertilizer) to produce a crop thereby making it only marginally profitable. These lands can include areas on farms such as fields with poor soils, oldfields, horse pastures, drainage areas (which collectively constitute Class IV and Class V land in Ontario), as well as nearby forest remnants; and areas among farms such as road-side ditches (Wright and Wimberly 2013). The marginal land issue is especially important, for two reasons. First, these areas may be beneficially serving as *de facto* pollinator habitat, particularly for nesting. Second, these areas may be highly appropriate for habitat restoration on farms. Waste areas may be converted to resource-rich plant communities, replacing invader- or weed-dominated communities with pollinator-friendly (i.e., high flowering forb diversity, high nesting habitat) plant communities that, in turn, create spill-over benefits for crop plants. Given the explosion of food prices globally, especially for corn and soybeans, farmers are likely unable to contemplate planting pollinator-friendly plant communities on Class I-III land (Wright and Wimberly 2013). However, conversion of marginal land represents a potential win-win situation, by increasing pollinator habitat, and elevating pollination services to nearby pollinator-dependent crop plants.

Research to date on pollinators has commonly focused on one comparison, that between pollinator diversity and services on organic versus conventional farms (see Kennedy et al. 2011), effectively treating the latter as homogenous in the quality of pollinator food and nesting resources. This fails to acknowledge, however, that conventional farms can both be very different from each other, as well as ‘internally’ heterogeneous usually due to within-farm variation in habitat quality, thus with potentially variable impacts on pollinators. This is especially true in many parts of southern Ontario, where farms often contain many fields with single-species, non-organic monocultures but also some diverse collections of forest, crops, pasture, and wetland (Statistics Canada, 2011). My work will examine whether this habitat diversity on intensively managed conventional farms influences on-farm pollinator communities, even though these areas tend to occupy a relatively small footprint compared to fields in intensive monoculture.

Tallgrass Prairie

The planting of tallgrass prairie on farms in Ontario is being conducted increasingly for a range of purposes including biofuels, soil carbon storage, pasture forage for beef cattle, and wildlife habitat (e.g., the endangered bobwhite quail [*Colinus virginianus*]) but may also serve to bolster native pollinator populations. In testing for the overall impact of habitat on pollinators, I will also investigate the impact of tallgrass prairie (TGP) restoration on pollinator communities (diversity, composition, and abundance), and estimate its potential contribution to pollination services. Historically, TGP covered somewhere between 1,000-2,000 square kilometers in Ontario, but currently less than 3 percent remains as a result of agricultural land clearance and urbanization (Rodger 1998). Because this prairie habitat type was relatively open compared to forested areas of southern Ontario, TGP was aggressively and immediately colonized by European settlers starting in the early 1800s. Habitat loss in Ontario thus occurred within a few decades, and remnant areas that have persisted into the present-day are typically on soils unsuitable for agricultural (coarse glacial tills) or are associated with old railway corridors (e.g., the old Grand Trunk rail-line south of Cambridge, Ontario) and cemeteries (e.g. Rice Lake Plains south of Peterborough, Ontario). These remnant areas are never found on conventional farms.

Typically consisting of a mixture of nectar-rich forbs and other wildflowers as well as grass species such as Indian grass, big and little bluestem, and switch grass, TGP systems may provide foraging and nesting resources for native bee species, including the endangered rusty-patch bumblebee (*Bombus affinis*) (COSEWIC 2010), in addition to a multitude of other ecosystem services (e.g. carbon sequestration, nitrogen fixation, and soil stabilization - Rodger 1998). Some farmer organizations have already begun planting prairie in marginal areas in hopes to increase these services, although the effectiveness of these plantings is unclear. I worked with a farmers organization from Norfolk County, Ontario (ALUS- http://www.norfolkalus.com/). This group is especially keen to determine possible economic spill-over benefits of prairie restoration on marginal lands, in a sense trying to solve the pollinator paradox (increasing pollinator loss coupled with increasing human dependence on bee-pollinated crops) by managing for crop production but also pollinator habitat with the latter potentially benefitting the former (more pollinators = greater crop production). A number of ALUS farms have planted TGP mostly on marginal areas of their farms – my research focused on a subset of these farms.

This perspective on managing for a range of services and cover types is contrary to the typical approaches of intensive agriculture, which rarely consider pollinator habitat other than bringing in hives of European honey bees when needed. Due to the lack of value that intensive farming tends to place on ecological integrity (i.e., managing beyond crop production), vital ecosystem services upon which we depend may be suffering, including pollinators. Several different valuation systems have been proposed to integrate pollinator management within current agroeconomic models (i.e., so farmers can better appreciate the economic contribution of pollinators towards their financial bottom line). Winfree (2011) suggests that using a method termed "attributable net income" is the most practical way of valuing insect crop pollination services. Attributable net income values only the pollen utilized in producing fruit, and can be separated into different functional groups (native and managed, for example). Alternatively, “cost of replacement” methods estimate the cost of alternate methods of pollination without honey bees or native pollinators (e.g. pollen dusting, hand pollination, hive rental) (Allsopp et al. 2008). This is estimated by subtracting the annual production value using pollinator replacement from the annual production value attributed to insect pollination (Allsopp et al. 2008). A key limitation in both of these models, however, is a lack of field data that quantifies (i) the actual diversity, distribution, and abundance of pollinators on agricultural landscapes, (ii), the influences of various farming practices to increase these measures, and (iii) how differences in diversity, composition, and abundance of pollinators influences crop yields. These short-comings in data have inhibited the determination of economic yield-based benefits of pollinator management, a short-coming targeted in Canada and in Ontario by organizations such as CanPolin, Pollination Canada (http://www.pollinationcanada.ca/), and other similar groups.

QUESTIONS & HYPOTHESIS

My research aimed to test the impact of habitat diversity on pollinator community composition and abundance on conventional farms, focusing on farms that include fields that are monocultures of crops but are also being managed for increased habitat diversity via the planting of tallgrass prairie and oak savannah on marginal areas. The target of my research is to address key issues related to the diversity, composition and abundance of native pollinators (as discussed previously) on multiple ALUS farms, where I attempt to answer the following questions:

1. What is the diversity, composition (both species and functional-group levels) and abundance of pollinators in restored prairie?
2. How does this compare with three other habitat types typically found on farms in Norfolk county – intensive crops fields (conventional), waste areas (i.e. ditches), and adjacent forest patches which tend to have high concentrations of flowering understory forbs especially in spring?
3. What environmental features of the landscape (i.e. nesting or foraging materials) are most associated with a diverse and compositionally complex native bee community?
4. How do farms with varying habitat configurations compare in terms of pollinator community composition, diversity and abundance? And how do they compare in terms of the availability of potential foraging and nesting habitat?

Based on current knowledge of habitat-pollinator dynamics on farms, as reviewed above, I predict the following results based on my hypothesis that habitats with greater foraging and nesting resources will support a more complex, diverse and abundant native bee community:

P1: There will be a strong positive relationship between habitat type (as defined by ALUS, landowners and on the ground surveys) and pollinator diversity on the farms that I will be sampling, along a gradient from prairie (best) to conventional (poor), with marginal/waste areas and forested areas being intermediate.

P2: This positive relationship will be associated with several habitat features relating to food and nesting that I assume to occur more frequently in restored prairie – greater total availability of flowers per unit area, greater diversity of flower colours per unit area, greater availability of bare ground favored by ground nesting bees, and greater availability of coarse plant litter favored by cavity-nesting bees.

P3: There will be significantly greater pollinator diversity in marginal farms areas (e.g., ditches) and adjacent forested sites compared to intensively managed crop areas, consistent with the idea that marginal areas and forests are important for pollinators in farmed landscapes, but these areas will have less diversity compared to restored prairie.

METHODS

Three farms in Simcoe, Ontario participating in ALUS restoration projects were sampled three times throughout the summer of 2013, in June, July and August, each time being associated with different intensities and diversities of pollinator activity (late spring, midsummer, and late summer; Figure 1).

I worked through a list of almost twenty candidate farms with the ALUS staff, to identify the best configuration of habitat diversity and farm proximity. This was to reduce driving times among farms and to determine which candidate farms will be most suitable for this project, provide a range of habitat types, as well as a gradient of large to small TGP restoration areas. Of these, a select few had planted prairie and oak savannah that was well established, and where the landowners agreed to support our research. The three farms chosen and the area surveyed on each provide us with a gradient of relatively small to large farming areas, each with roughly the same proportion of total land restored to prairie (approximately 10%). The first farm, which has around 35-40% of the total land we surveyed restored to prairie (10% of the landowners total land- we did not survey the entire property), was the smallest of the three. The second farm, which was intermediate in size compared to the other two, has 60-70% of land restored to oak savannah with a small prairie restoration equaling approximately 10% of the land. The third farm, the largest of the three, has a large prairie restoration that accounts for 10-15% of the total farmland (Figs. 2, 3, 4). All three are intensively managed conventional farms, meaning that they utilize pesticides, and engage in tilling and other practices which some research suggests is detrimental to the success of pollinators. My research consisted mainly of observational, survey-based analysis and extensive statistical modeling. The observational study involved surveying numerous locations on each farm, to connect landscape features with organismal (plant and pollinator) diversity, abundance and pollinator behavior (in terms of habitat usage to determine what types of habitats are used for foraging and nesting, respectively). The modelling work combined the diversity, habitat, and spatial factors that I measured, to test their relationships both within and among the three farms.

Forty 4 x 4 m plots were placed strategically on each farm to capture the heterogeneous distribution of habitats (and thus, potential resources) (Figs. 2, 3, 4). Basically, I divided the farm into the major habitat types (e.g., crop fields, prairie), and then sampled randomly using survey plots (4 x 4 m) within each of these habitats, thus ensuring that I not only captured potentially variability within each habitat type but that I also captured ‘distance’ (e.g., locations in crop fields both near and far away from boundaries with prairie, and so on).

Within each plot on each of the participating farms, I conducted surveys of diversity, abundance, and nesting substrate availability. Geographical coordinates of each plot were obtained to within 1m or less using a Trimble handheld GPS unit. Estimates of nesting and foraging resources were assessed each month at each plot, and averaged overall. Nesting substrate availability was estimated using percent coverage of 5 substrate types (bare ground, mud, pithy stems/twigs, woody debris, and existing cavities over 2mm which may have been created by other insects or vertebrates) in order to cover the range of materials and strategies utilized by each bee genus (Packer et al. 2007, The Xerces Society 2011). Foraging resource availability was estimated as percent coverage (i.e. the percent coverage) of open white, blue and yellow flowers within each plot, presence of pollen and nectar availability (scored as a binary presence/absence for flowers known to produce nectar and those with visible pollen), and the richness of those plants currently in flower (at the lowest taxonomic level possible). The percent coverage of currently available floral resources provided an estimate of floral resource availability for generalist genera (Kremen et al. 2004).

Native bees were captured using a combination of day-glo fluorescent Kryolan spray painted pan traps (2 of each colour for a total of 4 pans per plot) and sweep netting using 15" diameter fine mesh nets (Spafford and Lortie 2013). The pan traps were filled with a mixture of 5 drops of Dawn Ultra dishsoap per 1000 mL of water. Pans were put out before 9 AM each day, and collected after 5 PM. Specimens were drained from pan traps into coffee filters, placed in zip-lock bags and frozen in order to preserve them prior to being taken back to the lab for pinning and identification (Droege et al. 2012). Sweep netting was conducted by myself and 3 field technicians between the hours of 10 AM and 2 PM to maximize catch rate at the time of day when bees are at their peak flight abundance (Droege et al. 2010). Sweep-netted specimens were placed into zip-lock bags and frozen. It is important to combine sampling methods, especially since pan traps can sometimes over-sample pollinator diversity (e.g., when flowers are scarce, coloured pan traps can quickly fill with pollinators, thereby 'over-sampling' – complimentary sweep netting helps control for this possibility) (Spafford and Lortie 2013).

Specimens were identified visually using keys for *Apoidea* found on discoverlife.org, Laurence Packer's "*The Bee Genera of Eastern Canada*" (Packer et al. 2007), and Steve Marshall's "*Insects: Their Natural History and Diversity*" (Marshall 2007). Ambiguous or difficult-to-identify specimens were sent for DNA barcoding at the Canadian Centre for DNA Barcoding in Guelph, Ontario. Records are stored in the Barcode of Life Data System (BOLD), and also include photographs of specimens (see 'ASGCB- Grassland Community Barcoding' file at http://www.boldsystems.org). The term DNA barcoding refers to the process of extracting and sequencing specific regions or markers in the genome of an organism, which in this case is the 648 base-pair cytochrome c oxidase-I (COI) gene (Ratnasingham and Hebert 2013). Identifications were retrieved using the BOLD nucleotide sequence identification search engine, which compared the COI sequences for my specimens from the CCDB to those of pre-existing, published sequences archived in the BOLD database (Ratnasingham and Hebert 2007). In cases where sequence divergence was greater than 2%, identifications were based on BINs (Barcode Index Number) within Taxon ID Trees generated by BOLD, and the most common published entries with the least amount of divergence were taken as the probable species identification (Ratnasingham and Hebert 2013). Details on how the barcoding was conducted, facilitated by the Alex Smith lab, are described in Ratnasingham and Hebert (2007).

Statistical Analyses

To analyze the results of this study, I utilized three major techniques in landscape ecology known as Principal Components of Neighboring Matrices (PCNM), Distance-Based Redundancy Analysis (db-RDA) and variation partitioning to perform ordination analysis on dissimilarity matrices of species abundance data and environmental data. These analytical techniques, which separate the relative multivariate influence of measured factors on my responses variables (e.g., pollinator diversity), allowed me to test the spatially relevant hypotheses of my thesis. PCNM analysis creates spatial explanatory variables at multiple spatial scales ranging from broad to fine, which can then be used in regression or RDA analysis and related to a species matrix (e.g., the matrix of diversity levels from all plots on each farm) and environmental variables (e.g., bare soil, flower diversity) and consists of three main steps (Borcard and Legendre 2002). First, the pairwise Euclidean distance matrix is calculated using the geographical distance between sampling points. Second, a threshold value is chosen and a truncated distance matrix is calculated. Lastly, principal coordinate analysis (PCoA) is performed on the truncated distance matrix (Dray et al. 2006). The principal coordinates that result from positive eigenvalues are utilized as explanatory variables in the redundancy analysis, and they represent the Euclidean components of the relationships within the truncated geographic distance matrix (Borcard and Legendre 2002).

For my analysis, a distance-based redundancy analysis using Jaccard distance was calculated and utilized as a species distance matrix. Distance-based redundancy analysis or db-RDA is a method of redundancy analysis combined with principal coordinate analysis (PCoA) and is based on an ecologically meaningful distance measures (Legendre and Anderson 1999). Using db-RDA gives you the freedom to choose between a wide variety of distance measures, and it also allows non-Euclidean distance measures to be utilized (Anderson et al. 2011). Euclidean distance measures are not as useful as non-Euclidean distance measures when looking at species composition, because they tend to focus on the distance between sites rather than the distance between species (Borcard et al. 2011). I chose Jaccard's similarity index because a binary presence-absence matrix does not focus on rare or abundant species, but rather allows us to look at the composition of a community when there is a large range of abundances and zero entries in our species data matrix (Borcard et al. 2011). Thus, a distance matrix using the preferred distance measure (i.e. Jaccard) is calculated. Second, the principal coordinates are calculated that maintain the distances from the matrix. Finally, redundancy analysis is used to look at the relationship between the species data and the resulting model, and permutation tests are used to determine the significance of each term of the model (Legendre and Anderson 1999). Minimum spanning trees were used to determine relationships between neighboring plots (Dray et al. 2006).

Forward selection was carried out on PCNM eigenvectors and environmental variables before the final db-RDA analysis. A double-stopping criterion was utilized in forward selection to avoid type I errors or overestimation of the amount of variation explained (Blanchet et al. 2008). Prior to proceeding with forward selection, the global test with all explanatory variables must prove to be significant when tested (which I found to be the case with my analyses). This method utilizes two stopping criterion, the first being the alpha significance level and the second being the adjusted coefficient of multiple determination with all explanatory variables (Blanchet et al. 2008). If a variable results in either value being over the given limit the procedure is no longer carried out, and it rejects that variable which caused the value to exceed the limit (Blanchet et al. 2008). Plots with no bee species recorded were removed in order to satisfy the requirements of the dissimilarity matrix determination (i.e., no zero entries).

The analyses were carried out using R statistical software version 3.0.2 (R Core Team, 2014), employing a number of downloadable "packages" for the software including vegan, capscale, packfor, and varpart (Borcard et al. 2011, Peres-Neto et al. 2006, Legendre & Legendre 2012). Identical analysis was also performed at the genera level, the corresponding data and figures for which is included in the appendix. The three months in which I sampled were pooled for each analysis, due to large differences in effective catch rate. Pollinator abundances were summed for each plot, whereas environmental variables were averaged over the three months.

My analyses were specifically constructed around the following sets of variables:

Explanatory variables:

1. Habitat type (dummy variables- categorized as binary 1 or 0)

    1. Restored tallgrass prairie (hereafter defined as planted prairie areas dominated exclusively by herbaceous plants – grasses and forbs).
    2. Cropland
    3. Forest
    4. Marginal lands (edge, ditch)
    5. Restored oak savannah (only present on Farm 2) (hereafter defined as planted prairie areas dominated by herbaceous plants – grasses and forbs – but also containing some cover of woody savanna species such as oak).
2. Availability of nesting and foraging resources (% coverage estimate)
    1. Yellow inflorescences (e.g., goldenrod, prairie sunflower)
    2. Blue/Purple inflorescences (e.g., vetch, some aster species)
    3. White inflorescences (e.g., queen anne's lace, some aster species)
    4. Flowering plant diversity (species per plot)
    5. Bare ground (% visible over per plot)
    6. Mud (% visible over per plot)
    7. Pithy stems and twigs (% visible over per plot)
    8. Woody substrate (% visible over per plot)
    9. Cavities (pre-existing) (% visible over per plot)
3. PCNM variables
4. Spatial variables (UTM coordinates)

Response variables (bees):

1. Community composition (dissimilarity measure using Jaccard's distance)
    i. Genus-level

ii. Species-level

RESULTS

Overview

Measured habitat conditions on the farms: All farms had mixtures of the four habitats. Farm 1 comprised approximately 60% crop (corn), 25% prairie (i.e., planted herbaceous flora species), 10% forest, and 5% marginal land. Farm 2 consisted of approximately 70% oak savannah (i.e., planted trees, shrubs, and herbaceous ground flora species), 15% Carolinian forest, 10% prairie and 5% marginal land, with a Saskatoon Berry crop at the top end. Farm 3 comprised approximately 70% crop (corn, soybeans, squash, pumpkin), 15% prairie, 10% Carolinian forest, and 5% marginal land. The prairie habitat had the greatest range of flower colour, reward type (nectar, pollen), nesting material, and bare ground (Tables 1-2). This is also demonstrated in the RDA biplots for each farm where prairie is consistently collinear with these environmental variables (Figs. 9, 10, 11). Next was forest, which was rich in nesting material but generally lacked flowers during my sampling periods. I may have missed early spring understory flowers, although it was a late spring due to early cool conditions and I still only recorded a few flowers in the woods. Marginal areas had mixtures of floral resources and nesting material, although flowering diversity was much lower in terms of number of species, percentage cover of floral resources, and range of flower colours in comparison to prairie habitat (Tables 1-2).

A large proportion of the bee genera and species were found in prairie areas on the farms, with the most abundant and diverse floral resources (pollen and nectar) (Tables 1-2, 4). This result can also be seen in the RDA biplots for each farm where the environmental variable “PRICH” (flowering plant richness) is highly predictive of a more complex and dissimilar bee community (using Jaccard’s distance, see Figs 9-11). Compared with prairie habitat, fewer bee genera and species were found in marginal areas or forest, depending on the farm (Table 4). Very few bees were captured in crop fields such as corn, except some in areas in close proximity to habitats with abundant floral resources (Tables 4-5). The maximum distance of this was approximately 5-10 m (i.e., the maximum distance into the corn fields where I captured bees). Nesting resources varied from habitat to habitat, with pithy stems and twigs being abundant in prairie habitat, and bare ground to a lesser extent. Woody debris, pithy stems and twigs, and some bare ground were abundant in forested areas (Table 2). Bare ground was typically abundant in crop areas, but it is likely that this would not provide nesting habitat to bees due to frequent tilling on the farms we examined. Marginal areas varied from farm to farm, but they typically had a mixture of bare soil, pithy stems and twigs and some woody debris.

Bees: I captured 118 bee species from 22 bee genera totaling 1242 individuals (Table 3 – summary list of all species and genera and their abundances). DNA barcodes were used to identify species from certain morphologically challenging genera, which were difficult to distinguish based on visual inspection alone (i.e., *Lasioglossum, Andrena, Megachile,* and *Nomada*). The most abundant genera were *Lasioglossum, Agapostemon, Augochlorella, Ceratina,* and *Hoplitis*. The most abundant species was *Hoplitis pilosifrons,* followed closely by *Augochlorella aurata* (Table 3). The rarest genera were *Calliopsis,* *Colletes, Dieunomia, Svastra,* and *Xylocopa.* Thirty six species were collected only once in the entire survey (Table 4).

Most of the common genera would be considered floral generalists, based on their known associations with a range of flowers and habitat (Packer et al. 2007, The Xerces Society 2011). These include *Lasioglossum, Andrena,* and *Megachile*. *Megachile,* the leaf-cutting bee, which constructs nests out of cut-up leaf material, is generally considered to be one of the most effective pollinators as a result of its flying motion, hairy body, and ineffectiveness at carrying pollen which means it must make considerably more visits to inflorescences than other bees when foraging (Shebl 2008). There were some specialists. The parasitic genus *Nomada* specializes in foraging on nectar rich plants only, as it utilizes the pollen in the nests it parasitizes from the *Andrena* genera. The most abundant species, *Hoplitis pilosifrons,* is considered to be a specialist pollinator on the genus *Penstemon*, which occur commonly in planted/restored tallgrass prairie seed mixtures in Ontario. The most abundant genera, *Lasioglossum, Andrena, Megachile*, and *Nomada* are respectively considered to be ground, mining, leaf-cutting and parasitic nesters. The rarest genera, *Calliopsis, Colletes, Dieunomia, and Svastra*, are considered to be ground nesters with the exception of *Xylocopa*, which is a carpenter bee and constructs its nest in wood (Packet et al. 2007, The Xerces Society 2011).

For the most part, the same abundant genera and species tended to be found on all three farms- *Lasioglossum, Andrena, Agapostemon*, and *Augochloropsis* (as well as sub-genera *Augochlora/Augochlorella)*. However, there were some genera that were specifically found on only one farm or to a much lesser extent on the other two farms. The genera *Hoplitis*, for example, was almost exclusively found on Farm 2 in abundant numbers (Farm 2 had a large planted oak savannah, tallgrass prairie, Carolinian forest and a small Saskatoon berry orchard). *Ceratina* was also found to be strikingly more abundant on Farm 2, as compared with the other two farms. *Melissodes* was found to be much more abundant on Farm 1, as compared with the other two farms. This is interesting because although, as detailed further on, all farms displayed similar results in terms of which environmental variables had a significant relationship with community composition, there are some subtle differences (such as nesting habitat availability) which may influence the differences in genera found among farms.

There were also differences among habitats, with respect to the bee community. Prairie habitats supported 68% of the full range of bee species that I recorded (Table 5). Marginal or "edge" areas were the next most important, supporting 55% of all the species that I saw. Crop was next – this area supported 28% of all species. And lastly, forest supported only 18% of species (most likely due to this area not containing floral resources later in the spring and summer). Although I did not survey farms with and without restored prairie, my data suggest that the latter supports less diversity etc. than the former. If I exclude prairie and restored oak savannah from my data, only looking at marginal lands, forest, and crops (the typical profile for farms in Ontario), I would see a 33% reduction in richness, a 72% reduction in abundance, and would not have detected 39 species at all (which were exclusively found in prairie and oak savannah habitats). Approximately 41%

of all species detected were exclusively found in one type of habitat only, supporting the idea that habitat heterogeneity increases the diversity of bees found within farms.

In addition to the differences in genera and species abundance and diversity between farms and habitats within farms, there were also differences between the months we sampled from the late spring to late summer. Abundance peaked in June, with a total of 754 specimens caught amongst all farms in this month and the most abundant genera being *Augochlorella, Agapostemon, Andrena, Ceratina, Hoplitis*, and *Lasioglossum*. July showed a strong drop in abundance, with the number of specimens caught across all farms dropping down to 223, and the most abundant genera being *Augochlorella, Apis* (most likely as a result of managed honey bees being brought onto farms for pollination services), *Ceratina* and *Lasioglossum*. Again in August, a total of only 250 specimens were captured across all farms, with the most abundant genera being *Agapostemon, Bombus, Lasioglossum, Melissodes*, and *Peponapis*. Differences in genera abundance across the seasons can most likely be attributed to a changing host of floral resources from spring to summer. Understory plants of Carolinian forest flower in early spring prior to leaf canopy closure – as mentioned, my sampling in late spring (delayed because of cold weather) appears to have missed this early floral bloom in forested areas on my farms. Similarly, flowering forbs of prairie also tend to flower in early summer, with diminishing floral resources later into the summer as the native C_4 grasses such as big-blue stem start to dominate the grassland canopy. Reduced capture of bees also likely reflects differences in the effectiveness of my sampling among the three time periods [see Methods] – because of this I pooled my three months together for my analyses.

The db-RDA allowed me to test the structure of my general findings, especially the relative importance of spatial and habitat-based factors on the abundance, composition, and richness of pollinators for each farm. 'Spatial' factors refer to distributional or abundance patterns that strictly relate to spatial patterns with no detectable association with habitat – for example, bees may be clustered in some areas but not others because of dispersal limitation. 'Habitat' factors refer to distributional or abundance patterns that strictly relate to habitat features - for example, bees may be clustered in some areas but not others because of the availability of floral resources. Typically, spatial and habitat factors combine to explain distribution and abundance (Cottenie 2005, Pinto et al. 2010, Germain et al. 2013).

Variation decomposition

In general, the db-RDA analysis of each farm revealed spatial and environmental structuring although the environmental variables contributing to this structure differed on each farm. Through variation decomposition we see that isolated spatial and pure environmental signals alone are somewhat weaker on their own (Figs. 21-23). Pure environmental variation had adjusted R^2 values of 0.009, 0.089, and 0.050, while pure spatial variation had adjusted R^2 values of 0, 0.020, and 0.048 for Farms 1-3 respectively. Combined explained variation adjusted R^2 values for spatial and environmental factors were 0.081, 0.082, and 0.029 for Farms 1-3 respectively. Also shown in figures 21-23 are adjusted R^2 values for identical analyses using genera-level data, where explained variation is notably higher than for species level data, most likely due to a high number of null abundances and a very wide range of abundance values at the species level. This combination of spatial and environmental structuring suggests that bees are non-randomly distributed due to the size and location of each habitat within the farm.

Spatial

i) PCNM eigenvector maps

The patterns seen in the PCNM eigenvector maps tend to correspond with specific habitat areas on each farm. These maps display patterns of community composition. In this study, because I used a dissimilarity measure (Jaccard's) to compute a dissimilarity matrix, these figures are showing plots (as black boxes, the larger the box the stronger the dissimilarity) where the community is more dissimilar in terms of species (i.e. more complex, and diverse). On Farm 1, the restored prairie area at the bottom along with the marginal ditch area located on the right hand border (Fig. 2, 8). This is evident in both the PCNM eigenvector maps for the genera level and species level analyses, indicating that these habitats have a strong influence on the structuring of native bee communities on this farm (note: by 'structuring', I mean influencing the richness, composition, and/or abundance of bees). The prairie habitat is collinear, as expected, with the same group of environmental variables in each case (flowering plant richness, yellow inflorescence abundance, white inflorescence abundance and blue inflorescence abundance) (Fig. 9-11). On Farm 2 the PCNM eigenvector maps tend to correspond with the location of the restored prairie (top right corner), the oak savannah (bottom) and potentially the Carolinian forest (right) (Fig. 12). Again this is seen at both the genus and species level. The environmental variable "prairie" is again collinear with flowering plant richness, and yellow and blue inflorescence abundance at both levels. Interestingly, on Farm 2, the environmental variable "oak savannah” is collinear with the abundance of white inflorescences, indicating that this habitat, while similar to prairie, is supporting specific species of plant, which then support specific species and genera of native bees. On Farm 3 the PCNM eigenvector maps correspond again with the location of the restored prairie and also the location of mixture of squash and pumpkin crops that are both bee pollinated flowering plants (top) (Fig. 13).

ii) UTM coordinates as explanatory variables

Pure spatial structuring (using UTM coordinates alone as explanatory variables in an RDA analysis with a species distance matrix) was marginally stronger on Farm 2 (adjusted R^2=0.1130384) compared with Farms 1 (adjusted R^2=0.05311849) and 3 (adjusted R^2=0.03632181) (Fig. 14, 15, 17). RDA analysis using positive as well as forwardly selected PCNM eigenvectors and UTM coordinates (used here as vectors) revealed similar results among the three farms, although once again the adjusted R^2 was marginally higher for the analyses performed on Farm 2 (Tables 7-9). These results indicate that both small scale (plot level - within habitat) and north-south (farm level- among habitats) spatial scales influence the distribution and composition of bees on this farm. This spatial structuring suggests that bees are non-randomly distributed due to the size and location of each habitat within the farm.

Environmental

On Farm 1 crop land supports a small and structurally simple bee community. On Farm 2 woody debris, flowering plant richness and oak savannah habitat have a significant positive impact on the abundance, diversity, and/or composition of the bee community. On

Farm 3 forest and prairie habitat strongly influenced the structure of the bee community. RDA analyses using environmental variables and species distance matrices yielded equally strong results for Farms 1 and 3 (F1 adjusted $R^2 = 0.08459262$; F3 adjusted $R^2 = 0.0858306$), while the analysis for Farm 2 showed the strongest results out of the three with the highest amount of variation being explained (F2 adjusted $R^2 = 0.2240407$) (Fig. 9-11). A second set of RDA analyses using only forwardly selected environmental variables yielded a similar set of results, with the adjusted R^2 values being similar for Farms 1 and 3, and higher for Farm 2 (F1 adjusted $R^2 = 0.09003045$; F2 adjusted $R^2 = 0.1703587$; F3 adjusted $R^2 = 0.07857744$). Forward selection of environmental variables resulted in the selection of "crop" as being significantly inversely related to the distribution and composition of native bees caught on Farm 1 (Fig. 9). Forward selection of environmental variables on Farm 2 resulted in "wood" (woody debris), "plant richness" (flowering plants), and "oak savannah" being forward-selected and having a positive significant influence on native bee distribution and composition (Fig. 10). Forward selection of environmental variables on farm 3 indicated that "forest" and "prairie" have a significant positive influence on the distribution and composition of native bees (Fig. 11). A relatively high adjusted R squared value for these forwardly selected environmental variables indicates that these habitats and resources (both floral and nesting material) are supportive of a compositionally complex bee community, structured by specific habitat features (as opposed to more spatial or 'neutral' distance based factors). In the case of Farm 1 the environmental variable "crop" is highly predictive of bee distribution and composition, albeit negatively as crop land supports a significantly lower number of bees and a compositionally less complex array of species than other habitats present on this farm. It may also be possible that it supports no species, and I merely captured individuals flying across the fields that happened to see my coloured dishes. If true, the low frequency of captures may mean that bees are more likely not to fly across unsuitable habitat [or I would have caught more], but this is a hypothesis that I cannot test given the data I collected (perhaps it could be tested by examining visitation rates to inflorescences in bee pollinated crops, and using a wide variety of emergence traps and nesting blocks to determine whether it provides any type of nesting habitat).

Pair-wise comparisons of environmental variables

The db-RDA yielded strong results for each farm, with those at the genus level generally being stronger than for species level, implying that those environmental and spatial variables that yielded high adjusted R squared values in RDA analysis are highly correlated with the distribution and composition of bee genera at each farm. The environmental variable “prairie” displayed collinearity with plant richness (PRICH), and abundance of yellow inflorescences on each farm (as would be expected, given that prairie has a high diversity of flowering plants), as shown in the RDA biplots for each farm and in the pairwise comparisons of environmental variables (Fig. 5-7, Table 6). In these pair-wise comparisons, larger coefficients (i.e. greater collinearity) are shown in larger font sizes to hi-light those environmental variables which are collinear. Each of these environmental variables was highly predictive of species distribution and abundance of bees on farmlands, indicating that prairie provides abundant floral resources that are highly important and utilized by native bees.

Procrustes analysis

Procrustes analysis is a method of comparing the output of two RDA analyses using least squares orthogonal mapping, essentially rotating and dilating the axes of one ordination plot to conform with the other and noting the difference between the two. Utilizing this method to compare the PCNM RDAs revealed that the results seen in the environmental variable analysis on each farm were highly similar (Table 10). Unfortunately, this analysis could only be performed at the genus level, as some plots needed to be removed at the species level to satisfy the requirements of the Jaccard distance measure to complete the distance based redundancy analysis. Despite this, the results seen between farms at the species level and comparing the species level to the genera level lead me to believe that the results would also be highly similar at the species level.

DISCUSSION

My research aimed to test the impact of habitat diversity on pollinators on conventional farms, focusing on farms that include some fields that are monoculture-based but also areas being managed for increased habitat diversity via the planting of tallgrass prairie and oak savannah on marginal areas. A question of interest is whether these plantings, even over small areas, could somewhat offset the ‘pollinator paradox’ by allowing farms to maintain yields while still providing habitat for bees that might be important for those yields of crops that are pollinator-dependent.

There are three key ecological mechanisms that may explain the relationship between species richness of bees and provisioning of pollination ecosystem services (Naeem et al. 2009): sampling effects, niche complementarity, and functional facilitation. Although I did not explicitly quantify the relative strengths of these processes due to time constraints of my Masters research (one growing season), they describe different ways by which pollinator diversity can affect visitation to crops. They also make the general prediction that pollinator diversity should be good for pollen flow and seed set, regardless of the exact mechanism. My research findings may offer insights into the relative importance of these processes in the places where I am working.

Sampling (selection) effects: These refer to the idea that in experimental designs where species richness is a variable, there is a higher chance of including a species that makes a disproportional contribution to ecosystem functioning in areas where richness is higher (Loreau 2000). The most efficient bee species, in terms of the seed set or pollen deposition per visit, could thus dominate pollination services, masking minor benefits by other species (Naeem et al. 2009). Species rich pollinator communities may enhance pollination services not because of diversity, but because they are more likely to include a particularly efficient pollinator. For example, experimental studies of watermelon crops along land use intensity gradients have shown that species rich communities may be the only ones containing the most effective pollinators (Larsen 2005). This phenomenon is thought to be a result of non-random local extinction processes, whereby declines occur in species richness but it is the loss of the large-bodied and most functionally effective pollinators that explains the reduction in pollination.

Niche complementarity: In direct contrast to the sampling effect hypothesis, niche complementarity relies on the assumption that a high level of species richness increases functional effectiveness by increasing the spatio-temporal efficiency of resource use within a community (Naeem et al. 2009). This hypothesis relies on the assumption that distinct resource partitioning occurs with the addition of each individual species, eventually reaching a plateau (Naeem et al. 2009). It is assumed to have evolved from intense competition among pollinators for resources, where selection reduces the overlap in foraging and nesting requirements between dominant and subordinate competitors (MacArthur 1957, Tilman 1982). Species can thus maximize their ability to obtain foraging and nesting resources by exploiting different spatio-temporal floral and nesting resources within the landscape (e.g. foraging on different parts of a flower and/or at different times of the day) (Naeem et al. 2009). Hoehn (2008) characterized species-specific differences in spatio-temporal patterns of Indonesian flower visitation in landscapes with high and low pollinator richness. Where richness was high, experimentally planted crop species had maximum seed output and species covered the entire spectrum of spatio-temporal niches (in terms of flower height and time of day). Where it was low, their seed output was significantly lower (compared to hand pollinated flowers), and few spatio-temporal niches were occupied (Hoehn et al. 2008). It may not be that the niches were unoccupied but that they simply did not exist due to low availability of nesting, foraging or overwintering habitat.

Crop studies in Indonesia indicated that niche complementarity, rather than sampling effects, was the predominant mechanism where a high quality and quantity of pollination services existed, and functional group richness (where species were classified *a priori* using groups of morphological and behavioral traits) provided the best explanation of pollination services (Hoehn et al. 2008, Klein et al. 2008). Species richness can also be beneficial to the provisioning of pollination services, when it provides redundancy in terms of functional groups of efficient pollinators. Redundancy is a little different from complementarity - in that it suggests that multiple species can perform a single function- although they can act together in terms of ensuring that pollination needs are met within a plant community. As described above, complementarity suggests that each pollinator species is specialized on a particular floral or nesting resource within a community (i.e. a high degree of specialization). Redundancy suggests that higher diversity means more compensation if one or more species happens to disappear, as would be the case if many pollinators in a community are generalists regarding the flowers they visit (i.e., they may still be specialized, but maybe on nesting type, or they will be specialized on certain floral resources but switch to other ones if the opportunity presents itself [as might occur if a competing pollinator specialist disappears locally]). In the latter case, redundancy can provide resilience, because pollinators may be somewhat interchangeable (it wouldn't matter if a few species are lost because they all perform similar functions within the ecosystem).

In Ontario systems, redundancy may be common because many pollinators are somewhat general in their foraging needs (unlike tropical systems, for example). However, complementarity is also often detected, suggesting that both co-occur (redundancy and complementarity). Chagnon (1993), for example, observed niche complementarity in the pollination of strawberry plants, where the foraging behavior of differently sized bees (large honey bees and small wild bees) in combination maximized pollination and fruit development. In this plant, pollination by small and large species is necessary to cover the gynoecium in pollen and form a full fruit. Hoehn (2008) also found a similar relationship between body size of bee species and their flower visiting behavior, in terms of height, duration of visit, and time of day of visitation. Several studies indicate that bee communities where different bee species forage on different floral resources are structured by behavioral niche differentiation, owing to a number of species-specific behavioral traits (e.g. body size, circadian rhythms, temperature tolerance, competition hierarchies, sociality) (Bishop and Armbruster, 1999, Pinkus-Rendon et al. 2005, Stone 1994, Stone et al. 1999).

Facilitation: Thirdly, different species of pollinators may facilitate each other's contribution to pollination, providing another way that bee richness can improve pollinator services. For example, wild bees functionally facilitate the successful pollination of sunflowers by encouraging commercially available honey bees to switch from male to female flowers instead of exclusively foraging for nectar on females and pollen on males (Greenleaf and Kremen 2006). The presence of both wild and honey bees also increased per visit pollination efficiency when honey bees visited sunflowers. A potential facilitative mechanism to explain this increase in efficiency implies that honey bees help to disperse clumped pollen left by wild bees. Similarly, there may be floral facilitation, where resource-rich flowering species attract pollinators thereby increasing visitation to neighboring flowering species that devote less to producing nectar or pollen (Callaway 2007).

Whether sampling effects, niche complementarity including redundancy effects, or facilitation best describe pollinator dynamics remains unclear. What we do know, however, is that anthropogenic changes relating to habitat loss, pollution and invasion by plants and pollinator disease are potentially transforming all of them if pollinator diversity is indeed declining. These issues are especially relevant on agricultural landscapes, where farming is both potentially reducing pollinator effectiveness while increasing the need for the services of native pollinators because they may be less prone to colony collapse (i.e., what I am calling the 'pollination paradox'). These anthropogenic changes could have their own 'sampling effects' if they happen to eliminate, or at least reduce the effectiveness of, a disproportionately important species or group of species. They may degrade the benefits of niche complementarity on net community-wide pollination by reducing the total number of pollinator species in the system. Similarly, by simplifying pollinator communities through lost diversity, they may disrupt network-level facilitative feedbacks that increase pollinator efficiency, in both native and agronomic plant communities.

Based on my sampling, I found high levels of bee richness, abundance, and composition on these intensively managed farms, with a portion of the bee community unique to the constructed prairies. This finding was largely consistent among the three farms despite differences in the size and spatial orientation of the constructed habitat on each farm. More specifically, there were strong relationships between habitat type and pollinator richness, and an identifiable gradient in this trend with croplands consistently having the fewest species (my first hypothesis). As well, these trends were associated with a range of habitat features that I measured, especially floral resources associated with the numbers of flowers available and flower color and, to a lesser degree, factors associated with nesting (my second hypothesis). I did observe significant levels of pollinator richness and abundance in marginal areas on the farms and, to a lesser degree, forested habitat (my third hypothesis), albeit at reduced levels compared to the prairie. This result for marginal habitat suggests that such areas could be currently contributing to maintaining pollinator communities on contemporary agricultural landscapes, and could be valuable to preserve even if they are suboptimal compared to prairie. Overall, the results suggest that pollinators are likely to be rare on intensively managed farms lacking suitable resources (an increasingly typical scenario in many rural areas of central North America - Wright and Wimberly 2013). In total, my work indicates that even small patches of restored high quality habitat constructed on marginal areas of farms can have big impacts on bee communities. This could be important for bee conservation, but also has the potential to increase pollinator services on non-organic farms.

Given that we are supposedly in the midst of a pollinator crisis, it was conceivable that I would detect very little activity in these small restored areas. This may have been especially likely because the region in which I worked is almost exclusively composed of habitat not assumed to be ideal – crops, forest, and marginal areas, with no high quality habitat especially in terms of seasonal availability of flowers. This was not the case. Clearly, native bees are abundant and form complex communities on these intensively managed farms. My work shows, apart from prairie, pollinators can be found also in marginal areas such as ditches and roadsides. All plants in these areas are oldfield grasses and forbs, but with much lower forb diversity compared to prairie. Although I did not measure the quality of floral resources among habitats (e.g., quantity of nectar per flower per species among oldfield species), the quantity of flowers per area is much lower compared to prairie. Nonetheless, marginal areas still captured 16% of the total numbers of specimens that I sampled, and 55% of the overall species richness. Forest also supported some species, possibly because of high quality nesting availability while flowers were rare. These results suggest that marginal areas could be a central area where bee populations are being maintained on current landscapes. These areas are typically unmanaged, or managed against pollinators as they can be sprayed, mowed, or even planted with grass for erosion control. As has recently been seen for the Monarch butterfly in the central US (Flockhart and Norris 2014), marginal habitat can play a huge role for pollinator dynamics even if they occur over a very small area. That study showed that marginal areas in farming landscapes supporting common milkweed, such as narrow roadside areas, are critical for the life history dynamics of the Monarch, and recent changes to management including the spraying of these areas with herbicide threatens the butterfly. My results imply that marginal areas on farms could play a similar role for pollinator communities – they are limited in areas, not necessarily ideal for richness and abundance compared to prairie, but nonetheless important for keeping them around. This should be taken into account when considering management efforts for pollinators in Ontario and elsewhere.

One indication of the importance of the prairie habitat with respect to providing resources (particularly floral resources) for native bees, was the strong explanatory signal from environmental factors in my analyses (i.e., flowering plant richness, percent coverage of blue, yellow and white inflorescences). In many variation partitioning analyses, spatial factors play a strong role in explaining variation due to dispersal limitation; this is especially so for plants (Cottenie 2005). Many seeds, for example, fall near the parent plants simply due to dispersal inefficiencies – this creates spatial clustering in the population that may have nothing to do with environmental conditions (Pinto & MacDougall 2010). Here, my pure spatial signals were relatively weak. This has potentially 2 causes – (i) that bees are relatively mobile and will forage across the farm for suitable resources (they are not that dispersal limited) and (ii) when there was 'spatial structure' in there distribution, it was associated with the underlying distribution of environmental factors (i.e., bees were spatially aggregated in prairie habitat with high flower diversity). The strong signal for some factors associated with nesting does suggest that rearing of juveniles is spatially restricted to certain areas including forest. However, unlike with plants, I did not detect any signals that individuals are more likely to be near nesting areas compared to farther away (as occurs with plants). Again, this fits with the dispersal life history of bees. It is also consistent with studies on bee foraging, which has reported typical foraging distances to range from under a kilometer to several kilometers across agricultural landscapes (Greenleaf et al. 2007, Figure 17).

In terms of habitat features, floral resources seem to be more critical than nesting resources. Litter and to a lesser degree bare soil, are abundant in most habitats, whereas flowering plants were more strongly associated with a particular habitat. I hypothesized that ground nesters might be rarer than cavity nesters given that bare soil tends to be rare on agricultural landscapes, but this was not the case. There are some similarities in floral resources between marginal areas and prairie, with for instance flowers present from early to late summer, and even into the fall. However, oldfield of marginal areas have a much higher abundance of grasses (e.g., smooth brome, red fescue), and much lower forb diversity compared to prairie (Hamden, MacDougall and Sikes 2011). There were also forbs in marginal areas with questionable value for pollinators, such as wind-pollinated species like horseweed.

In terms of bee richness and composition, I detected mostly generalists with smaller body sizes, e.g. from the genera *Augochlorella, Agapostemon, Andrena, Ceratina, Hoplitis*, and *Lasioglossum*. Most of the rarer genera were found in the prairie. My capture rates of 1242 individuals per 120 traps over three farms can be considered average or even high compared to other studies (Droege et al. 2010, Campbell and Hanula 2007). In terms of nesting guild composition, approximately 70 percent of the total specimens caught were ground nesters, 23 percent nested in pithy stems and twigs, 3 percent were cavity nesters, 2 percent were parasitic, and 0.4 percent were wood nesters. The most common genera (*Augochlorella, Agapostemon, Andrena and Lasioglossum*) were ground nesters, along with the carpenter bees *Ceratina* and *Hoplitis* which nests in pithy stems and twigs. There was a steep decline in the overall abundance and species richness of specimens caught in the second two months of the summer after June. This could be due to a multitude of different reasons, for example the bee species which live on these farms could be most active in the spring or early summer as opposed to late summer, or pesticide utilization on the farms throughout the summer could have caused a decline and disturbed nesting sites.

DNA barcoding was helpful in distinguishing among some of the trickier groups especially *Lasioglossum, Andrena*, and *Nomada*, separating 25 species from 15 genera (Table 3). Interestingly, 34/192 samples were contaminated with *Wolbachia* (the DNA of this bacteria was detected in the analysis). *Wolbachia* infections typically alter the reproductive capabilities of their hosts, and it is interesting that I detected it so frequently given that I conducted my DNA analyses on the legs of the individuals that I sampled. The consequences of *Wolbachia* infection in native bees is debated (Gerth et al. 2011, Smith et al. 2012), but it is clearly not rare with the native bees that I sampled on my farms.

In terms of differences among farms, there were shared trends but some unique features. The farm with Saskatoon berries and a large oak savannah restoration had a significantly higher number of captured specimens (667) compared with the other two farms that grew corn and soybeans (207 and 369 specimens captured). While the presence of prairie does seem to support a richer bee community, the presence of a crop that is not particularly pollinator-friendly (corn, soybeans) seems to be a detriment to their abundance. It may be that the presence of tallgrass prairie and oak savannah on that farm is what made it highly supportive of an abundant and rich native bee community. It is apparent from my results that the prairie provides a rich floral resource for the bees, while the oak savannah provides appropriate nesting habitat. The restored areas (particularly restored prairie) contained much more diverse flowering plant communities compared with forested and crop areas. Marginal edge areas were second to restored areas in terms of flowering plant richness, but because they are so variable from place to place it is difficult to say what value these types of lands have overall, if any, in places where they are truly degraded and contain few to no flowering plants.

What may prove to be most crucial to the health and persistence of native bees on agricultural lands may be the heterogeneity of habitat available. A patch of restored tallgrass prairie (minimum 10% of the overall land in a given area or in crop use is recommended), an adequately sized oak savannah (again, at least 10% of the overall land, to provide nesting materials and overwintering habitat), and marginal land (ditches, roadsides, margins and edges of properties) left uncultivated along with cropfields may provide native bees with the resources they need to persist in what would otherwise be a harsh and unwelcoming landscape. I found that a high proportion of the specimens caught were ground nesters, and that the overall capture rate dropped significantly after the first month. It may be the case that those bees nesting on the ground on farms are losing their nesting habitat when farming activities such as repeated tilling and pesticide spraying commence. If this is true, I would recommend that farms either try to adopt a “no-till” policy, limit pesticide use (particularly neonicontinoids), or try to make bare ground available in other areas for bees to nest in. Additionally, the abundance of other nesting guilds may be increased by providing artificial nests and putting out nesting material. For wood and cavity nesters, farmers can place wooden blocks with a variety of differently sized holes drilled into them (“nesting blocks”) as well as woody debris such as old wooden furniture or logs. Some species prefer sandy soils, so placing sand or a mixture of soil and sand on the property in close proximity to restored areas or crops is recommended.

The farms we sampled are intensively managed and utilize pesticides, till on a regular basis, and would not be considered organic according to ALUS and the respective landowners. Land owners participating in the ALUS restoration program are required to devote 10% of their land to restoration, which is a relatively small proportion of their overall land. Despite the intensive management and relatively small area that is restored, having an area on a farm restored to native tallgrass prairie still evidently provides some benefit for native pollinators in terms of habitat provisioning. This is of interest because most of the research to date tends to suggest that organic farming provides an arguable benefit to pollinators versus intensively managed farms (Kremen et al. 2002, Morandin and Winston 2005, Schuler et al. 2005). While the use of some pesticides (neonicotinoids) may be detrimental to pollinator health, not all pesticides have these same negative impacts on pollinators (Xerces Society 2012, Lawrence and Sheppard 2013). Also, with the need for food output required globally, relying only on organic farming with its reduced yields compared to intensive farms may make it difficult to make such increases. As far as native pollinators are concerned, it may be that the availability of suitable habitat plays a greater role in sustaining populations than does the distinction between organic and non-organic farms.

Overall, it is quite clear that, as I predicted, restored prairie does have an influence on the abundance, distribution and community composition of native bees. The results for each farm may differ slightly, but they all signal that the abundance and diversity of flowering plants within prairie habitats has a strong influence on native bees. Looking at the results of this study, many further questions and potential areas of exploration come to mind. While my study did have its potential drawbacks, there is room for further research into certain areas such as nesting habitat quantification. It was surprising that I did not see nesting habitat availability having more of an influence on the presence and composition of pollinators. This could be due to a number of reasons, including that I started field work later in the spring due to cold weather and may have missed key nest seeking periods. Even then, one would expect that bees would return to and be active near these nest areas (Tscharntke etl al. 1998). Additionally, the bees I did catch may simply be nesting in another area located outside the farms, or perhaps pan traps are not an accurate way of capturing bees if you want to estimate their nesting habitat usage. In future studies, a more robust and probably separate sampling should take place where emergence traps are used to capture those bees emerging from ground nests, or possibly artificial wood or twig nests are built and occupancy is tracked (Sardinas and Kremen 2014). Also, it may be informative to include a larger number of farms with a greater variety of crops, preferably bee-pollinated crops exclusively, or to compare those with restored tallgrass prairie to those without. I would have also liked to have directly tested for spill-over effects, but could not due to time and logistical constraints. One idea was to plant experimental plots of pollinator-dependent crop species at various locations on farms including at a range of distances from areas of restored prairie. This would allow me to test whether crop visitation and yield is positively affected by ‘spill-over’ of pollinators from planted prairie.

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TABLES AND FIGURES

Flowering plant species identified on farms				
Common name	**Family**	**Genus**	**Species**	**Habitat**
purple vetch	Fabaceae	Vicia	*Vicia americana*	R
fleabane	Asteraceae	Erigeron	*Erigeron sp*.	R, E
black eyed susan	Asteraceae	Rudbeckia	*Rudbeckia hirta*	R, E, F
queen annes lace	Apiaceae	Daucus	*Daucus carota*	R, E
purple prairie clover	Fabaceae	Dalea	*Dalea purpurea*	R
yellow evening primrose	Onagraceae	Oenothera	*Oenothera biennis*	R
horseweed/fleabane	Asteraceae	Conzya	*Conzya canadensis*	R
knotweed	Polygonaceae	Polygonum	*Polygonum sp*.	C
chickweed	Caryophyllaceae	Stellaria	*Stellaria media*	R, E, C
sweet clover	Fabaceae	Melilotus	*Melilotus alba*	R
Canadian thistle	Asteraceae	Cirsium	*Cirsium arvense*	R, E
wild teasel	Dipsacaceae	Dipsacus	*Dipsacus fullonum*	E
Canadian hawkweed	Asteraceae	Hieracium	*Hieracium canadense*	R, E
tumble mustard	Brassicaceae	Sisymbrium	*Sisymbrium altissimum*	E
goldenrod	Asteraceae	Solidago	*Solidago canadense*	R
Virginia mountainmint	Lamiaceae	Pycnanthemum	*Pycnanthemum virginianum*	R
Canada tick trefoil	Fabaceae	Desmodium	*Desmodium canadense*	R
field bindweed	Convolvulaceae	Convolvulus	*Convolvulus arvensis*	R
common mullein	Scrophulariaceae	Verbascum	*Verbascum thapsus*	R
alsike clover	Fabaceae	Trifolium	*Trifolium hybridium*	R
black medic	Fabaceae	Medicago	*Medicago lupulina*	R, C
cornflower	Asteraceae	Centaurea	*Centaurea cyanus*	R, E
oxeye daisy	Asteraceae	Leucanthemum	*Leucanthemum vulgare*	R, E
St John's wort	Hypericaceae	Hypericum	*Hypericum perforatum*	R, E, C
white vetch	Fabaceae	Lathyrus	*Lathyrus sativus*	R
red clover	Fabaceae	Trifolium	*Trifolium pratense*	R
wild bergamot	Lamiaceae	Monarda	*Monarda fistulosa*	R
common chicory	Asteraceae	Cichorium	*Cichorium intybus*	E
yarrow	Asteraceae	Achillea	*Achillea millefolium*	R
hoary vervain	Verbenaceae	Verbena	*Verbena stricta*	R
butterfly weed	Apocynaceae	Asclepias	*Asclepias tuberosa*	R
common milkweed	Aslepiadaceae	Asclepias	*Asclepias syriaca*	R

sweet potato	Convolvulaceae	Ipomoea	*Ipomoea batatas*	R
Penstemon eriantherus	Plantaginaceae	Penstemon	*Penstemon eriantherus*	R
greater water dock	Polygonaceae	Rumex	*Rumex orbiculatus*	R, E
sulphur cinquefoil	Rosaceae	Potentilla	*Potentilla recta*	R, F
common dandelion	Asteraceae	Taraxacum	*Taraxacum officinale*	R
garlic mustard	Brassicaceae	Alliaria	*Alliaria petiolata*	E, F
daisy fleabane	Asteraceae	Erigeron	*Erigeron annus*	R, E
hispid buttercup	Ranunculaceae	Ranunculus	*Ranunculus hispidis*	E
ground ivy	Lamiaceae	Glechoma	*Glechoma hederacea*	E
wild strawberry	Rosaceae	Fragaria	*Fragaria virginiana*	R
alfalfa	Fabaceae	Medicago	*Medicago sativa*	R
false solomon's seal	Asparagaceae	Maianthemum	*Maianthemum racemosum*	F
medicago	Fabaceae	Medicago	*Medicago sp.*	R, C
wild black raspberry	Rosaceae	Rubus	*Rubus occidentalis*	F
lily of the valley	Asparagaceae	Convallaria	*Convallaria majalis*	F
wild geranium	Geraniaceae	Geranium	*Geranium maculatum*	E
soybean	Fabaceae	Glycine	*Glycine max*	C
potato	Solanaceae	Solanum	*Solanum tuberosum*	R, C

Table 1. Flowering plant species identified on farms.

Farm	1				2				3			
Habitat	crop	forest	prairie	edge	oak savan	forest	prairie	edge	crop	forest	prairie	edge
min sum flwr	0	0	8.833333	12.16667	0	0	0	0	0	0	0	0
max sum flwr	0.333333	0.333333	32	25.33333	36.83333	0.166667	47	12.16667	11.66667	1.666667	2	3.333333
mean sum flwr	0.2	0.1	20.72222	15.9	11.86842	0.111111	18.66667	3.47619	1.555556	0.407407	0.433333	1.138889
min bg	33.33333	25	1.666667	1.666667	1.666667	0.166667	11.66667	11.66667	26.66667	8.333333	21.66667	33.33333
max bg	56.66667	45	35	1.666667	61.66667	48.33333	55	58.33333	88.33333	45	58.33333	85
mean bg	46.66667	33.1	11.12222	1.666667	18.53509	26.13889	29.375	27.14286	72.88889	22.7963	34.66667	70.27778
min m	28.33333	0	0	0	0	0	0	0	0	0	0	0
max m	31.66667	5	28.33333	1.666667	5	8.333333	0	0	0	11.66667	0	0
mean m	30.77778	1.333333	1.888889	0.333333	0.350877	1.388889	0	0	0	1.296296	0	0
min ptt	6.666667	10.16667	0	1.666667	0.166667	18.33333	5	0.166667	0	16.66667	0.166667	13.33333
max ptt	18.33333	36.66667	1.833333	1.666667	53.33333	33.33333	35	35	18.33333	33.33333	11.66667	18.33333
mean ptt	13.66667	24.4	0.877778	1.666667	26.67544	23.05556	13.125	12.66667	11.77778	24.25926	3.4	15.83333
min wd	0	5	0	0	0	18.33333	0	0	0	7.333333	0	0
max wd	0	15	0	0	8.333333	31.66667	11.66667	48.33333	1.666667	25	1.666667	10
mean wd	0	9.733333	0	0	1.412281	22.5	6.666667	11.66667	0.333333	17.85185	0.2	3.888889
min c	0	0	0	0	0	0	0	0	0	0	0	0
max c	0	0	0	0	0	0	0	5	0	0	0	1.666667
mean c	0	0	0	0	0	0	0	0.952381	0	0	0	0.277778
min prich	0	0	5	4	0	0	0	0	0	0	0	0
max prich	4	1	13	12	8	1	12	5	1	2	3	2
mean prich	1.333333	0.4	9.066667	6.4	2.736842	0.666667	7.5	1.428571	0.133333	0.555556	1.8	0.666667

Table 2. Summary statistics (min, max and mean) of nesting and foraging substrate availabilities in each habitat on each farm.

Total abundances of each species caught on all farms throughout the summer							
Genera	**Species**	**BOLD BIN #**	**Total # caught**	**Genera**	**Species**	**BOLD BIN #**	**Total # caught**
Augochlorella	*Augochlorella aurata*		111	Lasioglossum	*Lasioglossum foveolatum*		1
Augochloropsis	*Augochloropsis metallica*		1	Lasioglossum	*Lasioglossum furunculum*		5
Augochlora	*Augochlora pura*		1	Lasioglossum	*Lasioglossum fuscipenne*		30
Agapostemon	*Agapostemon sericieus*		30	Lasioglossum	*Lasioglossum gotham*		43
Agapostemon	*Agapostemon texanus*		61	Lasioglossum	*Lasioglossum hitchensii*		2
Agapostemon	*Agapostemon virescens*		38	Lasioglossum	*Lasioglossum leucocomum*	ACF2785	1
Apis	*Apis mellifera*		34	Lasioglossum	*Lasioglossum leucozonium*	AAA2322	24
Andrena	*Andrena cardina*		1	Lasioglossum	*Lasioglossum lineatulum*	AAA2141	4
Andrena	*Andrena commoda*	AAI4594	17	Lasioglossum	*Lasioglossum lustrans*		1
Andrena	*Andrena distans*	AAF0935	16	Lasioglossum	*Lasioglossum macoupinense*	AAB8845	3
Andrena	*Andrena dunningi*	AAB5093	2	Lasioglossum	*Lasioglossum oceanicum*		2
Andrena	*Andrena eriginae*		7	Lasioglossum	*Lasioglossum oenotherae*		1
Andrena	*Andrena nasonii*	AAB7413	2	Lasioglossum	*Lasioglossum paraforbesii*	AAD0523	1
Andrena	*Andrena nivalis*	AAB5093	1	Lasioglossum	*Lasioglossum pentinatum*		10
Andrena	*Andrena placata*	AAI4593	3	Lasioglossum	*Lasioglossum pectorale*	AAB3614	21

Andrena	*Andrena platyparia*		1	Lasioglossum	*Lasioglossum perpunctatum*	AAC1122	2
Andrena	*Andrena robertsonii*	AAJ2126	1	Lasioglossum	*Lasioglossum quebecense*	ACE6243	4
Andrena	*Andrena splendons*		14	Lasioglossum	*Lasioglossum pilosum*		3
Andrena	*Andrena sp. i*	ABZ1483 (nearest)	6	Lasioglossum	*Lasioglossum rufitarse*		1
Andrena	*Andrena sp. Ii*	AAJ2126 (nearest)	1	Lasioglossum	*Lasioglossum sopinci*		1
Anthidiellum	*Anthidiellum notatum notatum*	AAD2040	1	Lasioglossum	*Lasioglossum vierecki*	AAB4651	25
Bombus	*Bombus affinis*		1	Lasioglossum	*Lasioglossum viridatum*		20
Bombus	*Bombus bimaculatus*		1	Lasioglossum	*Lasioglossum zonulum*	AAB3147	72
Bombus	*Bombus citrinus*		1	Lasioglossum	*Lasioglossum sp.(flagged as mixup/contaminated by BOLD, ID'd visually)*		16
Bombus	*Bombus impatiens*	ABZ2516	17	Megachile	*Megachile bimaculatus*		2
Bombus	*Bombus grisecollis*		1	Megachile	*Megachile campanulae*	AAD2929	3
Bombus	*Bombus rufocinctus*	AAB0152	2	Megachile	*Megachile latimanus*	AAA7749	5
Bombus	*Bombus sandersonii*		1	Megachile	*Megachile mendica*	AAC4239	4
Bombus	*Bombus variabilis*		2	Melissodes	*Megachile denticulata*		4
Calliopsis	*Calliopsis sp.(flagged as mixup/contaminaton by BOLD,*		1	Melissodes	*Megachile dentriventris*	ACE6030	4

	ID'd visually)						
Ceratina	*Ceratina calcarata*	AAA2368	8	Melissodes	*Megachile desponsa*	ACE6030	17
Ceratina	*Ceratina dupla*	AAA2368	56	Melissodes	*Melissodes druriella*	AAB3389	1
Ceratina	*Ceratina floridana*	AAA2368	8	Melissodes	*Melissodes subillata*		18
Ceratina	*Ceratina mikmaqi*	AAA2368	27	Melissodes	*Melissodes texana*	AAC1845	1
Ceratina	*Ceratina octoplenta*		1	Melissodes	*Melissodes trinodes*	ACE6030	2
Ceratina	*Ceratina strenua*	AAA2368	1	Nomada	*Nomada articulata*		4
Ceratina	*Ceratina sp.*	AAA2368	2	Nomada	*Nomada cressonii*	ACE6524	3
Colletes	*Colletes compactus*		1	Nomada	*Nomada denticulata*	ACE6522	1
Colletes	*Colletes inaequalis*	AAE1758	1	Nomada	*Nomada lepida*	AAI3547	2
Colletes	*Colletes validus*	AAE1758	1	Nomada	*Nomada pygmaea*	ABZ6834	10
Dieunomia	*Dieunomia nevadensis*		6	Nomada	*Nomada sayi*	ABZ1280	2
Halictus	*Halictus confusus*		9	Nomada	*Nomanda sp. i*	AAI3547	6
Halictus	*Halictus ligatus*		24	Nomada	*Nomada sp. Ii*	ACE3252	2
Hoplitis	*Hoplitis pilosifrons*	AAA7121	172	Osmia	*Osmia atriventris*	AAB8874	4
Hoplitis	*Hoplitis annulatus*		3	Osmia	*Osmia caerulescens*	AAD0313	1
Hoplitis	*Hoplitis paralellus*		13	Osmia	*Osmia distincta*	AAC0884	3
Hoplitis	*Hoplitis rubicundis*		3	Osmia	*Osmia georgica*	ABZ2181	1
Hoplitis	*Hoplitis truncata*	AAA7121	1	Osmia	*Osmia pumila*	AAC5789	2
Lasioglossum	*Lasioglossum acuminatum*		6	Osmia	*Osmia sp.*	AAD0313	1
Lasioglossum	*Lasioglossum albipenne*		34	Peponapis	*Peponapis pruinosa*		17
Lasioglossum	*Lasioglossum anomalum*	AAA7867	2	Perdita	*Perdita sp.*	ACK6347	1
Lasioglossum	*Lasioglossum ascheri*		3	Sphecodes	*Sphecodes coarctatus*	AAE2107	1

Lasioglossum	*Lasioglossum bruneri*	AAC7048	4	Sphecodes	*Sphecodes dichrous*	AAC8354	1
Lasioglossum	*Lasioglossum cintipes*		31	Sphecodes	*Sphecodes lateralis*	AAE2107	6
Lasioglossum	*Lasioglossum coriaceum*	AAB7007	10	Sphecodes	*Sphecodes persimilis*	ACE6810	2
Lasioglossum	*Lasioglossum cressonii*	ACE7675, AAA5973, AAD0913	4	Sphecodes	*Sphecodes stygius*	AAD7375	1
Lasioglossum	*Lasioglossum disparile*		3	Sphecodes	*Sphecodes sp. (flagged as mixup/contaminated by BOLD, ID'd visually)*		1
Lasioglossum	*Lasioglossum divergens*	AAB8845	3	Svastra	*Svastra aegis (flagged as mixup/contaminated by BOLD, ID'd visually)*		1
Lasioglossum	*Lasioglossum floridanum*		1	Xylocopa	*Xylocopa virginica*		1

Table 3. Summary of the total abundance of all species and genera found on all farms throughout the summer, and BIN references for DNA barcoded specimens where available.

Rare species found on farms, habitat captured in, and nesting type			
Species/Genus	**Number of farms (x/3 farms)**	**Habitat (x/4 types)**	**Nesting type**
Augochloropsis metallica	1	Oak savannah	Ground
Augochlora pura	1	Edge	Woody debris
Andrena cardina	2	Edge, forest	Ground
Andrena nivalis	1	Oak savannah	Ground
Andrena platyparia	1	Forest	Ground
Andrena robertsonii	1	Edge	Ground
Anthidiellum notatum notatum	1	Oak savannah	Cavity
Bombus affinis	1	Prairie	Ground
Bombus bimaculatis	1	Oak savannah	Ground
Bombus citrinus	1	Prairie	Ground (parasitic)
Bombus grisecollis	1	Prairie	Ground
Bombus sandersonii	1	Edge	Ground
Calliopsis sp.	1	Prairie	Ground
Ceratina octoplenta	1	Prairie	Pithy stems and twigs
Ceratina strenua	1	Prairie	Pithy stems and twigs
Colletes compactus	1	Prairie	Ground
Colletes validus	1	Edge	Ground
Hoplitis truncata	1	Oak savannah	Cavity
Lasioglossum floridanum	1	Crop	Ground
Lasioglossum foveolatum	1	Edge	Ground
Lasioglossum leucocomum	1	Prairie	Ground
Lasioglossum lustrans	1	Prairie	Ground
Lasioglossum oenotherae	1	Oak savannah	Woody debris
Lasioglossum paraforbesii	1	Oak savannah	Ground
Lasioglossum rufitarse	1	Crop	Ground
Lasioglossum sopinici	1	Forest	Ground
Megachile texana	1	Oak savannah	Ground
Melissodes druriella	1	Oak savannah	Pithy stems and twigs, Ground
Nomada denticulata	1	Prairie	Ground (parasite)

Osmia caerulescens	1	Prairie	Cavity
Osmia georgica	1	Oak savannah	Cavity, pithy stems and twigs
Sphecodes coarctatus	1	Oak savannah	Ground (parasitic)
Sphecodes dichrous	1	Prairie	Ground (parasitic)
Sphecodes stygius	1	Prairie	Ground (parasitic)
Svastra aegis	1	Edge	Ground
Xylocopa virginica	1	Crop	Woody debris

Table 4. Rare species present on farms, the habitat type in which they were found and their nesting substrate.

Abundance, species richness, and exclusive species in each habitat type			
Habitat	**Abundance**	**Species richness**	**# of exclusive species**
crop	142	34	3
forest	47	22	2
prairie	529	81	21
edge	197	65	9
oak savannah	327	62	14
total	**1242**	**118**	**49**

Table 5. Summary abundance, richness and number of exclusive species by habitat type and overall.

Overall comparison of general results between farms			
Analysis	**Farm 1**	**Farm 2**	**Farm 3**
Variation partitioning (genera, species)	Environmental: 0.078, 0.009 PCNM: 0.090, 0	Environmental: 0.076, 0.089 PCNM: 0.066, 0.020	Environmental: 0.078, 0.050 PCNM: 0.075, 0.048
R^2 for RDA of species distance matrix & PCNM axes	0.07669569	0.1019147	0.07652357
PCNM axes	2 (V3, x)	2 (V5, x)	3 (V1, V2, x)
Significant (forward selected) environmental variables	Crop (inverse)	Wood PRICH Oak savannah	Prairie Forest
R^2 value for RDA with species distance matrix & significant environmental variables	0.09003045	0.1703587	0.07857744
Collinearity among environmental variables	Prairie, PRICH, YFLWR, WFLWR, BFLWR	-Prairie, PRICH, YFLWR, BFLWR -Oak savannah, WFLWR	Prairie, PRICH, YFLWR, BFLWR
RDA using geographical coordinates	North-south (latitudinal gradient)	North-south (latitudinal gradient)	North-south (latitudinal gradient)
PCNM plots	Correspond w/ prairie & marginal/edge	Correspond w/ prairie, oak savannah, Carolinean forest	Correspond w/ prairie, crop (squash & pumpkin crop)

Table 6. Comparison of general results between farms. Similar results across farms are in black and variable results are in red.

Test name	Genera or species	Adjusted R squared
rda(F1sp.hel, F1xy)	Genera	0.07018681
rda(F1spdsist, F1xy)	Species	0.05311849
rda(F1sp.hel, F1.PCNM.pos)	Genera	0.1727945
rda(F1spdist, F1.PCNM.pos)	Species	0.09338649
rda(F1sp.hel, PCNM.red)	Genera	0.1773864
rda(F1spdist, PCNM.red)	Species	0.07669569
rda(F1sp.hel, F1env)	Genera	0.1459703
rda(F1spdist, F1env)	Species	0.08459262
rda(F1sp.hel, env.red)	Genera	0.1656174
rda(F1spdist, env.red)	Species	0.09003045

Table 7. PCNM RDA analysis adjusted R squared results for Farm 1.

Test name	Genera or species	Adjusted R squared
rda(F2sp.hel, F2xy)	Genera	0.1036463
rda(F2spdist, F2xy)	Species	0.1130384
rda(F2sp.hel, F2.PCNM.pos)	Genera	0.1732408
rda(F2spdist, F2.PCNM.pos)	Species	0.1329109
rda(F2sp.hel, PCNM.red)	Genera	
rda(F2spdist, PCNM.red)	Species	0.1019147
rda(F2sp.hel, F2env)	Genera	0.2368492
rda(F2spdist, F2env)	Species	0.2240407
rda(F2sp.hel, env.red)	Genera	0.2145217
rda(F2spdist, env.red)	Species	0.1703587

Table 8. PCNM RDA analysis adjusted R squared results for Farm 2.

Test name	Genera or species	Adjusted R squared
rda(F3sp.hel, F3xy)	Genera	0.02821814
rda(F3spdist, F3xy)	Species	0.03632181
rda(F3sp.hel, F3.PCNM.pos)	Genera	0.2232228
rda(F3spdist, F3.PCNM.pos)	Species	0.0763929
rda(F3sp.hel, PCNM.red)	Genera	
rda(F3spdist, PCNM.red)	Species	0.07652357
rda(F3sp.hel, F3env)	Genera	0.1635105
rda(F3spdist, F3env)	Species	0.0858306
rda(F3sp.hel, env.red)	Genera	0.1267989
rda(F3spdist, env.red)	Species	0.07857744

Table 9. PCNM RDA analysis adjusted R squared results for Farm 3.

Farm	**Procrustes sum of squares**
1 & 2	1.07722
2 & 3	0.652773
3 & 1	0.5856839

Table 10. Procrustes sum of squares results for genera level Procrustes analysis of environmental RDAs.

Families and genera of bees typically found in Eastern Canada and their characteristics								
Family	**Genus**	**Nest site**	**Forage site**	**Sociality**	**Season**	**Provinces**	**Abundance**	**# of species**
Melittidae	*Macropis*	Ground	Specialist (*Lysimachia* genus; loosetrife, pimpernel)	Solitary	Summer	ON-NS	Rare	2
Megachilidae	*Anthidiellum*	Mason		Solitary	Summer	ON,QC	Rare	1
	Anthidium	Cavities	Generalist	Solitary	Summer	ON-NS	C Urban	1
	Chelostoma	C+ST	Specialist (Hydrophyllaceae family; *Phacelia* and *Eriodictyon,* or mock orange)	Solitary	Summer	ON	C Urban	3
	Coelioxys	Parasite	Nectar only	Megachile	Summer	All	Common	10
	Dianthidium	Mason		Solitary	Summer	ON, QC	Rare	1
	Heriades	C+ST	Specialist (*Rhus typhina laciniata*)	Solitary	Summer	ON-NS	Uncommon	2
	Hoplitis	C+ST+M*	Generalist and specialist* (Pea, Mint, Figwort families)	Solitary	Summer	All	Local	8
	Megachile	ST,W*,C,G	Generalist and specialist* (Aster, Pea families; alfalfa)	Solitary	Summer	All	Abundant	18

	Osmia	C, UR*	Generalist (shrubs, small trees, rose family, fruit tree orchards; pollinate apple, cherry and plum)	Solitary	Sp+su	All	Abundant	23
	Stelis	Parasite	Nectar only	Megachilidae	Summer	All	Uncommon	10
	Anthophora	G+ST*	Generalist (long tongues; pollinate cherry tomatoes)	Solitary	Sp+Su	All	Local	1
Apidae	*Apis*	Hives	Generalist	PE	All	All	Abundant	1
	Bombus	RB,OG,IT	Generalist (willow, goldenrod; long tongues; larkspur, penstemon; pollinate tomatoes, watermelon, blueberries)	AE	All	All	Abundant	27
	Ceratina	ST	Generalist	Solitary	All	ON-NS	Abundant	3
	Epeoloides	Parasite	Lysimachia (yellow loosetrife)	*Macropis* bee	Summer	ON-NS	ER	1
	Epeolus	Parasite		*Colletes* bees	SU+fall	ON-NS	Local	11
	Holcopasites	Parasite		N/A	Summer	ON-NS	Uncommon	1
	Melissodes	Ground	Specialist (sunflowers, aster, daisy)	Solitary	Su+fall	ON-NS	Common	10
	Nomada	Parasite	Nectar only	Andrena, Agapostemon, Halictus, Lasioglossum	All	All	Abundant	37

	Peponapis	Ground	Specialist (squash, pumpkin, gourd, watermelon)	Solitary	Summer	ON	Local	1
	Svastra	Ground	Generalist and specialist (sunflowers; evening primrose; cactus)	Solitary	Summer	ON, QC	Rare	1
	Triepeolus	Parasite		N/A	Su+fall	ON-NS	Local	10
	Xylocopa	Wood	Generalist (large/open faced flowers; pollinates passionfruit, blackberry, pepper)	NS	All	ON, QC	C Urban	1
Andrenidae	*Andrena*	Ground	Generalist and specialist	S+Comm*	All	All	Abundant	75
	Calliopsis	Ground		Solitary	Summer	ON-NS	Local	1
	Perdita	Ground	Specialist (willow, lotus, asters, sunflowers, *Spurge*, *Phlox*)	S+Comm*	Summer	ON-NS	Local	5
	Protandrena	Ground		Solitary	Summer	ON-NS	Local	6
Halictidae	*Agapostemon*	Ground	Generalist (short tongue)	Comm+S	All	ON-NS	Common	4
	Augochlora	Wood	Generalist	Solitary	Summer	ON-NS	Common	1
	Augochlorella	Ground		AE	All	ON-NS	Common	1
	Augochloropsis	Ground		NS?	Summer	ON	Local	1
	Dufourea	Ground		Solitary	Summer	ON-NS	Local	3
	Halictus	Ground	Generalist (pollinate hybrid sunflowers, watermelon)	AE+S	All	All	Abundant	4
	Lasioglossum	G, W*	Generalist	S,Com,AE	All	All	Abundant	71
	Sphecodes	Parasite	Nectar only	Halictidae	All	All	Abundant	24

Colletidae	*Colletes*	Ground	Specialist*	Solitary	All	ON-NS	Common	16
			(*Asteraceae*) or Generalist					
	Hylaeus	ST, G*	Generalist	Solitary	Summer	All	Common	12

* uncommon option

UR: under rocks, PE: perennial eusocial, AE: annual eusocial, RB: rodent burrows, ST: stems and twigs, OG: on ground, IT: in trees,

ER: extremely rare, NS : nest sharing, C urban: common urban, comm: communal, S: solitary

1. ***Ground**: nests made by burrowing into the soil. **Mason**: nests made on a substrate from resin or mud. **Cavities**: nests made in naturally occurring cavities such as beetle borings in wood, snail shells, etc. **Wood**: nests excavated in woody substrates. **Stems**: nests excavated in pithy stems. **Under rocks**: (one species) brood cells made under rocks. **Hive**: the honey bee is the only species that nests in hives, although feral colonies can be found in other hollows and cavities. **Rodent burrows**: on the ground and in hollow trees; bumble bees nest in these diverse locations. **Parasites**: make no nests.*
2. ***Solitary**: females nest alone. **Annual eusocial**: overwintered queens start a nest in spring and produce workers before producing males and the next season's queens. **Communal**: females share a nest entrance but each constructs her own brood cells and forage for food for their own offspring. **Nest sharing**: a few females may share a nest, exact details rarely known. **Perennial eusocial**: the honey bee has colonies that last for many years.*
3. *Times of year are approximate and will depend upon location. For example, summer bees are unlikely to be found in May or after mid-August. All season means that the bees can usually be found from spring to the first frosts.*
4. *Bees listed as from all provinces can be expected to occur even in northern regions, such as Hudson's Bay and Labrador. Species listed as ON-NS – or subsets of these provinces, are not generally found far to the north. ON-NS also includes PEI although the bee fauna there has not been well studied yet.*
5. ***Abundant**: easily found almost anywhere. **Common**: seasonally abundant in most locations. **Common Urban**: common within urban settings, including gardens. **Local**: seasonally abundant within specific habitats and locations. **Uncommon**: seldom encountered but usually widespread. **Rare**: seldom encountered. **Extremely rare**: known recently from only a few specimens, possibly extirpated from most of former range.*

Adapted from Packer et al. 2007

Forage type adapted from The Xerces Society (2011); information still needed from historical accounts/literature containing info on life history of remaining genera

Table 11. Bee families and genera of interest that have been previously documented in Ontario, along with life history characteristics of interest to this study.

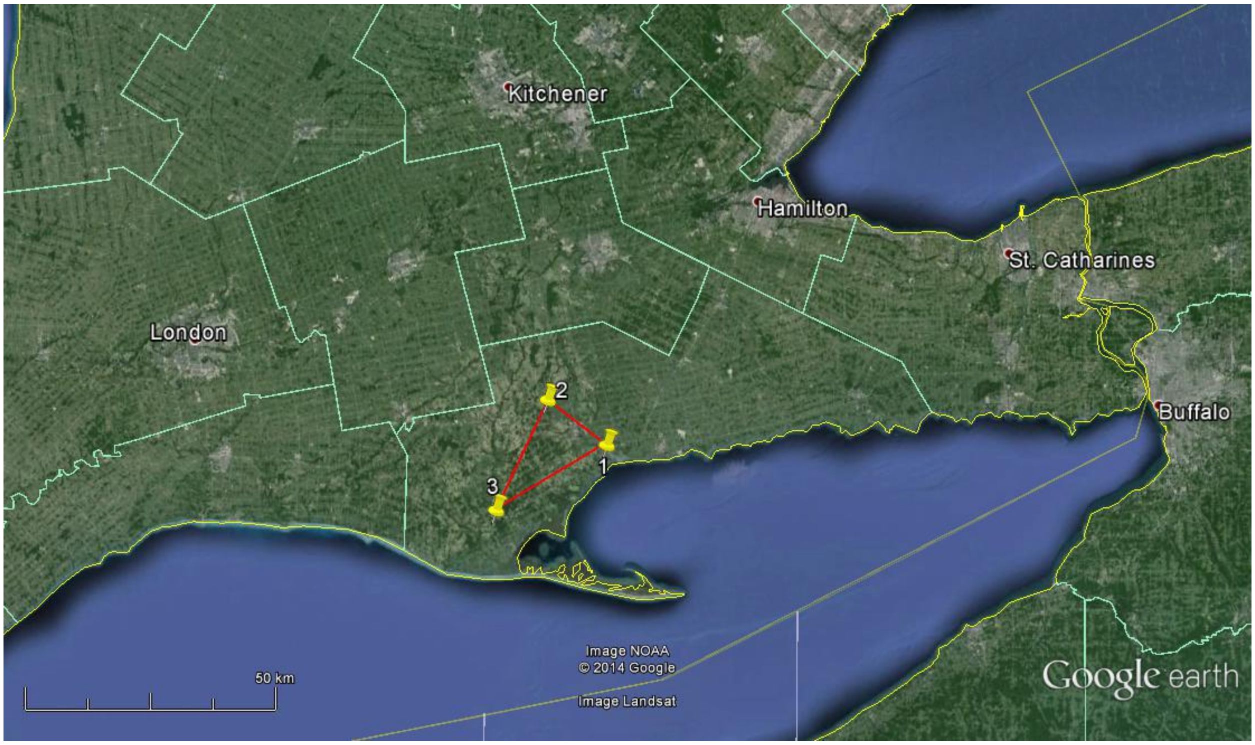

Figure 1. Map of study site locations in Norfolk County, Ontario, Canada.

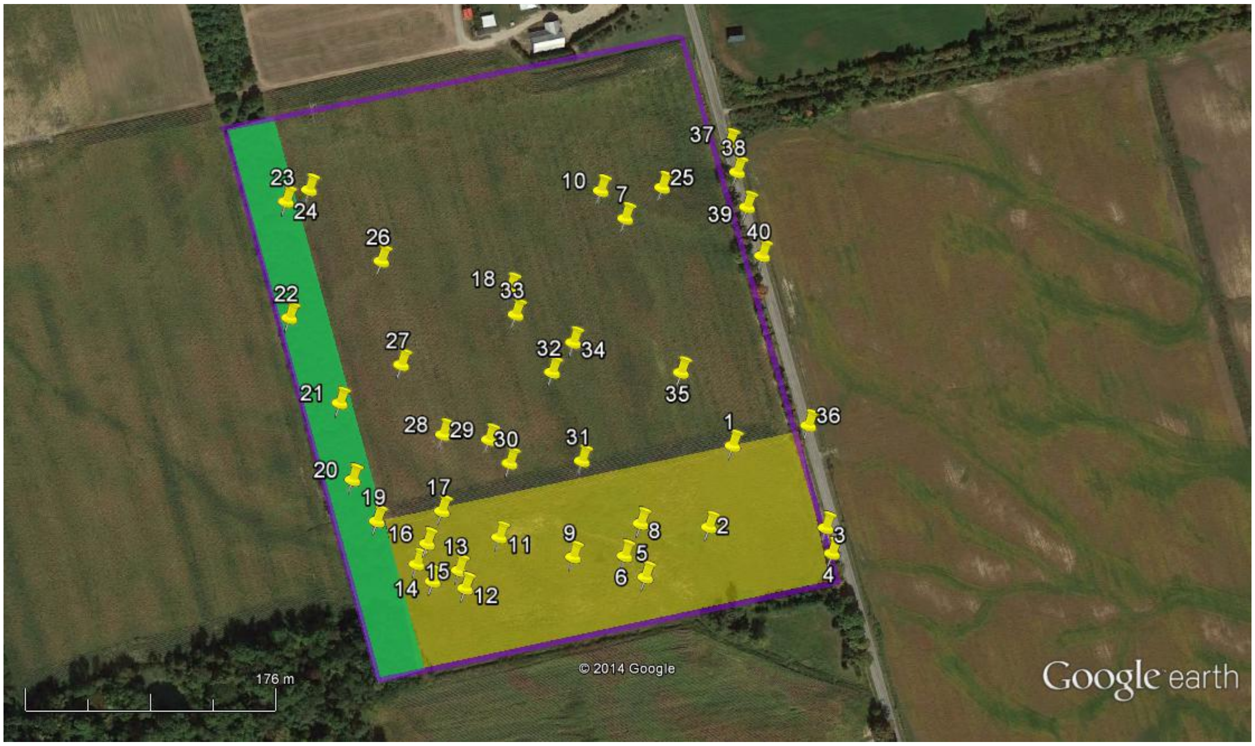

Figure 2. Map of Farm 1 (borders outlined in purple). Tallgrass prairie restoration is highlighted in yellow, and forest is in green.

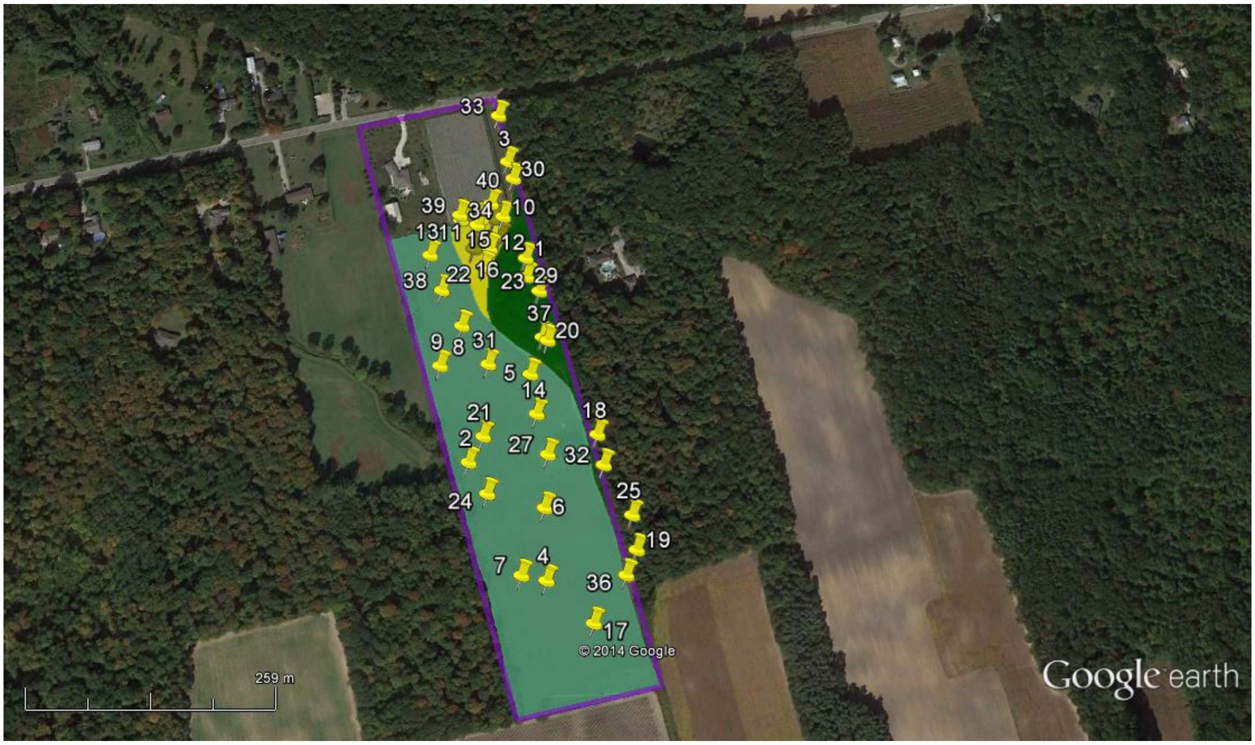

Figure 3. Map of Farm 2 (borders outlined in purple). Tallgrass prairie restoration is highlighted in yellow, forest is highlighted in dark green and restored oak savannah is in pale green.

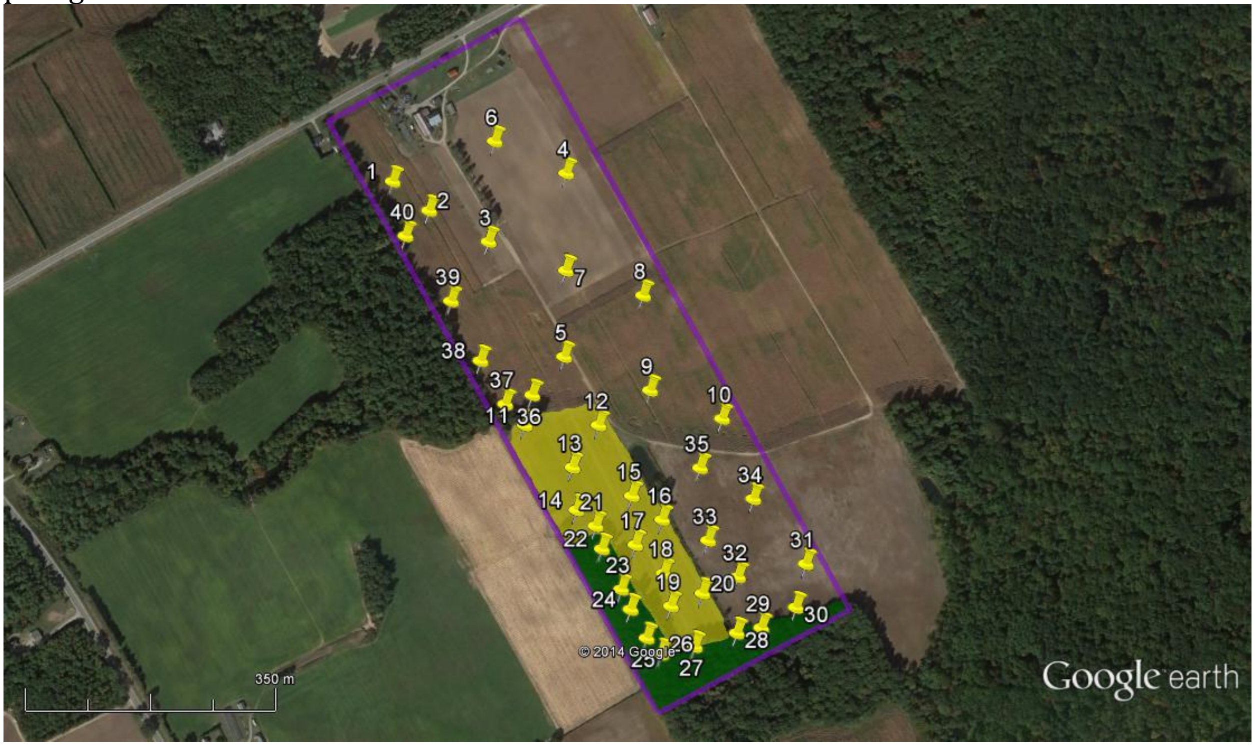

Figure 4. Map of Farm 3 (borders outlined in purple). Tallgrass prairie restoration is highlighted in yellow, and the forest is dark green.

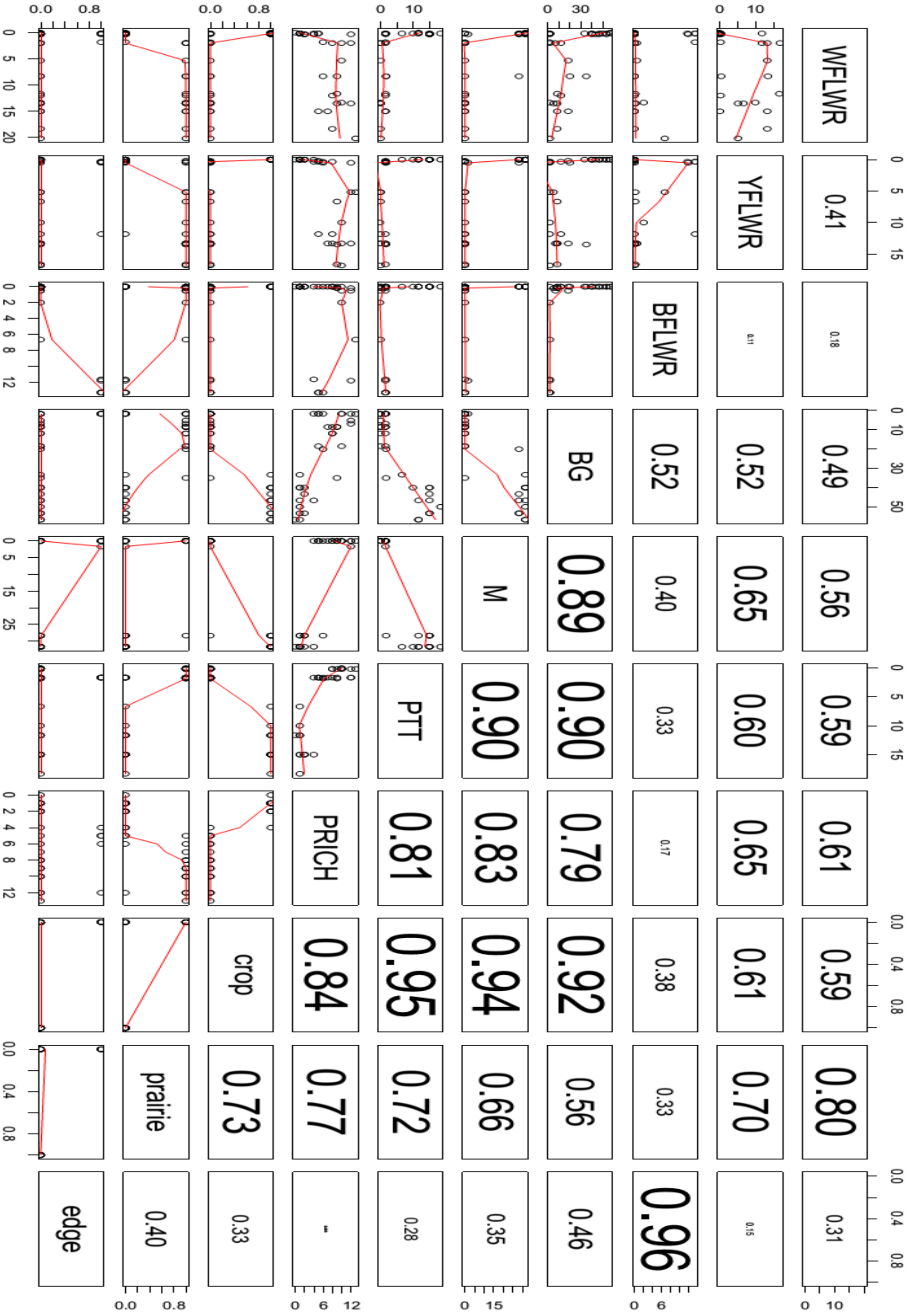

Figure 5. Pairwise comparison of environmental variables on Farm 1.

Figure 6. Pairwise comparison of environmental variables on Farm 2.

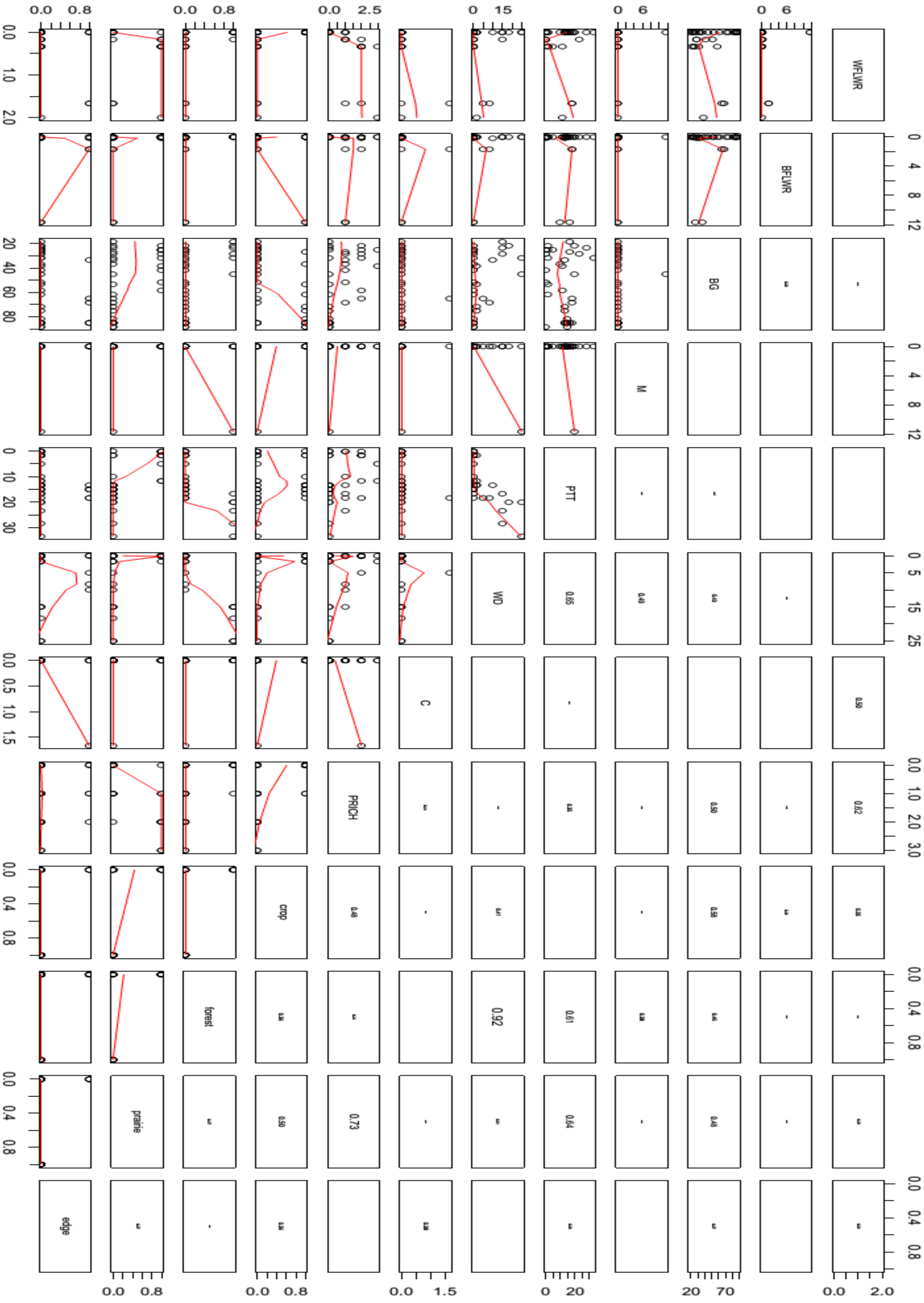

Figure 7. Pairwise comparison of environmental variables on Farm 3.

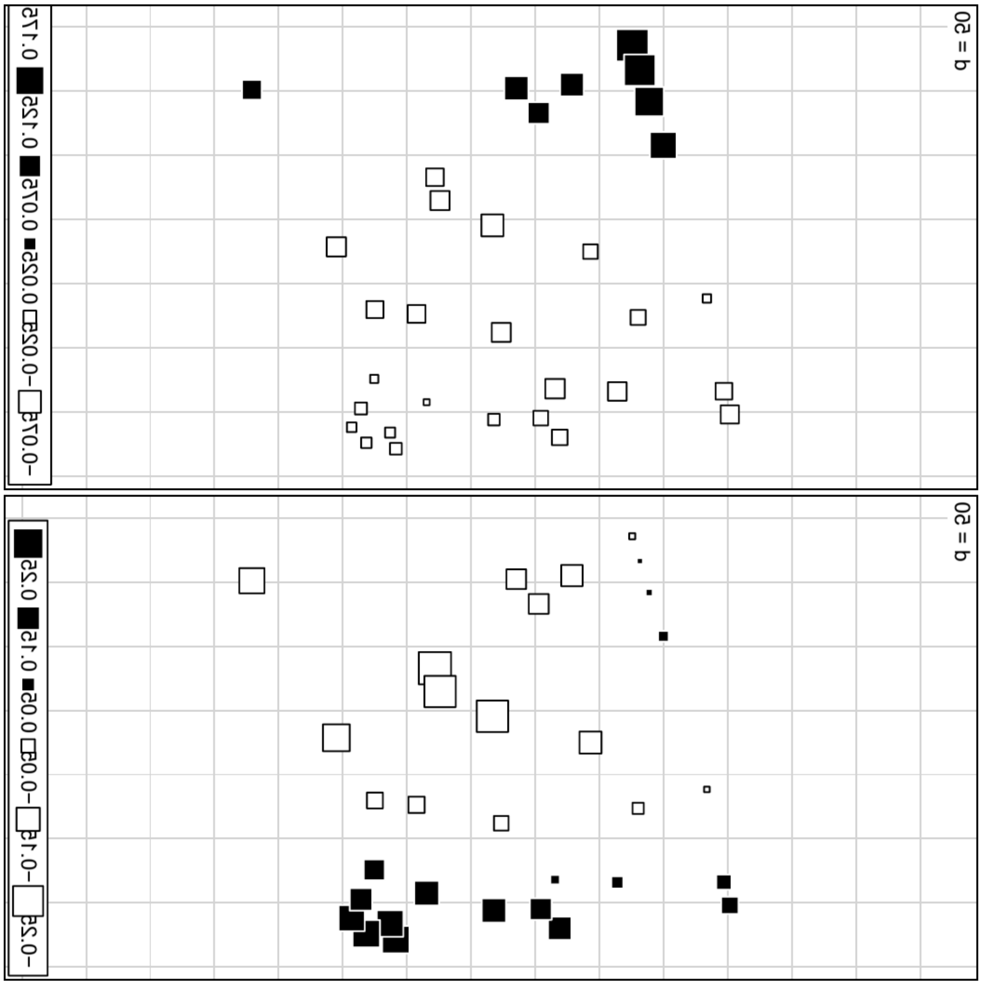

Figure 8. PCNM eigenvectors for Farm 1 species level analysis.

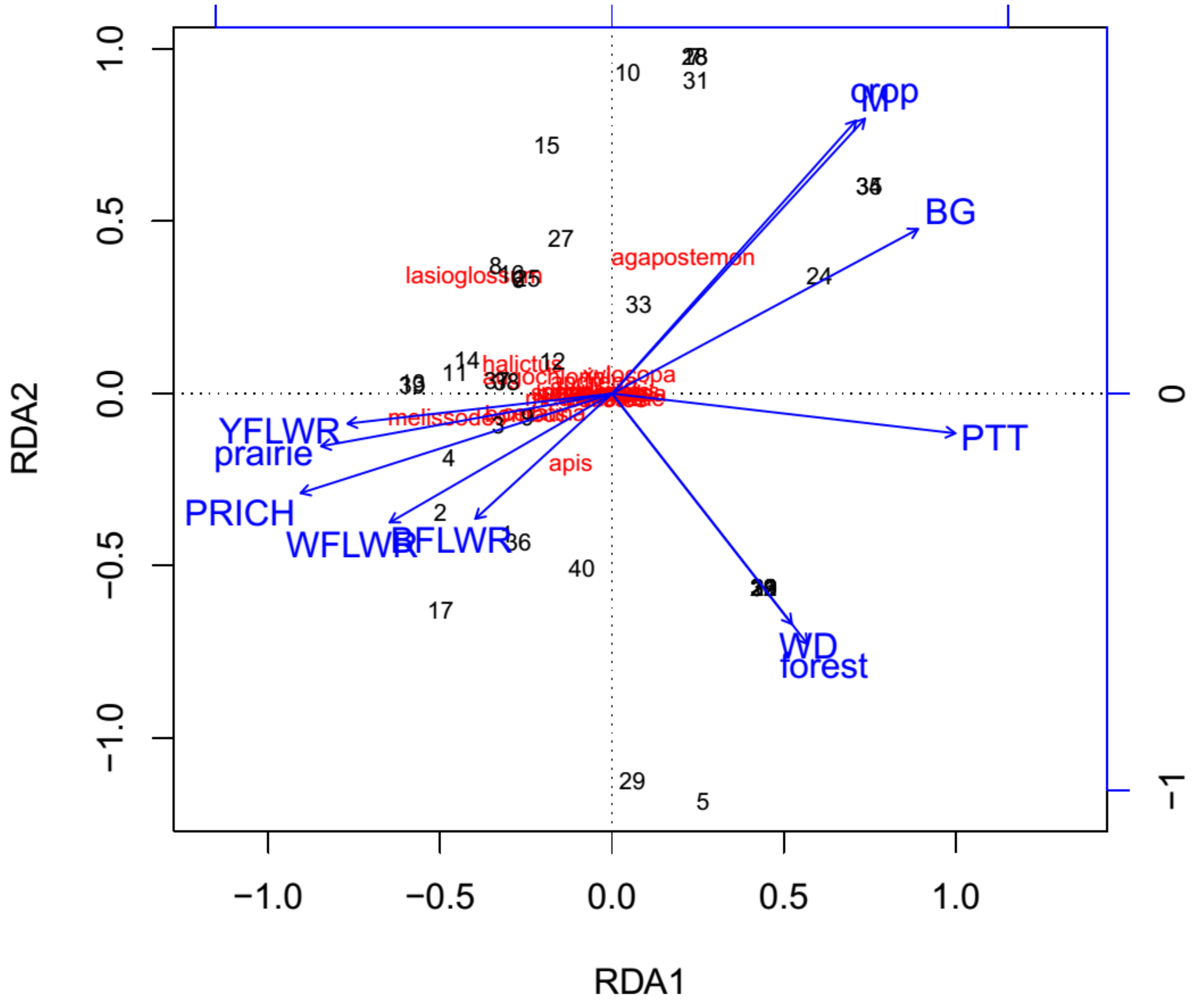

Figure 9a. PCNM RDA biplots for genera level analysis of environmental variables for Farm 1. Adjusted R squared values as follows for full models and reduced models (in brackets): 0.1459703 (0.1656174).

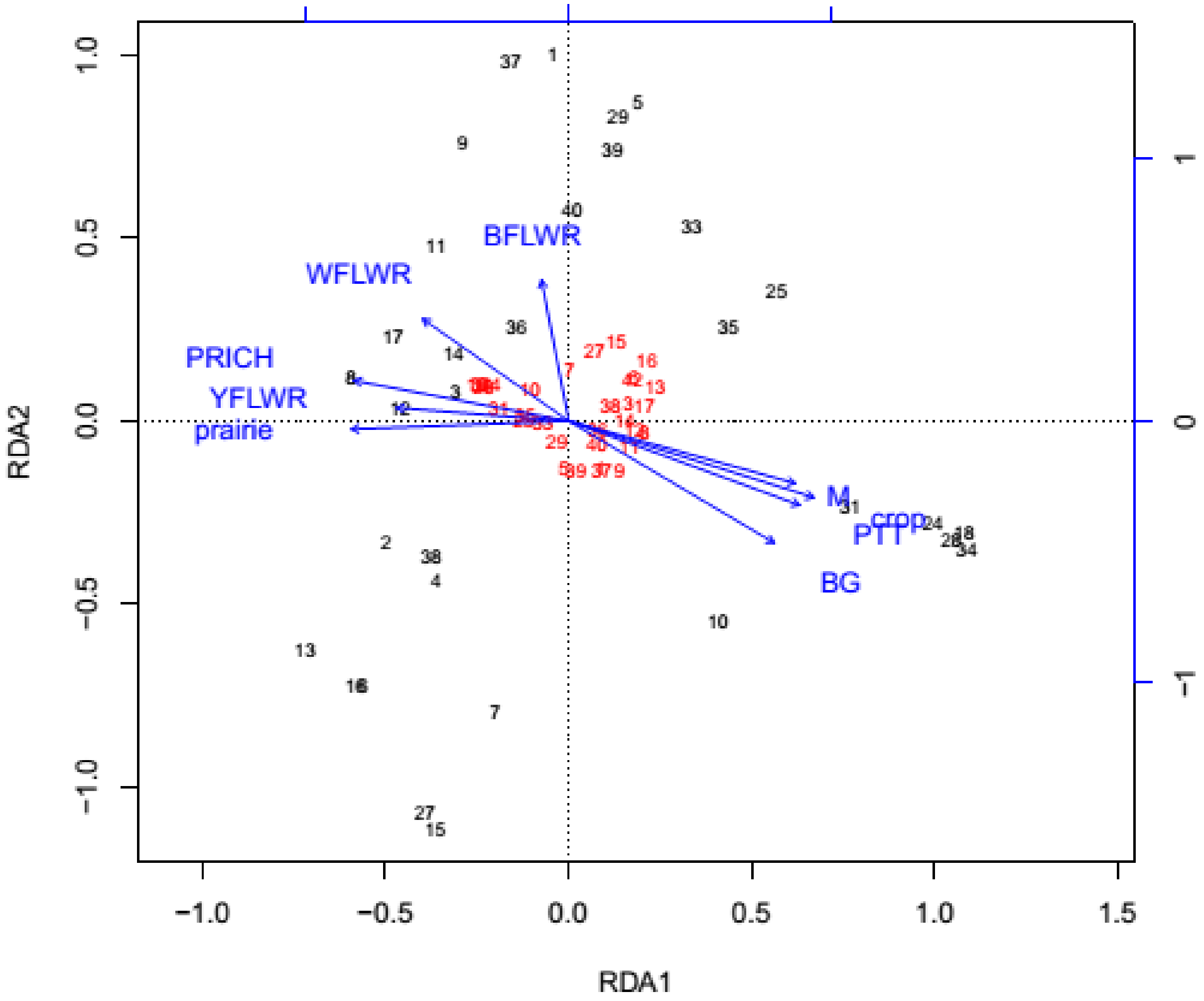

Figure 9b. PCNM RDA biplots for species level analysis of environmental variables for Farm 1. Adjusted R squared values as follows for full models and reduced models (in brackets): 0.08459262 (0.09003045).

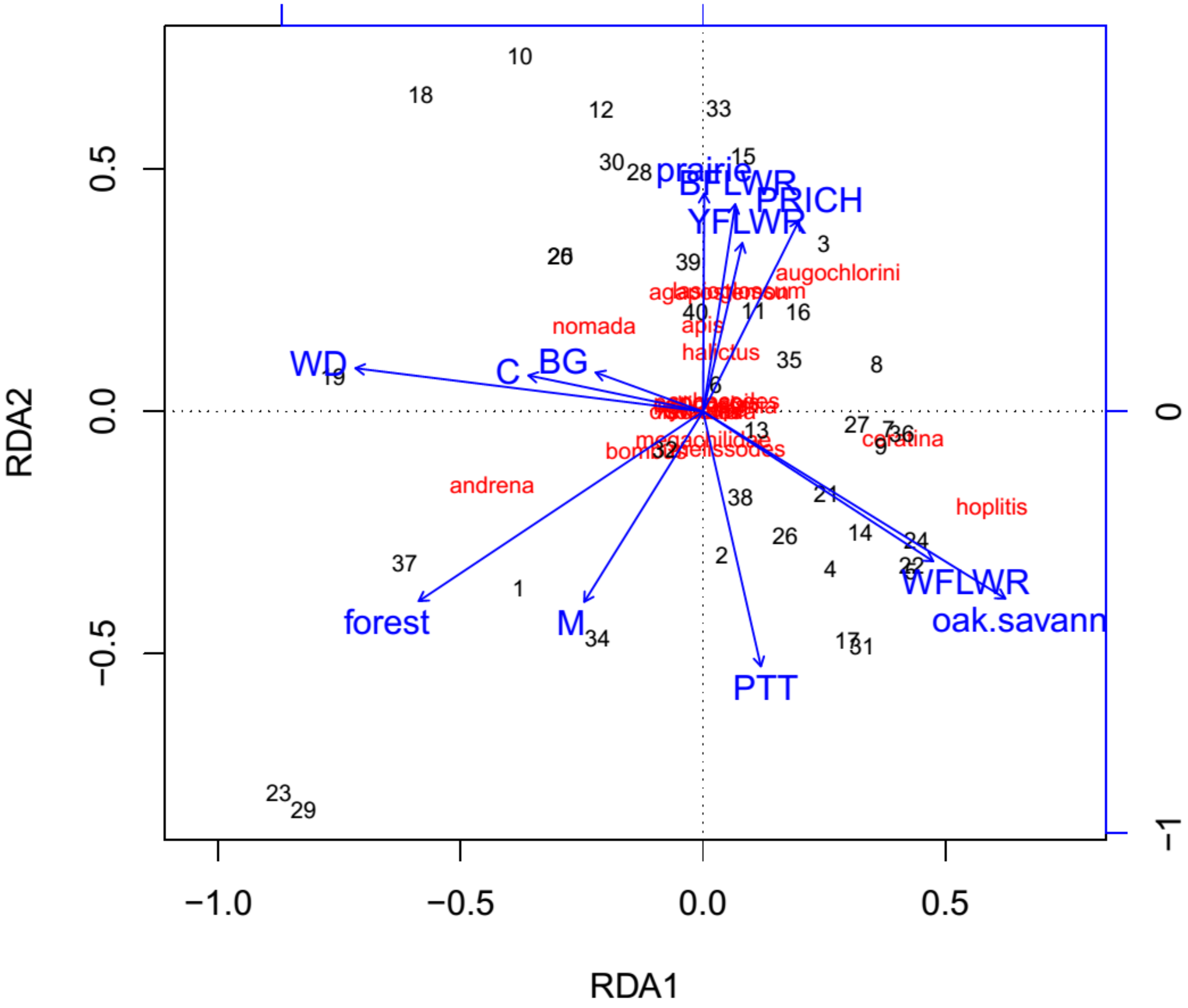

Figure 10a. PCNM RDA biplots for genera level analysis of environmental variables for Farm 2. Adjusted R squared values as follows for full models and reduced models (in brackets): 0.2368492 (0.2145217).

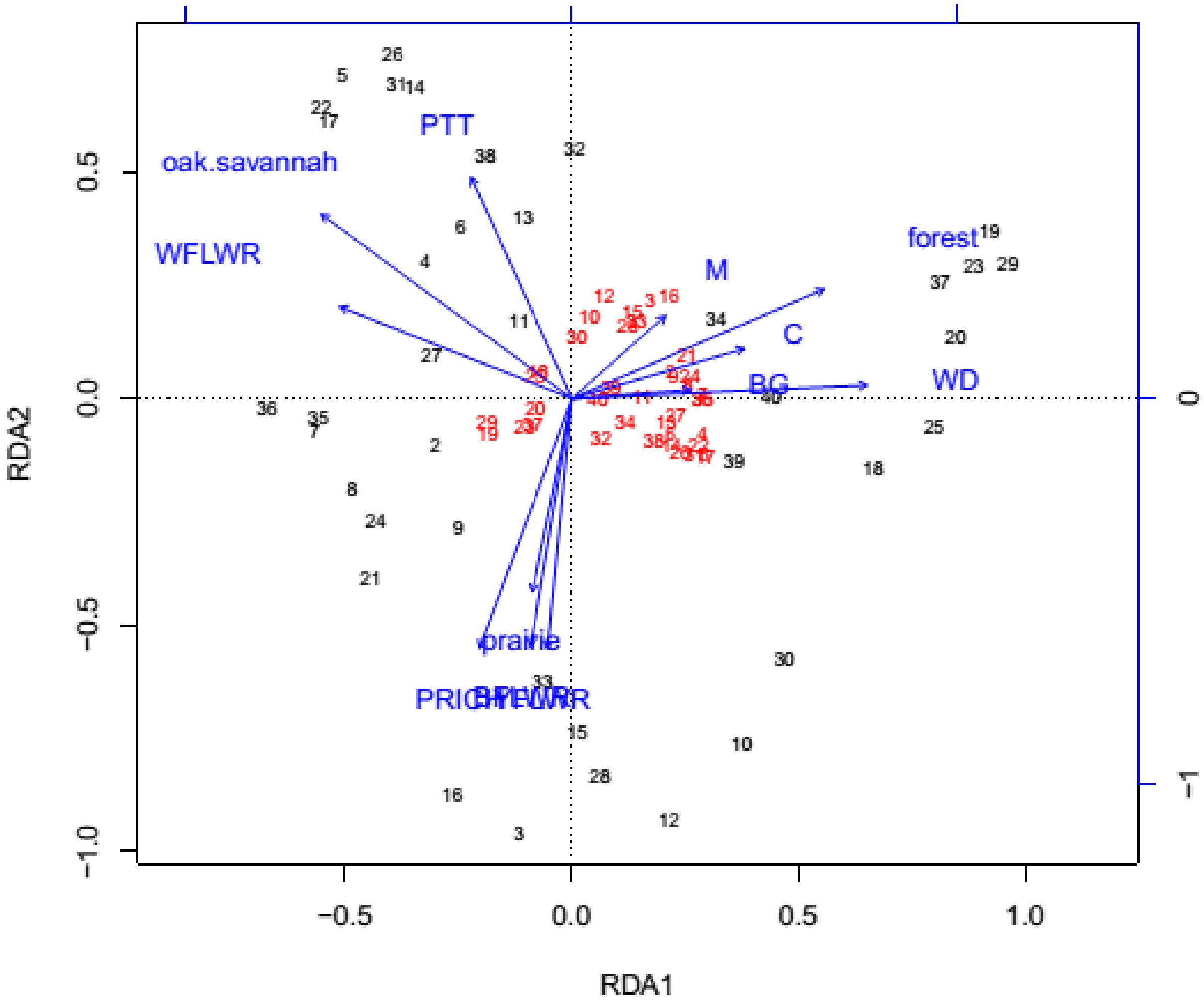

Figure 10b. PCNM RDA biplots for species level analysis of environmental variables for Farm 2. Adjusted R squared values as follows for full models and reduced models (in brackets): 0.2240407 (0.1703587).

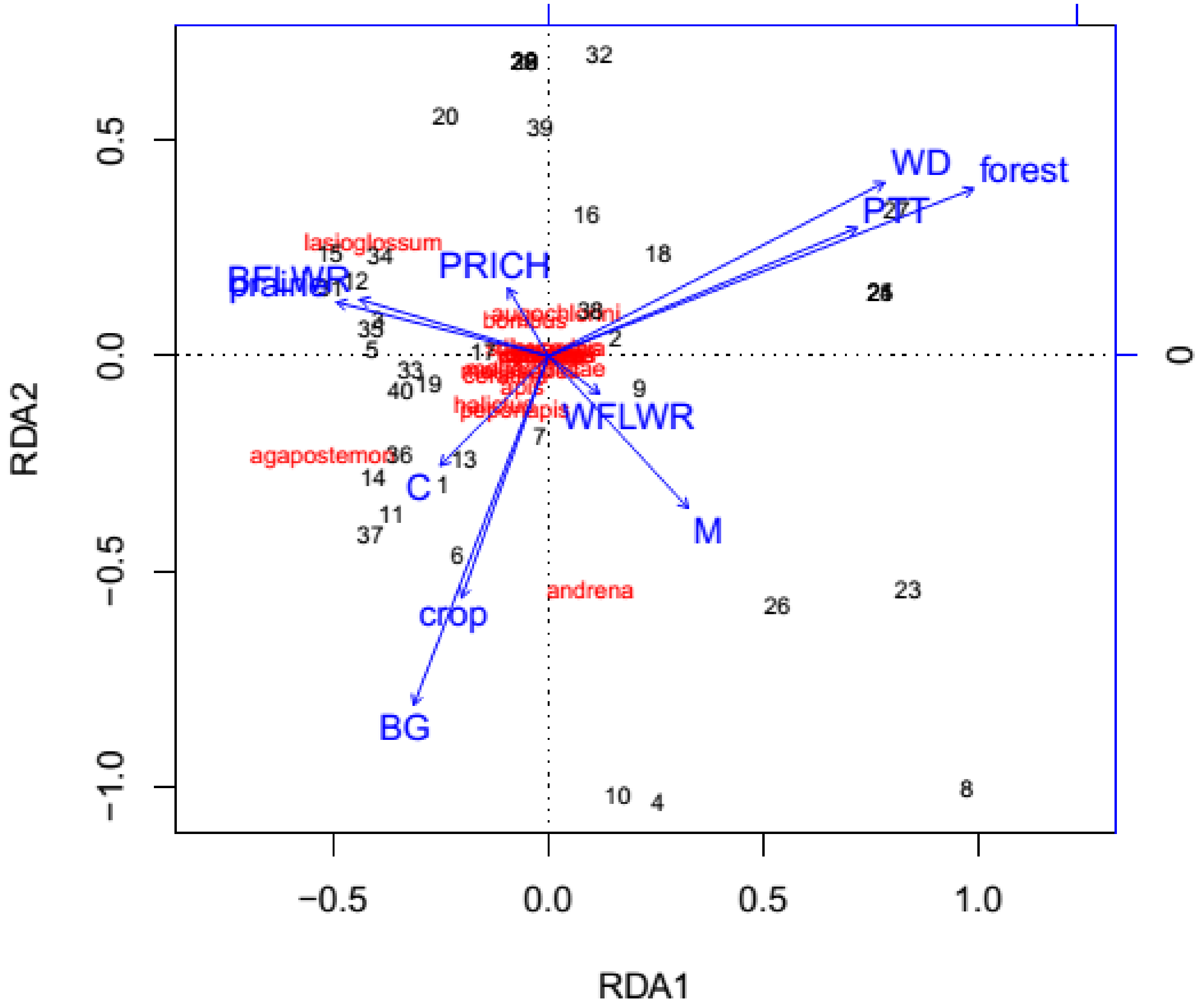

Figure 11a. PCNM RDA biplots for genera level analysis of environmental variables for Farm 3. Adjusted R squared values as follows for full models and reduced models (in brackets): 0.1635105 (0.1267989).

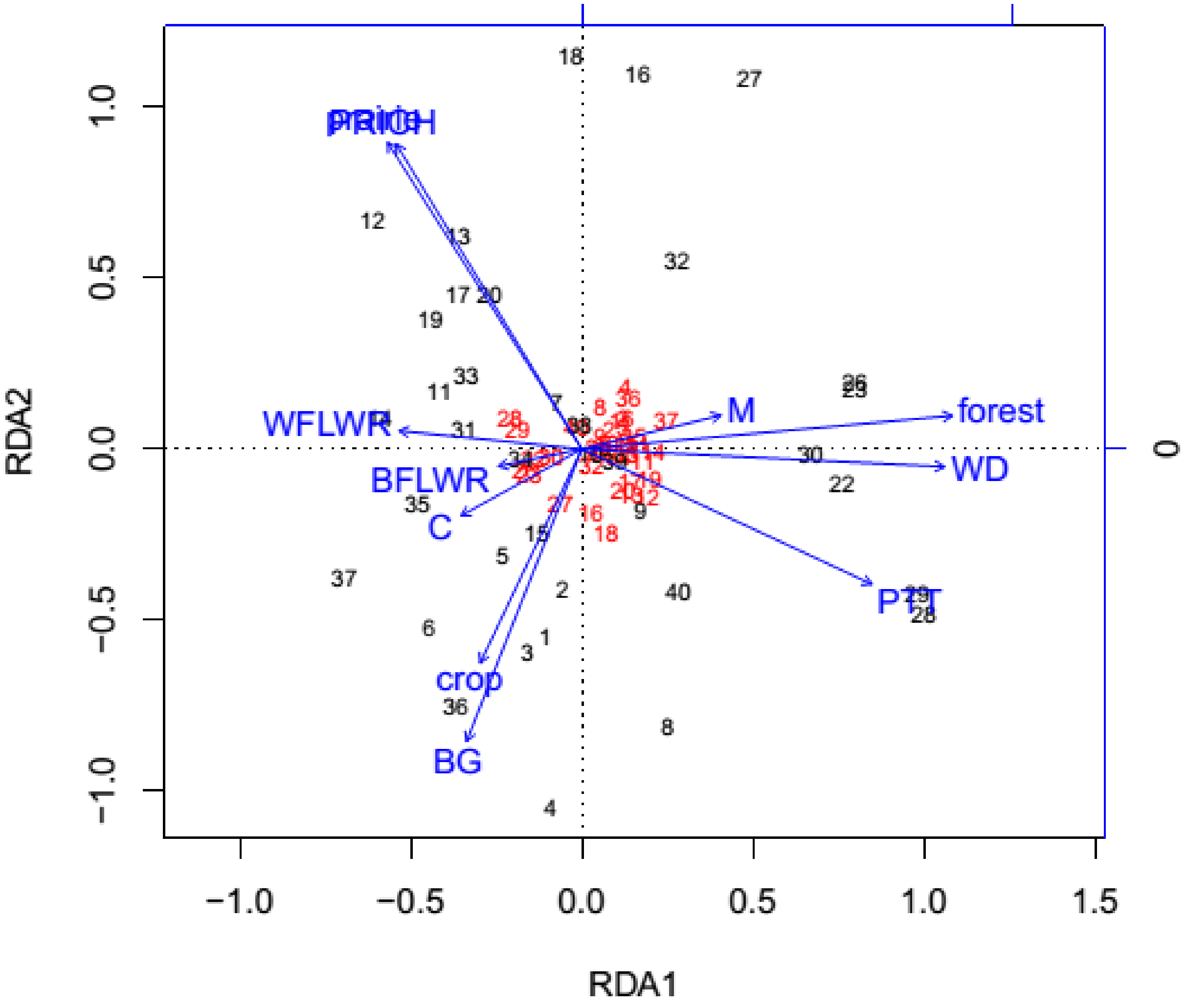

Figure 11b. PCNM RDA biplots for species level analysis of environmental variables for Farm 3. Adjusted R squared values as follows for full models and reduced models (in brackets): 0.0858306 (0.07857744).

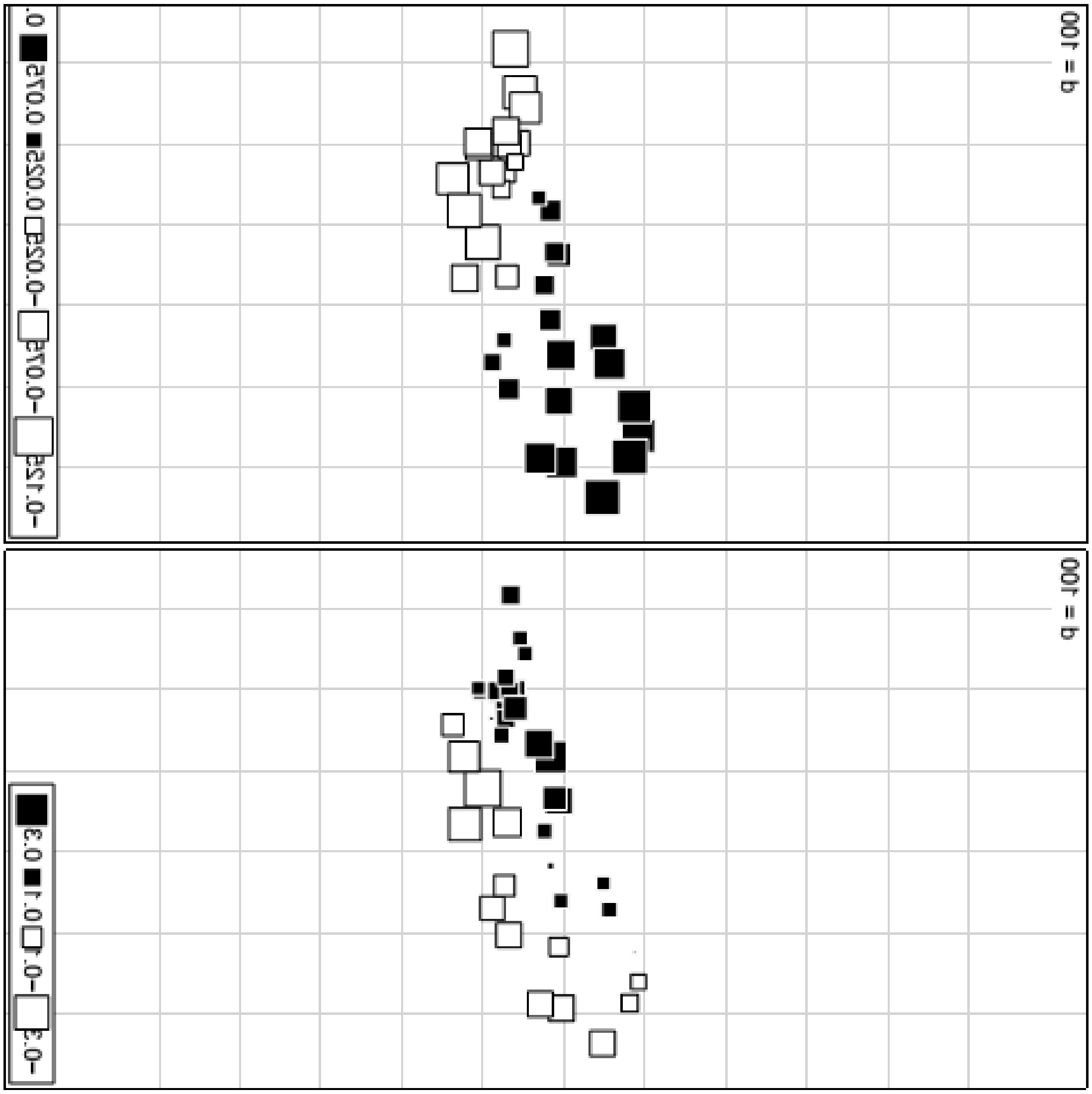

Figure 12. PCNM eigenvectors for Farm 2 species level analysis.

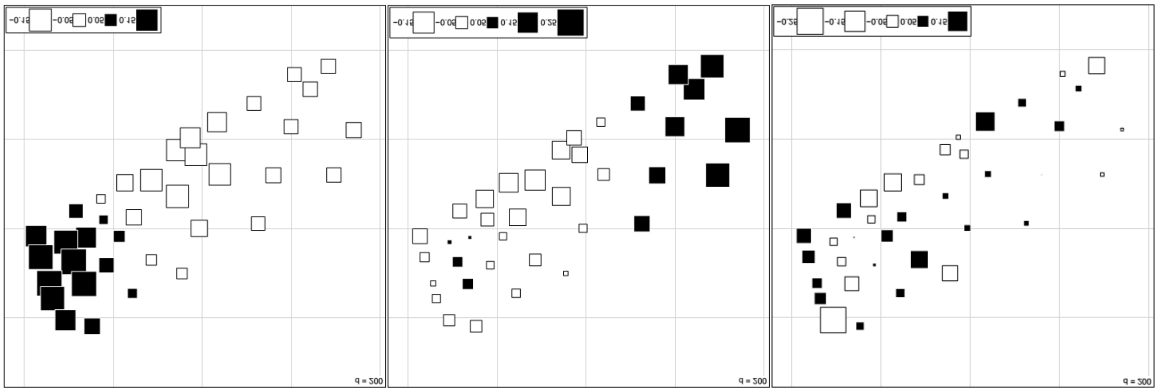

Figure 13. PCNM eigenvectors for Farm 3 species level analysis.

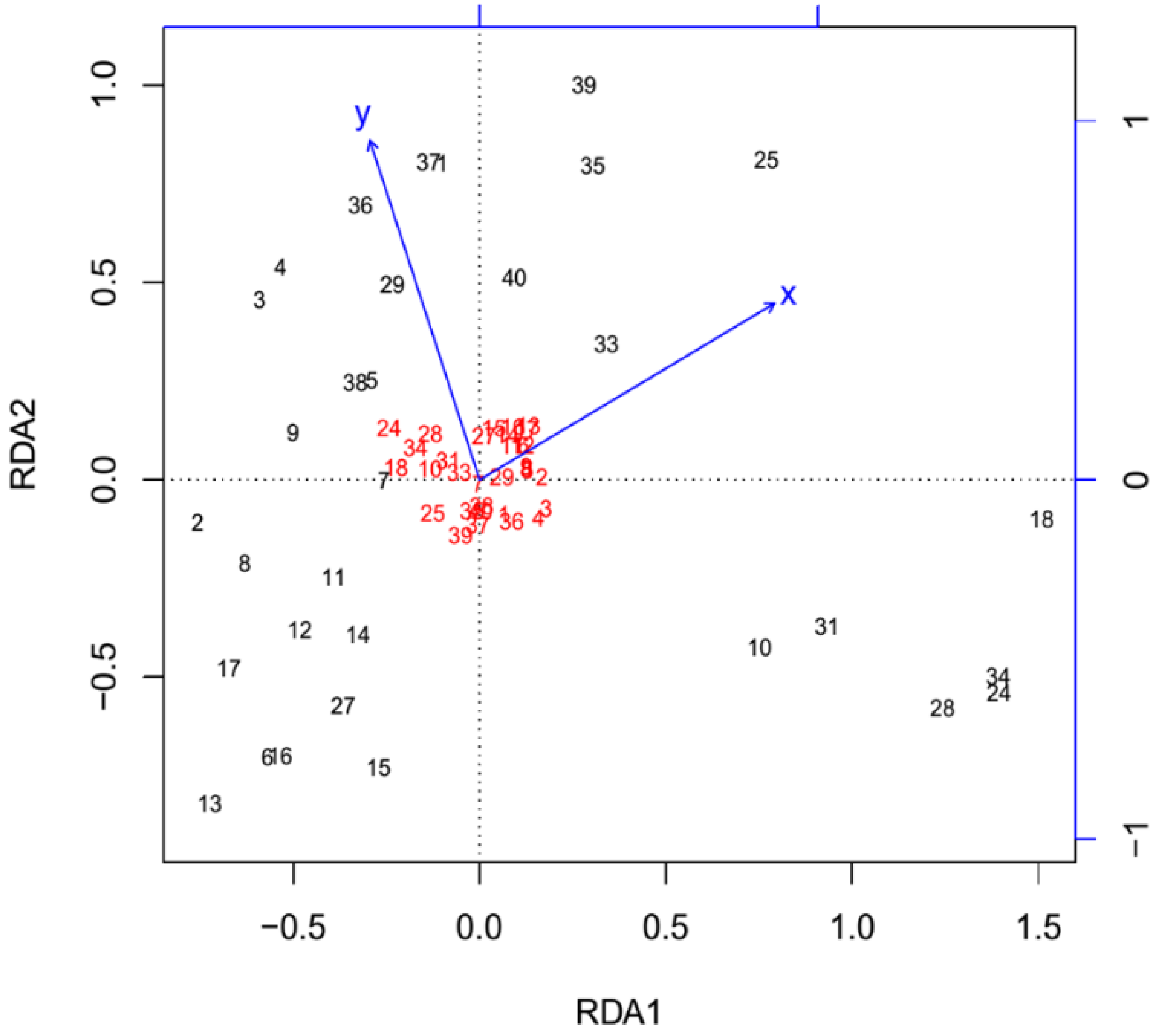

Figure 14. PCNM RDA biplots for species level analysis of spatial variables (using UTM coordinates as explanatory variables) for Farm 1. Adjusted R squared: 0.05311849.

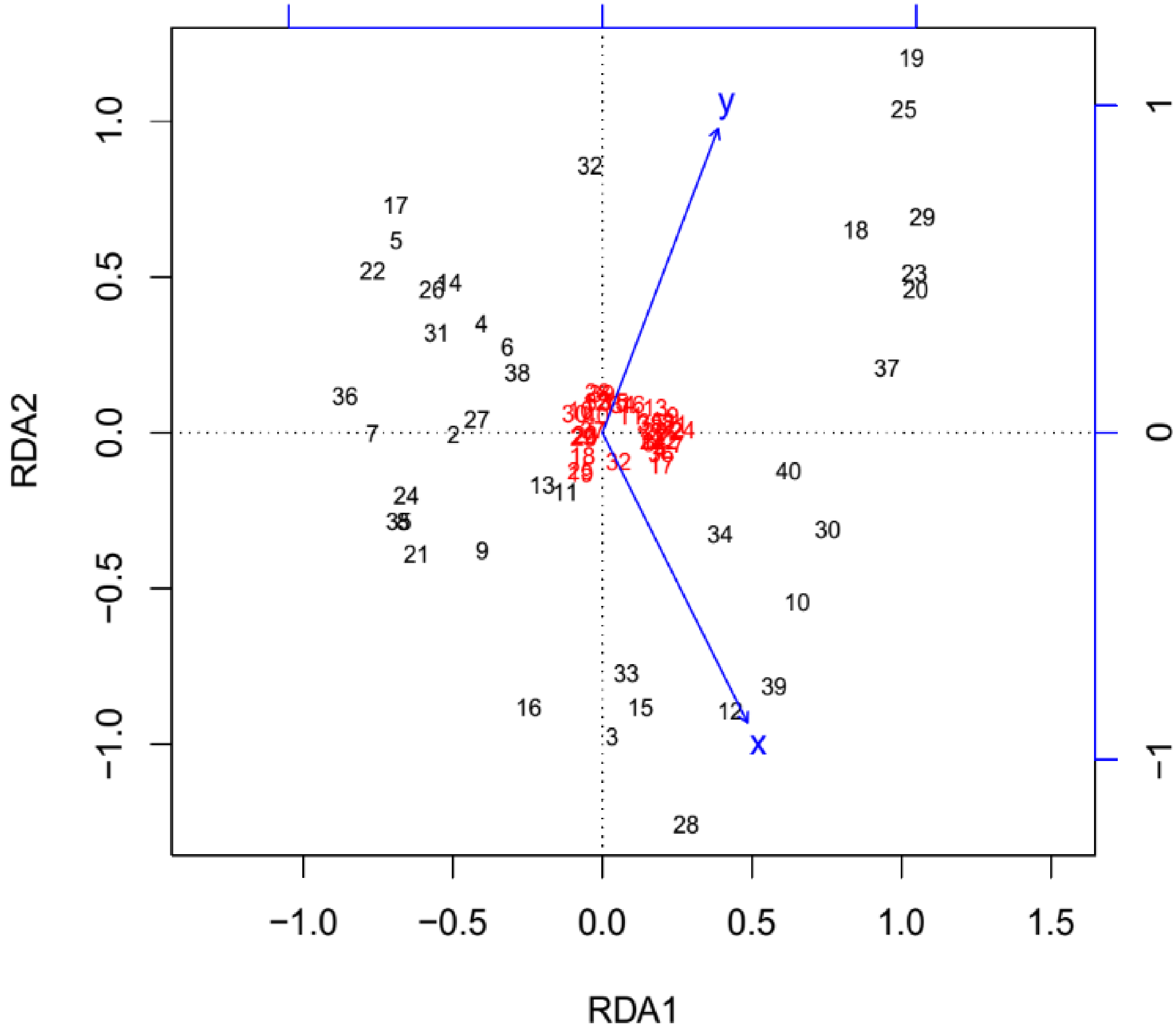

Figure 15. PCNM RDA biplots for species level analysis of spatial variables (using UTM coordinates as explanatory variables) for Farm 2. Adjusted R squared: 0.1130384.

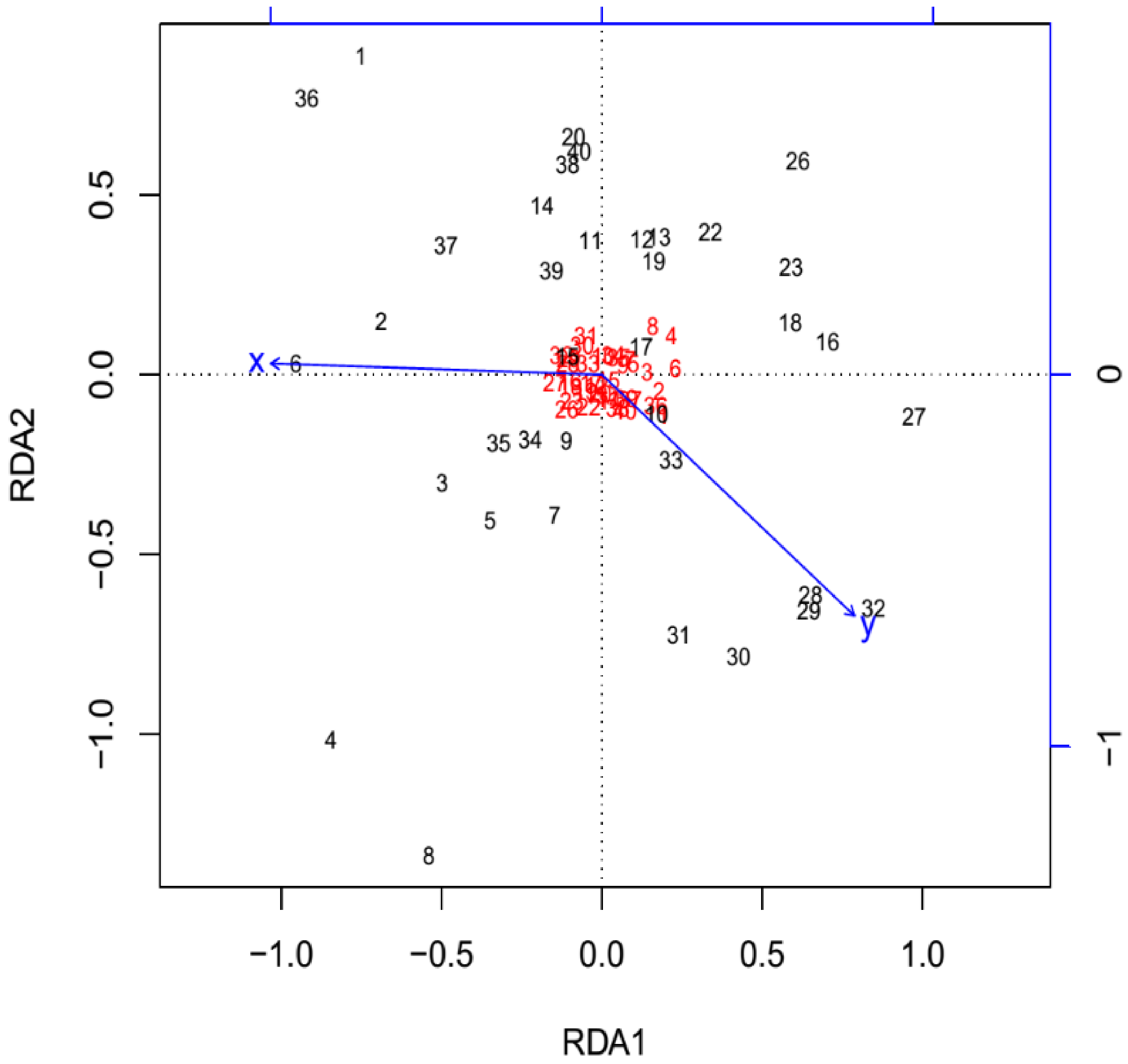

Figure 16. PCNM RDA biplot for species level analysis of spatial variables (using UTM coordinates as explanatory variables) for Farm 3. Adjusted R squared: 0.03632181.

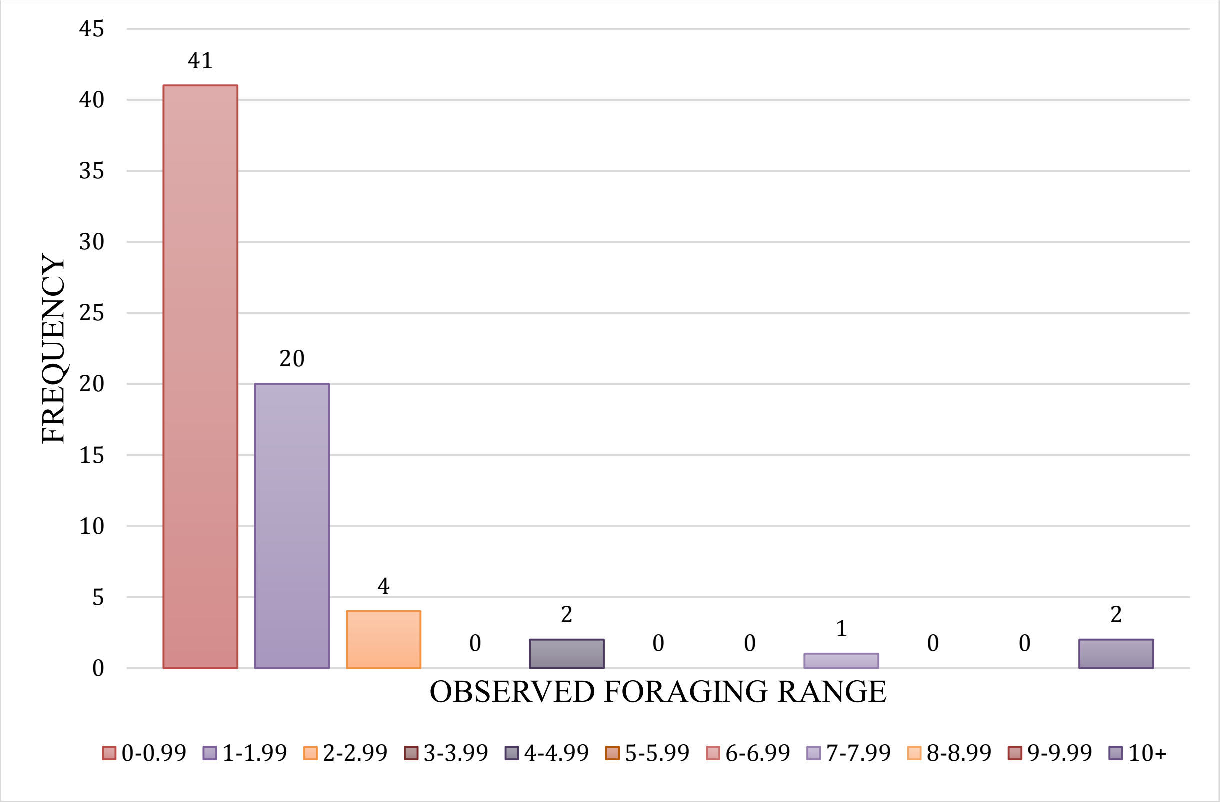

Figure 17. Observed foraging ranges of various bee species (adapted from Greenleaf et al. 2007, supplementary material).

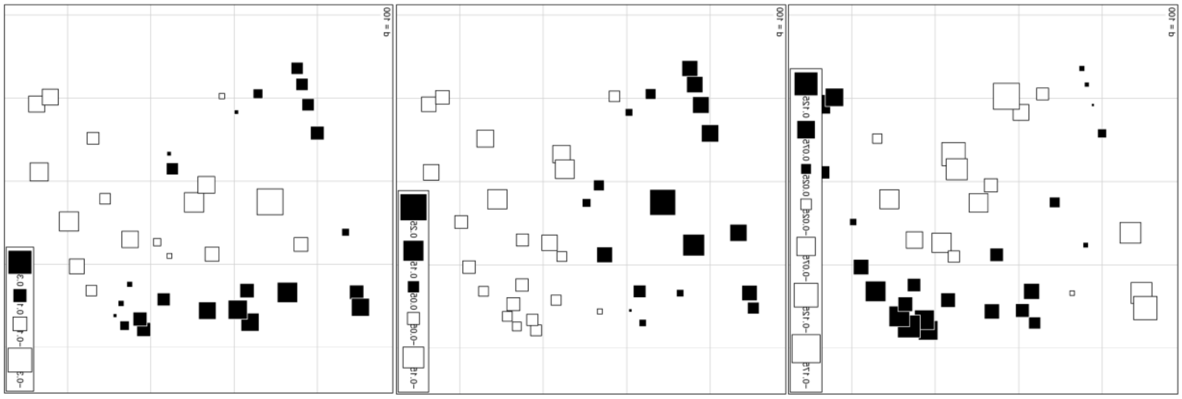

Figure 18. PCNM eigenvectors for Farm 1 genera level analysis.

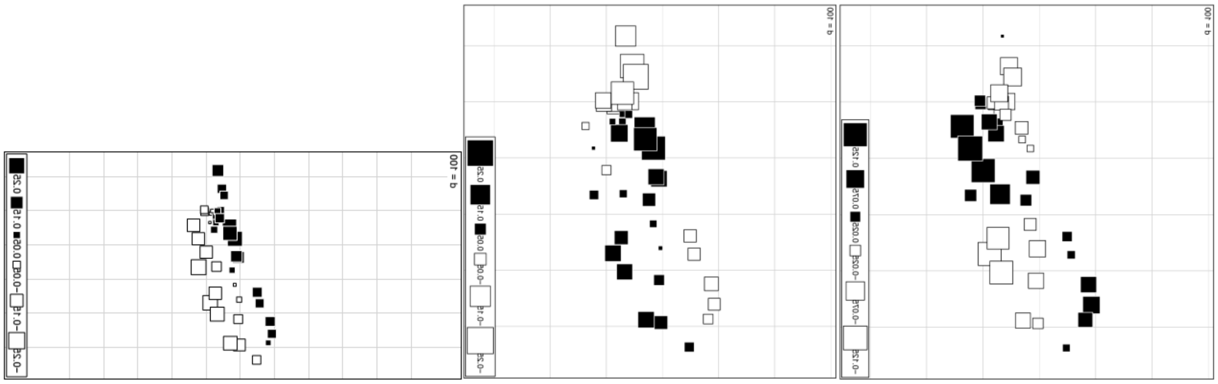

Figure 19. PCNM eigenvectors for Farm 2 genera level analysis.

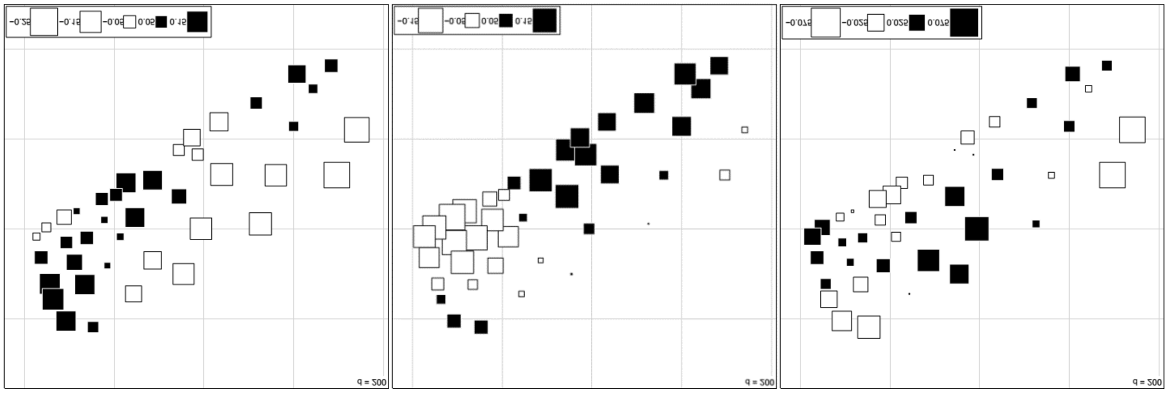

Figure 20. PCNM eigenvectors for Farm 3 genera level analysis.

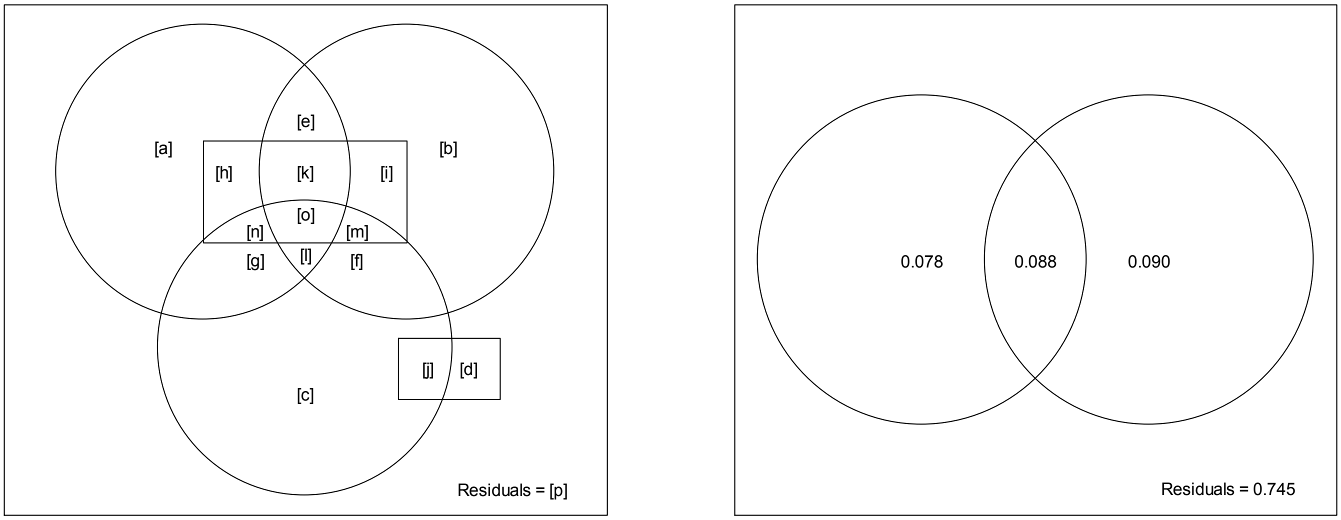

Figure 21a. PCNM variation partitioning results for Farm 1 genera level data. Fraction [a] represents the variation explained by forward selected environmental variables (adjusted $R^2 = 0.078$) and fraction [b] the variation explained by forward selected PCNM eigenvectors (adjusted $R^2 = 0.090$).

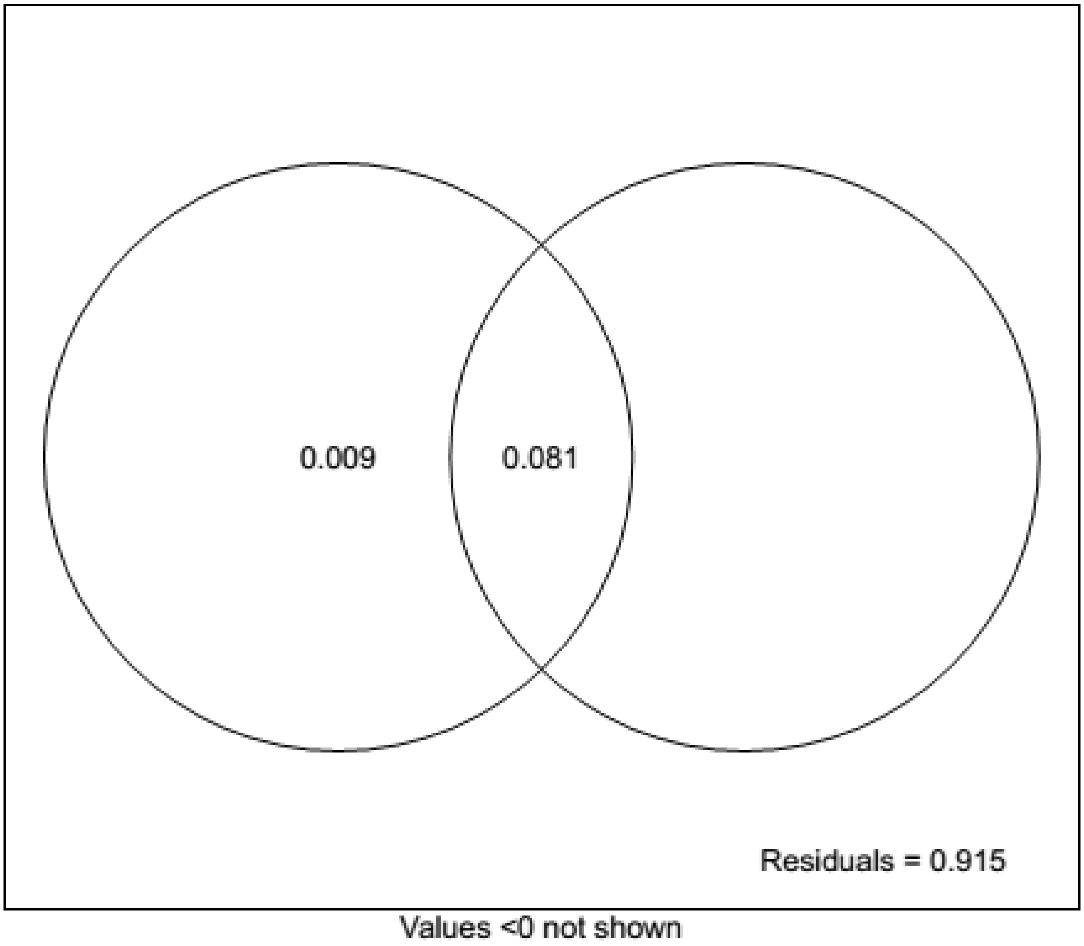

Figure 21b. PCNM variation partitioning results for Farm 1 species level data. Fraction [a] represents the variation explained by forward selected environmental variables (adjusted $R^2 = 0.009$) and fraction [b] the variation explained by forward selected PCNM eigenvectors (adjusted $R^2 < 0$).

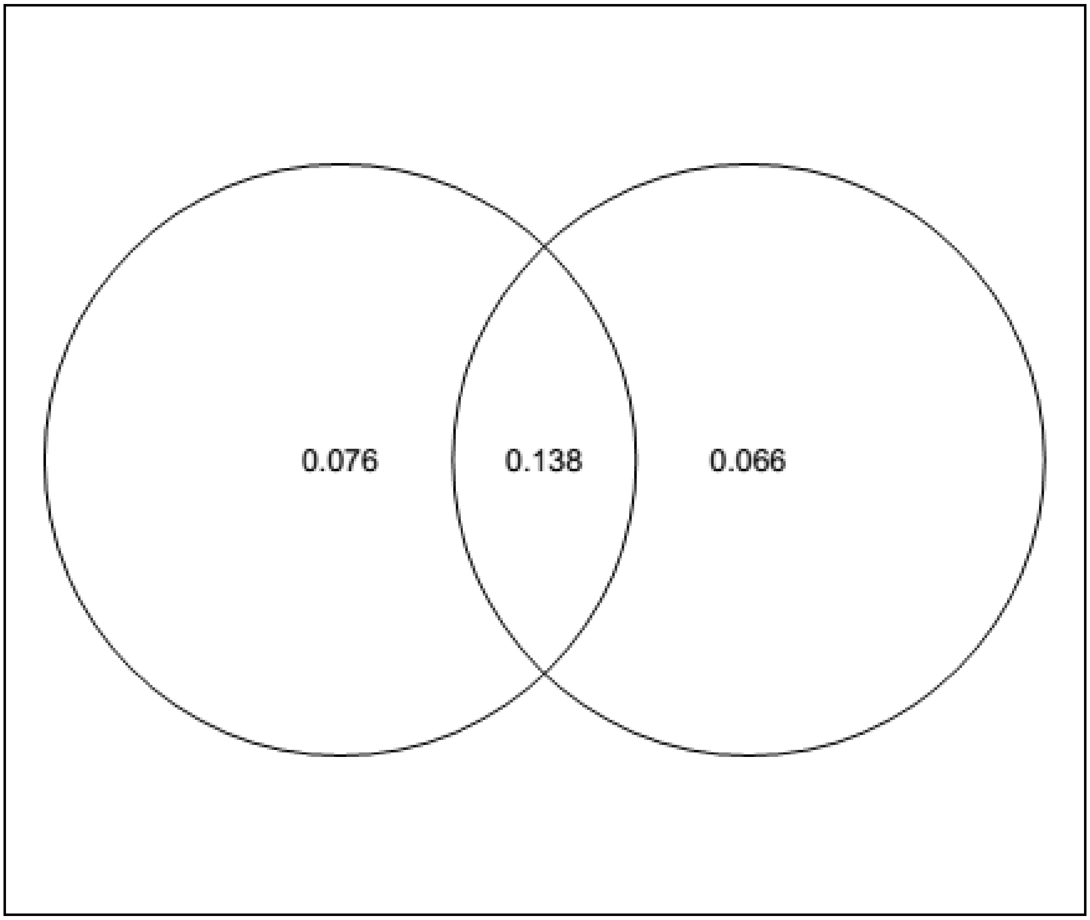

Figure 22a. PCNM variation partitioning results for Farm 2 genera level data. Fraction [a] represents the variation explained by forward selected environmental variables (adjusted $R^2 = 0.076$) and fraction [b] the variation explained by forward selected PCNM eigenvectors (adjusted $R^2 = 0.066$).

Figure 22b. PCNM variation partitioning results for Farm 2 species level data. Fraction [a] represents the variation explained by forward selected environmental variables (adjusted $R^2 = 0.089$) and fraction [b] the variation explained by forward selected PCNM eigenvectors (adjusted $R^2 = 0.020$).

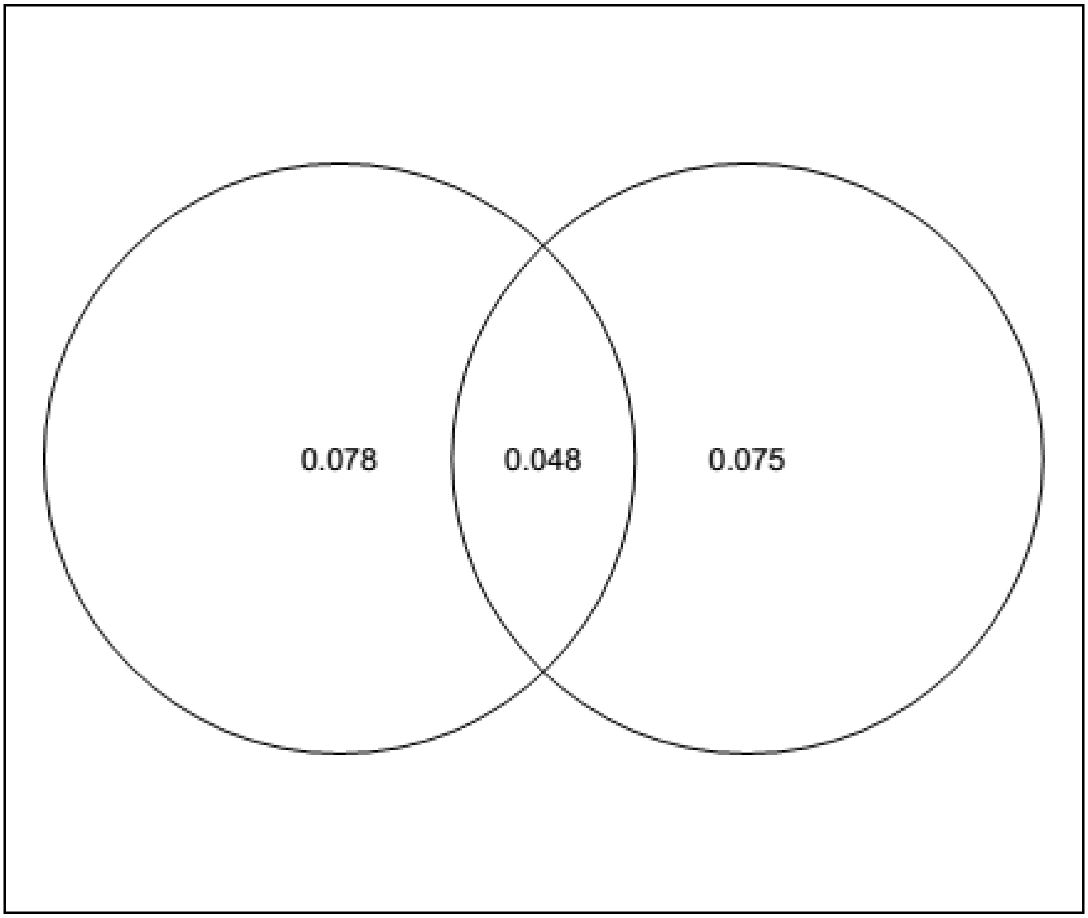

Figure 23a. PCNM variation partitioning results for Farm 3 genera level data. Fraction [a] represents the variation explained by forward selected environmental variables (adjusted $R^2 = 0.078$) and fraction [b] the variation explained by forward selected PCNM eigenvectors (adjusted $R^2 = 0.075$).

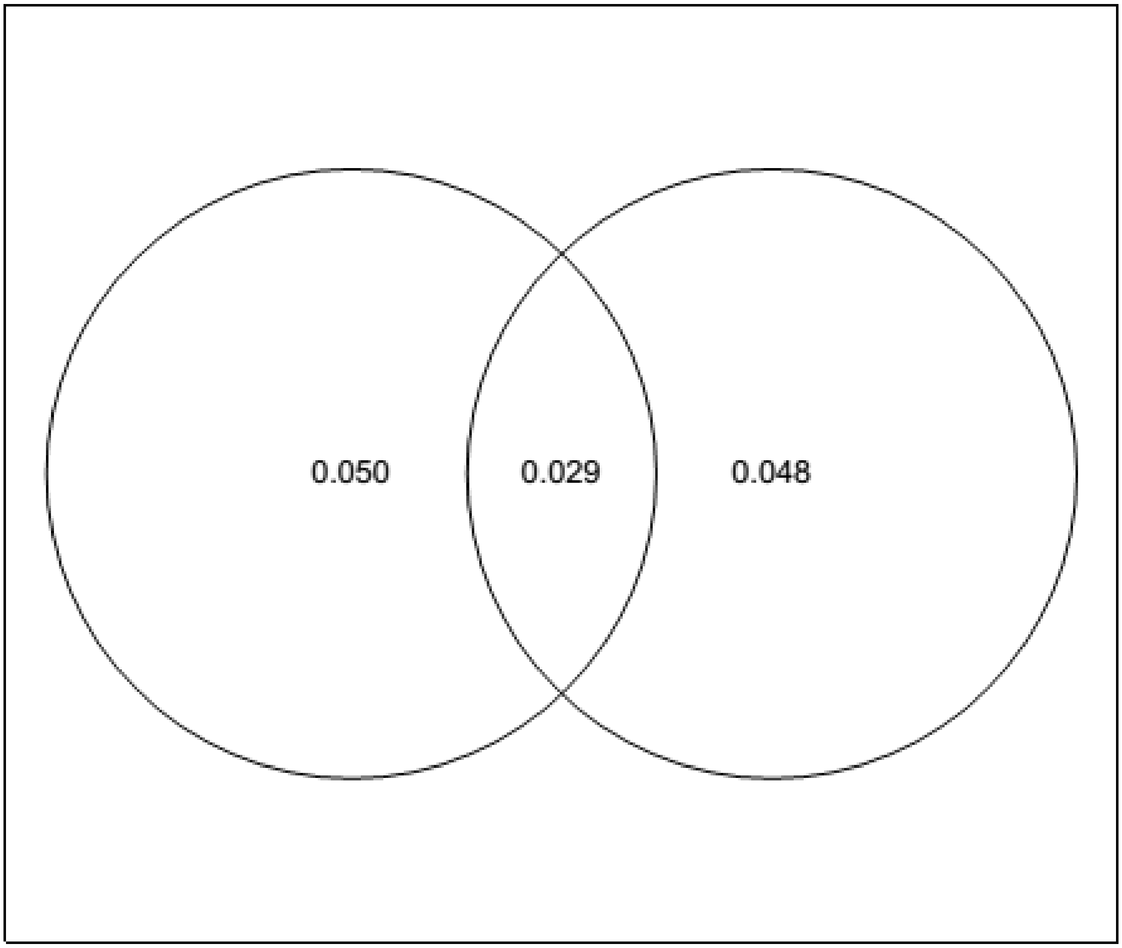

Figure 23b. PCNM variation partitioning results for Farm 3 species level data. Fraction [a] represents the variation explained by forward selected environmental variables (adjusted $R^2 = 0.050$) and fraction [b] the variation explained by forward selected PCNM eigenvectors (adjusted $R^2 = 0.048$).

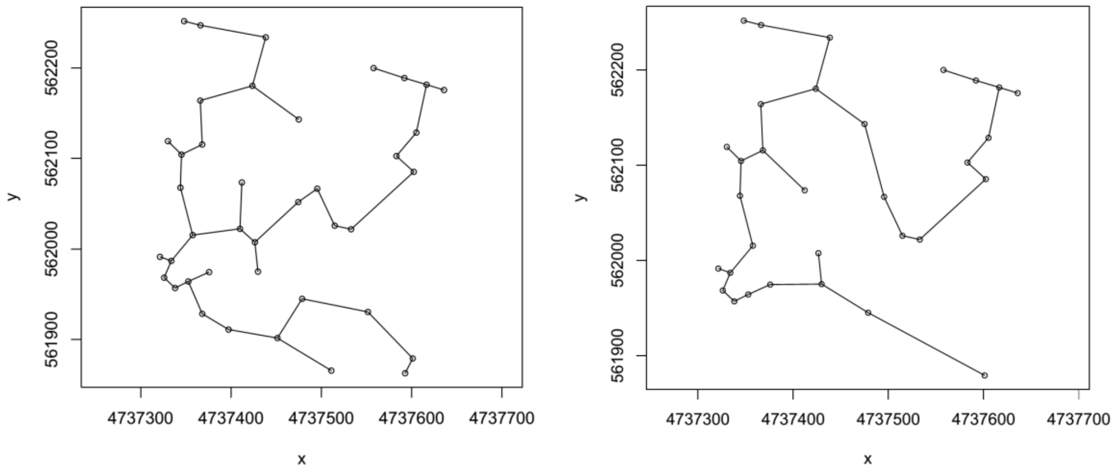

Figure 24. Minimum spanning trees for PCNM eigenvalues for Farm 1. Genera level data is on the left and species level data is on the right.

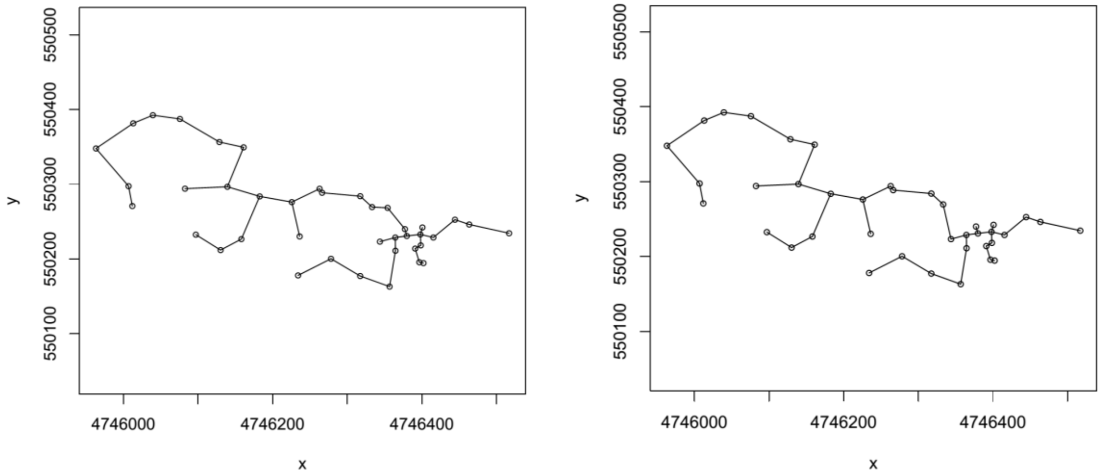

Figure 25. Minimum spanning trees for PCNM eigenvalues for Farm 2. Genera level data is on the left and species level data is on the right.

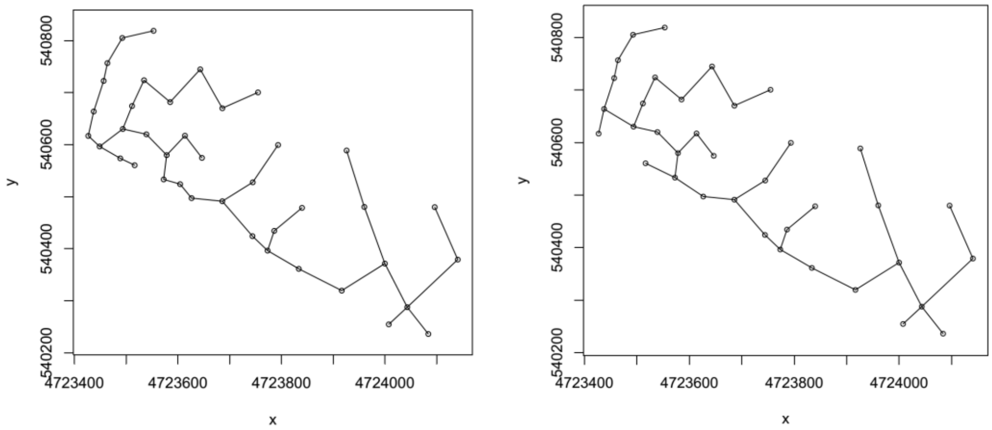

Figure 26. Minimum spanning trees for PCNM eigenvalues for Farm 3. Genera level data is on the left and species level data is on the right.