Does landscape heterogeneity affect bee diversity in farmland?

by

Sean Feagan

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fulfillment of the requirements for the degree of

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Abstract

Agricultural land conversion and management practices reduce spatial heterogeneity, which can affect the presence and distribution of species in farmland. Landscapes with more cover types (compositional heterogeneity) are expected to contain a greater diversity of resources, and thus should harbour more diverse species assemblages. The spatial distribution of landscape features (configurational heterogeneity) is expected to affect the distribution of species by determining the access to different required resources (landscape complementation). The objective of this study was to determine whether landscape heterogeneity, independent of habitat amount, affects the richness and abundance of a temperate bee assemblage in an agricultural region of Eastern Ontario, Canada. Bee diversity was sampled at roadside sites at the centre of each of 40 landscapes. A landscape selection process was used to minimize correlations between landscape predictor variables. The results indicate that bee richness responds to the amount of habitat in the landscape, but is not related by the heterogeneity of the landscape. However, heterogeneity did relate to the relative abundance of bees. In a *post hoc* analysis this was found to be driven by an increased abundance of common species in more configurationally heterogeneous landscapes. The results of my study suggest that in order to maintain a diverse bee assemblage, areas of semi-natural habitat must be maintained in farmland, and that reduced heterogeneity could decrease the sizes of bee populations.

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Introduction

Anthropogenic activities degrade ecosystems through the alteration of energy and chemical pathways and through the modification of the terrestrial surface (Vitousek *et al.* 1997). A large number of species have gone extinct in the modern era (Pereira *et al.* 2010), and even previously abundant species have experienced large population declines (Gompper and Hackett, 2005; Greenberg and Droege 1999; Julliard *et al.* 2003). Based on demographic, economic, and climatic trends, the human impact on the planet is expected to increase in the future, which will likely entail additional losses of biodiversity (Pereira *et al.* 2010). In response to current and projected threats to global biodiversity, there is a need to study the mechanisms by which anthropogenic activities affect biotic patterns, to develop evidence-based management strategies of prevention or mitigation. As agricultural activity is a large component of the total human impact on the biosphere (Matson *et al.* 1997), identifying the determinants of biotic patterns in farmland is central to the conservation of global biodiversity.

The total impact of agriculture on the biosphere has increased immensely throughout the modern era (Matson *et al.* 1997; Tilman 1999). Rates of agricultural land conversion began to spike in the pre-industrial period, such that the area of cultivated land expanded by 466% between 1700 and 1980 (Meyer and Turner 1992). The current global footprint of agriculture is immense, with 40% of the terrestrial surface currently in production (Foley *et al.* 2005). Agricultural conversion adversely affects biodiversity through the destruction and alteration of natural habitats such as forests and wetlands (Matson *et al.* 1997), although traditional farmland still maintains relatively large biotic assemblages (Benton *et al.* 2003). However, regions of extensive agriculture have

become increasingly inhospitable to biodiversity since the mid twentieth century, through a process referred to as agricultural intensification (Benton *et al.* 2003; Tilman 1999).

Agricultural intensification refers to changes in agricultural management practices to increase yields and farm profitability (Tilman 1999). Intensive practices are characterized by an increased per-area use of labour, capital, or technological inputs (Tilman 1999). Although intensification has allowed global food production to largely meet the energetic and nutritional needs of a large and expanding human population, these practices have had adverse ecological consequences at multiple spatial scales (Donald *et al.* 2001; Kremen *et al.* 2002; Matson *et al.* 1997).

The adverse ecological consequences of agricultural intensification are driven in part by alterations in material and energy flows that result from within-field management practices, such as an increased use of mechanization, irrigation, and chemical inputs such as fertilizers or biological control agents (Matson *et al.* 1997; McLaughlin and Mineau 1995). These practices degrade ecosystem function and adversely affect biodiversity through a variety of mechanisms, such as direct mortality (pesticides) and habitat destruction/alteration by soil compaction, nutrient depletion, and erosion (McLaughlin and Mineau 1995). The effect of these practices on biodiversity at local (farm field) scales has been shown through studies that compare the structure of biotic communities in organic versus intensive production systems. These studies generally show that organic fields support a higher abundance and/or richness of species for a variety of taxa (Hole *et al.* 2005). Within-field practices also adversely affect ecosystem processes and biodiversity at global and regional scales, through processes such as atmospheric pollution and wetland eutrophication (Matson *et al.* 1999; Tschamtkke *et al.* 2005).

Agricultural intensification has also affected biodiversity through changes in the pattern of land cover in agricultural areas (Tscharntke *et al.* 2005), which can affect the movement, distribution, and persistence of organisms in a landscape (Turner 2005). In intensive systems, managers often enlarge fields to maximize the area under production, at the expense of non-production cover such as hedgerows or field margins (Benton *et al.* 2003; Tscharntke *et al.* 2005). This trend has been driven in part by the development of larger farm machinery, as well as the consolidation of farm ownership (Benton *et al.* 2003; Fahrig *et al.* 2011). The removal of semi-natural cover features have caused agricultural regions to become increasingly devoid of potential habitat (Benton *et al.* 2003; Steffan-Dewenter *et al.* 2002). Remaining patches of natural habitat are smaller and increasingly isolated from each other (Tscharntke *et al.* 2005). Such patches are expected to contain fewer species as a result of decreased rates of immigration and increased probability of extinction (MacArthur and Wilson 1967). This prediction is supported by studies showing negative relationships between species diversity or abundance in natural habitat patches and the area of land under agricultural production in the surrounding landscape (Ockinger and Smith, 2006; Smith *et al.* 2010; Steffan-Dewenter *et al.* 2002).

While agricultural intensification drives the loss of habitat at the landscape scale, it has also affected landscape structure by reducing the heterogeneity of landscape features within agricultural landscapes (Benton *et al.* 2003; Fahrig *et al.* 2011). Spatial heterogeneity has long been recognized as a determinant of biotic patterns (Roth 1976). However only recently have ecologists considered the effects of heterogeneity in farmland at the landscape scale (Benton *et al.* 2003). Landscape heterogeneity can be

measured in terms of the composition and the configuration of cover (Figure 1; Benton *et al.* 2003; Fahrig *et al.* 2011). Compositional heterogeneity is usually measured by the richness and evenness of different cover types in the landscape, often combined into indices such as the Shannon Diversity index, while configurational heterogeneity can be measured in a number of ways, including the average size or density of patches in the landscape, or edge based metrics like average edge density or the Landscape Shape Index (McGarigal and Cushman 2002).

Landscapes of higher compositional heterogeneity contain higher resource diversity, and thus should harbour larger and more diverse species assemblages (Fahrig *et al.* 2011). Heterogeneity is also expected to favour species that require multiple habitat types, because as the evenness (compositional heterogeneity) or juxtaposition (configurational heterogeneity) of cover features increases, the accessibility to each required habitat will increase (Figure 2). This process is referred to as landscape complementation, and has been demonstrated empirically by Pope *et al.* (2002) who found that the density of northern leopard frogs (*Rana pipiens*) to be highest in breeding ponds that are situated in landscapes containing a mixture of breeding ponds and abundant summer foraging habitats. Configurational heterogeneity is also expected to facilitate landscape supplementation, which occurs when landscape structure facilitates the use of resource outside an organisms home habitat patch (Dunning *et al.* 1992). This allows smaller habitat patches that would otherwise have limiting resources to support larger and more diverse assemblages. For example, Morellet *et al.* (2011) found that roe deer (*Capreolus capreolus*) used hedgerow in agricultural landscapes only when their preferred woodland habitat was rare, a finding which suggests that *C. capreolus* uses

hedgerow as supplemental habitat. It is expected that in more configurational landscapes with greater juxtaposition of cover features, there would be greater access to supplemental habitats (Figure 2).

Agricultural intensification reduces the compositional heterogeneity of both the production and non-production components of agricultural landscapes (Fahrig *et al.* 2011). Heterogeneity of the cultivated area decreases through regional specialization of production systems and by farm consolidation, both of which decrease the diversity of crop or livestock types contained within the landscape (Matson *et al.* 1997; Fahrig *et al.* 2011). Compositional heterogeneity of the non-production portion of the landscape is reduced because as additional non-production cover is converted to agriculture, there are generally fewer types of semi-natural cover remaining in the landscape (Fahrig *et al.* 2011). Configurational heterogeneity has also been reduced by agricultural intensification through increased field sizes, farm consolidation, the loss of non-production cover, and the simplification of production systems (Fahrig *et al.* 2011; Tschardtke *et al.* 2005), such that agricultural landscapes are now generally composed of fewer, larger patches of cover.

Though many studies have looked at the effect of habitat availability in agricultural areas on biodiversity (Ockinger and Smith, 2006; Smith *et al.* 2010; Steffan-Dewenter *et al.* 2002), few have investigated whether landscape heterogeneity, measured independently from habitat amount, affects patterns of biodiversity in agricultural areas (Benton *et al.* 2003; Fahrig *et al.* 2011). Determining that heterogeneity *per se* is a strong determinant of biodiversity could benefit management efforts in that managers could support diverse farmland assemblages without sacrificing production area, by increasing

or maintaining spatial heterogeneity (Fahrig *et al.* 2011).

Pollinators are an essential component of biodiversity, as they facilitate the reproduction of the majority of wild plants, and permit the cultivation of many crops (Kearns *et al.* 1998). Bees are a particularly important group of pollinators, as they are abundant in most terrestrial ecosystems, and are efficient at pollination because they actively collect pollen (Kremen *et al.* 2002). The number of managed and wild *Apis mellifera* colonies has declined in both North America and Europe (De La Rua *et al.* 2009; Neumann and Carreck 2010), which could increase the relative importance of wild bees for pollination services (Winfree *et al.* 2007). However, there is also concern that populations of wild bee are declining due to anthropogenic stressors (Brown and Paxton 2009; Cane and Tepedino 2001), which could imperil global pollination services (Steffan-Dewenter *et al.* 2005; Kearns *et al.* 1998). While data regarding long-term bee population trends is lacking (Ghazoul 2005), some bee species have become extremely rare (Grixti *et al.* 2009; Williams and Osborne 2009). Concern over declines in bee populations and the pollination service they provide has driven research on the ecological determinants of bee diversity, particularly in agricultural settings. Measured bee diversity has been shown to respond to within-field management such as pesticide application (Plowright and Rodd 1980) or tillage (Shuler *et al.* 2005), proximity to semi-natural cover (Kim *et al.* 2006), floral resource availability at local (Hopwood 2002) and landscape scales (Hines and Hendrix 2005), and the amount of semi-natural habitat in surrounding landscapes (Steffan-Dewenter *et al.* 2002). However, no studies to date have looked at the effects of heterogeneity *per se* on bee diversity on farmland. Compositional heterogeneity could be an important determinant of bee diversity in farmland, as different species require

different floral and nesting resources. Complementarity could also drive patterns of bee diversity, as the floral and nesting resources bees require often occur independently in space (Gathmann and Tscharntke 2002). Configurational heterogeneity could also increase bee diversity by facilitating supplementation, as bees could better access supplemental resources in landscapes with higher juxtaposition of cover features.

My objective was to determine whether landscape heterogeneity, measured independently of the amount of habitat in the landscape, affects the structure of a temperate North American wild bee assemblage. I measured the relative abundance and richness of bees in a set of landscapes selected such that levels of compositional heterogeneity and configurational heterogeneity were not correlated across the sampled landscapes. The study aimed to test the predictions that both bee abundance and richness will be positively correlated with both compositional and configurational heterogeneity, and to determine the relative effects of these landscape predictor variables on bee richness and abundance.

Methods

Overview

I used a focal site design (Brennan *et al.* 2002) to study the effects of landscape heterogeneity and habitat amount on the richness and abundance of wild bees at 40 vegetated roadside sites across a rural area of eastern Ontario (Figure 3). I measured heterogeneity in terms of both the composition and the configuration of the landscapes surrounding the roadside sites. As a measure of compositional heterogeneity, I used Shannon's Diversity Index (SDI) which measures the number and proportional evenness of different cover types within the landscapes. I used the density of patches, i.e. number of patches per unit area, in the landscapes (patch density; PD) as a measure of configurational heterogeneity. I also calculated the proportion of semi-natural land cover classes as an estimate of the amount of bee habitat in the landscapes. I analyzed the effect of each landscape predictor variable at each of eight spatial scales, to determine the scale at which landscape structure most strongly affects wild bees. I then used AIC-based multi-model selection to determine which landscape predictors best describe the observed patterns in bee abundance and richness in the sampled landscapes.

Study region & site selection

The eastern Ontario study region features large, contiguous areas of relatively intensive agriculture interspersed by urban communities and remnant forest patches (Figure 3). Agriculture in the area primarily consists of annual row crop production, as well as large dairy operations supported by hayfields and pastures. The extent of the study region was defined by a 2008 version of the Southern Ontario Land Resource

Information System (SOLRIS) land classification for eastern Ontario. The original data set was modified to differentiate a conglomerate agricultural class into four component classes that included corn, soybean, cereal crops, and a layer consisting of all grass-based cover, corresponding to hayfields and pasture (Pasher *et al.* in review). I collapsed the 19 classes of the data set into 10 cover classes: forest, urban, open water, wetland, hedgerow, field margins, 'grassland ' (including fallow, hay, and pasture), corn (*Z. mays*), soybean (*G. Max*), and 'cereals' (including wheat [*Triticum* sp.], barley [*Hordeum vulgare*], and oat [*Avena sativa*]).

I used roadsides as focal sites for bee sampling, as they are relatively homogeneous in habitat structure, and have been described as potentially important bee habitat in human modified environments (Shepherd *et al.* 2003; Hopwood 2008). I used ArcGIS 9.3 (ESRI 2006) to select focal sites from a large group (>12 000) of randomly generated candidate roadsides in the study region. I first removed sites that were situated in primarily forested or urban areas, leaving approximately 9000 candidate sites. Landscape context (amount of each cover type, Shannon's Diversity Index of land cover, patch density) was then calculated for each candidate site, at four spatial scales, of radii 500m, 1000m, 1500m, and 2000m around each focal site, using Fragstats 3.3 (McGarigal and Cushman 2002). This range of scales is broadly similar to that used in other landscape-scale studies on wild bee diversity (Steffan-Dewenter *et al.* 2002), and contains the estimated maximum foraging distance of many solitary wild bees (<1000m: Gathmann and Tscharrntke 2002), a trait that can determine the scale at which an organism responds to landscape structure (Holland *et al.* 2005). To ensure all sites were in an agricultural context, I retained only candidate sites with at least 70% agriculture - corn, soybean,

cereal crops, and 'grasslands' (alfalfa, hay and pasture) - at each of the four scales. This reduced the number of candidate sites to 5740. The amount of bee habitat in each landscape was measured as the proportion of the landscape area composed of semi-natural cover that potentially contained resources for bee nesting and foraging, an approach that is similar to previous landscape-scale research on the effects of semi-natural cover on bee diversity (Steffan-Dewenter *et al.* 2002). I included hedgerows, other field boundaries, grassland (including hay, alfalfa, and pasture), and forest edge to a depth of 10m as semi-natural cover types. Since the main objective of this study was to determine effects of landscape heterogeneity (rather than habitat amount) on bee abundance and diversity, I attempted to limit the variation in bee habitat amount across sample sites by removing candidate sites with either extremely low ($< 15\%$) or high ($> 60\%$) amounts of bee habitat. This further reduced the number of candidate sites to 3240 sites.

Across randomly selected landscapes, compositional and configurational heterogeneity tend to be positively correlated. Therefore, to examine the effects of each aspect of landscape heterogeneity independently, I used a mensurative experimental approach to limit the correlation between SDI and PD across the sampled landscapes. I did this by first grouping candidate sites into four possible combinations of compositional and configurational heterogeneity (Figure 2). Then, I selected an equal number of sites from each quadrant, which limited the correlation between the two heterogeneity variables across sites. I further limited the selection of sites to those whose landscapes were spatially non-overlapping at the largest scale (2000m radius). This limited the set of potential sites to 265. Finally, I selected 40 non-overlapping sample sites ($> 4000\text{m}$ apart;

Figure 3) after visual field inspections during April 2010, to ensure sites were as similar as possible and were suitable as potential bee habitat (i.e., non-treed, mostly unmown).

Spatial data verification and recalculation of landscape predictor variables

The initial site selection was conducted using the best spatial data available before the field sampling season (summer 2010). However, the actual makeup of each of the 40 landscapes during the field season 2010 differed somewhat from the pre-sampling information due to crop rotation, other changes in land use, and some misclassifications in the remote land classification process. In addition, the "grassland" category in the remotely-sensed data included three qualitatively different (from a bee's perspective) component classes (hay, pasture, and alfalfa) that the remotely-sensed data were not able to differentiate. Therefore, during the field season I updated the descriptions of each of the 40 selected landscapes and included these three classes. This resulted in a 13-class land classification data set of each landscape in the study. Using these revised maps, I then recalculated each of the three landscape predictor variables (bee habitat amount, SDI, PD) at each of eight spatial scales, of radii 250m, 500m, 750m, 1000m, 1250m, 1500m, 1750m, and 2000m.

Bee surveys

I sampled bees at each of the 40 sites six times between May 12th and August 13th, 2010. Multiple site visits were conducted to increase the number of bees collected, and to minimize the effect of phenological changes in the bee fauna, or different environmental conditions within a given round of site visits. To randomize the order that I visited each site, I first categorized the compositional and configurational heterogeneity of each site as low or high, and then I subdivided the 40 sites into 10 groups, such that each group

contained one example landscape from each of the four possible combinations of compositional and configurational heterogeneity (Figure 2). Then I randomized the order in which I visited each group during each round of sampling.

I used pan-traps to sample bees. Pan-traps are coloured containers that act as decoy flowers that attract bees, which are then killed by liquid contained in the traps. They have been found to be an effective method to sample bee richness, and lacks collector bias (Wesphal *et al.* 2008). The pan-traps I deployed were 355 mL brightly-coloured non-UV reflectant plastic bowls filled with a soap (Blue Dawn dishwashing detergent) and water solution. The soap acts as a surfactant, such that small insects that would float in water due to surface tension actually sink.

I deployed the pan traps in a zigzag pattern along a 30m transect, the midpoint of which was the GPS location of the focal site (Figure 4). Equal numbers of blue, white, and yellow pan traps were deployed, to attract a wide variety of bees. I deployed 15 pan-traps during the first four rounds of sampling, and then deployed 30 traps during the two final rounds. Pan-traps were set out between 8:00 and 13:00 and were left in the field for 24 hours.

I also conducted a vegetation survey of each focal roadside site per sampling round, to assess local floral resource availability (Hines and Hendrix 2005; Hopwood 2008). The survey entailed counting and identifying the insect-pollinated plants contained within a 1m² quadrat, thrown randomly fifteen times along the 30m transect. Data from the entire sampling period was summarized into two measures of resource availability at each site: floral abundance (number of flowering ramets per visit) and floral richness (total number of flowering plant species observed at site). I primarily used Newcomb's Wildflower

Guide (Newcomb 1977) and Plants of the Kingston Region 1996 (Crowder *et al.* 1996), as resources in the identification of flowering plants.

As traffic can negatively affect animal populations adjacent to roads, and can be correlated with patterns of land use (Forman and Alexander 1998), I estimated traffic intensity at each site. Using a digital audio recorder (Toshiba DMR-850W Digital Voice Recorder), I recorded the sound of passing traffic during a 15 minute recording period twelve times at each roadside focal site throughout the sampling season (Figure 4). I then used digital audio software (NCH Software, WavePad Sound Editor v 4.59) to count the number of vehicle passes on each recording. I defined the traffic intensity at each site as the average number of vehicle passes across the twelve sampling events.

Identification of bee specimens and calculation of response variables

Specimens were first washed and then dried to remove any nectar and pollen that could impede identification. All specimens were identified to genus using a key specific to the bee fauna of eastern Canada (Packer *et al.* 2007). For identification to species I used a combination of published taxonomic keys and the online identification resource *discoverlife.org* to differentiate the sampled bees into 'morphotypes,' representing the finest unambiguous taxonomic resolution possible (Appendix B). Groups not identified to species included members of the genera *Nomada*, *Hylaeus*, *Sphecodes*, and the *Lasioglossum* subgenera *Dialictus* and *Evyulaeus*. Members of *Dialictus* were subdivided into 15 morphotypes using 10 morphological characters that were selected from previous *Lasioglossum* keys (Supplemental Information).

I used the total number of bee specimens caught at each site as a measure of relative bee abundance. I estimated species richness as the total number of morphotypes

observed at each site. *Apis mellifera* were disregarded in the analyses as their abundance is confounded by the existence of commercial colonies. Also excluded from the analysis were members of *Bombus*, because they are not as consistently sampled in pan-traps (Cane *et al.* 2000; Roulston *et al.* 2007) as other wild bees.

Statistical Analyses

To identify the spatial scale of strongest effect of the landscape variables on bee abundance and diversity, I conducted a simple regression of each response (richness and abundance) on each landscape predictor variable (HA, SDI, and PD) for each of the eight spatial scales. I considered the scale of maximum effect as the scale at which the R^2 was largest. Each response was also regressed on each of the three local variables (Floral Abundance, Floral Richness, Traffic Intensity) to determine whether these variables significantly correlated with either response variable, to decide whether they should be included in the multi-model selection procedure.

To determine the effects of the landscape variables on the bee responses I used Akaike's Information Criterion (AIC) in a multi-model selection procedure. This method defines the best model as that with the lowest AIC score. However, this model is considered the unambiguous best model only if the score of any of the other models does not come within 2 AIC values of the lowest AIC score (Mazerolle 2006). Using AIC weights, the average standardized regression coefficients weighted across models were calculated, which were used to infer the relative importance of each landscape predictor in influencing each bee response variable.

Results

I caught a total of 1334 bee specimens, which I differentiated into 89 morphotypes of 20 genera (Appendix A). I identified 69.4% (n=921) of collected specimens to species, while the remaining specimens were characterized to morphotype, of which 71% (n=293) were members of the *Lasioglossum* subgenus *Dialictus*. Approximately 69% of the collection was composed of members of either Halictidae or Andrenidae (Appendix A). On average, I caught 0.3 bees per bowl per 24 hour deployment period, with 33.3 +/- 9.9 individuals of 16.2 +/- 3.6 morphotypes collected at each site. There was a positive correlation between bee abundance and richness across sites ($r=0.77$, $p<0.01$).

Landscape structure correlated with patterns of bee diversity most strongly at scales ranging from 500m to 1000m (Figures 6 & 7). The scale of maximum effect of each predictor variable was the same for richness and abundance: habitat amount at 750 m, Shannon's Diversity Index at 500 m, and patch density at 1000 m. The relationship between bee richness and each landscape predictor is depicted in Figures 8, 9, and, 10, while the relationship between bee abundance and each landscape predictor is depicted in Figures 11, 12, and, 13.

There were no significant relationships between the relative abundance or richness of bees and any of the local variables: flower abundance, flower richness, or traffic intensity (Table 1). There also were no strong correlations between the local variables and the landscape predictor variables (all $r<0.33$; Figure 5). Therefore, the local variables were not included in the multi-model selection procedure (below).

The model containing habitat amount as the sole landscape predictor was the best

model of bee morphotype richness; this model had the lowest AIC value, no other model had an AIC value within 2 AIC units of this model, and the average standardized regression coefficient weighted across models for habitat amount was 25-50 times the magnitude of those for the other two landscape predictors (Table 2). To test whether the over-riding effect of habitat amount on bee morphotype richness was influenced by the fact that not all bees were identified to species, I repeated the model selection process on bee richness where only specimens identified to species were included. Habitat amount remained the dominant landscape predictor (Table 3).

For bee abundance, five of the seven candidate models had an AIC score with 2 AIC values of the best model, meaning that these top five models were indistinguishable in their ability to describe the pattern of abundance (Table 4). Based on the average standardized regression coefficients, habitat amount appears to have a slightly stronger effect than the two heterogeneity predictor variables, SDI and/or PD. However, each of the top models contained at least one of the two heterogeneity predictor variables, lending support to the hypothesis that landscape heterogeneity affects bee abundance (Table 4). Note that adding patch density to a model already containing habitat amount increased the model R^2 by approximately 38% (from 0.21 to 0.29), while adding Shannon's diversity index to a model already containing habitat amount increased the model R^2 by 24% (from 0.21 to 0.26), suggesting that the effect of landscape heterogeneity on bee abundance may be due mainly to configurational rather than compositional heterogeneity (Table 4).

If all bees positively respond to heterogeneity, than in more heterogeneous landscapes, there would be higher bee richness and abundance. However, I found that

heterogeneity was related to bee abundance, but not richness. This suggests that heterogeneity might have a positive effect on some bee species, but not others. Since certain species dominated the collection, I wanted to test the prediction that the more common species might be more positively affected by heterogeneity. I partitioned the species-only data set (morphospecies excluded) into common and rare species, such that each group represented as close to 50% of the collection as possible. The four most common species, *Andrena nasonii*, *Augochlorella aurata*, *Halictus confusus*, and *Ceratina dupla*, made up 53% of the total collection (Figure 14). I therefore conducted the model selection process for abundance of these four species and the remaining species in two separate analyses. An effect of heterogeneity on abundance of the common species but not the rarer species would support my *post hoc* hypothesis. A model containing only habitat amount was the best model predicting abundance of the rarer bees (Table 5), while for the common species the top 5 models were indistinguishable (Table 6). The fact that patch density was in the top two models supports our tentative conclusion (above) that the abundance of the common bee species is related to configurational heterogeneity. In fact, for these common bee species the model average standardized regression coefficient weighted by AIC weight was larger for patch density than for habitat amount (Table 6), suggesting a stronger effect of configurational heterogeneity than bee habitat availability on the abundance of the common species.

In a second *post hoc* analysis I tested for an expected cross-species relationship between bee dispersal ability and the scale of effect of the landscape. Dispersal ability (as inferred by body size) has previously been shown to be a determinant of the scale at which dead wood boring beetles respond to the landscape (Holland *et al.* 2005), and it

has been suggested as a reason for why *Apis* and non-*Apis* bees respond to landscape structure at different scales (Steffan-Dewenter *et al.* 2002). To test for the dispersal ability vs. scale of effect relationship, I calculated the scale of effect of habitat amount for the 15 most abundant species, using logistic regression of presence/absence data for species present at less than 90% of sites, and linear regression of relative abundance for species present at more than 90% sites. I then regressed the scale of effect on the maximum body length of the species. There was no relationship between the scale of effect and body length (Figure 15).

Discussion

Landscape predictors of bee richness

I found that bee morphotype richness was greater in landscapes containing more bee habitat. This finding supports previous research that suggests the amount of bee habitat in the landscape is a determinant of bee richness in agricultural systems (Brosi *et al.* 2007; Hines and Hendrix 2005; Steffan-Dewenter *et al.* 2002), and is consistent with the finding that the amount of habitat within a landscape generally has a positive effect on biodiversity (Fahrig 2003). The support for habitat amount as a landscape predictor of bee richness suggests that bees are affected by the relative size and isolation of habitat patches in these landscapes. As habitat patches become increasingly isolated, there is likely a decreased chance that bees can successfully disperse among habitat patches, and smaller patches are expected to have higher extinction rates (MacArthur and Wilson 1967). Thus, bee richness may have been lower in landscapes containing low amounts of habitat because patches with increased extinction probability and reduced immigration are expected to support fewer species. The effect of habitat amount also could have been driven through greater availability of floral resources in landscapes with more semi-natural cover, as weed species diversity (Roschewitz *et al.* 2005) and floral cover (Holzshuh *et al.* 2007) in farmland have been shown to be lower in landscapes with more cultivated land and less semi-natural cover.

Contrary to my predictions, landscape heterogeneity was not an important predictor of bee richness. Higher compositional heterogeneity should increase bee diversity by providing different habitat types required by different species and/or by providing multiple habitat types required by one species (landscape complementation).

The fact that compositional heterogeneity was not strongly related to bee diversity suggests that in this region different bee species generally use the same range of habitats, and that bees can attain their required resources without having to travel between patches of different habitats. It is also possible that landscape heterogeneity does affect patterns of bee diversity, but is relatively less important than habitat availability. As there was a large range in habitat amount across my sampled landscapes, perhaps an effect of heterogeneity was not detected because it was swamped by the large effect of habitat amount.

Landscape predictors of relative bee abundance

Relative bee abundance, as measured by the number of individual bees passively sampled at each site, increased in response to the amount of habitat within the sampled landscape. This finding supports the density-area relationship (Flather and Beavers 2002; Matter 2000), and also confirms previous studies that have found bee abundance responds positively to the amount of semi-natural cover in agricultural landscapes (Kremen 2004; Hines and Hendrix 2005; Steffan-Dewenter *et al.* 2002).

Relative bee abundance also increased in response to landscape heterogeneity. In a *post hoc* analysis, I determined that the effect of heterogeneity on bee abundance was driven by an increased abundance of the four most common species (*Andrena nasonii*, *Augochlorella aurata*, *Ceratina dupla*, and *Halictus confusus*), in landscapes of high configurational heterogeneity. In fact, configurational heterogeneity was a stronger determinant of abundance of these common species than was habitat amount. This is an interesting finding, as compositional metrics generally exert a stronger effect than configurational metrics on ecological responses (Fahrig and Nuttle 2005; Flather and

Beavers 2002).

The effect of configurational heterogeneity on the abundance of the four common species may have been driven through an increased availability of marginal linear habitats in landscapes of high configurationally heterogeneity. Floral resources from invasive plant species that often dominate edge habitat like field margins and roadsides (72% of flower species encountered at roadsides were non-native; Appendix B), which occur at higher density in landscapes composed of more patches. As these four species are generalist pollinators (Mitchell 1960; 1962), they likely could use the resources provided by non-native flower species, while perhaps the rarer species are more specialized in their floral associations and thus do not benefit from an increased availability of the resources provided by non-native plants.

The scale of effect of landscape structure

Bee diversity was most strongly related to landscape structure within 500m to 1000m surrounding the focal roadside sites. This supports previous research (Hines and Hendrix 2005; Kleijn and Langevelde 2006; Steffan-Dewenter *et al.* 2002; Taki *et al.* 2007). In addition, these scales coincide with estimated foraging ranges of many wild bees (Gathmann and Tscharntke, 2002), a trait which is often thought to determine the scale of effect of the landscape (Holland *et al.* 2004). It is important to note, however, that this scale is likely representative of an average operating range of the entire assemblage, which itself is comprised of a large number of species of various sizes and dispersal abilities, such that some species likely respond to landscape structure at a scale larger than 1000m.

Contrary to previous research (Holland *et al.* 2005; Steffan-Dewenter *et al.* 2002),

I found no evidence of a relationship between estimated dispersal ability (as inferred from body size) and the scale at which a bee species responds to landscape structure. However, since the relationship between habitat amount and either the abundance or presence/absence of each species was statistically significant for only 4 out of 16 species, the overall strength of this analysis is likely limited.

Local determinants of bee diversity

There was no relationship between the abundance or richness of floral resources in the focal roadside and either measure of bee diversity. However, as the encountered flower species were predominately non-native (Appendix B), this finding may confirm the results of Hopwood (2008) who found that species richness of bees along roadsides was significantly correlated with floral richness only in sites that were restored with native wildflowers, and not in unaltered roadside sites with predominately non-native 'weedy' flowering species. Alternatively, floral resource availability may be a determinant of bee diversity in this system only at a larger scale than the 50m linear transect at which floral resources were quantified in this study.

Similar to previous research (Hopwood 2008), roadside bee abundance and diversity was found to be unrelated to local traffic intensity. This suggests that mortality or disturbance due to traffic is may not be an important factor affecting bee populations in roadside habitats.

Overall, bee diversity was unresponsive to environmental conditions at scales smaller than 250 m. Neither landscape structure at 250m nor local floral resource availability nor traffic intensity was a significant predictor of bee richness or abundance. Perhaps bee diversity is affected by local factors other than floral resources that I did not

measure, such as management practices (Holzschuh *et al.* 2007) or nest site availability (Steffan-Dewenter and Schiele 2008). Alternatively, floral resource availability at scales larger than the 30m linear roadside transect may be important in the determination of the structure of a bee assemblage in roadsides.

Study limitations

The effect of landscape structure on bee diversity may have been driven in-part through possible colinearity between the landscape predictor variables and relative management intensity across sites. However, as I was unable to quantify the relative impact of management practices within my sampled landscapes, the degree to which these two factors are correlated is unknown. As the amount of semi-natural habitat was negatively correlated with the area of row crops across the sampled landscapes ($r=0.74$, $p<0.01$), it is possible that landscapes with less habitat may have had greater levels of chemical inputs such as fertilizers and pesticides, which can adversely affect wild bees directly through lethal and sub-lethal effects and indirectly through decreased floral resource availability (Batra 1982; Richards 2001). The amount of cultivated land likely also adversely affects bees through increased tillage, which is detrimental to ground nesting species (Roulston and Goodell 2011). Ground nesting species comprised a large proportion of my entire collection, as approximately 69% of the collection was comprised of members of the families Andrenidae and Halictidae, which consist entirely and predominately of ground nesting species, respectively (Michener 2000).

I used a morphotype approach in the identification of some of my specimens. This method seems to have adequately represented local bee diversity, as I identified relatively strong relationships between patterns of bee diversity and landscape structure. In a *post*

hoc analysis, I found stronger relationships between richness and abundance when 'morphotypes' of a lower taxonomic resolution than species were included in the analysis. However, by using a morphotype approach, I overlooked some diversity, particularly within the *Lasioglossum* subgenus *Dialictus*. By underestimating diversity at some sites, I may have detected weaker relationships between bee richness and landscape structure than what actually exists in these landscapes.

Future research

Similar to previous research (Steffan-Dewenter *et al.* 2002), I measured all cover types considered as potential habitat to have an equal contribution to the total availability of habitat in the landscape. Future research should be conducted to create empirically based habitat selection models for the distribution of particular bee species, and should attempt to determine the relative importance of different habitat types. This approach could also identify the specific cover types that are used by different species of bees that vary in ecological characters such as nesting behaviour, sociality, or floral specificity. For example, I would predict that forest edge, hedgerow and other habitats containing woody growth would be more important to bees that nest in stems (ex. *Ceratina* sp.) than those that nest in the ground (ex. *Andrena* sp.).

Habitat models rely on two dimensional land classification data sets to approximate the distribution of complex multidimensional ecosystems (Guisan and Thiller 2005). These models overlook variation in environmental conditions such as resource availability or the distribution of predators that can be important determinants of species distributions. Perhaps the availability of floral and nesting resources in the

landscape could be incorporated into cover-based habitat models to better explain patterns of bee diversity in farmland. Such an approach was used by Hines and Hendrix (2005), who determined that bumble bee richness was better explained by the landscape resource index (a measure of the relative amount of floral resources in the landscape) than by the total area of grassland in the landscape.

Implications to bee management

My research suggests that, in order to maintain a large and diverse bee assemblage at a target site (such as an orchard requiring pollination services) land managers such as farmers need to maintain open semi-natural habitat within the surrounding landscape at a scale of approximately 750 to 1000m from that site. However, in order to target all bee species, such efforts may need to target the landscape beyond 1000m, as *Apis mellifera* and members of *Bombus* (which were not included in this study) have been shown to respond to landscape structure at larger spatial scales (Steffan-Dewenter *et al.* 2002).

The results of this study suggest that bees, particularly common generalist species, could be more abundant in areas of high configurational heterogeneity composed of more and smaller patches. As decreased configurational heterogeneity could depress the local abundance of these common species, farmers that are attempting to maintain pollination services may want to limit the sizes of fields in their agricultural landscapes.

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Tables

Table 1. Summary of simple regressions of (A) bee morphotype richness and (B) relative bee abundance on local variables.

(A) Richness					
Predictor Variable	Scale	R²	β	F	<i>p</i>
Floral Abundance	L	0.02	-0.13	0.63	0.43
Floral Richness	L	0.01	0.08	0.22	0.64
Traffic Intensity	L	0.01	-0.07	0.18	0.67
(B) Abundance					
Floral Abundance	L	0.02	-0.16	0.95	0.34
Floral Richness	L	0	0	0	0.99
Traffic Intensity	L	0	-0.04	-0.06	0.81

Table 2. Multi-model selection procedure for the effects of the three landscape variables (HA, habitat amount; PD, patch density; SDI, Shannon's Diversity Index) on bee morphotype richness.

The 7 possible models are ranked in order of increasing ΔAIC . β : standardized regression coefficients. $\hat{\beta}$: average standardized regression coefficient weighted by the relative AIC weight of each model. (*) denotes significance at $p < 0.05$.

Rank	Predictor Variable(s)	β HA	β SDI	β PD	R^2	P	ΔAIC	AIC Weight
1	HA	0.55	-	-	0.31	<0.01*	0	0.56
2	HA, PD	0.54	-	0.06	0.31	<0.01*	2.1	0.19
3	HA, SDI	0.52	0.06	-	0.31	<0.01*	2.2	0.18
4	HA, PD, SDI	0.52	0.04	0.05	0.31	<0.01*	4.6	0.06
5	SDI	-	0.38	-	0.13	0.02*	8.8	0.01
6	PD, SDI	-	0.340	0.07	0.14	0.06	11	0.01
7	PD	-	-	0.20	0.04	0.22	13	0.01
$\hat{\beta}$		0.54	0.02	0.01				

Table 3. The seven models for each possible combination of landscape predictor variables, in relation to bee species richness (morphotypes excluded). The 7 possible models are ranked in order of increasing ΔAIC . β : standardized regression coefficients of each model variable.

$\hat{\beta}$: average standardized regression coefficient weighted by the relative AIC weight of each model. (*) denotes significant at $p < 0.05$.

Rank	Predictor Variable(s)	β HA	β SDI	β PD	R^2	P	ΔAIC	AIC Weight
1	HA	0.52	-	-	0.27	<0.01*	0	0.56
2	HA, SDI	0.48	0.06	-	0.24	<0.01*	2.2	0.19
3	HA, PD	0.52	-	<0.01	0.27	<0.01*	2.3	0.17
4	HA, SDI, PD	0.49	0.07	- 0.01	0.28	<0.01*	4.7	0.05
5	SDI	-	0.35	-	0.13	0.02*	7.4	0.01
6	SDI, PD	-	0.35	0.01	0.13	0.06	9.8	<0.01
7	PD	-	-	0.14	0.02	0.22	12	<0.01
$\hat{\beta}$		0.50	0.02	0.00				

Table 4. The seven models for each possible combination of landscape predictor variables, in relation to relative bee abundance. The 7 possible models are ranked in order of increasing

ΔAIC . β : standardized regression coefficients of each model variable. $\hat{\beta}$: average standardized regression coefficient weighted by the relative AIC weight of each model. (*) denotes significant at $p < 0.05$.

Rank	Predictor Variable(s)	β HA	β SDI	β PD	R^2	p	ΔAIC	AIC Weight
1	HA, PD	0.38	-	0.29	0.29	<0.01*	0	0.28
2	HA, PD, SDI	0.27	0.21	0.24	0.32	<0.01*	0.94	0.18
3	PD, SDI	-	0.36	0.26	0.27	<0.01*	1.2	0.16
4	HA, SDI	0.28	0.29	-	0.26	<0.01*	1.4	0.14
5	SDI	-	0.46	-	0.21	<0.01*	1.9	0.11
6	HA	0.46	-	-	0.21	<0.01*	2.0	0.10
7	PD	-	-	0.39	0.15	0.01*	4.8	0.03
$\hat{\beta}$		0.24	0.19	0.18				

Table 5. The seven models for each possible combination of landscape predictor variables, in relation to relative abundance of the rare bee species. The 7 possible models are ranked in order of increasing ΔAIC . β : standardized regression coefficients of each model variable. $\hat{\beta}$: average standardized regression coefficient weighted by the relative AIC weight of each model. (*) denotes significant at $p < 0.05$.

Rank	Predictor Variable(s)	β HA	β SDI	β PD	R^2	p	ΔAIC	AIC Weight
1	HA	0.45	-	-	0.21	< 0.01*	0	0.55
2	HA, PD	0.46	-	0.01	0.21	0.01*	2.3	0.17
3	HA, SDI	0.46	-0.07	-	0.21	0.01*	2.3	0.17
4	HA, PD, SDI	0.46	0.01	-0.23	0.21	0.04*	4.8	0.05
5	SDI	-	0.31	-	0.09	0.06	5.3	0.04
6	PD, SDI	-	0.34	-0.07	0.09	0.01	7.5	0.01
7	PD	-	-	0.09	0.01	0.58	8.9	0.01
$\hat{\beta}$		0.43	0.01	0.01				

Table 6. The seven models for each possible combination of landscape predictor variables, in relation to relative abundance of the common bee species. The 7 possible models are ranked in order of increasing ΔAIC . β : standardized regression coefficients of each model variable. $\hat{\beta}$: average standardized regression coefficient weighted by the relative AIC weight of each model. (*) denotes significant at $p < 0.05$.

Rank	Predictor Variable(s)	β HA	β SDI	β PD	R^2	p	ΔAIC	AIC Weight
1	HA, PD	0.25	-	0.28	0.18	0.03*	0	0.22
2	PD	-	-	0.35	0.12	0.03*	0.25	0.19
3	SDI	-	0.35	-	0.12	0.03*	0.41	0.18
4	PD, SDI	-	0.23	0.24	0.16	0.04*	0.80	0.15
5	HA	0.33	-	-	0.11	0.04*	0.95	0.14
6	HA, SDI	0.15	0.23	-	0.13	0.08	2.3	0.07
7	HA, SDI, PD	0.21	0.52	0.26	0.18	0.07	2.4	0.06
$\hat{\beta}$		0.12	0.14	0.18				

Figures

Figure 1: Sample landscapes showing independent variation in compositional (Shannon's Diversity Index) and configurational (Patch Density) landscape heterogeneity. (a) high compositional heterogeneity, low configurational heterogeneity; (b) high compositional heterogeneity, high configurational heterogeneity; (c) low compositional heterogeneity, low configurational heterogeneity; (d) low compositional heterogeneity, high configurational heterogeneity.

Figure 2. Levels of complementation and supplementation depend on landscape structure. The left hand side of the figure depicts that for species that require two habitat types, complementation (A) is low when compositional evenness and configurational heterogeneity are low, but increases as (B) the relative evenness of the two required habitat types increases or (C) the juxtaposition of cover features increases. The right hand side of the figure depicts that supplementary habitats that can support species residing in small focal habitats (*f*) are expected to be more evenly distributed and hence more accessible when (E) configurational heterogeneity is high, than when low (D).

Figure 3. Locations of 40 sampled landscapes in eastern Ontario, Canada. Black areas are urban development, while grey and white areas are forest and agriculture, respectively. Each landscape is depicted as the area surrounding each focal roadside bee sample site (●) within a 2 km radius, the largest of eight analyzed spatial scales. Landscapes are shown as categorized into four classes based on levels of compositional and configurational heterogeneity, although these were analyzed as continuous variables.

Figure 4. Sampling design at each focal roadside, showing the GPS location of the site (▲) as the midpoint of a 30m transect running parallel to the road. Roadside width varied, so average roadside width is shown. Pan traps (⊙) were set along the transect at approximately regular intervals in a zigzag pattern while alternating the bowl colour (blue, white, yellow). A digital audio recorder (★) placed near the transect midpoint was used to record vehicle passes to estimate traffic intensity at each site.

Figure 5. Correlations matrix depicting relationship between response variables (AB = relative bee abundance, RI = relative bee richness), landscape predictor variables (HA = habitat amount, PD = patch density, SDI = Shannon's Diversity Index), and local variables (TRA = log traffic intensity, FR = floral resource richness, FA = floral resource abundance). Landscape predictor variables are measured at the scale of maximum response with each response (see Figures 5 and 6). The upper right half of the figure gives the Pearson's correlation coefficients while the lower half shows the corresponding bivariate plots.

Figure 6. . Scatter plot of R^2 from simple linear regressions of bee richness on each landscape predictor variable at multiple spatial extents (nested circular areas surrounding the focal roadside bee sample sites). HA = Habitat Amount; SDI = Shannon's Diversity Index; PD = Patch Density.

Figure 7. Scatter plot of R^2 from simple linear regressions of bee abundance on each landscape predictor variable at multiple spatial extents (nested circular areas surrounding the focal roadside). HA = Habitat Amount; SDI = Shannon's Diversity Index; PD = Patch Density

Figure 8. Relationship between habitat amount, as measured by the proportion of the landscape composed of semi-natural cover types (see text for definition), within a radius of 750m from the focal site, and bee morphotype richness across 40 sampled landscapes.

Figure 9. Relationship between compositional heterogeneity, as measured by the Shannon's Diversity Index of land cover classes, within a radius of 500m from the focal site, and bee morphotype richness across 40 sampled landscapes.

Figure 10. Relationship between configurational heterogeneity, as measured by the density of patches within the landscape within a 1000m radius of the focal roadside sites, and bee morphotype richness across 40 sampled sites.

Figure 11. Relationship between habitat amount, as measured by the proportion of the landscape composed of semi-natural cover types (see text for definition), within a radius of 750m from the focal site, and relative bee abundance across 40 sampled landscapes.

Figure 12. Relationship between compositional heterogeneity, as measured by the Shannon's Diversity Index of land cover classes, within a radius of 500m from the focal site, and relative bee abundance across 40 sampled landscapes.

Figure 13. Relationship between configurational heterogeneity, as measured by the density of patches within the landscape within a 1000m radius of the focal roadside sites, and relative bee abundance across 40 sampled sites.

Figure 14. Number of individuals caught of each specimen type identified to species.

Figure 15. Scatter plot of the relationship between body length and the scale of maximum effect of the landscape for the 15 most abundant bee species. The scale of maximum effect was determined using either occurrence data (◆; 12 species), or abundance data (+ ; 3 species). (○) signifies a significant ($p < 0.05$) relationship between and the scale of maximum effect.

Appendices

Appendix A. Summary of the bee collection. This table depicts the relative number of specimens and recorded morphospecies of each collected genus, as well as the primary taxonomic resources used in identification.

Family	Genus (subgenus)	#Specimens	#Morphotypes	Taxonomic Resolution	Primary Resource
Apidae	<i>Ceratina</i>	186	2	species	Mitchell 1962; Rehan and Richards 2008
	<i>Melissodes</i>	7	5	species	<i>discoverlife.org</i>
	<i>Peponapis</i>	3	1	species	Packer <i>et al.</i> 2007
	<i>Nomada</i>	25	1	genus	Packer <i>et al.</i> 2007
	<i>Epiolus</i>	1	1	genus	Packer <i>et al.</i> 2007
Halictidae	<i>Agapostemon</i>	9	3	species	<i>discoverlife.org</i>
	<i>Augochlorella</i>	120	1	species	Packer <i>et al.</i> 2007
	<i>Augochlora</i>	2	1	species	Packer <i>et al.</i> 2007
	<i>Augochloropsis</i>	1	1	species	Packer <i>et al.</i> 2007
	<i>Halictus</i>	113	4	species	Mitchell 1960
	<i>Lasioglossum</i> (<i>Dialictus</i>)	299	14	morphospecies	Mitchell 1960
	<i>Lasioglossum</i> (<i>sensu stricto</i>)	86	4	species	<i>discoverlife.org</i>
	<i>Lasioglossum</i> (<i>Evylaeus</i>)	8	1	subgenus	<i>discoverlife.org</i>
	<i>Specodes</i>	16	1	genus	Packer <i>et al.</i> 2007
Andrenidae	<i>Andrena</i>	300	26	species	<i>discoverlife.org</i>
	<i>Calliopsis</i>	3	1	species	Packer <i>et al.</i> 2007
Megachilidae	<i>Chelostoma</i>	10	2	species	<i>discoverlife.org</i>
	<i>Coleoxys</i>	1	1	species	<i>discoverlife.org</i>
	<i>Hoplitis</i>	39	4	species	<i>discoverlife.org</i>
	<i>Megachile</i>	17	9	species	<i>discoverlife.org</i>
	<i>Osmia</i>	35	6	species	Mitchell 1962; <i>discoverlife.org</i>
Colletidae	<i>Hylaeus</i>	53	1	genus	Packer <i>et al.</i> 2007
Total:		1334	89		

Appendix B. List of flowering plant species encountered during floral survey, denoting the species name, common name, and family of each species. ‘Status’ indicates whether the species is (N) native to North America, or (I) introduced.

Species	Common Name	Family	Status
<i>Asclepias syriaca</i>	Common Milkweed	Asclepidaceae	N
<i>Cerastium arvense</i> L. spp. <i>arvense</i>	Field Chickweed	Caryophyllaceae	I
<i>Silene vulgaris</i> (Moench) Garcke	Bladder Campion	Caryophyllaceae	I
<i>Stellaria media</i> (L.) Villars	Chickweed	Caryophyllaceae	I
<i>Achillea millefolium</i> L. spp. <i>millefolium</i>	Yarrow	Compositae	I
<i>Aster lanceolatus</i> Willd	Panicked Aster	Compositae	N
<i>Aster lateriflorus</i> (L.) Britton	Calico Aster	Compositae	N
<i>Aster marcophyllus</i> L.	Large-leaved Aster	Compositae	N
<i>Chrysanthemum leucanthemum</i> L.	Ox-eye Daisy	Compositae	I
<i>Cichorium intybus</i> L.	Chicory	Compositae	I
<i>Cirsium arvense</i> (L.) Scop	Canada Thistle	Compositae	I
<i>Erigeron annuus</i> (L.) Pers.	Daisy Fleabane	Compositae	N
	Philadelphia		
<i>Erigeron philadelphicus</i> L. spp. <i>philadelphicus</i>	Fleabane	Compositae	N
<i>Erigeron strigosus</i> Muhlenb. Ex Willd	Lesser Fleabane	Compositae	N
<i>Eupatorium maculatum</i> L.	Joe Pye Weed	Compositae	N
<i>Rudbeckia hirta</i> L.	Black-eyed Susan	Compositae	N
<i>Solidago canadensis</i> L.	Canada Goldenrod	Compositae	N
<i>Sonchus arvensis</i> L. spp. <i>arvensis</i>	Field Sow Thistle	Compositae	I
<i>Sonchus asper</i> (L.) Hill spp. <i>Asper</i>	Spiny Sow Thistle	Compositae	I
<i>Tanacetum vulgare</i> L.	Tansy	Compositae	I
<i>Taraxacum officinale</i> G. Weber	Dandelion	Compositae	I
<i>Tragopogon dubius</i> Scop.	Goat’s Beard	Compositae	I
<i>Barbarea vulgaris</i> R. BR.	Wintercress	Cruciferae	I
	Wormsweed		
<i>Erysimum repandum</i> L. spp. <i>cheiranthoides</i>	Mustard	Cruciferae	I
<i>Hypericum perforatum</i> L.	Common St. John’s Wort	Guttiferae	I
<i>Sisyrinchium montanum</i> Michaux	Blue-eyed Grass	Iridaceae	N
<i>Prunella vulgaris</i> L. spp. <i>vulgaris</i>	Selfheal	Labiatae	I
<i>Lotus corniculatus</i> L.	Bird’s foot Trefoil	Leguminosae	I
<i>Medicago lupulina</i> L.	Black Medick	Leguminosae	I
<i>Medicago sativa</i> L. spp. <i>sativa</i>	Alfalfa	Leguminosae	I
<i>Melilotus alba</i> Medikus	White Sweet Clover	Leguminosae	I
<i>Melilotus officinalis</i> (L.) Pallas	Yellow Sweet	Leguminosae	I

Clover			
<i>Trifolium aureum</i> Pollich.	Yellow Hop Clover	Leguminosae	I
<i>Trifolium campestre</i> Schreber	Smaller Hop Clover	Leguminosae	I
<i>Trifolium hybridum</i> L. ssp. <i>elegans</i> (Savi) Asch. & Graebner	Alsike Clover	Leguminosae	I
<i>Trifolium pratense</i> L.	Red Clover	Leguminosae	I
<i>Trifolium repens</i> L.	White Clover	Leguminosae	I
<i>Vicia cracca</i> L.	Cow Vetch	Leguminosae	I
<i>Lythrum salicaria</i> L.	Purple Loosestrife	Lythraceae	I
<i>Oxalis stricta</i> L.	Yellow Wood Sorrel	Oxalidaceae	I
<i>Anemone canadensis</i> L.	Canada Anemone	Ranunculaceae	N
<i>Ranunculus acris</i> L.	Tall Buttercup	Ranunculaceae	I
<i>Fragaria virginiana</i> Miller ssp.	Wild Strawberry	Rosaceae	N
<i>Potentilla inclinata</i> Villars (= <i>P. argentea</i> x <i>P. recta</i>)	Downy Cinquefoil	Rosaceae	I
<i>Linaria vulgaris</i> Miller	Butter and Eggs	Scrophulariaceae	I
<i>Daucus carota</i> L.	Queen Anne's Lace	Umbelliferae	I
<i>Pastinaca sativa</i> Walter	Wild Parsnip	Umbelliferae	I