



Factors affecting bee communities in forest openings and adjacent mature forest



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ARTICLE INFO

Article history:

Received 13 January 2017

Accepted 27 March 2017

Available online 12 April 2017

Keywords:

Early-successional forest

Forest opening

Group selection

Mature forest

Bee

Silviculture

ABSTRACT

Anthropogenic disturbance of habitat is considered a contributing factor of pollinator declines, but some disturbances such as silviculture, may have positive implications for pollinator communities. Silviculture is a key source of disturbance in the eastern USA and thus, developing a better understanding of its ramifications for these keystone species is important for effective ecosystem conservation. We sampled bees in 30 forest openings created by group selection harvest as well as 30 sites in adjacent mature forest to examine the extent to which small forest openings support bees, to identify environmental variables influencing bee abundance and diversity, and to gauge their potential to augment bee populations in adjacent unmanaged forest. Bees were significantly more abundant and diverse in forest openings than in mature forest, but species composition did not differ. There was no relationship between opening size and abundance or diversity of bees in openings or adjacent mature forest. Both abundance and diversity were generally positively related to the amount of early-successional habitat on the landscape. Within openings, overall abundance and diversity decreased with vegetation height and increased with a metric representing floral richness and abundance. Notably, social, soft-wood-nesting, and small bees exhibited the opposite pattern in adjacent forest, increasing with vegetation height in openings and decreasing with greater floral richness and abundance within openings. Our results suggest that the creation of small forest openings helps to promote bees both in openings and adjacent mature forest, but this pattern is not consistent for all guilds.

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1. Introduction

Pollinators are vital to both ecosystems and humans worldwide, providing essential services for reproduction to the large majority of flowering plants (Kearns et al., 1998; Ollerton et al., 2011). Of all pollinating taxa, bees are the most effective at carrying out this critical ecological role (Winfree, 2010). There are over 4000 species of native bees in North America (Cane and Tepedino, 2001), which contribute significantly to the pollination of both native plants and crops (Klein et al., 2003; Winfree et al., 2007a, 2008). A growing body of evidence indicates that bees and other pollinators are declining globally (Bartomeus et al., 2013; Biesmeijer et al., 2006; Burkle et al., 2013; Cameron et al., 2011; Koh et al., 2016). Anthropogenic disturbances that result in the loss, fragmentation, or degradation of pollinator habitats have been implicated as a major contributing factor to these declines (Aizen and Feinsinger,

2003; Goulson et al., 2008; Potts et al., 2010); however, not all disturbances are detrimental for bees since many species are associated with open, early-successional habitats that are created by disturbance (Grundel et al., 2010; Michener, 2007). Thus, developing a complete understanding of how anthropogenic disturbances influence bees is an important step toward effective pollinator conservation.

In a broad-scale meta-analysis, Winfree et al. (2009) presented evidence that human disturbances negatively impact bees on the whole, but when broken down by disturbance type, logging exerted a positive (albeit non-significant) influence on bee abundance. Indeed, recent studies have shown that certain silvicultural practices can promote bees (e.g., Hanula et al., 2015; Taki et al., 2010a). This suggests that silviculture, which is a common form of disturbance throughout the eastern USA and responsible for roughly 78% of all early-successional habitats in New England (King and Schlossberg, 2012), may contribute considerably to bee populations.

Even-aged silviculture appears to be effective at promoting overall bee communities (Hanula et al., 2015; Romey et al., 2007;

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Wilson et al., 2014), but has declined in favor of uneven-aged management throughout much of the U.S. (Oswalt and Smith, 2014). Stands managed with single-tree selection support more bees than unmanaged stands (Nol et al., 2006), but far fewer bees and lower diversity than even-aged regimes (Romey et al., 2007). Proctor et al. (2012) found that group selection, an uneven-aged method where groups of adjacent trees are removed from a mature forest matrix (Smith et al., 1997), supported significantly more bees than mature forest and suggested it was more effective at promoting bees than single-tree selection. These studies reinforce the notion that bees likely benefit from most forms of silviculture, but stop short of examining habitat characteristics (e.g., patch area), which can vary considerably among harvests and have been shown to be important for other taxa (e.g., Costello et al., 2000; Moorman and Guynn, 2001). Identifying the factors important for bee communities in various forest management scenarios will help conservationists and forest managers maximize the conservation value of their efforts.

Bees display considerable variation among species in several ways including dietary breadth (i.e., pollen specificity), sociality, body size, and nesting substrate. Accounting for these guilds can be of critical importance in understanding how bees respond to the environment as well as anthropogenic disturbances (Cane et al., 2006; Williams et al., 2010; Wray et al., 2014). Silviculture has the potential to impact guilds in different ways. For example, soil disturbance is common among silvicultural prescriptions, which may be beneficial for ground-nesting bees, but opening the canopy may also promote a floral community that is not conducive for floral specialists. Elucidating guild-specific responses to different silvicultural practices will be necessary in order to render a clear picture of how forest management shapes the pollinator community.

Landscape-level factors, in addition to microhabitat (Potts et al., 2003) and patch-level variables (Diaz-Forero et al., 2013), are important for bees (e.g., Winfree et al., 2007b). The presence of certain habitat types on the landscape such as grasslands have been shown to improve pollination in adjacent agricultural systems (Taki et al., 2010b). Because silviculture generally appears to promote bees (Hanula et al., 2016), it could have similar beneficial implications for pollination in adjacent unmanaged areas. This has not been thoroughly studied (although see Cartar, 2005 and Jackson et al., 2014), but could provide guidance to restoring pollination services to forested landscapes, the lack of which has been implicated in the decline of some mature forest plants (Willis et al., 2008) as well as other flora around the globe (Biesmeijer et al., 2006).

Heightened concern about native bee populations as well as increased emphasis on uneven-aged management suggests the importance of a more detailed understanding of the application of these methods for supporting these important pollinators. The objectives of this study were to (1) compare the bee community within forest openings to that of adjacent mature forest to illustrate the impact of group selection on bee communities, (2) identify microhabitat-, patch-, and landscape-level factors influencing bee abundance and diversity in both openings and adjacent forest, (3) quantify bee abundance and diversity at a range of distances from forest openings to gauge the potential for openings to augment bee populations in adjacent mature forest, and (4) examine the habitat associations of individual species.

2. Methods

2.1. Study area

We conducted this study in western Massachusetts, USA (42.46°N, -72.32°W; Fig. 1) in 2014 and 2015. The landscape

was over 90% forest, characterized as hardwoods-white pine and was primarily made up of red maple (*Acer rubrum*), red oak (*Quercus rubra*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*). Human development comprised <5% of the immediate landscape. Forest openings ranged in size from 0.08–1.29 ha and were created 4–8 years prior to sampling. The average nearest-neighbor edge-edge distance between forest openings was 43 m within harvest sites. Vegetation within openings consisted primarily of birches (*Betula* spp.), red maple, white pine, *Rubus* spp., mountain laurel (*Kalmia latifolia*), and various fern species. Residual woody debris from harvests was prevalent in all openings. The primary flowering plants during this study included *Acer rubrum* (early spring), blueberry (*Vaccinium* spp.; spring), *Aralia hispida* (summer), *Rubus* spp. (summer), and *Lysimachia quadrifolia* L. (summer). Few non-native plants were detected in openings.

2.2. Bee and microhabitat surveys

We randomly selected thirty openings for sampling across six harvest sites using bins based on opening size to ensure that a gradient of sizes were included. Sampling took place during three periods: spring (26 April–14 May), summer (1 July–17 July), and late summer (23 August–8 September). We collected bees once during each period using bowl traps, which consisted of 96 milliliter plastic cups (Solo®, Highland Park, IL) filled with water mixed with soap (blue Dawn® Liquid Dish Soap, original scent). To sample bees within openings, we established a transect of 5 sample points 5 m apart in each opening 15 m from the forest and parallel to the opening edge. To sample bees in forest, we established a second transect of 5 sample points 10 m apart starting 10 m from the opening and running perpendicular to the opening edge into the forest along east-west bearings to control for the effects of aspect (Matlack, 1994). We placed three bowls at each sampling point, one white, one fluorescent yellow, and one fluorescent blue, on the ground approximately 1 m apart. These colors have been shown to be most attractive to bees of eastern North America (Campbell and Hanula, 2007). We conducted sampling on sunny, calm days when the average temperature was >10 °C. We placed forest transects such that surrounding sources of shrubland habitat were never closer to points along the transect than the focal opening. After 24 h, bowls were collected and bees removed from bowl traps and stored in 70% ethyl alcohol. We cleaned, dried, pinned, labeled, and identified bees to species using online keys such as Discoverlife.org (Ascher and Pickering, 2016) and published references (e.g., Mitchell, 1960, 1962). We sent bees with uncertain identities to specialists Sam Droege, Michael Veit, and Dr. Jason Gibbs for confirmation.

We measured vegetation at 20 random locations within each opening. At each point, we placed a 3-m pole vertically and recorded the identity and height of the tallest plant species in contact with the pole or a vertical projection of the pole if vegetation was taller than 3 m. We used median vegetation height and coefficient of variation of vegetation height in the analyses to characterize vegetation structure. During each visit, we recorded the number of flowers by species within a 1-m radius of each sampling point. Absolute flower abundance yielded extremely heterogeneous data that over represented species that produce compound flowers made up of dozens of very small flowers (e.g., *A. hispida*). Flowering species richness was also not particularly descriptive of the floral community within openings because richness along transects only exceeded 3 species once for a single opening. To better describe the floral community within openings, we calculated the flowering species richness at each individual sampling point and summed those values for all 5 sample points in each transect. This new metric, which we refer to as “floral index,” allowed us to



Fig. 1. Map of study area in western Massachusetts, USA (42.46°N, -72.32°W). Black stars indicate harvest sites where bees were collected in early spring, mid-summer, and late summer in 2014 and 2015.

coarsely account for both abundance ($r = 0.61$) as well as richness ($r = 0.86$), while not overly representing plants that produce numerous compound flowers.

2.3. Patch and landscape metrics

We quantified the area of each opening and the percentage of the surrounding landscape containing shrubland habitat (PLAND) using FRAGSTATS software, version 4 (McGarigal et al., 2012). We chose to examine area because there is a lack of consensus regarding the influence of patch size on bees (e.g., Bommarco et al., 2010 and Brosi et al., 2008). We chose PLAND because landscape composition has been shown to be important in determining bee communities (e.g., Winfree et al., 2007b), but few studies of bees have examined early-successional habitat at a landscape level (see Diaz-Forero et al., 2013 and Rubene et al., 2015). In this study, the PLAND metric represents the percent of the landscape that consisted of shrubland habitat within a specified search-radius from the centroid of each opening. We used both 200 m and 500 m radii because bee guilds have been shown to display varying responses to landscape features at different scales (Benjamin et al., 2014). To facilitate the calculation of these metrics in FRAGSTATS, we first delineated forest openings using ArcGIS 10.2.1 (Environmental Systems Research Institute, Inc., Redlands, CA) and then rasterized them using a grid size of 3 m.

2.4. Statistical analysis

Generalized linear mixed models (GLMM; Zuur et al., 2009) were the primary framework under which we analyzed data in this study. We used GLMMs to compare differences in bee abundance and diversity (Shannon's Diversity Index) by habitat type, model abundance and diversity as a function of microhabitat, patch, and

landscape variables, model abundance and diversity in mature forest as a function of distance to openings, and examine habitat associations of individual species. Environmental variables included vegetation height, coefficient of variation (CV) of vegetation height, and floral index at the microhabitat level, opening area at the patch level, and the amount of early-successional habitat within 200 m and 500 m (PLAND200 and PLAND500 respectively) at the landscape level. We used Akaike's information criterion (AIC; Burnham and Anderson, 2002), to compare poisson and negative binomial distributions for modeling abundance and gaussian and gamma distributions for modeling diversity. We also considered zero-inflated models when dependent variables appeared to have more zero values than would be expected under the distributions used (Zuur et al., 2009). We included site as a random effect to account for variations in abundance and diversity among sites. We modeled abundance using a log link and diversity using an identity or inverse link depending upon the distribution. We pooled bees caught at sample points within transects for all community analyses except for that of the effect of distance to forest openings for which we used individual sample points.

We modeled overall bee abundance and diversity as well as individual species abundance as a function of habitat by including a single categorical fixed effect representing habitat type (opening or forest). We only modeled habitat associations for species with >30 individuals collected across both habitats. We modeled relationships with microhabitat, patch, and landscape variables for all species combined and by guild. We included the following guilds: dietary breadth (broad or "polylectic" versus narrow or "oligolectic"), sociality (solitary, eusocial, parasitic), nest substrate (soil, cavity, soft wood, pith), and body size (small, medium, large). We gathered information about diet, sociality, and nesting substrate from primary literature and personal communications with experts. We estimated body size by first measuring the

intertegular length (Cane, 1987) of at least 5 randomly selected bees of each species. We then estimated dry body mass using the known exponential relationship with intertegular length established by Cane (1987). We categorized bees as small if their estimated weight was <4 mg, medium if their estimated weight was 4–16 mg, and large if their estimated weight was >16 mg, in accordance with Winfree et al. (2007b). We included unidentified species (nearly all were identified to genus; Appendix A) in analyses of abundance of all bees combined and certain guilds (if they could be clearly placed in a particular guild, e.g., *Nomada*), but excluded from analyses of diversity and body size.

We assessed correlations among predictor variables using Pearson correlation. For all variable comparisons, r was ≤ 0.51 . We scaled continuous variables with $\bar{x} = 0$ and $\sigma = 1$ to facilitate model convergence. We used scatterplots to examine the nature of relationships between dependent and independent variables. All relationships appeared linear, with the exception of PLAND500, which consistently demonstrated a unimodal pattern where abundance and diversity peaked at intermediate levels. To account for this potential non-linear relationship, we included a quadratic term in addition to a linear term in models containing this variable.

Since we had no *a priori* variable combinations of interest and there was a risk of over-fitting models if more variables were included (due to a small sample size of $n = 30$), relationships were modeled using only a single fixed effect variable. Covariates were considered strongly supported if the 95% confidence interval (CI) for their coefficient did not overlap zero (Chandler et al., 2009). We considered a sequential Bonferroni procedure (Holm, 1979) to account for the likelihood of a Type I error given the number of models applied to similar data, but we did not use this method because we felt it was too conservative and would exclude relationships that are biologically meaningful. We fit models and estimated parameters using the glmmADMB package (Skaug et al., 2015) in R statistical software version 3.1.1 (R Development Core Team, 2016).

To visualize differences in community composition between opening and forest habitats, we ordinated opening and forest samples using nonmetric multidimensional scaling (NMDS; McGarigal et al., 2000). NMDS plots sample-entities in low dimensional space such that the entity distance in the ordination has the same rank order as the original dissimilarity matrix (McGarigal et al., 2000). We used a Bray-Curtis measure of ecological distance. We assessed the fit of the ordination distances to the original data by calculating stress where values closer to zero indicate better fit. Because

abundance was anticipated as a distinguishing factor between habitats, we created NMDS plots using a raw and binary dataset to assess community compositions with and without the influence of species abundance. We performed NMDS using the vegan package (Oksanen et al., 2013) in R statistical software version 3.1.1.

3. Results

We collected 2404 bees (74 species) in forest openings and 574 bees (49 species) in mature forest representing 5 families, 14 genera, and 76 identifiable species (Appendix A). Approximately 10% of bees collected could not be identified to species (most of which were of the genera *Nomada* and *Lasioglossum*) due to a lack of information on taxonomy for certain groups of bees and the poor condition of some specimens. We collected three exotic species (*Andrena wilkella*, *L. leucozonium*, and *Osmia cornifrons*), totaling 18 individuals. Nine species represented approximately 64% of all individuals. The two most common species were *N. maculata* (456 individuals; a cleptoparasite primarily of *Andrena* spp.) and *Augochlorella aurata* (368 individuals). The majority of identified bees were polylectic (96% of individuals) and soil-nesting (66% of individuals) bees. Cavity, soft wood, and pith-nesting bees made up 14%, 11%, and 9% of bees that could be assigned nesting substrates, respectively. Solitary and eusocial bees represented roughly equal proportions (37% and 36% respectively), while cleptoparasitic bees made up the remaining 27%. When we examined habitats separately, guild proportions were similar. Oligolectic bees were uncommon with only 116 individuals (8 species) collected, of which 86 individuals were *A. uvulariae*, a species thought to specialize on the plant genus *Uvularia* (M. Arduser, P. Bernhardt, and S. Droege, pers. comm.). Twenty-seven species were only found in openings (Appendix A), all of which were low in abundance. *Bombus perplexus* and *L. foxii* were the only species that only occurred in forest, but these were only represented by single individuals.

Bees abundance ($\beta = -1.478$, $SE = 0.172$, $z = -8.61$, $P < 0.001$) and diversity ($\beta = -0.528$, $SE = 0.113$, $z = -4.65$, $P < 0.001$) were significantly greater in openings than in adjacent forest (Fig. 2). NMDS ordinations appeared to show a separation of opening and forest communities when raw data was used, but there was no clear separation when ordinated using binary data (Fig. 3). Overall, opening points were more tightly clustered than forest points in ordination plots, indicating less variation in their community

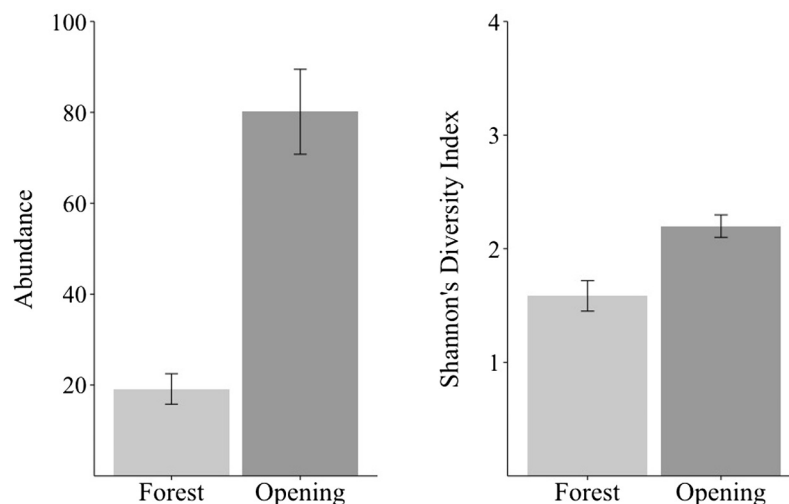


Fig. 2. Mean bee abundance and diversity per transect in openings and mature forest in western Massachusetts, USA. Bars represent standard error. Data comes from bowl trap surveys conducted in early spring, mid-summer, and late summer in 2014 and 2015.

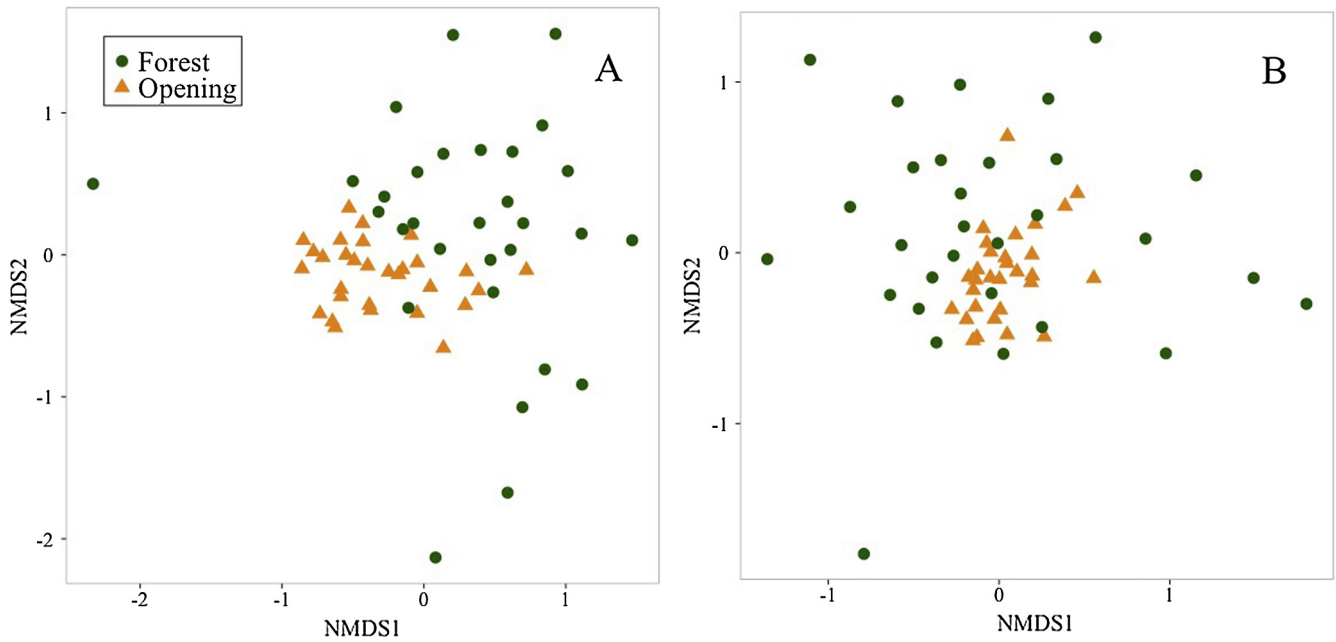


Fig. 3. Non-metric multidimensional scaling ordination of opening and forest transects with raw (A) and binary (B) community data. The two habitat types appear to separate within ordination space using raw data, but when abundance is removed there is no apparent separation. Data comes from bowl trap surveys conducted in early spring, mid-summer, and late summer in 2014 and 2015 in western Massachusetts, USA.

makeup (Fig. 3). Relatively low stress values for both raw and binary ordinations (0.19 and 0.2 respectively) and inspection of Shepard's plots suggested acceptable fits. Bee abundance ($\beta = -0.012$, $SE = 0.007$, $z = -1.76$, $P = 0.08$) and diversity ($\beta = -0.006$, $SE = 0.004$, $z = -1.52$, $P = 0.13$) in the forest showed no significant relationship with distance to forest opening, but appeared to decrease further from openings.

Bee abundance and diversity in openings was unrelated to patch area (Table 1). Diversity of all bees combined as well as abundance of parasitic, soil-nesting, soft-wood-nesting, and small bees were positively related to PLAND200. The quadratic term for PLAND500 was strongly supported for all guilds except eusocial, pith-nesting, and medium size bees. Coefficients of the quadratic term of PLAND500 were all negative, indicating a unimodal relationship with the dependent variables (Fig. 4). Abundance and

diversity of all bees combined, as well as polylectic, eusocial, solitary, cavity and pith-nesting, and medium size bees, displayed strong negative relationships with vegetation height. Only diversity of all bees combined and soft-wood-nesting bees were positively related to coefficient of variation of vegetation height. Abundance and diversity of all bees combined as well as polylectic, eusocial, solitary, soil, cavity, and pith-nesting, and medium and large bees displayed positive relationships with floral index.

Patch area had no apparent influence on the abundance or diversity of bees within adjacent mature forest (Table 2). Abundance of all bees combined as well as polylectic, solitary, soil-nesting, and large bees exhibited positive relationships with PLAND200. Abundance of all bees combined, as well as polylectic, oligolectic, solitary, parasitic, soil-nesting, and medium and large bees displayed positive relationships with the linear PLAND500

Table 1

Parameter estimates for fixed-effect variables in generalized linear mixed models of the relationship between abundance and diversity of bees in forest openings and environmental variables. Standard errors are given in parentheses. Models only included one fixed-effect variable, with the exception of models of PLAND500, which also included PLAND500². Coefficients were only shown if 95% CI did not overlap zero.

Group	Measure ^a	Microhabitat ^b			Patch Area	Landscape ^c		
		Height	CV	Flower		PLAND.200	PLAND.500	PLAND.500 ²
All bees	Abund	-0.19 (0.097)		0.268 (0.092)				-0.224 (0.096)
	SDI	-0.174 (0.074)	0.162 (0.076)	0.172 (0.074)		0.168 (0.079)		-0.169 (0.08)
Polylectic	Abund	-0.203 (0.097)		0.273 (0.096)				-0.197 (0.1)
Oligolectic	Abund							-0.613 (0.186)
Eusocial	Abund	-0.306 (0.137)		0.410 (0.134)				-0.212 (0.097)
Solitary	Abund	-0.324 (0.086)		0.337 (0.081)				-0.469 (0.176)
Parasitic	Abund					0.364 (0.151)		-0.469 (0.176)
Soil	Abund			0.267 (0.119)		0.238 (0.116)		-0.306 (0.124)
Soft wood	Abund		0.355 (0.159)			0.461 (0.211)		-0.458 (0.203)
Cavity	Abund	-0.282 (0.103)		0.225 (0.103)				-0.257 (0.01)
Pith	Abund	-0.725 (0.141)		0.627 (0.170)				
Small	Abund					0.315 (0.139)		-0.401 (0.151)
Medium	Abund	-0.233 (0.089)		0.272 (0.084)				
Large	Abund			0.395 (0.197)				-0.638 (0.255)

^a Abund = abundance; SDI = Shannon's Diversity Index.

^b Height = median vegetation height; CV = coefficient of variation of vegetation height; Flower = floral index.

^c PLAND = percent early-successional habitat within 200 m (PLAND200) and 500 m (PLAND500) of the centroid of forest openings.

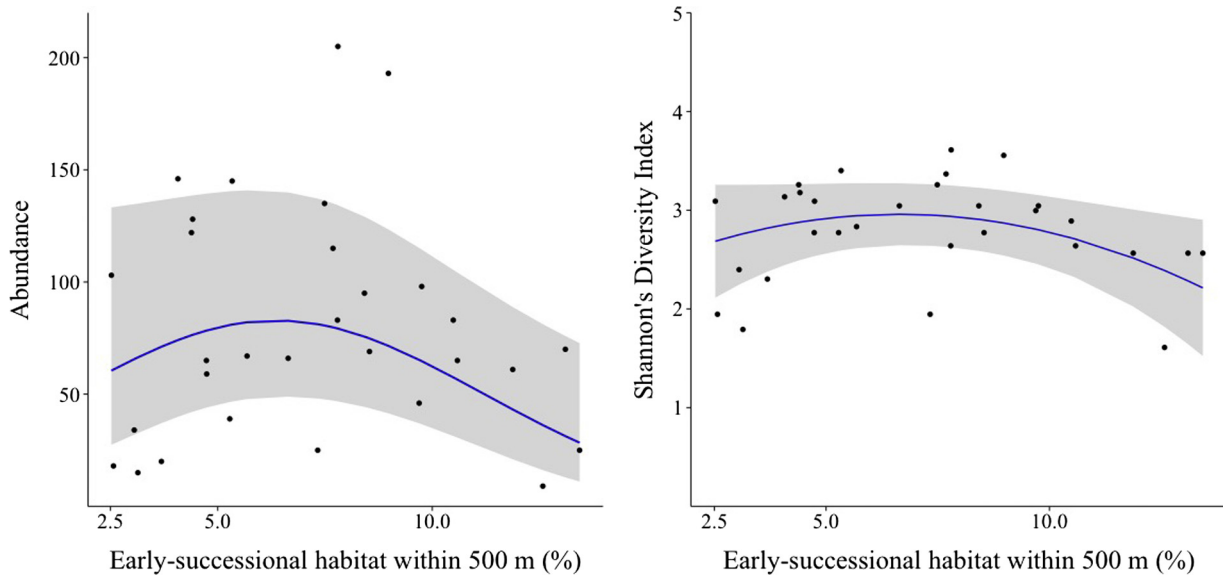


Fig. 4. Abundance and diversity of bees in forest openings in relation to the percent of the surrounding landscape that was early-successional habitat within 500 m (PLAND500). Lines and shaded areas represent the predicted values of generalized linear mixed models and 95% CI respectively. Models included a linear and quadratic term for PLAND500 as fixed effects and site as a random effect. Data comes from bowl trap surveys conducted in early spring, mid-summer, and late summer in 2014 and 2015 in western Massachusetts, USA.

Table 2
Parameter estimates for fixed-effect variables in generalized linear mixed models representing the relationship between abundance and diversity of bees in mature forest and environmental variables. Standard errors are included in parentheses. Models only included one fixed-effect variable with the exception of models including PLAND500, which also included PLAND500². Coefficients were only included if 95% CI did not overlap zero.

Group	Measure ^a	Microhabitat ^b			Patch Area	Landscape ^c		
		Height	CV	Flower		PLAND200	PLAND500	PLAND500 ²
All bees	Abund					0.408 (0.169)	0.432 (0.184)	-0.435 (0.208)
	SDI							-0.317 (0.162)
Polylectic	Abund					0.392 (0.17)	0.454 (0.196)	
Oligolectic	Abund						0.672 (0.325)	
Eusocial	Abund	0.462 (0.18)		-0.389 (0.173)				
Solitary	Abund					0.483 (0.163)	0.484 (0.169)	-0.457 (0.181)
Parasitic	Abund						0.844 (0.244)	-0.667 (0.217)
Soil	Abund					0.375 (0.176)	0.611 (0.166)	-0.527 (0.177)
Soft wood	Abund	0.666 (0.244)		-0.698 (0.242)				
Cavity	Abund							-0.450 (0.227)
Pith	Abund							
Small	Abund	0.652 (0.276)		-0.638 (0.281)				
Medium	Abund						0.486 (0.189)	-0.513 (0.214)
Large	Abund		NC ^d			0.528 (0.2)	0.753 (0.245)	

^a Abund = abundance; SDI = Shannon's Diversity Index.

^b Microhabitat within forest openings; Height = median vegetation height; CV = coefficient of variation of vegetation height; Flower = floral index.

^c PLAND = % early-successional habitat within 200 m (PLAND200) and 500 m (PLAND500) of the centroid of forest openings.

^d NC = non-convergent model.

term. A negative quadratic term for PLAND500 was a strong predictor of abundance and diversity of all bees combined, as well as solitary, parasitic, soil and cavity-nesting, and medium size bees. Abundance of eusocial, soft-wood-nesting, and small bees displayed positive relationships with the vegetation height within forest openings. Coefficient of variation of vegetation height within openings exhibited no apparent influence on any guild. Abundance of eusocial, soft-wood-nesting, and small bees displayed negative relationships with floral index within forest openings.

Seventeen bee species were abundant enough to compare between openings and mature forest (Table 3). Of these species, 11 were significantly more abundant in openings than mature forest including: *A. vicina*, *A. aurata*, *Ceratina calcarata*, *C. dupla*, *L. cressonii*, *L. ephialtum*, *L. taylorae*, *N. luteoloides*, *N. maculata*, *O. atriventris*, and *O. pumila*. Two species, *L. coeruleum* and *L. versans*, were more abundant in forest than in openings, but only *L. versans*

was significantly more abundant. Species that did not show strong associations with a particular habitat type were *A. carlini*, *A. uvulariae*, *L. planatum*, *L. subviridatum*.

4. Discussion

The perceived decline of bees (Koh et al., 2016), poses a threat to both biodiversity and the ecosystem services that bees provide (Klein et al., 2007). Forests cover roughly one third of the North American land area (World Bank, 2016) and silviculture is widespread (Oswalt and Smith, 2014). Thus, it is important to paint a detailed picture of how silviculture impacts these keystone species if effective conservation actions are to be implemented. With this study, we demonstrate that group selection harvests foster a considerably more abundant and diverse bee community than

Table 3

Results of species habitat associations using generalized linear mixed models. We included a single fixed effect representing habitat type (opening or forest) and a random effect of site in all models. Negative β values indicate greater abundance in openings. Only species that occurred >30 times were examined.

Species	n	β	SE	z	P
<i>Andrena carlini</i>	159	-0.67	0.4	-1.71	0.09
<i>Andrena uvulariae</i>	86	-0.21	0.23	-0.9	0.37
<i>Andrena vicina</i>	44	-2.66	0.75	-3.55	<0.01
<i>Augochlorella aurata</i>	368	-2.64	0.38	-6.95	<0.01
<i>Ceratina calcarata</i>	166	-2.22	0.34	-6.63	<0.01
<i>Ceratina dupla</i>	102	-2.97	0.54	-5.49	<0.01
<i>Lasioglossum coeruleum</i>	87	-0.01	0.31	-0.03	0.97
<i>Lasioglossum cressonii</i>	44	-1.36	0.44	-3.09	<0.01
<i>Lasioglossum ephialtum</i>	37	-2.11	0.66	-3.2	<0.01
<i>Lasioglossum planatum</i>	55	-0.77	0.72	-1.07	0.28
<i>Lasioglossum subviridatum</i>	144	-0.31	0.35	-0.88	0.38
<i>Lasioglossum taylorae</i>	138	-1.84	0.34	-5.48	<0.01
<i>Lasioglossum versans</i>	32	0.89	0.46	1.94	0.05
<i>Nomada luteoloides</i>	67	-1.42	0.31	-4.61	<0.01
<i>Nomada maculata</i>	456	-2.61	0.28	-9.42	<0.01
<i>Osmia atriventris</i>	171	-1.674	0.25	-6.66	<0.01
<i>Osmia pumila</i>	133	-1.75	0.27	-6.54	<0.01

closed-canopy forest, enhancing habitat for these important pollinators. These results are consistent with those of Proctor et al. (2012) in Ontario and contribute to the growing body of evidence that forest management can benefit native bee populations (Hanula et al., 2016).

Our observations suggest that bees are relatively insensitive to patch area within the context of group selection. There is little consensus in the literature on bees and patch size, with studies reporting positive relationships with patch area (Aizen and Feinsinger, 1994; Bommarco et al., 2010; Diaz-Forero et al., 2013; Krauss et al., 2009; Meyer et al., 2007; Rubene et al., 2015), no relationships (Brosi et al., 2008), or mixed responses by guild (Cane et al., 2006; Donaldson et al., 2002; Neame et al., 2013). Ockinger et al. (2012) found that there was a significant effect of patch area on bee richness in grasslands; however, in agreement with our findings, when their analysis was restricted to patches within a forested matrix, the effect of patch area was no longer significant. Ockinger et al. (2012) did not suggest an explanation for this phenomenon, but their findings highlight the importance of considering matrix type when studying pollinators. Since the variety of resources (e.g., nectar, pollen, nest substrates, and nest-construction materials) necessary for bees to complete their life cycle (Muller et al., 2006) often come from different habitats (Westrich, 1996), opening size may not have influenced bee communities because the surrounding forest matrix was able to supplement resources in even the smallest openings. Indeed, other studies of wildlife in fragmented habitats have provided similar explanations (Brotons et al., 2003; Neame et al., 2013).

We observed that most guilds displayed non-linear unimodal relationships with the amount of early-successional habitat within 500 m, indicating that while early-successional habitat beyond the boundaries of the treatment area can increase abundance and diversity, there appears to be a threshold beyond which its influence subsides. Landscape composition has been examined with respect to bees (Dauber et al., 2003; Hirsch et al., 2003; Taki et al., 2007, 2010b; Watson et al., 2011; Winfree et al., 2007b), but few studies have investigated how the extent of early-successional forest habitat at the landscape level affects bees. Rubene et al. (2015) measured the amount of early-successional habitat within 2 km of clearcuts, but found no relationship with species richness. This discrepancy might be explained by differences in surrounding matrices (see Ockinger et al., 2012) or

the differences in the scales examined. Research has shown that stretches of forest habitat are not effective barriers to certain eusocial (Kreyer et al., 2004) and solitary (Zurbuchen et al., 2010) bees. If this is also true for other bees, and they were not restricted to single openings in this study, it is not surprising that abundance and diversity increased with greater early-successional cover because openings supported more abundant and diverse communities than adjacent forest (see Section 2.3) and the scales examined (200 m and 500 m) are within the feasible foraging distance for many bees captured in this study (Gathmann and Tscharrntke, 2002). It is more difficult to explain the eventual subsidence of this effect. One hypothesis is that there may be a threshold at which local resources become abundant enough that movement among openings, especially those further away, is no longer necessary and as a result fewer bees visit each opening.

Similar to the potential value for natural habitats to supplement crop pollination (Benjamin et al., 2014; Klein et al., 2003; Ricketts et al., 2008), greater pollinator numbers in forest openings could promote pollination services in adjacent forest where bees are generally scarce. Our results provide some evidence to this point. Although not statistically significant, we observed a pattern of greater abundance and diversity of bees at individual sample points that were closer to openings. In addition, the landscape-level analysis showed that overall bee abundance and diversity in the forest increased with the amount of early-successional habitat on the landscape at both scales. The lack of a statistically significant effect of distance to opening along transects might be explained by the fact that the furthest sample point was only 50 m from openings, which is likely well below the foraging distance of most bees (Gathmann and Tscharrntke, 2002). Therefore, we may not have sampled far enough into the woods to measure a change in the bee community. Similarly, Jackson et al. (2014) did not observe elevated bee abundance near early-successional habitat along old logging roads. The positive relationship with early-successional habitat at the landscape-level suggests that group selection does promote pollinators in adjacent forest and thus may translate to elevated pollinator services for flowering plants associated with mature forest. However, abundance and diversity followed a unimodal trend for the amount of early-successional habitat at 500 m similar to that within openings, indicating that extensive logging may not improve pollinator services if the resulting early-successional cover is too great. Further attention needs to be given to examining this relationship and identifying when the benefits of early-successional habitat may diminish.

Group selection may not benefit all guilds in adjacent mature forest. Eusocial, soft-wood-nesting, and small bees showed no response to the amount of early-successional habitat nearby and were negatively related to the floral index of openings. Similarly, other studies have reported reduced density (Cartar, 2005) and species richness (Diaz-Forero et al., 2013) of *Bombus* spp. near early-successional habitats. Both of these studies suggest that this phenomenon may be the result of bees prioritizing foraging efforts in young forest where there is elevated floral abundance. This pattern, and the increased abundance of eusocial, small, and soft-wood-nesting bees in mature forest with taller vegetation within openings, show that microhabitat characteristics can directly influence not only the bee community within that opening, but also in surrounding habitat. Despite our observation that creating forest openings appears to augment overall bee populations (and therefore possibly pollination) in adjacent forest, silviculture could have the opposite effect if eusocial, soft-wood-nesting, and small bees are more effective pollinators of forest flora. Indeed, Cartar (2005) suggested that early-successional forests may cause reduced pollination rates in forest plants and Proctor et al. (2012) expressed concern that *Rubus*, a prolific flowering

plant genus and aggressive colonizer of disturbed areas, may “monopolize” pollinators and negatively impact the reproductive success of neighboring forest plants. Future research should consider measuring the reproductive success of forest plants to definitively assess the impact of silviculture.

Evidence suggests that microhabitat characteristics are of considerable importance in determining bee communities (Murray et al., 2012; Williams and Winfree, 2013) and our results were supportive of this. Bees in openings were generally positively related to floral index, which is consistent with other studies (e.g., Potts et al., 2003; Roulston and Goodell, 2011; Torne-Noguera et al., 2014). Guilds that showed no response to floral index were oligolectic, cleptoparasitic, soil and soft-wood-nesting, and small bees. Oligolectes require certain types of pollen to provision their young (Roulston and Goodell, 2011) and thus are more likely driven by the presence of their host plants. Similarly, cleptoparasites are associated with the presence of their host species (Sheffield et al., 2013) as opposed to the floral community, since they do not provision their young (Rozen, 2001). Small-bodied bees may have been primarily driven by the relative isolation of openings since body size is linked to shorter flight distances (Gathmann and Tschamtkke, 2002; Greenleaf et al., 2007). It is difficult to explain why soil and soft-wood-nesting bees did not respond to floral index.

Our findings that all bees combined and many individual guilds were negatively associated with vegetation height in openings supports the widely held belief that many bees prefer early-successional, open habitats (Michener, 2007). Other studies have identified similar relationships (Gikungu, 2006; Sudan, 2016; Taki et al., 2013). This pattern is possibly the result of factors associated with lower vegetation such as elevated light levels, which can stimulate the growth of flowering plants (Romey et al., 2007; Vallet et al., 2010) and improve nesting suitability for certain species (Potts and Willmer, 1997). This relationship between vegetation height and floral index is reflected by their correlation ($r = -0.51$, $P < 0.01$).

Similarly, the observed increase in bee diversity and abundance of soft-wood-nesting bees with more varied vegetation height may also have been the product of associated factors such as light levels. However, CV of vegetation height did not appear to be related to floral index ($r = 0.16$, $P = 0.4$) or vegetation height ($r = -0.17$, $P = 0.36$), indicating that CV of vegetation height is likely driving other factors. To our knowledge, the impacts of CV of vegetation height on bees has not been studied, but edge habitats, which typically represent a wide range in vegetative structure, have been shown to be important for bees (Diaz-Forero et al., 2013; Osborne et al., 2008; Sepp et al., 2004).

Habitat requirements are largely unknown for many bee species. While research has shown that some species are associated with late-successional habitats (Taki et al., 2007; Winfree et al., 2007b), most species are thought to prefer open, early-successional habitats (Michener, 2007). Our analyses partly support this line of thought, demonstrating clear preferences toward openings by certain species, but other species did not appear to utilize one habitat more than the other, and one species, *L. versans*, was more abundant in the forest ($P = 0.05$). In contrast, Proctor et al. (2012) captured the vast majority of *L. versans* in group selection openings, not mature forest. This difference could be due to the fact that our study may have sampled mature forest habitat closer to openings (although Proctor et al. (2012) did not specify how far unmanaged sites were from group selection openings) and thus the *L. versans* we captured in the forest likely came from openings. This is further supported by the fact that *L. versans* is a soil-nesting species (Giles and Ascher, 2006) and bare ground was far more abundant in openings than in the forest (personal observation).

Bee guilds differ with respect to their sensitivity to disturbance (Cane et al., 2006; Williams et al., 2010; Wray et al., 2014) and thus examining community makeup with respect to guilds can provide information as to the extent that group selection harvests contribute to bee conservation. For example, floral specialists (oligolectes) are of heightened conservation concern because they are at greater risk of decline (Biesmeijer et al., 2006; Winfree, 2010). Although oligolectes typically represent a sizeable proportion (~30%) of species in temperate bee communities (Minckley and Roulston, 2006), they comprised only 11% of the species and less than 4% of individuals collected in this study, suggesting that silvicultural openings do not promote floral specialists. Interestingly, despite the limited representation of specialists, we collected a notably large number of female and male *A. uvulariae*, a possible specialist of *Uvularia* spp. While less abundant than both eusocial and solitary bees, cleptoparasitic bees were common both in mature forest and openings, making up approximately 27% of total captures and contributing the most frequently captured species (*N. maculata*). This may reflect the overall good health of the bee community, as suggested by Sheffield et al. (2013), who argued for the use of cleptoparasites as indicator taxa due to their stabilizing role in communities, their sensitivity to negative disturbances, and their inherent reflection of the presence of their host bee species.

Although bowl traps avoid collector bias, which may affect samples collected by opportunistic netting techniques (Westphal et al., 2008), bowl traps tend to catch fewer large-bodied bees and fewer individuals of certain genera (Cane et al., 2000; Cane, 2001; Roulston et al., 2007). Nevertheless, we know of no reason to expect that the species not represented in our bowls would exhibit different patterns of abundance relative to opening and forest habitat conditions than the species we were able to collect. There is also concern that bowl traps are potentially biased as a function of floral abundance, collecting fewer bees when resources are plentiful (Baum and Wallen, 2011; Wilson et al., 2008). Our observation of a positive relationship between bee captures in bowls and floral index suggests this source of bias was not influencing our sampling. Furthermore, studies of the vertical distribution of bees in forests suggest that low encounter rates in forest understories reflect the failure to sample bees in the canopy, where some species appear to be abundant (Ulyshen et al., 2010). Nevertheless, bees do appear to favor open forest habitats in general (Hanula et al., 2016). Finally, our study did not encompass a complete gradient of landscape conditions, no openings were completely isolated, nor did any openings have more than 13% of the surrounding landscape (within 500 m) consisting of early-successional habitat. These limitations should be kept in mind when comparing the results of this study with results based on netting or other sampling techniques, and caution exercised when extrapolating these results to less forested landscapes.

5. Conclusions

Public and private conservation and management entities are receiving encouragement to create habitat for pollinators (Obama, 2014). While plantings and gardens are effective at achieving this goal (Vaughn et al., 2015), there are considerable associated monetary costs, especially at large spatial scales. This research demonstrates that creating forest openings within largely forested landscapes can promote native bees, not only within openings, but also in surrounding mature forest. Managers may be able to boost pollinator services to surrounding habitats with the strategic placement of young forest, but it is unclear whether creating openings will translate to increased pollination rates within adjacent forest because certain guilds may be drawn out

of forests into openings, potentially depriving forest habitats of their pollination services.

These findings suggest that within stands managed with group selection, it is the total proportion of the landscape converted to early-successional habitat rather than size of individual openings that is important for predicting bee abundance and diversity, with an optimal level of approximately 5–10% of the landscape (within 500 m) as early-successional habitat. Capture rates in openings in this study were lower than those of open meadow habitats dominated by perennial flowering plants (Gezon et al., 2015), nevertheless, the broad extent of silvicultural habitats in the eastern U.S. (e.g., Schlossberg and King, 2015) suggests that the aggregate contribution of silviculture to pollinator populations may be significant.

Acknowledgments

We are grateful to A. Hulsey and E. Dalton for providing field assistance and M. Akresh for providing analytical support. S. Droege, M. Veit, and J. Gibbs were extremely helpful with bee identification. This work was funded by the USDA Natural Resources Conservation Service Conservation Effects Assessment Program, Agreement # 68-7482-13-519. Additional funding was provided by the USDA Forest Service Northern Research Station. We would also like to thank K. McGarigal, B. Byers, A. Vitz, J. Grogan, and one anonymous reviewer for their comments on previous drafts of this manuscript. The Massachusetts Department of Conservation and Recreation and Harvard Forest provided access to field sites.

Appendix A. Bees collected using bowl traps in early spring, mid-summer, and late summer in 30 forest openings and adjacent mature forest in western Massachusetts, USA in 2014 and 2015.

Species	Opening		Forest		Total	Orig ^a	Nest ^b	Diet ^c	Soc ^d
	2014	2015	2014	2015					
Colletidae									
<i>Colletes inaequalis</i>	3	0	0	0	3	N	S	P	S
<i>Hylaeus affinis</i>	1	0	0	0	1	N	C	P	S
<i>Hylaeus modestus</i>	1	2	0	0	3	N	C	P	S
Halictidae									
<i>Augochlorella aurata</i>	269	79	13	7	368	N	S	P	E
<i>Augochlora pura</i>	9	8	2	0	19	N	SW	P	S
<i>Agapostemon virescens</i>	1	0	0	1	2	N	S	P	S
<i>Sphecodes coronus</i>	4	0	2	0	6	N	S	P	P
<i>Sphecodes mandibularis</i>	0	3	0	0	3	N	S	P	P
<i>Sphecodes townesi</i>	3	0	1	0	4	N	S	P	P
<i>Halictus rubicundus</i>	3	1	3	0	7	N	S	P	E
<i>Lasioglossum acuminatum</i>	4	2	3	2	11	N	S	P	S
<i>Lasioglossum athabascense</i>	1	0	0	0	1	N	S	P	S
<i>Lasioglossum atwoodi</i>	4	1	1	0	6	N	S	P	E
<i>Lasioglossum coeruleum</i>	14	26	17	30	87	N	SW	P	E
<i>Lasioglossum coriaceum</i>	11	3	5	2	21	N	S	P	S
<i>Lasioglossum cressonii</i>	26	9	6	3	44	N	SW	P	E
<i>Lasioglossum ephialtum</i>	29	4	3	1	37	N	S	P	E
<i>Lasioglossum foxii</i>	0	0	1	0	1	N	S	P	S
<i>Lasioglossum laevisimum</i>	2	1	1	0	4	N	S	P	E
<i>Lasioglossum leucozonium</i>	1	0	0	0	1	E	S	P	S
<i>Lasioglossum nelumbonis</i>	1	0	0	0	1	N	S	O	S
<i>Lasioglossum nigroviride</i>	6	0	0	0	6	N	S	P	E
<i>Lasioglossum oblongum</i>	4	0	1	2	7	N	SW	P	E
<i>Lasioglossum planatum</i>	14	29	6	6	55	N	S	P	E
<i>Lasioglossum quebecense</i>	11	1	11	2	25	N	S	P	S
<i>Lasioglossum subviridatum</i>	44	37	30	33	144	N	SW	P	E
<i>Lasioglossum taylorae</i>	66	53	15	4	138	N	S	P	E
<i>Lasioglossum tegulare</i>	2	2	0	1	5	N	S	P	E
<i>Lasioglossum versans</i>	10	0	18	4	32	N	S	P	E
<i>Lasioglossum versatum</i>	2	0	0	0	2	N	S	P	E
<i>Lasioglossum viridatum</i>	4	1	0	0	5	N	S	P	E
<i>Lasioglossum spp.</i>	25	44	9	18	96				
Andrenidae									
<i>Andrena bradleyi</i>	6	2	0	0	8	N	S	O	S
<i>Andrena carlini</i>	74	32	23	30	159	N	S	P	S
<i>Andrena carolina</i>	3	1	0	1	5	N	S	O	S
<i>Andrena cressonii</i>	3	0	0	0	3	N	S	P	S
<i>Andrena forbesii</i>	1	0	0	0	1	N	S	P	S
<i>Andrena frigida</i>	1	0	0	0	1	N	S	O	S

(continued on next page)

Appendix A. (continued)

Species	Opening		Forest		Total	Orig ^a	Nest ^b	Diet ^c	Soc ^d
	2014	2015	2014	2015					
<i>Andrena imitatrix</i>	2	1	1	0	4	N	S	P	S
<i>Andrena mandibularis</i>	2	0	1	0	3	N	S	P	S
<i>Andrena melanochroa</i>	2	0	0	0	2	N	S	O	S
<i>Andrena nigrihirta</i>	1	3	0	0	4	N	S	P	S
<i>Andrena rufosignata</i>	15	2	3	2	22	N	S	P	S
<i>Andrena rugosa</i>	6	0	7	0	13	N	S	P	S
<i>Andrena tridens</i>	9	0	8	0	17	N	S	P	S
<i>Andrena uvulariae</i>	31	17	10	28	86	N	S	O	S
<i>Andrena vicina</i>	40	1	3	0	44	N	S	P	S
<i>Andrena violae</i>	1	3	1	1	6	N	S	O	S
<i>Andrena wilkella</i>	0	1	0	0	1	E	S	P	S
<i>Andrena spp.</i>	0	2	0	0	2				S
Megachilidae									
<i>Hoplitis producta</i>	0	1	0	0	1	N	P	P	S
<i>Osmia atriventris</i>	73	71	21	6	171	N	C	P	S
<i>Osmia bucephala</i>	0	2	0	0	2	N	C	P	S
<i>Osmia cornifrons</i>	1	6	0	9	16	E	C	P	S
<i>Osmia georgica</i>	0	1	0	0	1	N	C	P	S
<i>Osmia inspergens</i>	3	2	0	0	5	N	C	P	S
<i>Osmia lignaria</i>	0	1	0	0	1	N	C	P	S
<i>Osmia proxima</i>	0	1	0	0	1	N	C	P	S
<i>Osmia pumila</i>	31	82	6	14	133	N	C	P	S
<i>Osmia virga</i>	2	5	0	0	7	N	C	O	S
Apidae									
<i>Ceratina calcarata</i>	27	123	1	15	166	N	P	P	S
<i>Ceratina calcarata/dupla</i>	1	0	0	0	1	N	P	P	S
<i>Ceratina dupla</i>	32	65	0	5	102	N	P	P	S
<i>Ceratina mikmaqi</i>	3	4	1	1	9	N	P	P	S
<i>Nomada armatella</i>	0	1	0	0	1	N	S	P	P
<i>Nomada composita</i>	2	0	1	0	3	N	S	P	P
<i>Nomada cressonii</i>	3	0	3	0	6	N	S	P	P
<i>Nomada depressa</i>	4	1	3	1	9	N	S	P	P
<i>Nomada gracilis</i>	4	1	0	1	6	N	S	P	P
<i>Nomada gracilis/xanthura</i>	1	0	0	0	1	N	S	P	P
<i>Nomada illinoensis</i>	0	1	0	0	1	N	S	P	P
<i>Nomada imbricata</i>	2	2	0	0	4	N	S	P	P
<i>Nomada luteoloides</i>	43	11	8	5	67	N	S	P	P
<i>Nomada maculata</i>	353	70	23	10	456	N	S	P	P
<i>Nomada pygmaea</i>	12	5	3	4	24	N	S	P	P
<i>Nomada sayi/illinoensis</i>	11	0	0	0	11	N	S	P	P
<i>Nomada spp. (bidentate)^e</i>	117	25	15	17	174		S	P	P
<i>Bombus bimaculatus</i>	3	2	1	2	8	N	C	P	E
<i>Bombus impatiens</i>	20	5	2	2	29	N	C	P	E
<i>Bombus perplexus</i>	0	0	1	0	1	N	C	P	E
<i>Bombus sandersoni</i>	8	3	4	0	15	N	C	P	E
<i>Bombus sandersoni/vagans</i>	1	0	1	0	2	N	C	P	E
<i>Bombus vagans</i>	9	3	2	3	17	N	C	P	E
Unknown	1	0	0	0	1				
Total	1539	865	301	273	2978				

^a Origin of species: exotic (E) or native (N).^b Nest substrate: cavity (C), pith (P), soil (S), soft wood (SW).^c Pollen-specificity: polylectic (P) or oligolectic (O).^d Sociality: eusocial (E), solitary (S), and parasitic (P).^e Bidentate *Nomada* that are not of the species *N. maculata* and could not be determined due to incomplete taxonomy.

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