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Bee Assemblages in Managed Early-successional Habitats in Southeastern New Hampshire

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and David I. King⁴

Abstract - We examined the abundance and species richness of bees at 10 sites managed for *Sylvilagus transitionalis* (New England Cottontail Rabbit) in southeastern New Hampshire. In 2015, we sampled bees using a streamlined bee-monitoring protocol (SBMP) developed for rapid assessment of bee communities, and in 2015 and 2016, we employed bee bowls (modified pan traps) painted fluorescent blue, yellow, or white and filled and with soapy water that were intended to mimic flower colors and attract bees. We compared the abundance of all species combined and species richness among management treatments (clearcuts, old fields, and gravel pits), patch area, and time since management action. We also compared the combined captures from bee bowls to relative abundance indices from the SBMP, as well as flower abundance and richness. Neither captured bee abundance nor species richness differed among management treatments; however, by removing a possible outlier, both abundance and richness were greatest in gravel pits compared to other habitats. There was no correlation between bee captures and the SBMP, and no correlation between captures and flower abundance or floral diversity. Our study demonstrates that habitats managed for New England Cottontail support a diverse assemblage of native bees. Gravel pits are potentially valuable targets for native bee conservation, but old fields and clearcuts offer alternatives in landscapes without gravel pits. Native bees are essential to support ecosystem function, and understanding their distribution and natural history is important to develop habitat-management efforts that benefit not only bees but multiple species of conservation concern within early-successional habitats.

Introduction

Native bees are key components of biodiversity and ecosystem health. Over 85% of flowering plants found worldwide rely on insects or other animals to transport pollen required for successful reproduction (Ollerton et al. 2011). Insects are by far the most important animal pollinators (~90% of angiosperms are pollinated by insects; Schoonhoven et al. 1998), and among insects, bees (Hymenoptera: Anthophila) are the most important pollinator group; many species have specialized structures for collecting and transporting pollen required to provision their young (Danforth et al. 2006, Michener 2007, Winfree 2010). As a result, pollinators are vital to agriculture and support the structure and function of natural communities. Recent declines of managed *Apis* spp. (honey bees; NRC 2007), and some wild bee populations, have

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been observed worldwide (e.g., Bartomeus et al. 2013, Biesmeijer et al. 2006, Goulson and Nicholls 2016). In the northeastern US, the genus *Bombus* seems particularly affected (Cameron et al. 2011, Colla and Packer 2008, Goulson et al. 2008). These declines have prompted substantial activity to understand the causes (e.g., NRC 2007) and to identify approaches that may restore or enhance bee communities (e.g., ToniETTO et al. 2017, Winfree 2010, Wratten et al. 2012).

Many environmental and human-caused factors (e.g., habitat degradation, fragmentation, invasive species, introduced diseases, pesticide use, and climate variation) affect the abundance and distribution of the ~20,000 described species of bees (Ascher and Pickering 2012, Potts et al. 2010), of which roughly 4000 species of bees are known from North America. A meta-analysis by Winfree et al. (2009) of responses by bees to human disturbances found that habitat loss and fragmentation had a substantial negative effect on native-bee abundance and species richness; however, some disturbances, including grazing, fire, and logging, can have a positive effect on species richness and abundance. These positive responses suggest that habitats altered by management actions such as clearcutting, mowing, or plantings may benefit bees by providing floral resources within the flight range of suitable nesting sites (Cane 2001). However, restoration activities may influence bee communities by selecting for bees with specific life-history traits, such as aboveground or belowground-nesting bees, or excluding bees sensitive to disturbance (Tonietto et al. 2017, Williams 2011).

In forest-dominated regions, the abundance and diversity of bees can vary with patch size (Rubene et al. 2015) and among seral stages (Taki et al. 2013), suggesting that bees are likely responding to biotic (e.g., plant species composition) and abiotic (e.g., soil moisture and temperature) features that change with forest succession. The northeastern US is dominated by forests that are subjected to natural and human-caused disturbances (Lull 1968). Intensity and frequency of those disturbances affect succession (Lorimer and White 2003), and thus influence the structure (Aber 1979) and plant species composition (Howard and Lee 2003) of these forests. Recently, attention has focused on shrub-dominated and young-forested habitats that are in short supply in the Northeast because a variety of vertebrates and invertebrates, including several species of conservation concern, are dependent on these habitats (Litvaitis et al. 1999). As a result, governmental (Natural Resources Conservation Service [NRCS], US Fish and Wildlife Service, and state fish and wildlife agencies) and non-governmental organizations (e.g., Environmental Defense Fund, National Fish and Wildlife Foundation, National Wild Turkey Federation, Wildlife Management Institute, and local land trusts) have been working to increase the availability of these vegetation types (Warren et al. 2016). For example, there are currently efforts underway to develop and maintain >20,000 ha of early-successional forests or shrub-dominated habitat specifically to benefit *Sylvilagus transitionalis* Bangs (New England Cottontail Rabbit; hereafter, NEC), a species of conservation concern, on public and private lands (Fuller and Tur 2012).

We were interested in understanding how early-successional habitats managed for NEC may affect local bee communities. Examining the patterns of bee

abundance and species richness in managed early-successional habitats in comparison to such parameters as habitat treatment (e.g., cutting forests, mowing of old fields, and gravel-pit reclamation), size of managed area, and time-since-management treatment can aid in developing conservation programs that maintain habitats for bees and other target species. Additionally, we were interested in identifying a bee-sampling protocol that can be applied to the large number of habitats being managed for NEC. Therefore, our specific objectives were to: (1) examine bee abundance and diversity in relation to habitat treatment because we suspected floral (and nesting) resources used by bees would vary by treatment, (2) analyze bee abundance and richness as a function of patch area and time (years) since treatment, (3) examine the relationship between bee abundance and floral abundance and richness, and (4) compare 2 methods used to inventory bee communities.

Study Area

We conducted this study at 10 sites in Strafford County, NH, that were undergoing management prescriptions designed to support NEC (Table 1, Fig. 1). These sites are owned by either private citizens or townships and were voluntarily enlisted in programs supervised by NRCS personnel to create habitats suitable for NEC.

Strafford County consists of a mix of second-growth forests, idle and active agricultural lands, and suburban and urban development (Johnson et al. 2006). Common overstory species include *Acer* spp. (maples), *Quercus* (oaks), *Pinus strobus* L. (Eastern White Pine), and *Tsuga canadensis* L. (Eastern Hemlock). Among old fields and regenerating forests, the groundcover is comprised of native and introduced grasses and forbs, especially *Solidago* spp. (goldenrods), *Asclepias* spp. (milkweeds), *Vicia* spp. (vetches), *Daucus carota* (Queen Anne's Lace), and *Potentilla* spp. (cinquefoils). Native shrubs include *Viburnum* spp. (viburnums), *Cornus* spp. (dogwoods), and *Juniperus communis* L. (Ground Juniper). Invasive

Table 1. Characteristics of 10 early-successional sites in Strafford County, NH, where bees were inventoried during 2015 and 2016. Time since treatment refers to number of years prior to 2015 treatment last occurred.

Site	Original habitat	Treatment	Time since treatment (y)	Size (ha)
CC-1	Forest	Clearcut	4	3.7
CC-2	Forest	Clearcut	2	3.3
CC-3	Forest	Clearcut	2	8.0
CC-4	Forest	Clearcut (and trees left at site)	4	2.9
OF-1	Old Field	Excavator-mounted mower, re-set to young forest and large shrubs	3	5.8
OF-2	Old Field	Excavator-mounted mower, re-set to young forest and large shrubs	1	10.1
OF-3	Old Field	Excavator-mounted mower, re-set to young forest and large shrubs	4	3.1
OF-4	Old Field	Selective cutting and herbicide control	4	6.8
GP-1	Gravel Pit	Tree and shrub plantings and wetland restoration	6	7.6
GP-2	Gravel Pit	Tree and shrub plantings	4	6.8

shrubs include *Eleagnus umbellata* (Autumn Olive), *Rosa multiflora* (Multiflora Rose), *Frangula alnus* Mill. (Glossy Buckthorn), *Rhamnus cathartica* L. (Common Buckthorn), and *Euonymus alatus* Thunb. (Burning Bush) (Johnson et al. 2006), though we did not encounter the latter 2 species on our sampling transects. The reversion of agricultural land to forest and the growing human population of southeastern New Hampshire have caused a marked decline in early-successional habitats in this region (Litvaitis 1993), hence, the need to increase their abundance because this region is one of 2 areas in New Hampshire where NEC still occur (Tash and Litvaitis 2006).

We classified study sites as 1 of 3 major categories: recently cut second-growth forests, old fields that were managed by mowing to prevent canopy closure and increase woody-stem density, and depleted gravel mines that have had some level of restoration, including seeding and planting pollinator-friendly plants, such as *Chamaecrista fasciculata* Michx. (Partridge Pea) and *Rudbeckia hirta* (Black-eyed Susan) (Mader et al. 2011). Time since last treatment varied from 2 to 8 y at the initiation of the study. All sites were dominated by herbaceous plants, young trees, and shrubs. We considered these areas attractive to bees because they provided habitat features necessary for their survival, including an abundance of flowering plants as forage and a variety of nesting sites (e.g., exposed soil, pithy stems of forbs and shrubs, beetle burrows in trees, and decaying wood in slash piles).

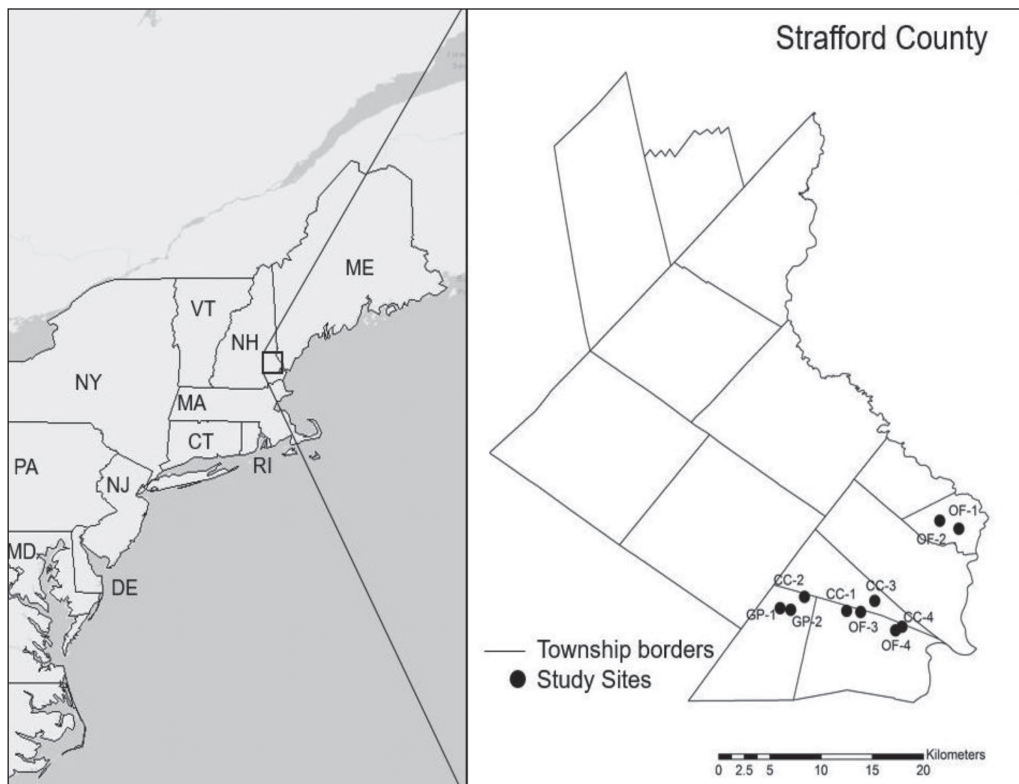


Figure 1. Location of 10 sites in southeastern New Hampshire used to examine bee responses to managed early-successional habitats during 2015 and 2016.

Methods

Bee sampling

We employed 2 methods to sample bees. We deployed bee bowls along established transects following LeBuhn et al. (2003) and followed a streamlined bee-monitoring protocol (SBMP) for assessing pollinator habitat (Ward et al. 2014). We established transects within each opening at least 100 m from the treatment edge. We used these transects for both bee bowls (2015 and 2016) and SBMP (2015). Bee bowls consisted of 100-ml plastic bowls left unpainted (white) or painted fluorescent blue or yellow and filled two-thirds full with soapy water. At each site, we distributed a total of 15 bowls at 3-m intervals along a transect, alternating the 3 colors. Bowl colors were selected to mimic flowers that attract pollinators (Campbell and Hanula 2007). We left bee bowls out for 24 h to ensure capture of bees active at different times of the day (LeBuhn et al. 2003). For each transect, we combined the contents of all bowls into a single sample and placed the bees in a plastic Whirl-Pak[®] bag with 70% ethanol. We took all specimens to the lab, where they were washed, dried, pinned, labeled, and identified. We deployed bee bowls on 3 occasions throughout the growing season (June, August, and late September/early October) in 2015 and 2016 to collect bee species that are active at different times of the year. We deployed bowls at the same locations both years during fair weather with no rain or high winds and ambient temperatures ≥ 15.5 °C. When possible, we identified to species bee specimens collected in bowls, or to genera for species for which accurate keys are not yet available or for specimens that were in poor condition. J. Milam, who has experience with bee identification, used a variety of keys, both online (Discoverlife.org) and print (e.g., Gibbs 2010, 2011; Mitchell 1962) to identify our specimens. We sent specimens that required additional expertise to taxonomists Michael Veit (Pepperell, MA) and Sam Droege (USGS Patuxent Wildlife Research Center, Laurel, MD) for identification. Specimens were deposited in the University of New Hampshire Insect Collection (Durham, NH). We summarized behavioral traits associated with nesting, sociality, and foraging behavior (polylectic or oligolectic) by species, based on information on North American bees (Giles and Ascher 2006, Goldstein and Ascher 2016, Hurd 1979). We included in the total species count but excluded from analysis *Apis mellifera* (European Honey Bee, hereafter Honey Bee) captured in bowls because their response to treatments is confounded by the placement of hives by farmers, as well as to allow for comparison with the transect captures. For the same reason, we excluded Honey Bees from the SBMP totals.

The SBMP recorded the number of bees visiting flowers along two 30.5-m transects established at each of the 10 sites in 2015. Although this approach does not identify bees to species or provide ecological or behavioral data, it does provide a measure of bee diversity and abundance (Ward et al. 2014). Monitoring can evaluate the performance of restoration practices across space and time and amongst habitat actions, ages, and sizes. We monitored transects on the same dates that we deployed the bee bowls (June, August, and late September/early October, respectively). During each visit, we monitored the 2 transects for 7.5 min each for a total of 15 minutes per site by recording the number of native bees observed on

the reproductive structures of a flower for more than 0.5 second within 1 m of each of the two 30.5-m transects. We recorded native bees as present but did not identify them to species.

Relative abundance of flowering plants

During the SBMP, we identified to species flowering plants known to support bees (Lee-Mäder et al. 2016, Mader et al. 2011, Vaughan et al. 2015) along each transect and then ranked them by relative abundance, where 1 = low, 2 = medium, and 3 = high. We summed these ranks over all plant species for each site, and used the summed values to rank the sites in terms of floral abundance (Ward et al. 2014). We also used bee counts from SBMP to rank sites following Ward et al. (2014) and employed these ranks in comparisons with those obtained from captures in bowls.

Data analyses

We calculated bee abundance for each site as the number of bees collected in bee bowls. Bee abundance was calculated for all species combined, as well as for bee species comprising >3% of all bees captured; a smaller sample size would subject analyses to potentially spurious results. We estimated bee species richness for each site using the program SPECRICH (<http://www.mbr-pwrc.usgs.gov/software/specrich.html>) to compensate for the influence of different capture rates among sites and treatments on species richness estimates.

We tested bee abundance and richness for normality, compared them among treatments using one-way analysis of variance (ANOVA) and employed least-squares regression with respect to patch-size (based on continuity of understory vegetation) and time since treatment. We compared the abundance of individual bee species relative to treatment, patch size, and time since treatment using generalized linear models with either a Poisson or negative binomial distribution, as appropriate. These analyses included a term for year interaction, and in cases where interaction terms were not significant, we summed abundance of all bees combined over years, and averaged richness over years.

We compared ranks of captures from bee bowls to ranks based on SBMP counts using Spearman-rank correlations. We also compared ranks of bee captures to relative floral abundance and richness using Spearman-rank correlations.

Results

We captured a total of 968 individual bees in bowls, representing 78 species, 5 families, 22 genera, and 2 morphospecies (Table 2). For analyses, we treated morphospecies as a single species, although this method may have underrepresented the total number of species captured because, at this time, it is unknown how many species are represented within morphospecies group designations. We identified all other individuals to species, except for those for which the taxonomy is poorly defined and could not be resolved with existing keys, including female *Hylaeus* keyed to nr.-*H. affinis* ($n = 41$) and bidentate *Nomada* keyed to bidentate non-*maculata* ($n = 2$). Species captured spanned a range of ecological and life-history

Table 2. Bees captured in bowl traps at 10 shrubland sites that included 4 clearcuts (CC), 2 reclaimed gravel pits (GP), and 4 old fields (OF) in southeastern New Hampshire during 2015 and 2016. [Table continued on following page.]

Species	2015			2016			Total
	CC	GP	OF	CC	GP	OF	
Colletidae							
<i>Colletes americanus</i> Cresson	0	1	0	0	2	0	3
<i>Hylaeus (Prosopis) affinis</i> (Smith) (males)	1	0	2	0	3	2	8
<i>Hylaeus</i> female keys to nr. <i>affinis</i>	1	3	8	6	11	12	41
<i>Hylaeus (Prosopis) modestus</i> Say (males)	1	0	1	1	0	0	3
Halictidae							
<i>Augochlorella aurata</i> (Smith)	25	12	14	33	12	27	123
<i>Augochloropsis (Paraugochloropsis) metallica</i> (Fabricius)	2	0	0	2	0	0	4
<i>Agapostemon (Agapostemon) texanus</i> Cresson	1	3	0	3	3	1	11
<i>Agapostemon (Agapostemon) virescens</i> (Fabricius)	1	0	1	8	12	4	26
<i>Sphecodes cressonii</i> (Robertson)	0	0	0	0	0	1	1
<i>Sphecodes davisii</i> Robertson	0	0	0	0	1	0	1
<i>Sphecodes illinoensis</i> (Robertson)	0	0	0	0	1	0	1
<i>Sphecodes mandibularis</i> Cresson	0	1	0	0	0	0	1
<i>Sphecodes ranunculi</i> Robertson	0	1	1	0	0	0	2
<i>Sphecodes townesi</i> Mitchell	0	0	0	1	0	0	1
<i>Halictus (Odontalictus) ligatus</i> Say	6	13	4	34	65	16	138
<i>Halictus (Protohalictus) rubicundus</i> (Christ)	1	1	0	0	0	0	2
<i>Halictus (Seladonia) confusus</i> Smith	1	1	1	1	6	1	11
<i>Lasioglossum (Lasioglossum) acuminatum</i> McGinley	0	0	0	1	1	0	2
<i>Lasioglossum (Lasioglossum) coriaceum</i> (Smith)	21	2	25	15	10	10	83
<i>Lasioglossum (Leuchalictus) leucozonium</i> (Schrank)	0	0	0	1	3	3	7
<i>Lasioglossum (Dialictus) atwoodi</i> Gibbs	0	0	1	0	0	0	1
<i>Lasioglossum (Dialictus) bruneri</i> (Crawford)	1	0	0	0	0	0	1
<i>Lasioglossum (Dialictus) cressonii</i> (Robertson)	4	0	27	5	1	4	41
<i>Lasioglossum (Dialictus) ephialtum</i> Gibbs	0	0	0	1	0	0	1
<i>Lasioglossum (Dialictus) fattigi</i> (Mitchell)	0	0	1	0	0	0	1
<i>Lasioglossum (Dialictus) hitchensi</i> Gibbs	1	0	0	0	0	0	1
<i>Lasioglossum (Dialictus) imitatum</i> (Smith)	0	0	0	0	1	0	1
<i>Lasioglossum (Dialictus) katherineae</i> Gibbs	0	0	0	1	0	0	1
<i>Lasioglossum (Dialictus) laevisimum</i> (Smith)	0	0	0	1	0	4	5
<i>Lasioglossum (Dialictus) leucocomum</i> (Lovell)	0	4	0	2	12	0	18
<i>Lasioglossum (Dialictus) oblongum</i> (Lovell)	0	0	0	0	1	0	1
<i>Lasioglossum (Dialictus) oceanicum</i> (Cockerell)	0	0	0	0	2	0	2
<i>Lasioglossum (Dialictus) pilosum</i> (Smith)	0	27	0	0	12	1	40
<i>Lasioglossum (Dialictus) taylorae</i> Gibbs	0	0	0	1	0	0	1
<i>Lasioglossum (Dialictus) tegulare</i> (Robertson)	9	2	3	10	0	4	28
<i>Lasioglossum (Dialictus) versans</i> (Lovell)	0	0	0	0	0	1	1
<i>Lasioglossum (Dialictus) versatum</i> (Robertson)	19	0	9	7	0	28	63
<i>Lasioglossum (Dialictus) weemsi</i> (Mitchell)	2	0	1	0	0	0	3
<i>Lasioglossum (Hemihalictus) birkmanni</i> (Crawford)	0	0	1	0	0	0	1
<i>Lasioglossum (Hemihalictus) foxii</i> (Robertson)	1	0	1	0	0	0	2
<i>Lasioglossum (Hemihalictus) macoupinense</i> (Robertson)	0	0	2	0	0	0	2
<i>Lasioglossum (Hemihalictus) pectorale</i> (Smith)	3	2	4	3	8	2	22
<i>Lasioglossum (Sphecodogastra) oenotherae</i> (Stevens)	1	0	0	0	0	0	1
<i>Lasioglossum (Sphecodogastra) quebecense</i> (Crawford)	1	0	3	0	0	3	7

traits, including soil nesters (55.7%) and cleptoparasites (15.2%; bees that do not collect pollen or build a nest, rather they lay their eggs in the nests of other “host” bee species). Cavity-, pithy-stem-, and soft-wood–nesting bees made up 13.9%, 7.6%, and 2.5%, respectively, while 5.1% were those that establish annual hives. Behavior types included solitary (41.8%), eusocial (34.2%), parasitic (15.2%), solitary–communal (6.4%), and subsocial (5.1%). Oligolectic bees were uncommon

Table 2, continued.

Species	2015			2016			Total
	CC	GP	OF	CC	GP	OF	
Andrenidae							
<i>Andrena (Cnemidandrena) canadensis</i> Dalla Torre	0	0	0	1	0	0	1
<i>Andrena (Holandrena) cressonii</i> Robertson	1	0	2	0	0	0	3
<i>Andrena (Melandrena) carlini</i> Cockerell	2	2	4	1	0	0	9
<i>Andrena (Melandrena) nivalis</i> Smith	2	0	2	1	0	0	5
<i>Andrena (Melandrena) vicina</i> Smith	0	1	0	1	0	0	2
<i>Andrena (Ptilandrena) distans</i> Provancher	3	0	2	0	0	0	5
<i>Andrena (Simandrena) nasonii</i> Robertson	1	0	2	0	0	1	4
Megachilidae							
<i>Anthidium (Proanthidium) oblongatum</i> (Illiger)	0	2	0	0	0	0	2
<i>Stelis (Stelis) lateralis</i> Cresson	0	0	1	0	0	0	1
<i>Hoplitis (Alcidamea) pilosifrons</i> (Cresson)	0	1	0	0	0	0	1
<i>Hoplitis (Alcidamea) producta</i> (Cresson) 2	0	0	3	1	6	12	
<i>Hoplitis (Alcidamea) spoliata</i> (Provancher)	0	0	0	1	0	0	1
<i>Osmia (Melanosmia) atriventris</i> Cresson	0	0	1	0	0	0	1
<i>Osmia (Melanosmia) bucephala</i> Cresson	1	0	0	0	0	0	1
<i>Osmia (Melanosmia) pumila</i> Cresson	0	0	0	0	0	1	1
<i>Megachile (Litomegachile) brevis</i> Say	1	1	0	0	1	0	3
<i>Megachile (Litomegachile) mendica</i> Cresson	0	0	0	1	1	0	2
<i>Megachile (Megachile) montivaga</i> Cresson	0	0	0	0	0	1	1
<i>Megachile (Xanthosaurus) gemula</i> Cresson	1	0	0	0	0	1	2
<i>Coelioxys (Boreocoelioxys) octodentata</i> Say	0	1	0	0	0	0	1
Apidae							
<i>Ceratina (Zadontomerus) calcarata</i> Robertson	8	2	8	12	13	31	74
<i>Ceratina (Zadontomerus) dupla</i> Say	4	2	4	3	6	25	44
<i>Ceratina (Zadontomerus) mikmaqi</i> Rehan and Sheffield	6	2	9	3	3	8	31
<i>Nomada articulata</i> Smith	0	0	1	1	0	0	2
<i>Nomada bidentate non-maculata</i>	1	0	0	1	0	0	2
<i>Nomada luteoloides</i> Robertson	0	0	1	0	0	0	1
<i>Triepeolus pectoralis</i> (Robertson)	0	0	0	1	0	0	1
<i>Melissodes (Eumelissodes) druriellus</i> (Kirby)	0	0	1	0	0	0	1
<i>Melissodes (Eumelissodes) illatus</i> Lovell and Cockerell	0	0	0	0	0	1	1
<i>Melissodes (Melissodes) bimaculata</i> (Lepeletier de Saint Fargeau)	1	0	0	0	0	0	1
<i>Peponapis (Peponapis) pruinosa</i> (Say)	1	1	0	0	0	0	2
<i>Bombus (Pyrobombus) bimaculatus</i> Cresson	0	0	1	0	0	0	1
<i>Bombus (Pyrobombus) impatiens</i> Cresson	0	0	0	8	3	2	13
<i>Bombus (Pyrobombus) vagans</i> Smith	0	0	0	1	0	0	1
<i>Apis (Apis) mellifera</i> L.	5	0	5	1	6	4	21

(6 species). We captured 2 naturalized exotic species: Honey Bees (2.2% of total bees), most likely from managed hives and not from feral colonies, and the adventive *Lasioglossum leucozonium* (a solitary sweat bee; 0.72% of total bees), a species introduced from Europe and northern China (Zayed et al. 2007.) We collected 2 specimens of the mason bee *Anthidium oblongatum* (0.2% of total bees), an aggressive species native to Europe that was first detected in North America in 1963 (Hoebeke and Wheeler 1999, Jaycox 1967) and has rapidly spread throughout North America (Maier 2009).

Capture rates varied by year, with the greatest number of captures in 2015 ($n = 384$) in early June followed by mid-August, and late September (224, 105, and 55, respectively), compared to 2016 ($n = 584$) (185, 131, and 268, respectively). Both abundance and species richness of bees captured in bowls were normally distributed and treatment * year interaction terms were not significant ($P > 0.05$); thus, we combined data over years and examined differences among treatments with ANOVA. There were no differences among treatments in either abundance ($F_{(2)}=1.30$, $P = 0.33$) or richness ($F_{(2)}=0.75$, $P = 0.50$) (Fig. 2). However, examination of the residuals suggested 1 site (CC-3) was potentially an outlier (Cook's $D > 4/n$; Bollen and Jackman 1990). With that site removed, the difference in abundance ($F_{(2)} = 4.84$, $P = 0.056$) and richness ($F_{(2)} = 4.57$, $P = 0.062$) among treatments was nearly significant, with abundance greater in gravel pits compared to clearcuts ($t_{(2)} = -3.11$, $P = 0.02$), and marginally greater in gravel pits than old fields ($t_{(2)} = -2.07$, $P = 0.08$). Similarly, species richness was also greater in gravel pits compared to clearcuts ($t_{(2)} = -3.02$, $P = 0.02$), although not different from old fields ($t_{(2)} = 1.79$, $P = 0.12$).

Ten bee species met the threshold of 3% of total captures, and we compared their abundance among treatments (Fig. 3). There was a significant treatment * year interaction for *Lasioglossum coriaceum*, so we analyzed the abundance of this species separately by year, and showed that abundance differed among treatments

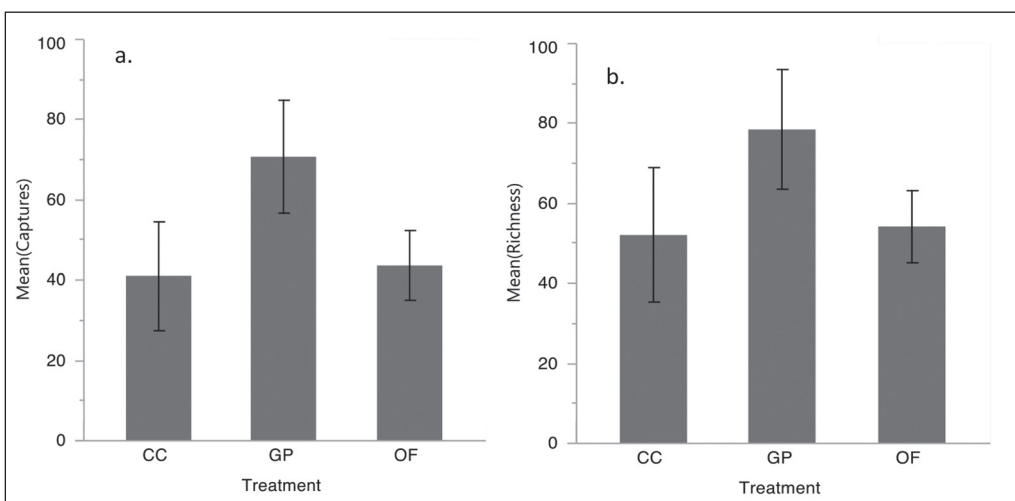


Figure 2. (a) Average bee captures and (b) species richness among clearcuts (CC), reclaimed gravel pits (GP), and old fields (OF) in southeastern New Hampshire, 2015 and 2016 combined.

in 2015 (Wald $\chi_{(2)}^2 = 6.22$, $P = 0.01$) with multiple comparisons indicating that their numbers were greater in old fields than gravel pits ($t_{(2)} = -2.49$, $P = 0.04$) and marginally higher in clearcuts than gravel pits ($t_{(2)} = -2.24$, $P = 0.06$). Abundance of *L. coriaceum* did not differ among treatments in 2016 ($\chi_{(2)}^2 = 2.43$, $P = 0.30$). There were no treatment * year interactions for any of the other species, so they were analyzed for years combined. Abundance of *L. cressonii* differed among treatments ($\chi_{(2)}^2 = 16.6$, $P < 0.001$), and multiple comparisons showed that their numbers were greater in old fields than clearcuts ($t_{(2)} = -3.27$, $P = 0.003$) or gravel pits ($t_{(2)} = -2.70$, $P = 0.01$; Fig. 3). Abundance of *L. tegulare* (Epaulette Metallic Sweat Bee) differed among treatments ($\chi_{(2)}^2 = 8.18$, $df = 2$, $P = 0.02$), and multiple comparisons showed their numbers were greater in clearcuts than old fields ($t_{(2)} = 2.26$, $P = 0.03$) or gravel pits ($t_{(2)} = -2.10$, $P = 0.05$). Abundance of *L. pilosum* (a sweat bee) differed among treatments ($\chi_{(2)}^2 = 27.3$, $P < 0.001$), and multiple comparisons showed that their numbers were greater in gravel pits than either old fields ($t_{(2)} = 4.70$, $P < 0.001$) or clearcuts ($t_{(2)} = -2.39$, $P = 0.02$).

During the SBMP conducted in 2015, we recorded 544 bees along transects at the 10 sites. Of these, 160 records were for Honey Bees. Average bee richness across sites was 9.9 taxa. Seasons showed variation in abundance of bees: spring = 128, summer = 232, and fall = 184. We recorded 84 species of flowering plants. Average floral richness across sites was 22.3 species. Plants with the highest relative abundance were *Rubus allegheniensis* (Blackberry), *Potentilla simplex* (Common

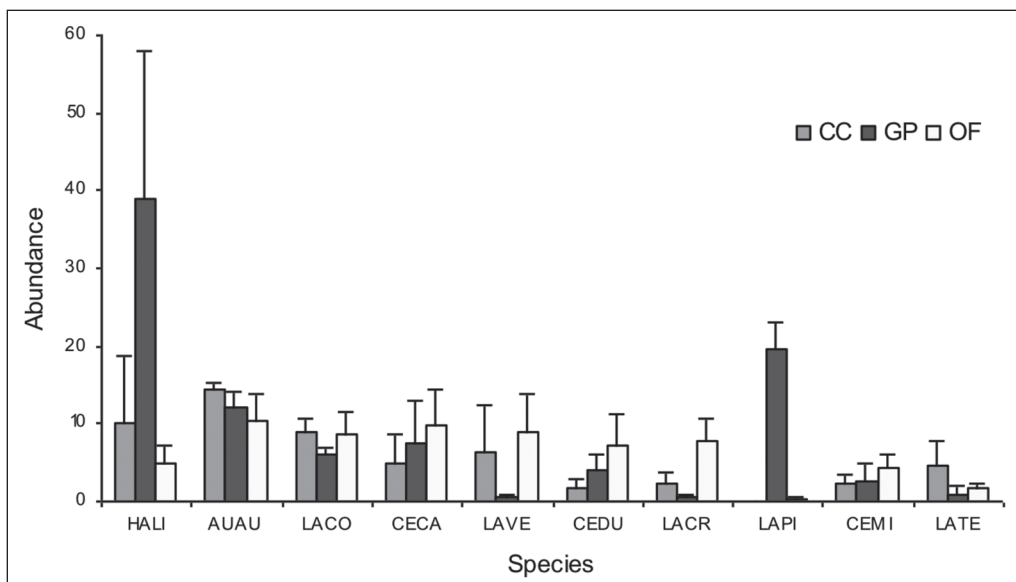


Figure 3. Captures of individual bee species comprising >3% of all captures compared among clearcuts (CC), reclaimed gravel pits (GP), and old fields (OF) in southeastern New Hampshire, years 2015 and 2016 combined. Species codes are HALI = *Halictus ligatus*, AUAU = *Augochlorella aurata*, LACO = *Lasioglossum coriaceum*, CECA = *Ceratina calcarata*, LAVE = *L. versatum*, CEDU = *C. dupla*, LACR = *L. cressonii*, LAPI = *L. pilosum*, CEMI = *C. mikmaqi*, and LATE = *L. tegulare*.

Cinquefoil), *Solidago canadensis* (Canada Goldenrod), *Solidago rugosa* (Rough Goldenrod), *Euthamia graminifolia* (Grass-leaved Goldenrod), and *Symphotrichum lateriflorum* (Calico Aster). These plants supported summer- and fall-flying bees. *Zizia aurea* (Golden Alexanders), *Viola* (violet) and *Fragaria* (strawberry) provided floral resources for spring-flying bees. We did not record flowering shrubs, such as *Salix* (willow), *Amelanchier* (shadbush), and *Vaccinium* (blueberry), that are important to bees that are out flying in early spring. A detailed summary of flower abundance is provided in Appendix 1.

There was no relationship between patch area and abundance ($F_{(1)} = 1.51, P = 0.25$) and species richness ($F_{(1)} = 3.25, P = 0.11$) (Fig. 4) or time since treatment and abundance ($F_{(1)} = 0.005, P = 0.95$) or species richness ($F_{(1)} = 0.31, P = 0.59$). There were no relationships between bee captures in bowls and counts on transects ($\rho = 0.48, n = 10, P = 0.16$; Fig. 5) or between bee captures and flower relative

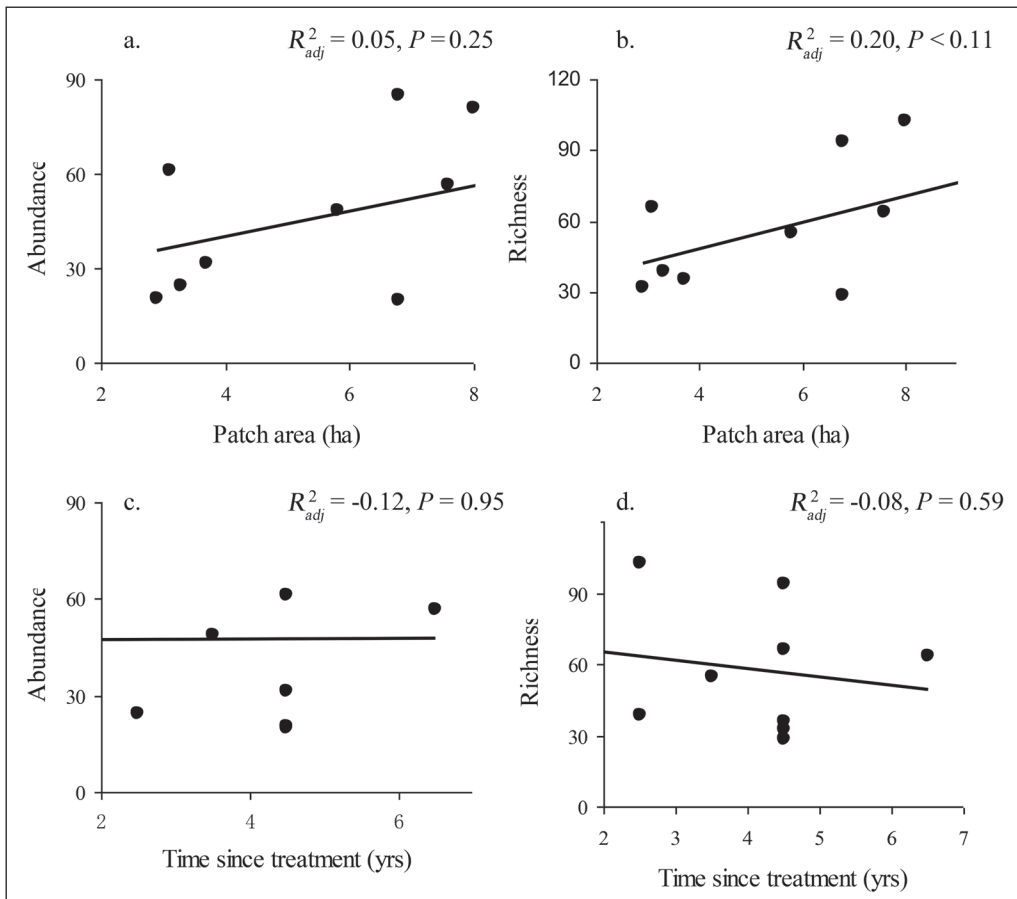


Figure 4. Bee abundance and species richness based on captures in soap-filled bowls with specific comparisons between (a) bee abundance and patch area, (b) bee species richness and patch area, (c) bee abundance and time since treatment, and (d) bee species richness and time since treatment. Comparisons are based on 10 shrubland sites in southern New Hampshire sampled during 2015 and 2016 (years combined).

abundance ($\rho = 0.28$, $n = 10$, $P = 0.43$) or flower species richness ($\rho = -0.27$, $n = 10$, $P = 0.45$).

Discussion

Early-successional habitats managed for NEC supported diverse bee communities that were similar to those reported in other studies from the region, thus validating the potential of managed habitats for pollinators. For comparison, our total of 79 species from bowl captures was similar to the 80 species collected by Roberts et al. (2017) in clearcuts in neighboring Massachusetts, and the 95 species collected at 4 pollinator-enhancement sites surveyed from 2015–2017 in Cheshire County, NH (A. Littleton, Cheshire County Conservation District, Walpole, NH, pers. comm.); but was not as numerous as the 118 bees collected from Strafford County, NH, by Tucker and Rehan (2017) and was less than half as many species (182 species)

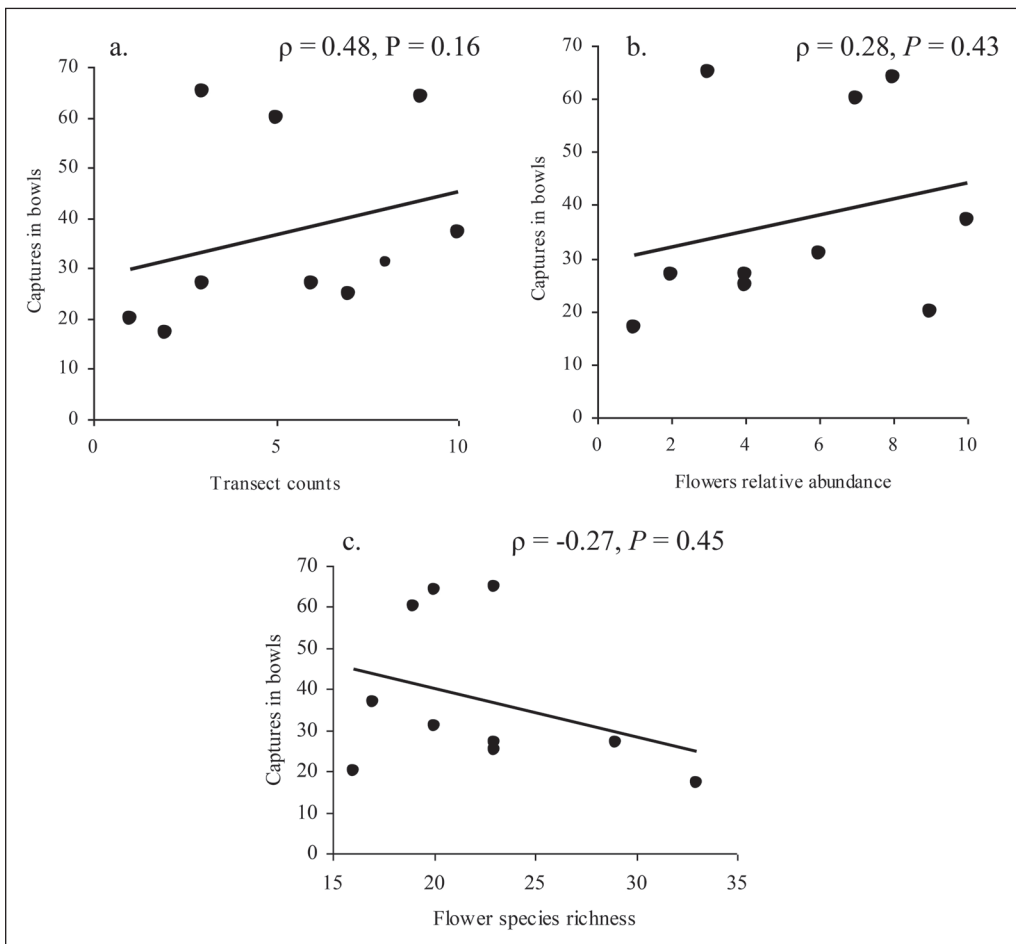


Figure 5. Rank correlations between (a) bee captures in bowls and bee counts from transects, (b) bee captures and relative abundance of flowers, and (c) bee captures and flower-species richness. Data are from 10 shrubland sites in southern New Hampshire sampled during 2015.

collected by Goldstein and Ascher (2016) on Martha's Vineyard, MA. It should be noted that our study and Roberts et al. (2017) collected bees using only bee bowls, whereas Tucker and Rehan (2017) and Goldstein and Ascher (2016) used a combination of bee bowls and net sweeping, which may account for the difference in species totals (see Grundel et al. 2011). Our findings are consistent with studies that documented a diverse range of species benefitting from management of early-successional forests and shrubland habitats including bees (Russell et al. 2005), butterflies (Berg et al. 2016), and birds (Askins et al. 2012, King and Byers 2002).

Bee-monitoring protocols

The SBMP was developed for land managers and conservationists to provide a gauge of species abundance and richness in response to habitat management without the collection and identification of specimens (Ward et al. 2014). Our findings indicate that captures in bowls and observations along transects do not yield comparable results. Observations along SBMP transects may be biased toward counts of larger, more readily observable bees. Regardless of whether observations are useful for rapid assessments, only collecting specimens (e.g., in bee bowls) will yield the type of species-specific information needed to assess life-history information and conservation status (e.g., Colla and Packer 2008) of most wild bee species that cannot be reliably identified in the field. Furthermore, museum specimens are a valuable resource that can be used to assess species' distributions and provide future opportunities for taxonomic revisions.

Role of managed habitats

Initially, we found no difference among management treatments in either bee abundance or species richness; however, subsequent analyses suggested 1 site may have been an outlier, and once eliminated, gravel pits showed higher abundance and richness in comparison to clearcuts and old fields. We did not identify any characteristic of the outlier site that would explain its influence on the analyses. The abundance and richness of bees in gravel pits was not entirely unexpected. These habitats tend to have a combination of weedy vegetation and xeric soils that may provide high-quality nesting habitat for sand-associated bees (Goldstein and Ascher 2016). However, managing gravel pits will not be a useful strategy for augmenting bee numbers in landscapes where they are not present. In those instances, other strategies would be more suitable, including maintaining old fields (Ginsberg 1983, Gixti and Packer 2006), or engaging in forest management (Roberts et al. 2017).

Among individual species reported from this study, *Lasioglossum cressonii* were more abundant in old fields than in clearcuts or gravel pits. This result was not expected because *L. cressonii* nests in soft wood that is typically abundant in clearcuts. *L. pilosum* were more abundant in gravel pits than in old fields or clearcuts, which conforms with reports of associations between this species and sandy soils (Grundel et al. 2011). *L. tegulare* were more abundant in clearcuts than old fields or gravel pits, which contrasts with the findings of Roberts et al. (2017) but is consistent with findings by Milam et al. (unpubl. data) in treated *Pinus rigida* (Pitch Pine) habitats

in Massachusetts. Although these species exhibited differences among treatments, most species did not. This apparent similarity among species could be because several of these species, including some of the most abundant ones (e.g. *Halictus ligatus* and *Augochlorella aurata*) are known to be generalists with respect to foraging resources (Goldstein and Ascher 2016), and thus would not be expected to exhibit differences among treatments.

Our findings that bee abundance and species richness are not related to patch area are consistent with other studies (Howell et al. 2017, Roberts et al. 2017). The expectation that abundance would increase in relation to patch area is largely based on studies reporting increases in abundance or occurrence of species such as birds (Chandler et al. 2009, Roberts et al. 2017). The inference of those studies is that smaller patches are not large enough to provide sufficient resources to support a variety of species. Bees are small bodied, and thus may not respond to area limitations in the range of patch sizes we examined, and the predominantly generalist species that we captured in this study may have fulfilled their resource needs in the smaller patches.

Floral abundance and diversity is clearly essential because bees rely on nectar for energy and pollen to provision their young, and it plays a role in structuring bee communities (Howell et al. 2017, Michener 2007, Potts et al. 2003). The importance of these resources has provided the basis for recommendations to increase floral abundance and duration through management practices and seeding (Eric Lee-Mäder, Pollinator Program Co-Director, The Xerces Society for Invertebrate Conservation, Portland, OR, pers. comm.). However, we did not observe a relationship among bee abundance or richness with flower abundance or richness. Similarly, Carper et al. (2014) did not find a relationship between bee abundance or richness and flower richness in 1 of 2 years of their study, which they attributed to unmeasured factors obscuring a potential relationship or the stochastic nature of floral resources.

Early-successional habitat has declined substantially in the northeastern US because of a reduction in agriculture, expanding urban and suburban developments, and modified timber harvests (Litvaitis 1993, Thompson and DeGraaf 2001). In this region, a variety of insects, birds, reptiles, and mammals are dependent on shrubby thickets and young forests (e.g., King and Byers 2002, Litvaitis 1993, Litvaitis et al. 1999).

Habitat management has the potential to provide a variety of nesting sites and abundant and diverse foraging opportunities for bees throughout their nesting and overwintering seasons. (Black et al. 2007). Historically, bees may have benefited from forest openings created by natural disturbances, such as periodic fires, ice-storm damage, high-wind events, or flooding (Potts et al. 2005, Winfree et al. 2007). Early-successional shrubland habitats have been declining throughout the Northeast due to reversion to forests from agriculture (Litvaitis 1993), alteration of natural-disturbance regimes (King and Schlossberg 2014), and loss of habitat development. As a result, areas with managed forests likely support higher bee diversity by providing a range of seral stages. All bee species require access to

pollen and nectar for energy and reproduction within flight range of suitable nesting sites (e.g., Greenleaf et al. 2007, Westrich 1996). However, the nesting habits of many bees remain unknown because nest sites are difficult to locate (Roulston and Goodell 2011). As a result, management actions to benefit bees often emphasize floral-resource enhancement rather than nest resources (Sardinas et al. 2016, Winfree 2010). Forest management can be used to support higher bee-diversity by encouraging increased abundance and diversity of flowering plants through increased ground-level light after removing canopy cover. Timber harvests can provide nesting sites in the form of bare ground, standing dead tree-snags, piles of rotting wood, and plant stems (Hanula et al. 2016, Jackson et al. 2014). A range of soil temperatures associated with managed forests also may benefit developing bee larvae (Cane 1991, Romey et al. 2007).

Importance of bees in early-successional habitats

Our study supports the growing body of research that indicates creating and managing early-successional habitats supports bees. Although, we did not find a relationship between time-since treatment and bee richness and abundance or floral diversity, the optimal age-range of early-successional habitats to support the maximum abundance of floral and nesting resources used by bees is unclear. Taki et al. (2013) looked at a range of successional stages between 1 and 178 years of age and found that early-successional stages of naturally regenerated and planted forests supported high abundance and richness of solitary bees and their associated cleptoparasites, but social bees responded differently to stand age. Black et al. (2007) suggested that periods between managed burns at a site be spaced 3–10 years apart based on their summary of studies on fire and the recovery period of pollinator populations. Similarly, Black et al. (2007) with the Xerces Society, recommended that habitat-management seek to maintain a range of early-successional stages by implementing activities in mosaic patches alternating over several years to provide refugia from habitat alteration and, thus provide time for pollinator populations to recover. Those authors recommended maintaining a range of early-successional stages at managed sites. Our records of the ecological and life-history traits for bees collected at our sites provide information on how these species may respond to anthropogenic and natural environmental habitat change (Williams et al. 2010). Supplemental planting of specific host plants for oligolectic bees may increase species richness. Likewise, additional information on how specific alterations (e.g., leaving slash piles) affect bee abundance and diversity would be useful in developing management guidelines to support a diversity of native bees.

We believe that it is important that private landowners, and local, state, and federal governments take an active role in the conservation of these habitats. Bees are essential for the reproduction of native shrubs that provide forage and cover for many reptiles, mammals, and the New England Cottontail. Thus, efforts to maintain habitats that support multiple species should include consideration of promoting rich bee communities for the pollination services they offer.

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Appendix 1. Relative abundance of flowering plants encountered on 10 sites managed for New England Cottontails in southeastern New Hampshire. Sites were partitioned as old fields (OF), clearcuts (CC), and gravel pits (GP). Within a row, flower abundances were ranked as 1 = low, 2 = moderate, and 3 = high abundance. Total abundance and richness were compared among sites.

Flower species	OF-1	OF-4	CC-2	OF-2	CC-3	OF-3	GP-2	GP-1	CC-4	CC-1
<i>Achillea millefolium</i> L. (Yarrow)	1	1		1		1	1			
<i>Agalinis</i> sp. (false foxglove)			1							
<i>Aralia hispida</i> Vent. (Bristly Sarsaparilla)					1					
<i>Aronia melanocarpa</i> Elliott (Black Chokeberry)	1									
<i>Celastrus orbiculatus</i> Thunb. (Oriental Bittersweet)			3							1
<i>Cicuta maculata</i> L. (Water Hemlock)				1						
<i>Cirsium</i> sp. (thistle)										
<i>Coreopsis lanceolata</i> L. (Lance-Leaf Coreopsis)								1		
<i>Daucus carota</i> L. (Queen Anne's Lace)						1	1	1		
<i>Doellingeria umbellata</i> (P. Mill.) Ness (Tall White Aster)	1	1		1		2	1		2	1
<i>Elaeagnus umbellata</i> Thunb. (Autumn Olive)		1							1	1
<i>Epilobium</i> sp. (willow herb)			1							
<i>Erechtites hieracifolius</i> Raf. (American Burnweed)										2
<i>Erigeron annuus</i> (L.) Pers. (Eastern Daisy Fleabane)			1							
<i>Erigeron strigosus</i> Muhl. (Prairie Fleabane)			1	1					1	
<i>Eupatorium perfoliatum</i> L. (Common Boneset)			1							
<i>Euthamia graminifolia</i> (L.) Nutt. (Flat-top Goldenrod)	2		2		2	1	1	1	2	1
<i>Eutrochium maculatum</i> (L.) E.E. Lamont (Spotted Joe Pye Weed)	1	1								
<i>Fragaria</i> sp. (strawberry)			1							
<i>Frangula alnus</i> Mill. (Glossy Buckthorn)	1	1	3			1				3
<i>Gaillardia aristata</i> Pursh (Blanketflower)								1		
<i>Geranium maculatum</i> L. (Spotted Geranium)	1	2	2							1
<i>Hieracium aurantiacum</i> L. (Orange Hawkweed)	1									
<i>Hieracium caespitosum</i> Dumort. (Yellow Hawkweed)	1					2	2			
<i>Hieracium pilosella</i> L. (Mouse-Ear Hawkweed)							1			1
<i>Hieracium</i> sp. (hawkweed)								1		1

Flowers species	OF-1	OF-4	CC-2	OF-2	CC-3	OF-3	GP-2	GP-1	CC-4	CC-1
<i>Houstonia caerulea</i> L. (Azure Bluet)				1			1		1	1
<i>Hypericum perforatum</i> L. (Saint Johnswort)	2	1		1	1		1	1		
<i>Impatiens capensis</i> Meerb. (Jewelweed)			2						1	
<i>Ionactis linarifolia</i> (L.) Greene (Stiff Aster)						3				
<i>Lespedeza capitata</i> Michx. (Round-Head Lespedeza)						1				
<i>Leucanthemum vulgare</i> Lam. (Ox-Eye Daisy)	1					1	1			
<i>Linaria vulgaris</i> Mill. (Yellow Toadflax)						1				
<i>Lobelia inflata</i> L. (Indian Tobacco)			1							1
<i>Lotus corniculatus</i> L. (Birdsfoot Trefoil)		3				3	3	3		
<i>Lupinus polyphyllus</i> Lindl. (Blue Lupine)							3			
<i>Lysimachia</i> sp. (loosestrife)			1							
<i>Lythrum salicaria</i> L. (Purple Loosestrife)		2								
<i>Oenothera biennis</i> L. (Evening Primrose)						1				
<i>Oxalis stricta</i> L. (Yellow Wood Sorrel)						1				1
<i>Packera aurea</i> (L.) Á. Löve & D. Löve (Golden Ragwort)										
<i>Plantago major</i> L. (Broadleaf Plantain)		1								
<i>Potentilla canadensis</i> L. (Dwarf Cinquefoil)		1	1	1						
<i>Potentilla simplex</i> Michx. (Common Cinquefoil)	3	3	1	2	2	1	1	1	1	1
<i>Ranunculus</i> sp. (ranunculus)			2	1						
<i>Robinia pseudoacacia</i> L. (Black Locust)								1		
<i>Rosa multiflora</i> Thunb. (Multiflora Rose)			1							
<i>Rubus allegheniensis</i> Porter (Blackberry)	3	3	3		1	3	3		3	3
<i>Rubus flagellaris</i> Willd. (Common Dewberry)					1				1	
<i>Rubus hispida</i> L. (Bristly Dewberry)					1		2	1	1	
<i>Rubus idaeus</i> L. (Red Raspberry)			3							
<i>Rubus occidentalis</i> L. (Black Raspberry)	1			1					3	
<i>Rudbeckia hirta</i> L. (Black-Eyed Susan)					1			1		
<i>Sisyrinchium angustifolium</i> Mill. (Narrowleaf Blue-Eyed Grass)			1			1				
<i>Solanum dulcamara</i> L. (Woody Nightshade)				1						1
<i>Solidago altissima</i> L. (Late Goldenrod)		2		1						2
<i>Solidago arguta</i> Aiton (Cut-Leaved Goldenrod)			1							

Flowers species	OF-1	OF-4	CC-2	OF-2	CC-3	OF-3	GP-2	GP-1	CC-4	CC-1
<i>Solidago caesia</i> L. (Bluestem Goldenrod)										1
<i>Solidago canadensis</i> L. (Canada Goldenrod)	2	2	2	2	1	2			2	2
<i>Solidago gigantea</i> Aiton (Smooth Goldenrod)						1			3	
<i>Solidago juncea</i> DC. (Early Goldenrod)	1				1		2	2		
<i>Solidago nemoralis</i> Aiton (Field Goldenrod)	1				1		3	1		
<i>Solidago puberula</i> Nutt. (Downy Goldenrod)							1			1
<i>Solidago rugosa</i> Mill. (Wrinkle-Leaved Goldenrod)	2	2	1	2		3		1	3	1
<i>Solidago speciosa</i> Nutt. (Showy Goldenrod)					1					
<i>Spiraea alba</i> Du Roi (Meadowsweet)	1		1			1	1		1	
<i>Spiraea tomentosa</i> L. (Steeplebush)	1									2
<i>Symphotrichum cordifolium</i> (L.) G.L. Nesom (Blue Wood Aster)				3			1		1	
<i>Symphotrichum dumosum</i> (L.) G.L. Nesom (Bushy Aster)		1		1		1			2	
<i>Symphotrichum ericoides</i> (L.) G.L. Nesom (White Heath Aster)	1						3			
<i>Symphotrichum laeve</i> (L.) A. Löve & D. Löve (Smooth Blue Aster)		1	1	1			1			
<i>Symphotrichum lateriflorum</i> (L.) A. Löve & D. Löve (Calico Aster)		2	2	3	1	1	1		1	
<i>Symphotrichum novae-angliae</i> (L.) G.L. Nesom (New England Aster)		1	2				1			1
<i>Symphotrichum puniceum</i> (L.) A. Löve & D. Löve (Bristly Aster)		2	1		3					
<i>Symphotrichum racemosum</i> (Elliott) G.L. Nesom (Small White Aster)				1		2		1		
<i>Taraxacum officinale</i> F.H. Wigg (Dandelion)			1	1						
<i>Trifolium pratense</i> L. (Red Clover)		1	3	1				1		
<i>Trifolium repens</i> L. (White Clover)		3	3				1			1
<i>Verbena hastata</i> L. (Blue Vervain)		2								
<i>Veronica officinalis</i> L. (Common Speedwell)				1	1					1
<i>Viburnum acerifolium</i> L. (Maple-Leaved Viburnum)			1			1	1		1	
<i>Vicia cracca</i> L. (Tufted Vetch)	1		1	3						
<i>Viola</i> sp. (violet)										1
<i>Zizia aurea</i> (L.) W.D.J. Koch (Golden Alexanders)		3								
Total abundance	29	35	55	34	19	27	42	26	34	24
Species richness	20	23	33	23	17	19	29	20	23	16