DEVELOPING GUIDELINES FOR PROMOTING POLLINATOR SERVICES AND SHRUBLAND BIRDS IN THE NORTHEAST

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Executive Summary: Once prevalent on the landscape, early-successional habitats are now increasingly threatened in the northeastern United States. As a result, many species that rely on or require habitats dominated by shrubs, young trees, grasses, and forbs have experienced precipitous population declines, leading many to list shrubland habitats and constituent wildlife as a conservation priority. Even-aged forest management (e.g. clearcutting) has been shown to be an efficient and effective means for creating early-successional habitat for certain taxa such as shrubland birds, but is unfeasible in many situations in southern New England due to public opinion and increased parcelization. Group selection harvests create shrubland conditions in the form of relatively small forest openings (< 1 ha); however, limited attention has been directed toward understanding the extent to which these methods contribute to the conservation. In order to assess the conservation value of small forest openings for wildlife in southern New England, We studied two distinct communities associated with early-successional habitats, shrubland birds and bees (Hymenoptera: Apiformes), in openings created by group selection harvests and patch-cutting.

In 2014 and 2015, birds were surveyed in small forest opening in western Massachusetts in an effort to describe relationships between species occupancy and patch area as well as other microhabitat-, patch-, and landscape-scale variables. Black-and-white warblers, common yellowthroats, chestnut-sided warblers, eastern towhees, and gray catbirds were likely to be present in openings at least 0.3 ha in size, while indigo buntings and prairie warblers had minimum area requirements of 0.55 and 1.07 ha, respectively. Variables within microhabitat-, patch-, and landscape-scales were important for predicting species occurrence. Most notably, prairie warblers were more likely to occur in openings closer to large patches of habitat such as powerline corridors, even if those openings were small in size. We conclude that, despite their inability to support the entire community of shrubland species in this region, small forest openings can provide habitat for several species of conservation concern if proper attention is given to promoting suitable microhabitat, patch, and landscape characteristics.

Bees were sampled in openings as well as adjacent mature forest in an effort to describe the bee community, identify environmental variables influencing bee abundance and diversity, and examine the extent to which openings created by forest management may support bees, as well as potentially augment bee populations within adjacent unmanaged forest. Bees were significantly more abundant and diverse in forest openings than mature forest, but species composition was indistinguishable between openings and forest. Abundance and diversity displayed no relationship with opening size in either openings or forest, but were generally positively related to the amount of early-successional habitat on the landscape. Vegetation characteristics within openings were important in shaping bee communities in openings with abundance and diversity decreasing with vegetation height and increasing with floral abundance. Notably, eusocial and small bees exhibited the opposite pattern in adjacent forest, increasing with the succession of openings and decreasing with greater floral abundance within openings. These results suggest that the creation of small forest openings may help to promote bees both in openings and adjacent mature forest, but certain guilds may be negatively affected.

SECTION I.
Patch Area Thresholds Provide New Guidance for Managing Shrubland Birds

1.1 Introduction

Many bird species that breed in early-successional shrubland habitats are currently experiencing severe population declines in eastern North America (Askins 1993, Hagan 1993, Hunter et al. 2001). These negative trends are in part attributed to the loss of required early-successional disturbance-dependent habitats (Litvaitis 1993, Askins 2001, Thompson and Degraaf 2001, Foster et al. 2002), which are concurrently declining at a rate of at approximately 2.5% per year across the northeastern United States (King and Schlossberg 2014). Disturbances such as windthrow, wildfire, beaver (*Castor canadensis*) activity, and flooding, which once naturally sustained these ephemeral habitats (Brawn et al. 2001, Lorimer 2001, Lorimer and White 2003), have largely been suppressed by humans (DeStefano and Deblinger 2005, Spetich et al. 2011). As a result, maintaining disturbance-dependent early-successional habitats is now considered a conservation priority in the northeast (Askins 2001, Oehler et al. 2006, King and Schlossberg 2014).

In an effort to simulate the effect of natural disturbances on the landscape, land-managing agencies and organizations have implemented anthropogenic disturbance strategies such as prescribed fires, mowing, and silvicultural methods. Schlossberg and King (2015) recently assessed the extent and origin of shrubland habitats in Massachusetts, finding that about 20% of all shrublands can be attributed to federal or non-governmental organization land management practices. This suggests that human efforts to create and maintain early-successional habitats are of considerable importance. Developing a better understanding of how these management strategies influence wildlife distributions and dynamics will be greatly beneficial for conservation.

Recent research has indicated that mechanically treated wildlife openings provide high quality habitat for a wide range of shrubland bird species (Chandler et al. 2009a, King et al. 2009a, Smetzer et al. 2014) and may be more effective than traditional silvicultural practices for certain species (Smetzer et al. 2014). However, land treatments associated with wildlife openings can be labor-intensive and expensive (Thompson and DeGraaf 2001, Oehler 2003), making widespread use of wildlife openings impractical. Silvicultural practices have been advocated for creating early-successional habitat not only because they are effective in promoting many shrubland species (DeGraaf and Yamasaki 2003), but also because costs can be offset by timber revenue.

Timber harvesting currently plays an important role in supporting shrubland bird populations, creating about 78% of the early-successional habitat in New England (King and Schlossberg 2012). Several studies indicate that clearcutting is the most effective silvicultural approach for creating shrubland bird habitat (e.g. Annand and Thompson 1997, Costello et al. 2000, King and DeGraaf 2000). In recent years, however, harvest methods in New England have shifted toward uneven-aged approaches (Trani et al. 2001) in response to negative public reaction to even-aged management, particularly clearcutting (Gobster 2001). Additionally, the parcel size of most forest owners in southern New England has been decreasing (Butler et al. 2007), and clearcutting is not

practical on these smaller properties. Of uneven-aged-practices, only group selection, where multiple adjacent trees are removed from a mature forest matrix (Smith et al. 1997), creates shrubland habitat suitable in structure for shrubland birds. However, patches created by group selection (typically < 1.0 ha) are too small to support more area-sensitive shrubland bird species (Costello et al. 2000; Alterman et al. 2005). Nevertheless, small forest openings still provide potential breeding habitat for species less sensitive to patch area that are of regional concern, and thus group selection may enable managers to contribute to conservation on sites where the creation of patches large enough to support more sensitive species is not practical. The precise area thresholds for these species have not been established, and thus the conservation value of forest openings too small to support complete shrubland bird communities remains poorly understood.

Although for forest birds the importance of landscape characteristics is well documented (Robinson et al. 1995, Howell et al. 2000, etc), landscape effects have been given less attention with respect to shrubland birds. Landscape composition is considered a potentially important factor for shrubland birds (Schlossberg and King 2007), but studies have lacked complete consensus. Some have found significant relationships between abundance and landscape composition, but have reported conflicting results for certain species (Hagan et al. 1997, Lichstein et al. 2002), while others have shown limited relationships with composition (Chandler et al. 2009b, Askins et al. 2007), or none at all (Chandler 2006). Research has also indicated that large patches of habitat in particular may increase the value of smaller adjacent shrubland patches (Buffum and McKinney 2014). While not in complete agreement, the existing research shows that the landscape conditions may influence patch suitability for many shrubland-obligate species and highlights the need for more detailed information to support the development of management guidelines.

The goal of this study was to investigate the potential for forest openings <1.5 ha in size to support shrubland birds. Objectives were to (1) identify species-specific minimum-area requirements for shrubland birds capable of occupying these openings, and (2) identify additional microhabitat-, patch-, and landscape-level factors that can promote occupancy of small forest openings.

1.2 Methods

1.2.1 Study Area and Site Selection

This study was conducted during 2014 and 2015 in the heavily forested northern region of the Quabbin Reservation in western Massachusetts, USA (42.46°N, -72.32°W; Fig. 1) on Massachusetts Department of Conservation and Recreation and Harvard Forest land. The dominant forest type of this region is transitional hardwoods-white pine, consisting primarily 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*). Forest openings in this study were created with group selection harvests, with the exception of three openings, which were the product of single patch-cuts. Forest openings contained seedlings and saplings of all adjacent tree species,

principally birches (*Betula* spp.), red maple, white pine, as well as *Rubus* spp., mountain laurel (*Kalmia latifolia*), and numerous fern species. Residual debris from harvests was prevalent in all openings.

Study openings were randomly selected from a list of 146 forest openings present across 10 stands (Fig. 1), 90 openings in 2014 and 104 in 2015. Openings ranged from 0.02-1.29 ha and had been harvested between 2006 and 2010. The number of forest openings within each stand ranged from one to 40 and varied in density. The nearest-neighbor distance between all openings was ≤ 106 m with a mean of 44 m. To ensure openings represented the entire range of opening sizes, openings were chosen randomly from 4 bins representing different size ranges. Fourteen of the smallest openings were added in 2015 in order to fully capture the lower range in opening sizes.

1.2.2 Bird and Vegetation Surveys

Each year birds were surveyed 3 times from late May to early July with 10-minute, 50-m radius point counts at the center of each opening (Ralph et al. 1995). Surveys commenced 15 minutes after sunrise and continuing until 1100 hours. Surveys were only conducted on calm days with no precipitation. To minimize bias, visits to each survey point occurred at different times of day and were mostly separated by ≤ 10 days. Wind speed (Beaufort scale) and cloud cover was recorded before each survey. Location, sex, and detection method of all birds noted during point counts were recorded on scaled orthoimagery. Survey points were visited by at least two different technicians during each year in order to reduce observer bias (Ralph et al. 1995). Fly-overs and birds detected outside of the 50-m radius were not included in the analysis.

Vegetation structure and composition was measured at 20 random locations within each opening using random bearings and distances (1-25 m) and starting from point count locations. We recorded species and maximum height of the plant species in contact with a 1.5-cm-diameter vertical pole within four height classes: 0-0.5 m, 0.5-1.4 m, 1.4-3.0 m, and > 3.0 m (Breeding Biology Research & Monitoring Database 1997). Mature trees within openings were rare and therefore were not accounted for.

1.2.3 Patch and Landscape Metrics

Patch and landscape variables were calculated using FRAGSTATS, version 4 (McGarigal et al. 2012) and ArcGIS 10.2.1 (Environmental Systems Research Institute, Inc., Redlands, CA). To facilitate analysis in FRAGSTATS, shapefiles delineating shrubland habitat boundaries were first created using ArcGIS and then rasterized using a 3-m cell size. Two patch-level metrics, area and Shape Index (SHAPE), were measured for each opening. SHAPE quantifies patch shape complexity by dividing the perimeter of a patch by the minimum possible perimeter of a patch equal in area. This eliminates bias associated with using the perimeter-to-area ratio metric on patches that vary in size. We chose to examine patch shape in addition to area because there is evidence that it is an influential factor for shrubland birds (Weldon and Haddad 2005, Shake et al. 2012). One landscape-level metric, Percentage of Landscape (PLAND), was used to measure the

amount of the shrubland habitat within the surrounding landscape. PLAND was calculated using a specified search-radius from the centroid of each opening. Since the scale at which birds respond to their surroundings is largely unknown, PLAND was calculated at 100 m, 200 m, 300 m, 400 m, and 500 m scales. We measured the distance from each opening to the nearest large patch of shrubland habitat using ArcGIS. We defined "large patches" as any powerline corridor > 50 m wide or patches of shrubland habitat > 5.0 ha in area. Patches of this size are sufficiently large enough to accommodate even the most area-sensitive birds in this area (King et al. 2009a, King et al. 2009b).

1.2.4 Statistical Analysis

Shrubland bird occupancy was related to environmental variables using single-season occupancy models that allow the incorporation of detection probability, which reduces bias associated with imperfect detection (Mackenzie et al. 2002, MacKenzie 2006). This framework uses replicated point counts to estimate detection probability (Thompson 2002). Single season occupancy models are valid under the assumption of closure where no immigration, emigration, and mortalities occur (Royle and Dorazio 2008). This assumption was considered fulfilled given territoriality and the relatively short amount of time allowed between replicate counts ($\leq$ 10 days; Smetzer et al. 2014).

We restricted the analysis to males that were detected inside openings and to species that occurred in $\geq$ 10% of plots. Occupancy and detection probability were related to respective covariates using a logit link. Data from each year was modeled separately because not all sites were sampled in both years, and to assess the agreement of results across years. Collinearity was assessed and variables with $r > 0.5$ were deemed highly correlated. Since patch area was of primary concern to this study, any variables that were correlated with area were removed, leading us to remove PLAND at the 100 m scale. We also removed variables describing forb, fern, and grass cover as well as needleleaf vegetation cover because they were correlated with broadleaf vegetation cover, which we hypothesized was likely more important for the majority of the species in this study. Measurements of PLAND for the 200 m, 300 m, 400 m and 500 m scales were highly correlated, but were retained because only the best predictive scale would eventually be chosen for each variable type. In order to promote model convergence, all continuous variables were scaled with $\bar{x} = 0$ and $\sigma = 1$. Predictor variables included percent broadleaf cover, median vegetation height, coefficient of variation (CV) of vegetation height, area, SHAPE, distance to large patch, and PLAND. Detection covariates included observer, date, time, wind speed, and cloud cover.

We employed an information-theoretic approach to determine best-performing model(s) (Burnham and Anderson 2002). We used Akaike's information criterion (AIC) adjusted for over-dispersion and small sample sizes ($QAIC_c$) to compare models (Burnham and Anderson 2011). Prior to model selection, fit of the data was assessed by conducting a goodness-of-fit bootstrap (1,000 bootstraps) of models containing all detection and occupancy covariates for each species for each year (MacKenzie and Bailey 2004) using the AICcmodavg package (Mazerolle 2015) in the R software environment, version 3.1.1 (R Development Core Team 2016). These bootstraps produced over-dispersion parameters ($\hat{c}$), which were used to inflate standard errors and

influence the subsequent selection of models (MacKenzie and Bailey 2004). All species with $\hat{c} \leq 1.0$ were assigned a value of one.

To begin the model selection process, we first determined best detection covariates for predicting occupancy for each species, which were subsequently included in all candidate models. This was done by fitting all subsets of detection covariates while including as many occupancy variables as possible while still allowing models to converge. Detection covariates were retained if they were statistically significant at $P \leq 0.1$, in models with a $\Delta QAIC_c \leq 2$, and performing better than a null model with respect to $QAIC_c$.

Next, with detection covariates fixed in all models, and using the same selection criteria, we separately assessed the importance of predictor variables within microhabitat, patch, and landscape scales. This resulted in a collection of variables, which were then combined into a final construction of models that included all scales. Since assessing the influence of area on shrubland birds was a primary objective, it was included in the final construction of models, even if it was not previously selected as important. In this way, patch area could still be subsequently excluded from the final models if it truly had no influence. Non-convergent models were removed and $QAIC_c$ values and model weights (w_i) were recalculated. Distance to large patch was included in 2015 prairie warbler model construction post hoc, because of its potential relevance for management and to compare coefficients between years. We also attempted to include an interaction coefficient between opening area and distance to large patch for prairie warblers post hoc, but no models including this term would converge. We used the unmarked package (Fiske and Chandler 2011) to fit models and estimate parameters in the R software environment, version 3.1.1 (R Development Core Team 2016).

In the final assessment, occupancy covariates were considered supported if included in models with a $\Delta QAIC_c \leq 2$ and strongly supported if 95% confidence intervals (CI) of their coefficients did not include zero, following Chandler et al. (2009a). Species-variable relationships were illustrated by plotting weighted-average model predictions using Akaikie weights (Burnham and Anderson 2002) across all models that included the focal variable while holding all other variables at their mean. To examine how the relationship between prairie warbler occurrence and distance to nearest large patch varied by patch size, we plotted this relationship while holding patch area constant at a range of sizes. We avoided model averaging parameter estimates because there are uncertainties about the most appropriate methods for averaging variable coefficients that are not included in all models (Burnham and Anderson 2002), parameter estimates are influenced by the total number of variables included in a model, and multicollinearity can influence the interpretation of parameters.

Following Shake et al. (2012), we calculated the "minimum-area requirement" and "optimal area" of each species by identifying the area at which probability of occurrence equaled 0.5 and 0.9 respectively. Although birds do occur within patches below their minimum-area requirements as defined using this procedure, since this value indicates the area below which occupancy is less than random, it has been adopted as a standard metric for quantifying area-sensitivity (Robbins 1989, Vickery 1994, Shake et al. 2012), which facilitates comparison among species and studies.

1.3 Results

In total, 2,285 birds of 49 species were detected in 2014 and 2,527 birds of 45 species were detected in 2015 (Appendix 1). Sixteen of 41 species identified as core shrubland birds of New England by Schlossberg and King (2007) were documented. Seven of these species had sufficient sample sizes for analysis: black-and-white warbler (*Mniotilta varia*), common yellowthroat (*Geothlypis trichas*), chestnut-sided warbler (*Setophaga pensylvanica*), eastern towhee (*Pipilo erythrophthalmus*), gray catbird (*Dumetella carolinensis*), indigo bunting (*Passerina cyanea*), and prairie warbler (*S. discolor*). American redstart (*S. ruticilla*) and veery (*Catharus fuscescens*), two species not commonly grouped with the shrubland bird community, were also included in the analysis because they were frequently observed nesting and defending territories within openings. Sufficient sample sizes were only available for indigo buntings in 2014 and veerys in 2015.

We found evidence of relationships between occupancy of study species and microhabitat-, patch-, and landscape-scale variables (Table 1). Forest opening area appeared in top models ($\Delta QAIC_c \leq 2$) for all species in both years and was strongly supported in at least one year for all species except for American redstart and veery (Table 1). Of the seven species that showed a strong relationship with area (Fig. 2), black-and-white warbler, common yellowthroat, chestnut-sided warbler, eastern towhee, and gray catbird were capable occupying smaller openings, with minimum-area requirements of 0.3 ha or less and optimal areas of 0.51 ha or less compared to indigo bunting and prairie warbler, which exhibited greater area sensitivity, with minimum-area requirements of 0.55 ha and 1.07 ha respectively and optimal areas of 0.69 ha and 1.25 ha respectively (Table 2).

American redstarts were strongly related to vegetation height (positive) and distance to large patch of shrubland habitat (positive) in both years and broadleaf vegetation (negative) in 2015, but weakly associated with patch area (positive) in both years (Table 1). Common yellowthroats were positively related to patch area in both years, but this relationship was only strong in 2015. Common yellowthroats also showed weak relationships with distance to large patch of shrubland habitat (positive) in 2014 as well as vegetation height (negative) and amount of shrubland habitat on the landscape within 500 m (negative) in 2015. Chestnut-sided warblers were strongly positively related to broadleaf vegetation in 2014 and patch area in 2015 and weakly positively related to patch area and distance to nearest large patch of shrubland in 2014. Eastern towhees showed only a weak positive relationship with area in 2014, but strong relationships with area (positive) and broadleaf vegetation (negative) in 2015. In 2014, gray catbirds were strongly related to vegetation height (positive), coefficient of variation of vegetation height (negative), patch area (positive), and amount of shrubland on the landscape within 300 m (positive). In 2015, gray catbirds showed strong associations with patch area (positive), weak associations with distance to nearest large patch of shrubland (positive) and both strong and weak associations with coefficient of variation of vegetation height (negative) depending on the model and amount of shrubland habitat on the landscape within 200 m (positive). Black-and-white warblers were weakly associated with area (positive) in 2014 and the coefficient of variation of vegetation height (negative) in 2015, but showed strong relationships with patch area (positive) and shape (negative) in 2015.

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Indigo buntings displayed strong positive relationships with patch area and weak negative relationships with vegetation height, patch shape, and the amount of shrubland within 500 m in single models in 2014. Veerys showed weak positive relationships with vegetation height and patch area in 2015. Prairie warbler was the only species to show a negative relationship with distance to the nearest large patch (Table 1). In 2014 prairie warblers were strongly related to patch area (positive), distance to nearest large patch of habitat (negative), and amount of shrubland habitat on the landscape within 500 m (negative). In 2015, prairie warblers showed both strong and weak associations with the amount of shrubland habitat within 500 m (negative) and weak associations with vegetation height (negative), area (positive), and distance to the nearest large patch of shrubland (negative). Prairie warblers also appeared more likely to occupy smaller openings if they were near larger patches (Fig. 3).

1.4 Discussion

Previous research has demonstrated that certain shrubland birds that are present in large patches are consistently absent from patches < 1 ha (Rodewald and Smith 1998, Robinson and Robinson 1999, Costello et al. 2000, Alterman et al. 2005, Tozer et al. 2010), but little progress has been made identifying the area thresholds below which species are not likely to occur. This information is important for conservation because without knowledge of how individual species respond to our management practices we cannot fully understand the impact of management efforts. Shake et al. (2012) determined minimum-area requirements for prairie warblers and yellow-breasted chats (*Icteria virens*) in North Carolina and determined there were distinct thresholds in patch area use for these species, information that will be useful for conserving these species. We have supplemented the efforts of Shake et al. (2012) with results for prairie warblers in a different region of the United States and have also included other species that occur in smaller openings in order to provide information of the utility of these smaller openings for bird conservation. This study is the first to systematically sample a fine gradient of patch sizes small enough to determine both the occupancy thresholds for species with less restrictive area requirements as well as the value of these smaller openings for conserving more area-sensitive shrubland bird species.

The finding that prairie warbler, chestnut-sided warbler, common yellowthroat, black-and-white warbler, eastern towhee, indigo bunting, and gray catbird were positively associated with patch area is consistent with the findings of others (Annand and Thompson 1997; Rodewald and Smith 1998; Costello et al. 2000; Moorman and Guynn 2001; King and Degraaf 2004). Indigo buntings were only likely to occur in openings larger than 0.55 ha. This contrasts with other studies that frequently encountered indigo buntings in openings that were smaller than 0.55 ha (Kerpez 1994; Robinson and Robinson 1999; Moorman and Guynn 2001). This difference might be explained by the minimal forb cover in openings in this study, which has been related to indigo bunting abundance (King et al. 2009a, Smetzer 2014) and was the dominant vegetation type in at least one of these studies (Moorman and Guynn 2001). Since forb coverage was low in most openings in this study, indigo buntings may have only been able to occupy larger openings with a greater breadth of resources. Prairie warblers were the most area-sensitive species that occurred frequently enough in openings to be

modeled, with an estimated a minimum-area requirement of 1.07 ha. This is estimate is close to the estimate of 1.1 ha by Shake et al. (2012) in North Carolina as well as the suggested opening size by Kerpez (1994) in Virginia, which was also 1.1 ha. Such consistency of estimated area requirements throughout the prairie warbler range suggests that our results are generalizable beyond our study area.

Group selection opening sizes can substantially influence both the composition and structure of regenerating vegetation (Smith et al. 1997), thus a plausible explanation for the apparent area-sensitivity of species that we observed could be that smaller openings simply foster unsuitable vegetative conditions below each species' respective threshold. However, if this were the case, vegetation variables would have played a more prominent and consistent role in the models than they did. An alternative explanation, provided by Askins et al. (2007), suggests that the primary factor determining area-sensitivity is a species' territory size and whether it can fit within a given opening. Lending some general support to this idea, prairie warblers, which were the most area-sensitive species in this study, appear to have larger territories on average than the species that we identified as less area-sensitive (DeGraaf and Yamasaki 2001). However, a lack of thorough analytical studies of territory size for these shrubland species makes it difficult to make definitive statements about the role of area-sensitivity in species-specific patterns of areas sensitivity.

Patch area appeared in top models for American redstarts and veerys, but neither species displayed a strong relationship with area, and for American redstarts occupancy appeared to be driven more by microhabitat-level characteristics. Contrary to their common designation as mature forest species, some studies have noted that American redstarts and veerys will readily utilize early-successional habitat (Degraaf 1991, King and Degraaf 2000) or even prefer it (Hunt 1996). These species may be primarily influenced by understory conditions regardless of whether there is mature tree canopy present, which is in contrast with early-successional shrubland species that mostly require sparse or open canopy (Smetzer et al. 2014).

Very little attention has been given to how proximity of large shrubland patches influences shrubland birds in smaller adjacent patches. Although Buffum and McKinney (2014) did not specifically examine distance to large patches as an independent variable, they found that the size of adjacent wetland shrub patches within 50 m increased occupancy of five species in small patches of upland shrubland in Rhode Island. Similarly, we observed that prairie warblers occurred more frequently in openings closer to large patches of shrubland, indicating that shrubland habitats may be enhanced with proximity to large upland shrublands, in addition to wetland shrublands. Furthermore, prairie warblers were capable of occupying openings considerably smaller than their standard territory size (typically > 1.0 ha [Nolan 1978, DeGraaf and Yamasaki 2001]), if the opening was located close to a large patch. For example, one individual was found breeding in a 0.22 ha opening that was approximately 60 m from a powerline right-of-way. This observation suggests that prairie warblers have flexible territory sizes and are willing to sacrifice the benefits of larger territories for proximity to large patches. These findings also illustrate the importance of landscape context in shrubland bird communities.

Occupancy by American redstarts increased with increasing distance to the nearest large patch of shrubland habitat, which directly contrasts with previous research

that has suggested American redstarts are more abundant both within (Hunt 1996) and in proximity to (King et al. 1997; Hagan and Meehan 2002) early-successional habitats. Given these findings, we believe it is unlikely that birds of this species are in fact avoiding large patches of habitat. Instead, since the vast majority of American redstarts occurred at only two sites that were located several km away from any large patches of shrubland habitat, we suggest that a separate unmeasured environmental variable may have been driving occurrence at these sites, thus giving the perception that they were responding to the distance to large patches.

      Landscapes that contain a higher proportion of shrubland habitat may be favored by shrubland birds for several reasons including conspecific attraction (Ward and Schlossberg 2004), availability of breeding sites to choose from during settlement (Badyaev et al. 1996), increased possibilities for within-breeding-season dispersal (Schlossberg and King 2007), and perhaps increased potential for extra-pair copulations (e.g. Byers et al. 2004). Landscape composition has been shown by other studies to be important for several of the species in this study (Hagan et al. 1997, Hagan and Meehan 2002, Lichstein et al. 2002); however, we found that only two species, gray catbirds and prairie warblers, were strongly associated with the amount of early-successional habitat in the landscape. Gray catbirds responded positively to the extent of shrubland habitat on the landscape, which is consistent with findings of Hagan et al. (1997). However, Askins et al. (2007) found that gray catbirds did not appear to respond to the amount of early-successional habitat on the landscape. This discrepancy may be due to the fact that residential areas, which Askins et al. (2007) found are positively related to gray catbird abundance, were absent from the study area of Hagan et al. (1997).

      My finding that prairie warbler occupancy decreased with more shrubland habitat in the landscape was unexpected in light of prior reports that this species prefers larger openings and our own finding that this species was more likely to occur closer to large patches of shrubland. While area and the amount of shrubland within 500 m were not correlated enough to exclude from the modeling process, their negative correlation was statistically significant ($r = -0.42$, $P = < 0.001$). Therefore, one explanation for this pattern is that the apparent negative relationship with the amount of shrubland on the landscape in the models may be a product of the fact that there happened to be less shrubland surrounding larger openings, which are more likely to attract prairie warblers (Shake et al. 2012). Furthermore, the shrubland that surrounded most openings was in the form of small patches that typically will not host prairie warblers, thus in this group selection system, more shrubland on the landscape may not necessarily have the same positive effect for prairie warblers as it could for species that will readily occur in smaller openings.

      Avoidance of edges and increased predation rates near edges is well documented for shrubland birds (King and Byers 2002; Rodewald and Vitz 2005; Schlossberg and King 2008; Shake et al. 2011), thus shape complexity, which increases the amount of edge bordering a patch, has been speculated as a restrictive factor for shrubland birds. In this study, only black-and-white warblers indicated a strong sensitivity to shape. Several studies have examined the influence of patch shape (Chandler et al. 2009b; Shake et al. 2012); . The patches in this study may not have encompassed a sufficient range in variation of shape complexity to properly examine this factor for other species.

Vegetation variables were important for most species, but did not always influence occupancy in the manner that was expected. Other studies have also reported positive relationships between chestnut-sided warblers and broadleaf cover (Schlossberg and King 2007; King et al. 2009a). King et al. (2009a) reported that eastern towhees were positively related to coniferous cover, which was negatively correlated with broadleaf cover in this study. We are unable to account for the negative relationship we observed between American redstarts and broadleaf cover, given their previously reported association with deciduous cover (Hunt 1996). Vegetation height is widely reported to affect bird abundance (Keller et al. 2003, Schlossberg and King 2009); however, only gray catbirds and American redstarts showed strong relationships with vegetation height in this study. This was probably due to the fact that the study sites were all created within four years of each other and thus reflect relatively limited variation in vegetation height. Gray catbirds were significantly negatively associated with the CV of vegetation height, indicating these species occurred most frequently in openings with relatively uniform vegetative structure.

Forest openings in this study were occupied by birds of high conservation concern. Seven of the nine focal species (black-and-white warbler, common yellowthroat, chestnut-sided warbler, eastern towhee, indigo bunting, prairie warbler, and veery) are experiencing significant population declines (Sauer et al. 2008). Of these declining species, chestnut-sided warbler, eastern towhee, indigo bunting, and prairie warbler are listed as species of elevated conservation concern in the Partners in Flight North American Landbird Conservation Plan (Rich et al. 2004). Therefore, while unable to support the full early-successional bird community, openings as small as 0.3 ha can still provide habitat for at least five shrubland species, four of which are of conservation concern. This is particularly relevant to conservation because a larger proportion of forested parcels in southern New England can support openings 0.3 ha in size (Butler et al. 2007) and openings of this size are less likely to raise public opposition.

The clustered nature of openings in this study added clear limitations to the extent to which we were able to analyze certain factors. For example, although there was certainly variation in the amount of shrubland habitat surrounding openings, there were very few openings that were completely isolated. Moreover, most of the more isolated openings were larger, making it difficult to examine occupancy in very small isolated openings. Small and isolated anthropogenic openings are too scarce to study because there is no silvicultural prescription that results single, small openings. Furthermore, the limitations of small openings have been widely communicated to managers. Therefore, though we were unable to properly address the lower range of isolation for small openings, it is unlikely that this information would be useful for land managers because small, isolated openings are impractical either as a silvicultural prescription or a wildlife management strategy.

Another limitation was the focus on occurrence data, which is not necessarily indicative of habitat quality (Brawn and Robinson 1996). Nevertheless, we did locate nests in nearly every opening over the two years of the study, although we did not have sufficient resources to monitor them for nesting success. Thus we are confident birds were at least able to acquire mates in even the smallest openings. Although some studies report increased predation near edges (Suarez et al. 1997, Weldon and Haddad 2005, Shake et al. 2011), shrubland birds are able to nest successfully in group selection cuts in

extensively forested landscapes in the Northeast (King and DeGraad 2004), and appear to nest with similar success in group selection openings and clearcuts (King et al. 2001, Alterman et al. 2005). .

1.5 Conclusions

The results of this study have important implications for the management of shrubland birds. In situations where the goal is to accommodate the full suite of shrubland species, land managers should consider creating openings at least 1.25 ha in size to maximize the probability of occurrence for the most area-sensitive species in this study, however openings as small as 1.07 ha are still likely to support these species. If these sizes are not feasible operationally, openings 0.3 ha in size or greater can still provide habitat for species of high conservation concern. Managers should consider placing openings near preexisting large patches such as clearcuts > 5 ha in size or powerline corridors that are at least 50 m wide. This will increase the probability of prairie warbler occurrence and thus maximize conservation value of management efforts while also minimizing monetary expenses associated with habitat creation. Finally, the "minimum" patch size for prairie warblers was similar between our study and studies in North Carolina and Virginia, suggesting these guidelines may be applicable throughout a large portion of the range of this species.

Table 1: Parameter estimates of state covariates for occupancy models of bird occurrence with ΔQAICc ≤ 2. State covariates include: broadleaf cover (Broad), median height of vegetation (Height), coefficient of variation of vegetation height (CV), patch area (Area), shape complexity (Shape), distance to nearest large patch of shrubland habitat (Distance), and amount of shrubland habitat on the landscape at 200 m, 300 m, 400 m, and 500 m scales (PL200, PL300, PL400, PL500). Species include: American redstart (AMRE), common yellowthroat (COYE), chestnut-sided warbler (CSWA), eastern towhee (EATO), gray catbird (GRCA), prairie warbler (PRAW), black-and-white warbler (BAWW), indigo bunting (INBU), and veery (VEER). Coefficients in **bold** indicate that confidence intervals did not include zero. Data comes from surveys conducted in forest openings in 2014 and 2015 in western Massachusetts, USA**.**

Species	Year	Microhabitat			Patch	
		Broad	Height	CV	Area	Shape
AMRE	2014		**4.68 (1.52)**			
			4.99 (1.59)		0.5 (0.43)	
	2015	**-1.21 (0.54)**	**4.78 (1.29)**		3.38 (1.83)	
		-1.4 (0.62)	**4.41 (1.21)**			
COYE	2014				1.43 (0.77)	
					1.15 (0.72)	
	2015				**15.01 (4.38)**	
					14.68 (4.68)	
				-0.25 (0.293)	**13.71 (0.42)**	
CSWA	2014	**1.2 (0.39)**			0.68 (0.42)	
		1.17 (0.39)				
		1.1 (0.38)				
		1.16 (0.39)			0.63 (0.43)	
	2015				**21.3 (7.77)**	
EATO	2014				7.09 (10.5)	
	2015	**-0.91 (0.42)**			**12.27 (4.78)**	
GRCA	2014		**4.46 (1.79)**	**-1.05 (0.52)**	**1.83 (0.64)**	
			4.1 (1.58)		**1.83 (0.72)**	
	2015				**10.58 (2.57)**	
				-0.67 (0.4)	**11.22 (2.85)**	
					10.77 (2.59)	
				-0.73 (0.36)	**10.54 (2.45)**	
					10.04 (2.6)	
				-0.72 (0.44)	**10.86 (3.09)**	
					10.1 (2.54)	
PRAW	2014				**2.95 (1.17)**	
	2015				9.11 (7.04)	
		-1.1 (1.0)			9.52 (10.03)	
BAWW	2014				17.9 (9.35)	
	2015				**30.13 (12.09)**	**-1.27 (0.61)**
				-1.01 (0.67)	**25.64 (8.2)**	**-1.22 (0.53)**
					24.3 (8.7)	
INBU	2014				**3.46 (1.21)**	
					4.99 (1.90)	-1.72 (1.04)
					3.83 (1.53)	
			-1.42 (1.29)		**3.16 (1.24)**	
VEER	2015		30.2 (25.6)		38.1 (33.1)	

Species	Year	Landscape		Δ	w_i

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		Distance	PL200	PL300	PL400	PL500	QAICc	
AMRE	2014	**1.71 (0.56)**					0.00	0.70
		1.58 (0.56)					1.68	0.30
	2015	**2.23 (0.63)**					0.00	0.56
		2.51 (0.69)					0.47	0.44
COYE	2014						0.00	0.41
		0.65 (0.43)					0.36	0.34
		0.93 (0.5)					0.90	0.26
	2015						0.00	0.55
						-0.54 (0.42)	1.65	0.24
							1.96	0.21
CSWA	2014						0.00	0.34
							0.04	0.33
		0.44 (0.35)					1.18	0.19
		0.32 (0.36)					1.77	0.14
	2015						0.00	1.00
EATO	2014						0.00	1.00
	2015						0.00	1.00
GRCA	2014			**1.79 (0.72)**			0.00	0.72
				1.68 (0.7)			1.91	0.28
	2015		**1.45 (0.68)**				0.00	0.24
			1.35 (0.69)				0.54	0.18
							1.12	0.13
							1.14	0.13
		0.51 (0.36)	**1.36 (0.62)**				1.18	0.13
		0.56 (0.4)	**1.34 (0.65)**				1.75	0.10
		0.56 (0.34)					1.89	0.09
PRAW	2014	**-6.93 (2.72)**				**-1.49 (0.72)**	0.00	1.00
	2015	-2.92 (1.95)				**-2.14 (1.02)**	0.00	0.58
		-2.58 (2.2)				-1.39 (0.79)	0.64	0.42
BAWW	2014						0.00	1.00
	2015						0.00	0.50
							0.98	0.30
							1.84	0.20
INBU	2014						0.00	0.36
							0.25	0.31
						-0.97 (0.87)	1.43	0.17
							1.60	0.16
VEER	2015						0.00	1.00

Table 2: Forest opening areas at which the probability of occurrence equaled 0.5 (minimum) and 0.9 (optimal) for each species that showed a significant relationship with area. Estimates are included for years that area was significant. See Table 1 for species codes. Data comes from surveys conducted in forest openings in 2014 and 2015 in western Massachusetts, USA.

Species	Year	Forest Opening Area	
		Minimum	Optimal
CSWA	2015	0.05	0.16
COYE	2015	0.08	0.23
BAWW	2015	0.13	0.22
EATO	2015	0.13	0.31
GRCA	2014	0.16	0.45
GRCA	2015	0.30	0.51
INBU	2014	0.55	0.69
PRAW	2014	1.07	1.25
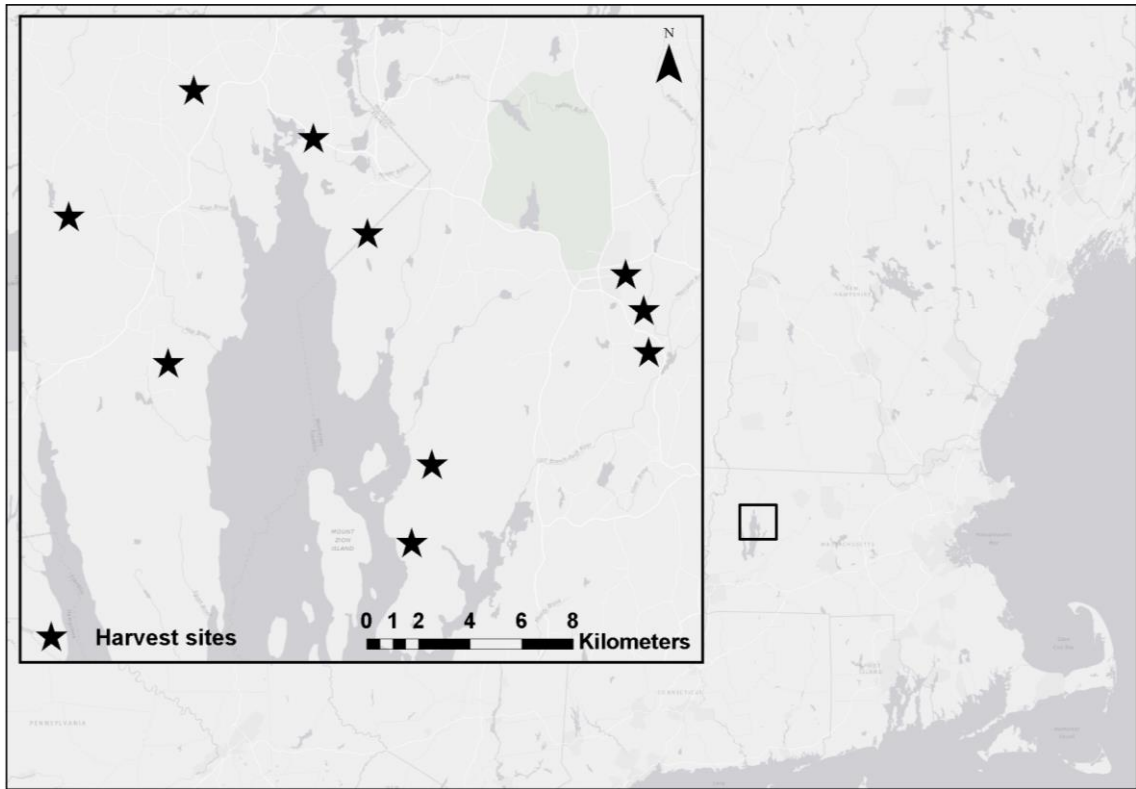
Figure 1: Northern region of the Quabbin Reservoir in western Massachusetts (42.46°N, -72.32° W). Black stars indicate harvest sites where bird and vegetation sampling took place. Data comes from surveys conducted in forest openings in 2014 and 2015 in western Massachusetts, USA.
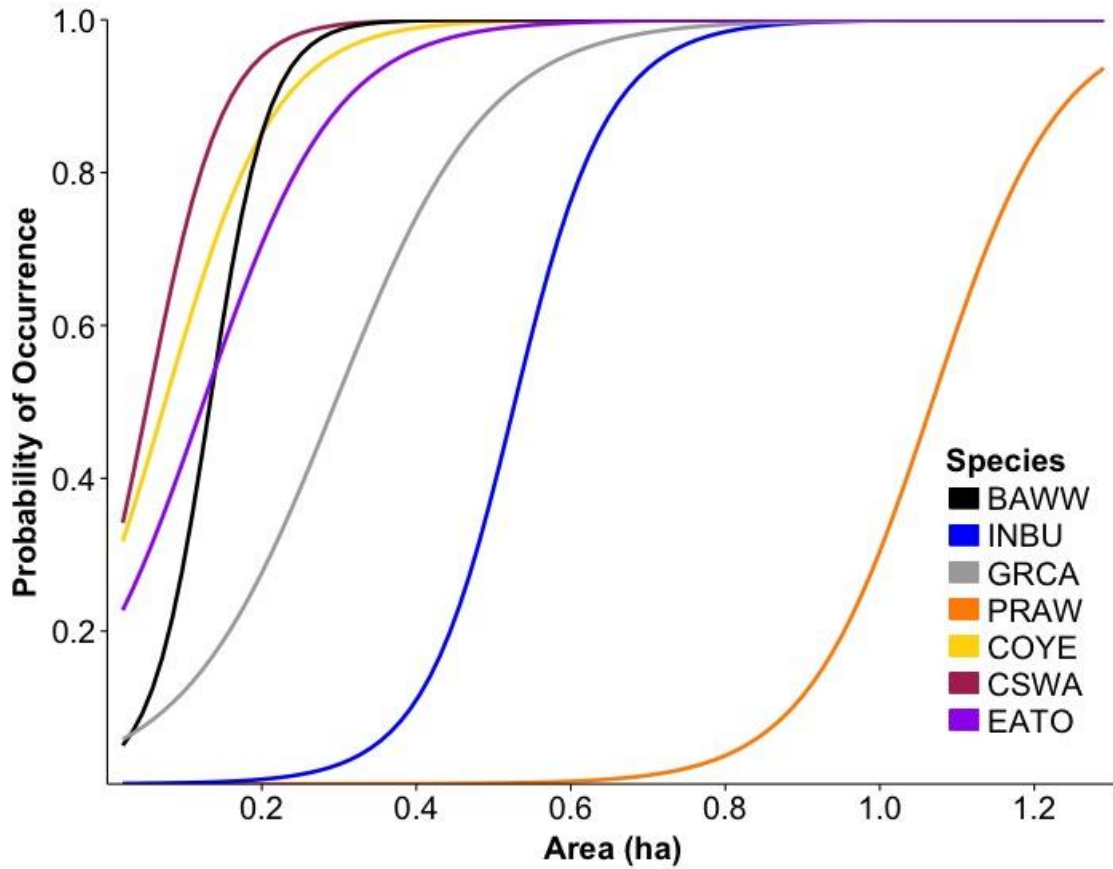
Figure 2: Occupancy model predictions demonstrating relationships between occurrence and patch area. See Table 1 for species codes. Data is only shown for species and years for which patch area was a strong predictor. Patch area was strong for gray catbird in both years, but only 2015 data is shown. Confidence intervals are excluded for better visualization. Data comes from surveys conducted in forest openings in 2014 and 2015 in western Massachusetts, USA.
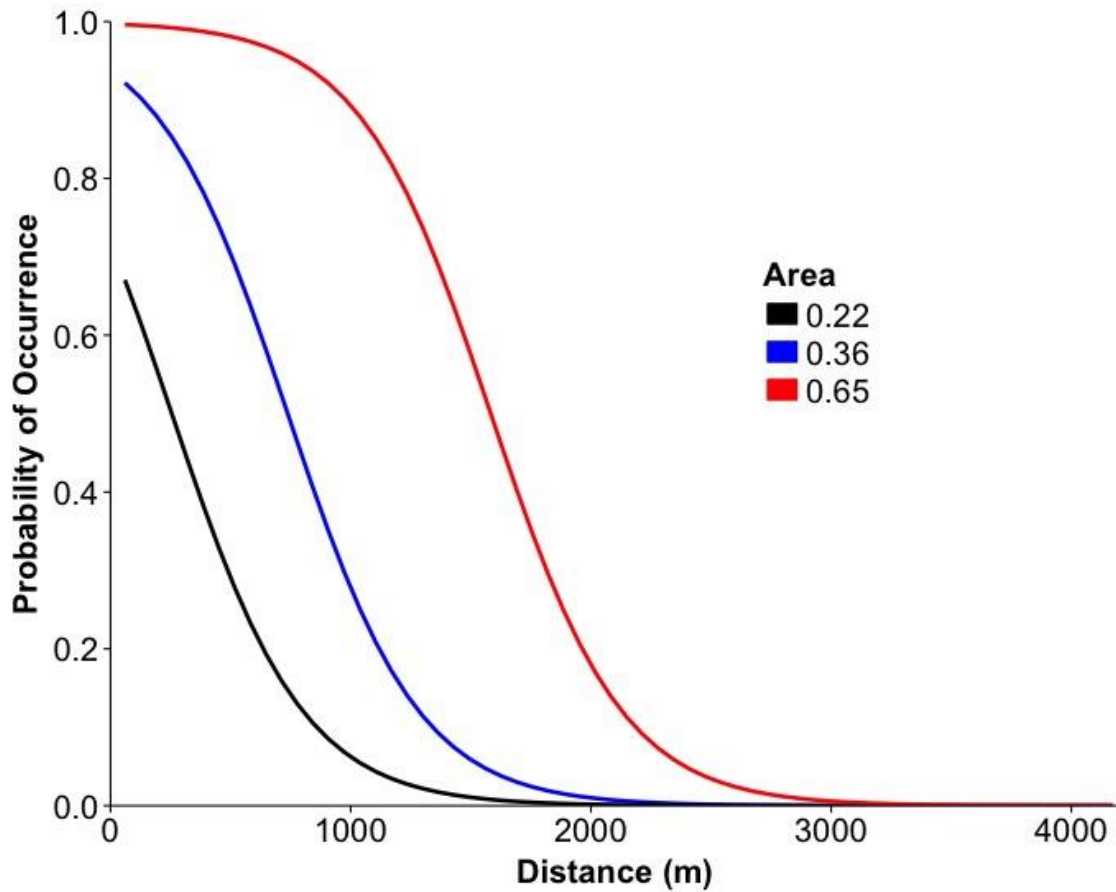
Figure 3: Occupancy model predictions demonstrating relationships between prairie warbler occurrence and the distance to the nearest large patch of shrubland habitat (> 5 ha) for different forest opening sizes. Data is only shown for 2014 in which distance was a strong predictor. Confidence intervals are excluded for better visualization. Data comes from surveys conducted in forest openings in 2014 and 2015 in western Massachusetts, USA.

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Section II

Enhancing Native Pollinator Populations Using Silviculture

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2.1 Introduction

Pollinators are a vital component of ecosystems, providing critical services for reproduction to the large majority of the world's flowering plants (Kearns et al. 1998). Pollinators also provide substantial ecosystem services to humans by pollinating approximately one third of plant-based food crops (Klein et al. 2007). Recent efforts to examine population trends have identified widespread pollinator declines (Biesmeijer et al. 2006; Potts et al. 2010; Bartomeus et al. 2013; Koh et al. 2016). While negative trends cannot be attributed to a single cause, the anthropogenic disturbance of pollinator habitats has been identified as a major contributing factor (Aizen and Feinsinger 2003; Goulson et al. 2008; Potts et al. 2010).

Of all the taxa that serve as pollinators, bees (Hymenoptera: Apiformes) are the most effective at carrying out this critical ecological role (Winfree 2010). Although a substantial proportion of North America's food crops are pollinated by introduced honeybees (Apis mellifera), the continent hosts over 4,000 species of native bees (Cane and Tepedino 2001), which contribute significantly to crop pollination (Klein et al. 2003, Winfree et al. 2007a). Recent evidence of declines of wild bee populations present a potential threat to ecosystem services on which both biodiversity and humans depend.

In a broad-scale meta-analysis, Winfree et al. (2009) synthesized the existing literature that addressed the impact of human disturbances on bees. Although overall their analysis indicated a significant, negative effect of human disturbances on bee abundance, the influence of disturbance on bees differed by disturbance type, with grazing, fire, agriculture and logging actually exerting a positive (albeit non-significant) influence on bee abundance (Winfree et al. 2009). Variation among human land use practices suggests additional research is needed to fully understand how human activities impact these ecologically and economically important species. Furthermore, understanding whether forest management can promote bee numbers could provide guidance to restoring pollination services to forested landscapes, the lack of which has been implicated in the decline of some forest plant species (citation).

One form of disturbance that appeared to be positively related to bee abundance in the analysis by Winfree et al. (2009) was logging. Logging is a dominant form of disturbance within the northeastern region of the United States and is responsible for roughly 78% of early-successional habitats in New England (King and Schlossberg 2012). Since many pollinators have traditionally been thought to prefer open, early-successional habitats (Michener 2007; Winfree et al. 2011), logging activities may have a positive influence on bee populations. Studies of pollinators in even-aged silvicultural treatments such as clearcuts report high abundance and diversity of native bees in comparison to late-successional habitats (Taki et al. 2013; Wilson et al. 2014, Hanula et al. 2015). Stands managed with uneven-aged single-tree selection support more bees than unmanaged stands (Nol et al. 2006), but still far fewer relative to even-aged systems

(Romey et al. 2007). Proctor et al. (2006) found that group selection supported significantly more bees than mature forests and suggested it was more effective at promoting bees than single-tree selection.

Given the fact that silviculture is the dominant disturbance agent over much of the northeast and that there is reason to believe it will positively influence bee populations, a better understanding of how bees respond to a range of uneven-aged silvicultural practices, both in post-logging and adjacent habitats, will contribute to our ability to conserve and manage these key pollinators. This study was undertaken to evaluate the response of bees to forest management. We focused specifically on group selection harvesting because larger openings created by even-aged management have been more thoroughly studied (Taki et al. 2013; Wilson et al. 2014; Rubene 2015) and single-tree selection is reported to support few bees (Romey et al. 2007) and is thus not likely a viable silvicultural approach for promoting bee populations.

The objectives of this study were to (1) compare the bee community within forest openings to that of adjacent mature forest to directly illustrate the impact of silviculture on bee communities relative to reference forest conditions, (2) identify stand-, patch-, and landscape-level factors influencing bee abundance and diversity in both openings and adjacent forest, since bees are known to respond to the environment at different scales (Diaz-Forero et al. 2013), (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 bee species .

2.2 Methods

2.2.1 Study Area

This study was conducted in 2014 and 2015 on lands managed by the Massachusetts Department of Conservation and Recreation land in western Massachusetts, USA (42.46°N, -72.32°W). The major land cover type in this region is mature forest characterized as transitional hardwoods-white pine and 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% the landscape when this study was conducted. Forest openings in this study ranged in size from 0.08-1.29 ha and were created by group selection harvests conducted between four and eight years prior to sampling. Vegetation within openings consisted of seedlings and saplings of tree species characteristic of the adjacent forest as well as mountain laurel (*Kalmia latifolia*), ferns and forbs.

2.2.2 Bee and Vegetation Surveys

Thirty openings were randomly selected 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 (April 26-May 14), summer (July1-July17), and late

summer (August 23-September 8). Bees were collected 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, a transect of 5 sampling points 5 m apart was established in each opening 15 m from the forest and parallel to the gap edge. To sample bees in forest, a second transect of 5 sample points 10 m apart was established starting 10 m from the opening and running perpendicular into the forest along east-west bearings to control for the effects of aspect (Matlack 1994). An additional sample point was placed at the forest edge between transects. At each sampling point, three bowls, one white, one fluorescent yellow, and one fluorescent blue, were placed 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). Sampling was only conducted on sunny, calm days when the average temperature was greater than 10° C. Forest transects were always placed such that surrounding sources of shrubland habitat were never closer to points along the transect than the focal opening. After 24 hours, bowls were collected and bees removed from bowl traps and stored in 70% ethyl alcohol. Bees were later cleaned, blown dry, pinned, labeled, and identified to species using online keys (discoverlife.org) and published references (e.g. Mitchell 1962). Bees with uncertain identities were sent out to specialists for confirmation.

Vegetation was measured 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. Number of flowers within a 1 m radius of each sampling point were recorded by species during each visit. Median and coefficient of variation of vegetation height were used in the analyses to characterize vegetation structure. Absolute flower abundance yielded extremely heterogeneous data that were primarily representative of certain species (e.g. *Aralia hispida*), which produce dozens of very small, but less conspicuous flowers that are not likely to individually attract pollinators to the same extent as larger flowers. Flowering species richness was also not representative of the floral characteristics because richness never exceeded three species 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 five sample points in each transect. This new metric allowed us to coarsely account for abundance, while not overly representing plants that produce numerous but less conspicuous flowers. Although it does not represent true floral abundance, we refer to this metric as floral abundance from this point forward.

2.2.3 Patch and Landscape Metrics

The area of each opening and the percentage of the surrounding landscape containing shrubland habitat (PLAND) were quantified using FRAGSTATS software, version 4 (McGarigal et al. 2012). Area was chosen because there is a lack of consensus regarding the influence of patch size on bee communities. PLAND was chosen 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 scale. To calculate these variables, forest openings were first delineated using ArcGIS 10.2.1 (Environmental Systems Research Institute, Inc., Redlands, CA) and

rasterized using a grid size of 3 m to facilitate analysis in FRAGSTATS. The PLAND metric represented the percent of the landscape that was shrubland habitat within a specified search-radius from the centroid of each opening. PLAND was measured using 200 m and 500 m radii because bee species have been shown to display varying responses to landscape features at different scales (Benjamin et al. 2014).

2.2.4 Statistical Analysis

Generalized linear mixed models (GLMM; Zuur et al. 2009) were the primary framework under which data were analyzed in this study. GLMMs were used to compare differences in abundance and diversity (Shannon's Diversity Index) by habitat type, model abundance and diversity as a function of stand, 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. Poisson and negative binomial distributions were compared using Akaike's information criterion (AIC; Burnham and Anderson 2002) for modeling abundance and gaussian and gamma distributions were compared for modeling diversity. Zero-inflated models were also considered when dependent variables appeared to have more zero values than would be expected under the distributions used (Zuur et al. 2009). Site was included 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.

Analyses of habitat (community and single-species) included a single categorical fixed effect representing habitat (opening or forest). Habitat associations were only modeled for species with > 30 individuals collected (excluding edge points). Relationships with stand, patch, and landscape variables were modeled for all species combined and by guild because bees vary in behavior and how they interact with the environment (Cane et al. 2006; Williams et al. 2010; Wray et al. 2014). Guilds included dietary breadth (broad or "polylectic" versus narrow or "oligolectic"), sociality (solitary, eusocial, or parasitic), nesting location (above or belowground), and body size (small or large). Information about diet, sociality, and nesting location were gathered 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. Dry body mass was then estimated using the known exponential relationship with intertegular length established by Cane (1987). Bees were categorized as small or large if they had body mass < 4 mg or > 16 mg respectively, in accordance with Winfree et al. (2007b). Bees that could not be identified to species were included 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.

Stand, patch, and landscape variables included vegetation height, CV of vegetation height, floral abundance, area of the forest opening, and percent of the landscape containing early-successional habitat within 200 m and 500 m (PLAND200 and PLAND500 respectively). Correlations among independent variables were assessed using Pearson correlation. For all variable comparisons, r was ≤ 0.51. Continuous variables were scaled with $\bar{x} = 0$ and $\sigma = 1$ to facilitate model convergence. Scatterplots were used 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 their coefficient 95% confidence interval did not overlap zero (Chandler et al. 2009). A sequential Bonferroni procedure (Holm 1979) was considered to account for the likelihood of a Type I error given the number of models applied to similar data; however, we did not use this method because we felt it was too conservative and would exclude relationships that are biologically meaningful. Models were fit and parameters were estimated using the glmmADMB package (Skaug et al. 2015) in R statistical software version 3.1.1.

To visualize differences in community composition between opening and forest habitats, opening and forest samples were ordinated 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. The fit of the ordination distances to the original data was assessed by calculating stress, where values closer to zero indicate better fit. NMDS plots were created using a binary dataset to assess community composition without the influence of abundance. NMDS was performed using the vegan package (Oksanen et al. 2013) in R statistical software version 3.1.1.

2.3 Results

In total, 3,316 bees representing 5 families, 15 genera, and 80 identifiable bee species were collected from forest openings and adjacent forest habitat (Appendix A). Approximately 9% of bees collected could not be identified to species (most of which were of the genera *Nomada* and *Lasioglossum*). Three exotic species (*Andrena wilkella*, *L. leucozonium*, and *Osmia cornifrons*), totaling 18 individuals, were collected. Nine species represented approximately 61% of all individuals. The two most common species were *N. maculata* (499 individuals) and *Augochlorella aurata* (402 individuals). The majority of identified bees were polylectic bees (96% of individuals) and bees that nest belowground (65% of individuals). Solitary and eusocial bees represented roughly equal proportions (37% and 36% respectively), while kleptoparasitic bees made up the remaining 26%. When habitats were examined separately, guild proportions were similar. Oligolectic bees were uncommon with only 126 individuals (eight species) collected, of which 94 individuals were *A. uvulariae*, a species that specializes on the plant genus *Uvularia* (Fowler and Droege 2016). *Bombus perplexus* and *L. foxii* were the only species that only occurred in forest, but these were only represented by single individuals.

Bee abundance (β = -1.478, SE = 0.172, z = -8.61, P = < 0.01) and diversity (β = -0.569, SE = 0.135, z = -4.22, P = < 0.01) were significantly greater in openings than in adjacent forest (Fig. 1). NMDS showed no clear separation of opening and forest communities when analyzed with binary data (Fig. 2). A relatively low stress value (0.2) and inspection of the Shepard's plot suggested an acceptable fit of the ordination. Bee

abundance (β = -0.012, SE = 0.007, z = -1.76, P = 0.08) and species diversity (β = -0.006, SE = 0.004, z = -1.52, P = 0.13) in the forest showed no significant relationship with distance to forest opening.

Bee abundance in openings were unrelated to patch area (Table 1). The abundance of parasitic, belowground-nesting, and small bees displayed a positive relationship with PLAND200. The quadratic term for PLAND500 was significant for all guilds except eusocial and aboveground-nesting bees. Coefficients of the quadratic term of PLAND500 were all negative, indicating a unimodal relationship with the dependent variables (Fig. 3). Abundance and diversity of all bees combined as well as polylectic, eusocial, solitary, and aboveground-nesting bees displayed significant negative relationships with vegetation height. Only diversity of all bees combined was positively related to CV of vegetation. Abundance and diversity of all bees combined as well as polylectic, eusocial, solitary, above and belowground-nesting, and large bees displayed positive relationships with floral abundance.

Patch area also 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, above and belowground-nesting, and large bees exhibited a positive relationship with PLAND200. Abundance of all categories except for eusocial, aboveground-nesting, and small bees displayed positive relationships with the linear PLAND500 term. A negative quadratic term for PLAND500 was significant for all bees combined, solitary bees, parasitic bees, and belowground-nesting bees. Abundance of eusocial, aboveground-nesting, and small bees displayed a positive relationship with the vegetation height within forest openings. CV of vegetation height within openings exhibited no apparent influence on any guild. Abundance of eusocial and small bees displayed a negative relationship with floral abundance 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. These species were *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. Additional species that did not show strong associations with a particular habitat type were *A. carlini*, *A. uvulariae*, *L. planatum*, *L. subviridatum*.

2.4 Discussion

Our findings that bee abundance and diversity were far greater in forest openings compared to closed-canopy forest demonstrate these practices greatly increase native bee abundance and diversity, and is consistent with the findings of Proctor et al. (2012) in Ontario. This is of interest from a conservation standpoint because of evidence that at least some native bee species are undergoing population declines (Bartomeus et al. 2013), and habitat loss has been implicated as potential cause of these declines (Potts et al. 2010). In addition to their value as biodiversity, bees provide important pollination services for native plants, and loss of pollination services has been suggested as a potential cause of declines in native flora in many regions of the globe (Biesmeijer et al. 2006, Willis et al. 2008). The creation of habitat through plantings and the establishment

of fallow fields is recommended by conservationists for supporting native pollinators (Vaughn et al. 2015). My results support the contention of Taki et al. (2013) who suggest that timber harvesting could be a potentially important tool for promoting bee populations and associated pollinator services.

Group selection as a habitat management tool has received a cool reception among conservationists interested in managing shrubland birds, since the habitat patches created by group selection are typically too small to support certain area-sensitive shrubland species (Costello et al. 2000; Schlossberg and King 2007). In contrast, our observations suggest that bees are relatively insensitive to patch area. Little consensus exists in the literature on bees and patch size, with some studies reporting positive relationships with patch area (Aizen and Feinsinger 1994; Meyer et al. 2007; Krauss et al. 2009; Bommarco et al. 2010; Diaz-Forero et al. 2013; Rubene et al. 2015), others no relationships (Brosi et al. 2008), or mixed responses by guild (Donaldson et al. 2002; Cane et al. 2006; 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) can 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 fragmented habitats have provided similar explanations (Brotons et al. 2003; Neame et al. 2013).

Landscape composition has been shown to be an important factor influencing bees (Dauber et al. 2003; Hirsch et al. 2003; Taki et al. 2007; Winfree et al. 2007b; Watson et al. 2011), but few studies have examined how the extent of early-successional forest habitat on the landscape affects bees. We observed that all guilds, apart from eusocial and aboveground-nesting bees, displayed unimodal relationships with the amount of early-successional habitat on the landscape within 500 m. These non-linear associations indicate 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. Rubene et al. (2015) sampled bees in post-logging habitats while also considering the amount of early-successional habitat on the landscape, but found no relationship between species richness and the amount of early-successional habitat within 2 km. 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 3) and the scales examined (200 m and 500 m) are within the feasible foraging distance for many bees (Gathmann and Tscharntke 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 is no longer necessary and as a result fewer bees visit each opening.

Similarly to the potential value for natural habitats to supplement crop pollination (Ricketts et al. 2008; Klein et al. 2003; Benjamin et al. 2014), greater pollinator numbers in forest openings could promote pollination services in adjacent forest where bees are scarce. However, our results were somewhat equivocal on this point. On the one hand there was no indication that bee abundance or diversity along transects was elevated near openings, while on the other hand 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 an effect of distance to opening 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 Tscharntke 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) failed to observe elevated bee abundance near early-successional habitat along old logging roads. The positive relationship with early-successional habitat that was found suggests that silviculture promotes pollinators in adjacent forest and thus may translate to elevated pollinator services for flowering plants associated with mature forest. It is critical to recognize, however, that abundance and diversity followed a unimodal trend for the amount of early-successional habitat at 500 m similar to that of bees 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.

Evidence suggests that local-scale factors 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 abundance, which is consistent with other studies (e.g. Potts et al. 2003; Roulston and Goodell 2011; Torne-Noruera 2014). The only guilds that showed no response to floral abundance were oligolectic bees, kleptoparasitic bees, and small bees. Oligoleges require certain types of pollen to provision their young (Roulston and Goodell 2011) and thus are more likely driven by the abundance of their host plants rather than the broader floral community. Similarly, kleptoparasites should be more driven by their host species (Sheffield et al. 2013) as opposed to the floral community especially since they do not provision 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 Tscharntke 2002; Greenleaf et al. 2007).

Abundance of eusocial and small bees in adjacent mature forest was negatively related to floral abundance in 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 due to the elevated flower abundance in young forests. This pattern, and the increased abundance of eusocial, small, and aboveground-nesting bees in mature forest with taller vegetation within openings show that stand characteristics can directly influence not only the bee community within that stand, but also in surrounding stands. These patterns also show that despite our expectation that high bee abundance in gaps might spill into adjacent forest and augment pollination in those habitats, post-logging habitats may in

fact have negative consequences for pollination services in adjacent forest. Indeed, Cartar (2005) suggested that early-successional forests may cause reduced pollination services to forest plants, while Diaz-Forero et al. (2013) postulated that young forests might be ecological traps for *Bombus* spp. In addition, 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 reproductive success of forest plants to definitively assess the impact of logging.

My findings that all bees combined and many individual guilds were negatively associated with vegetation height supports the wide-spread brief that most bees prefer early-successional, open habitats (Michener 2007). Other studies have identified similar relationships (Gikungu 2006; Taki et al. 2013; Sudan 2016). 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 Wilmer 1997). This relationship between vegetation height and floral abundance is reflected by their correlation ($r = -0.51$, $P = < 0.01$).

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

Although bees are often broadly lumped together as species of open habitats (Michener 2007), habitat requirements are largely unknown for many species and research has shown that some bees may in fact be associated with late-successional habitats (Winfree et al. 2007b; Taki et al. 2007). These analyses partly support this traditional line of thought, demonstrating clear preferences toward openings for 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, however, 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 probably sampled mature forest habitat that was 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 may have come 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 (oligoleges) are of heightened conservation concern because they have been shown to be at greater risk of decline (Biesmeijer et al. 2006; Winfree et al. 2010). Although oligoleges typically represent a far higher proportion (~30%) of species in temperate bee communities (Minckley and Roulston 2006), they comprised only 10% of the species and less than 4%

of individuals collected in this study, suggesting that silvicultural openings do not contribute to promoting floral specialists as much as other habitats. Interestingly, despite the limited representation of specialists, we collected a notably large number of *A. uvulariae,* a specialist of *Uvularia* spp. While less abundant than both eusocial and solitary bees, kleptoparasitic bees were common both in mature forest and openings, making up approximately 26% 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 kleptoparasites 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.

It should be noted that 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 bowl traps would exhibit different patterns of abundance relative to 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 (Wilson et al. 2008; Baum and Wallen 2011). My observation of a positive relationship between bee captures in bowls and floral abundance suggests this source of bias was not influencing our sampling. Finally, our study did not encompass a complete gradient of landscape conditions, no openings were completely isolated, nor did any openings have more than roughly 20% of the surrounding landscape containing 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.

2.5 Conclusions

Public and private conservation and management entities are receiving encouragement to create habitat for pollinators (Obama 2014), and plantings and pollinator gardens are recommended methods for achieving this goal (Vaughn et al. 2015). Although these methods are effective, there is a monetary cost associated with them, especially for creating them at a large spatial scale. This research demonstrates that forest management practices that create forest openings 0.08 - 1.29 ha within a landscape consisting of 5-15% early-successional habitat can promote native bee communities, not only within openings, but also in surrounding mature forest. 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 Massachusetts (Schlossberg and King 2015) suggests that the aggregate contribution of silviculture to pollinator populations in the region may be significant.

Although managers may be able to boost pollinator services to surrounding habitats with the strategic placement of young forest, but it is unclear whether creating gaps will translate to increased pollination rates within adjacent forest because certain

guilds may be drawn out of forests into gaps potentially depriving forest habitats of pollinator services.

Table 3: Parameter estimates for fixed-effect variables in generalized linear mixed models of abundance and Shannon's Diversity Index (SDI) of bees in forest openings. Standard errors are given in parentheses. Environmental variables include area of opening (Area), the amount of early-successional habitat within 200 m (PLAND200) and 500 m (PLAND500), a quadratic term for PLAND500 (PLAND500^2), median vegetation height within openings (Height), the coefficient of variation of vegetation height (CV), and floral abundance (Flower). Groups analyzed include all bees combined, polylectic bees, oligolectic bees, eusocial bees, solitary bees, parasitic bees, aboveground-nesting bees (above), belowground-nesting bees (below), small bees, and large bees. Models only included one fixed-effect variable, with the exception of models of PLAND500, which also included PLAND500^2. Coefficients were only shown if confidence intervals did not overlap zero. Data comes from bowl trap surveys conducted in early spring, mid-summer, and late summer in 2014 and 2015 in western Massachusetts.

Group	Measure	Area	PLAND.200	PLAND.500	PLAND.500^2	Height	CV	Flower
All Bees	Abundance				-0.224 (0.096)	-0.19 (0.097)		0.268 (0.092)
	SDI		0.168 (0.079)		-0.169 (0.08)	-0.174 (0.074)	0.162 (0.076)	0.172 (0.074)
Polylectic	Abundance				-0.197 (0.1)	-0.203 (0.097)		0.273 (0.096)
Oligolectic	Abundance				-0.613 (0.186)			
Eusocial	Abundance					-0.306 (0.137)		0.410 (0.134)
Solitary	Abundance				-0.212 (0.097)	-0.324 (0.086)		0.337 (0.081)
Parasitic	Abundance		0.364 (0.151)		-0.469 (0.176)			
Above	Abundance					-0.383 (0.083)		0.319 (0.086)
Below	Abundance		0.241 (0.116)		-0.305 (0.125)			0.266 (0.12)
Small	Abundance		0.315 (0.139)		-0.401 (0.151)			
Large	Abundance				-0.638 (0.255)			0.395 (0.197)

Table 4: Parameter estimates for fixed-effect variables in generalized linear mixed models of abundance and Shannon's Diversity Index (SDI) of bees in mature forest. Standard errors are included in parentheses. Environmental variables include area of opening (Area), the amount of early-successional habitat within 200 m (PLAND200) and 500 m (PLAND500), a quadratic term for PLAND500 (PLAND500^2), median vegetation height within openings (Height), the coefficient of variation of vegetation height within openings (CV), and floral abundance within openings (Flower). Groups analyzed include all bees combined, polylectic bees, oligolectic bees, eusocial bees, solitary bees, parasitic bees, aboveground-nesting bees (above), belowground-nesting bees (below), small bees, and large bees. Models only included one fixed-effect variable, with the exception of models including PLAND500, which also included PLAND500^2. Coefficients were only displayed if confidence intervals did not overlap zero. Data comes from bowl trap surveys conducted in early spring, mid-summer, and late summer in 2014 and 2015 in western Massachusetts.

Group	Measure	Area	PLAND.200	PLAND.500	PLAND.500^2	Height	CV	Flower
All Bees	Abundance		0.408 (0.169)	0.432 (0.184)	-0.435 (0.208)			
	SDI				-0.317 (0.162)			
Polylectic	Abundance		0.392 (0.170)	0.454 (0.196)				
Oligolectic	Abundance			0.672 (0.325)				
Eusocial	Abundance					0.462 (0.180)		-0.389 (0.173)
Solitary	Abundance		0.483 (0.163)	0.484 (0.169)	-0.457 (0.181)			
Parasitic	Abundance			0.844 (0.244)	-0.667 (0.217)			
Above	Abundance		0.404 (0.197)			0.411 (0.165)		
Below	Abundance		0.375 (0.176)	0.611 (0.166)	-0.527 (0.177)			
Small	Abundance					0.652 (0.276)		-0.638 (0.281)
Large	Abundance		0.528 (0.200)	0.753 (0.245)				

Table 5: Results of species habitat associations using generalized linear mixed models. A single fixed effect representing habitat type (opening or forest) and a random effect of site were included in all models. Only species that occurred > 30 times (excluding edge points) were examined.

| Species	n	β	SE	z	P
Andrena carlini	159	-0.674	0.395	-1.71	0.09
Andrena uvulariae	86	-0.209	0.233	-0.9	0.37
Andrena vicina	44	-2.66	0.75	-3.55	<0.01
Augochlorella aurata	368	-2.637	0.38	-6.95	<0.01
Ceratina calcarata	166	-2.222	0.335	-6.63	<0.01
Ceratina dupla	102	-2.965	0.54	-5.49	<0.01
Lasioglossum coeruleum	87	-0.01	0.31	-0.03	0.97
Lasioglossum cressonii	44	-1.358	0.44	-3.09	<0.01
Lasioglossum ephialtum	37	-2.11	0.6584	-3.2	<0.01
Lasioglossum planatum	55	-0.774	0.722	-1.07	0.28
Lasioglossum subviridatum	144	-0.313	0.354	-0.88	0.38
Lasioglossum taylorae	138	-1.835	0.335	-5.48	<0.01
Lasioglossum versans	32	0.886	0.457	1.94	0.05
Nomada luteoloides	67	-1.424	0.31	-4.61	<0.01
Nomada maculata	456	-2.611	0.277	-9.42	<0.01
Osmia atriventris	171	-1.674	0.251	-6.66	<0.01
Osmia pumila	133	-1.745	0.267	-6.54	<0.01
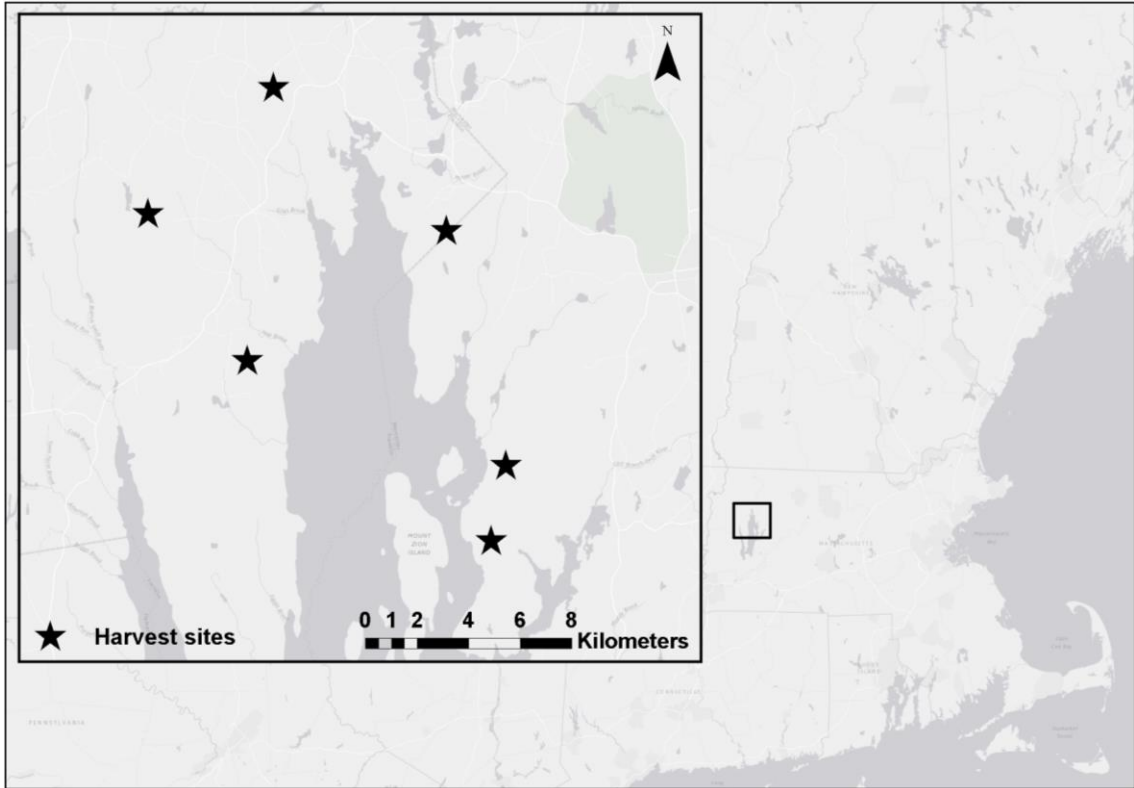
Figure 4: Northern region of the Quabbin Reservoir in western Massachusetts (42.46°N, -72.32° W). Black stars indicate harvest sites where sampling took place.
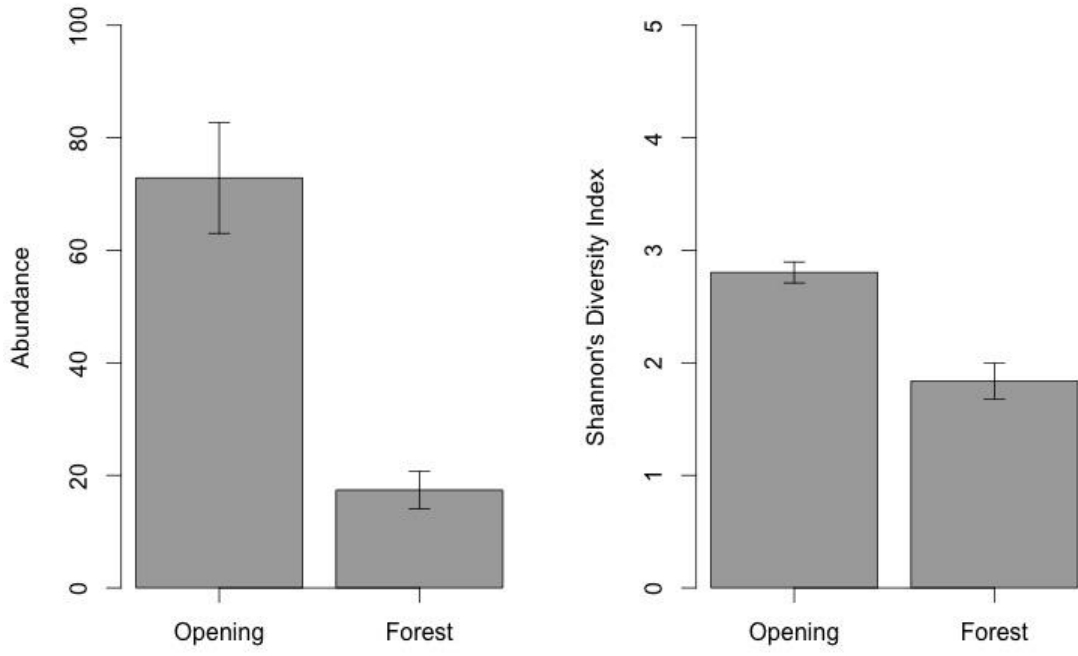
Figure 5: Bee abundance and diversity per transect in openings and mature forest. Bars represent standard error.
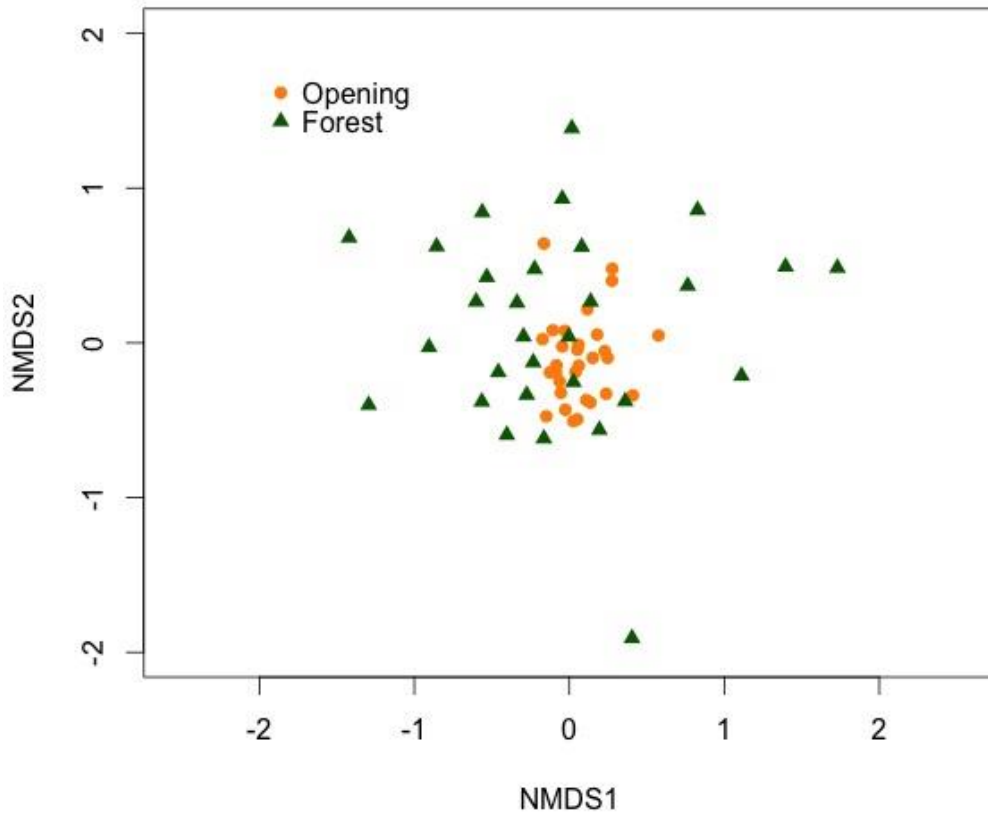
Figure 6: Non-metric multidimensional scaling ordination of opening and forest transects with binary community data.
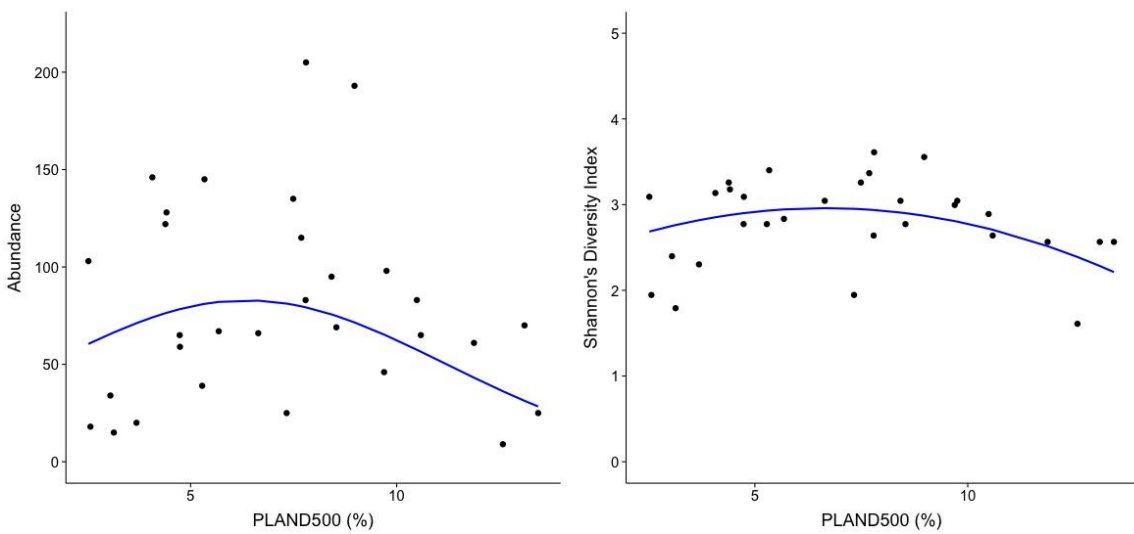
Figure 7: Bee abundance and Shannon's diversity index in openings in relation to the percent of the surrounding landscape that was early-successional habitat within 500 m (PLAND500). Lines represent the predicted values of fitted generalized linear mixed models that included a linear and quadratic term for PLAND500 as fixed effects and site as a random effect.

BEE SPECIES

Bee species collected at 30 locations in western Massachusetts in 2014 and 2015. Life history information is shown as well as abundance for opening transects, edge points, forest transects, and total combined, across all 30 locations. Life history information include: origin indicated by N (native) or E (exotic), pollen specificity (Diet) indicated by P (polylectic) or O (oligolectic), nesting location (Nest) indicated by B (below-ground nesting) or A (above-ground nesting), and sociality (Soc) indicated by E (social), S (solitary), or P (parasitic).

Species	Opening	Edge	Forest	Total	Origin	Diet	Nest	Soc
Agapostemon virescens	1	1	1	3	N	P	B	S
Andrena bradleyi	8	1	0	9	N	O	B	S
Andrena carlini	106	12	53	171	N	P	B	S
Andrena carolina	4	0	1	5	N	O	B	S
Andrena ceanothi	0	1	0	1	N	P	B	S
Andrena cressonii	3	0	0	3	N	P	B	S
Andrena forbesii	1	0	0	1	N	P	B	S
Andrena frigida	1	0	0	1	N	O	A	S
Andrena imitatrix	3	0	1	4	N	P	B	S
Andrena mandibularis	2	0	1	3	N	P	B	S
Andrena melanochroa	2	0	0	2	N	O	B	S
Andrena nigrihirta	4	0	0	4	N	P	B	S
Andrena rufosignata	17	3	5	25	N	P	B	S
Andrena rugosa	6	4	7	17	N	P	B	S
Andrena spp.	2	0	0	2				S
Andrena tridens	9	0	8	17	N	P	B	S
Andrena uvulariae	48	8	38	94	N	O	B	S
Andrena vicina	41	1	3	45	N	P	B	S
Andrena violae	4	0	2	6	N	O	B	S
Andrena wilkella	1	0	0	1	E	P	B	S
Augochlora pura	17	2	2	21	N	P	A	S
Augochlorella aurata	348	34	20	402	N	P	B	E
Augochloropsis metallica	0	1	0	1	N	P	B	S
Bombus bimaculatus	5	0	3	8	N	P	A	E
Bombus impatiens	25	5	4	34	N	P	A	E
Bombus perplexus	0	0	1	1	N	P	A	E
Bombus sandersoni	11	1	4	16	N	P	A	E
Bombus sandersoni/vagans	1	0	1	2	N	P	A	E
Bombus vagans	12	3	5	20	N	P	A	E
Ceratina calcarata	150	14	16	180	N	P	A	S
Ceratina calcarata/dupla	1	0	0	1	N	P	A	S
Ceratina dupla	97	10	5	112	N	P	A	S
Ceratina mikmaqi	7	0	2	9	N	P	A	S

Colletes inaequalis	3	1	0	4	N	P	B	S
Halictus confusus	0	2	0	2	N	P	B	E
Halictus rubicundus	4	3	3	10	N	P	B	E
Hoplitis producta	1	0	0	1	N	P	A	S
Hoplitis spoliata	0	1	0	1	N	P	A	S
Hylaeus affinis	1	0	0	1	N	P	A	S
Hylaeus modestus	3	1	0	4	N	P	A	S
Nr. *Lasioglossum abanci*	6	3	4	13	N	P	B	E
Lasioglossum acuminatum	6	4	5	15	N	P	B	S
Lasioglossum athabascense	1	0	0	1	N	P	B	S
Lasioglossum atwoodi	5	0	1	6	N	P	B	E
Lasioglossum coeruleum	40	9	47	96	N	P	A	E
Lasioglossum coriaceum	14	9	7	30	N	P	B	S
Lasioglossum cressonii	35	18	9	62	N	P	A	E
Lasioglossum ephialtum	33	4	4	41	N	P	B	E
Lasioglossum foxii	0	0	1	1	N	P	B	S
Lasioglossum laevissimum	3	1	1	5	N	P	B	E
Lasioglossum leucozonium	1	0	0	1	E	P	B	S
Lasioglossum nelumbonis	1	0	0	1	N	O	B	S
Lasioglossum nigroviride	6	0	0	6	N	P	B	E
Lasioglossum oblongum	4	0	3	7	N	P	A	E
Lasioglossum planatum	43	2	12	57	N	P	B	E
Lasioglossum quebecense	12	3	13	28	N	P	B	S
Lasioglossum spp.	63	13	23	99				
Lasioglossum subviridatum	81	25	63	169	N	P	A	E
Lasioglossum taylorae	119	25	19	163	N	P	B	E
Lasioglossum tegulare	4	0	1	5	N	P	B	E
Lasioglossum versans	10	6	22	38	N	P	B	E
Lasioglossum versatum	2	0	0	2	N	P	B	E
Lasioglossum viridatum	5	1	0	6	N	P	B	E
Nomada (bidentate)	72	13	23	108	N	P	B	C
Nomada armatella	1	0	0	1	N	P	B	C
Nomada composita	4	0	2	6	N	P	B	C
Nomada cressonii	3	2	3	8	N	P	B	C
Nomada depressa	5	0	4	9	N	P	B	C
Nomada gracilis	5	1	1	7	N	P	B	C
Nomada gracilis/xanthura	1	0	0	1	N	P	B	C
Nomada illinoensis	1	0	0	1	N	P	B	C
Nomada imbricata	4	1	0	5	N	P	B	C
Nomada luteoloides	54	7	13	74	N	P	B	C
Nomada maculata	423	43	33	499	N	P	B	C
Nomada pygmaea	17	0	7	24	N	P	B	C
Nomada sayi/illinoensis	11	2	0	13	N	P	B	C

Nomada spp.	68	6	8	82		P	B	C
Osmia atriventris	144	20	27	191	N	P	A	S
Osmia bucephala	2	0	0	2	N	P	A	S
Osmia cornifrons	7	0	9	16	E	P	A	S
Osmia georgica	1	0	0	1	N	P	A	S
Osmia inspergens	5	0	0	5	N	P	A	S
Osmia lignaria	1	0	0	1	N	P	A	S
Osmia proxima	1	0	0	1	N	P	A	S
Osmia pumila	113	10	20	143	N	P	A	S
Osmia virga	7	1	0	8	N	O	A	S
Sphecodes coronus	4	0	2	6	N	P	B	C
Sphecodes mandibularis	3	0	0	3	N	P	B	C
Sphecodes townesi	3	0	1	4	N	P	B	C
Unknown	1	0	0	1				

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