Contents lists available at ScienceDirect

Forest Ecology and Management

Pollinator communities vary with vegetation structure and time since management within regenerating timber harvests of the Central Appalachian Mountains

Codey L. Mathis [a,*], Darin J. McNeil Jr. [b], Monica R. Lee [a], Christina M. Grozinger [b], David I. King [c], Clint R.V. Otto [d], Jeffery L. Larkin [a]

[a] *Department of Biology, Indiana University of Pennsylvania, 1011 South Drive, Indiana, PA 15701, USA*
[b] *Department of Entomology, Pennsylvania State University, Millennium Science Complex, University Park, PA 16802, USA*
[c] *US Forest Service Northern Research Station, University of Massachusetts, Amherst, MA 01003, USA*
[d] *U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND 58401, USA*

ABSTRACT

Native pollinator populations across the United States are increasingly threatened by a multitude of ecological stressors. Although the drivers behind pollinator population declines are varied, habitat loss/degradation remains one of the most important threats. Forested landscapes, where the impacts of habitat loss/degradation are minimized, are known to support robust pollinator populations in eastern North America. Within heavily forested landscapes, timber management is already implemented as a means for improving forest health and enhancing wildlife habitat, however, little is known regarding the characteristics within regenerating timber harvests that affect forest pollinator populations. In 2018 and 2019, we monitored insect pollinators in 143 regenerating (≤9 growing seasons post-harvest) timber harvest sites across Pennsylvania. During 1129 survey events, we observed over 9100 bees and butterflies, 220 blooming plant taxa, and collected over 2200 pollinator specimens. Bee and butterfly abundance were positively associated with season-wide floral abundance and negatively associated with dense vegetation that inhibits the growth of understory floral resources. Particularly in late summer, few pollinators were observed in stands >6 years post-harvest, with models predicting five times more bees in 1-year-old harvests than in 9-year-old harvests. Pollinator species diversity was positively associated with floral diversity and percent forb cover, and negatively associated with percent tall (>1 m) sapling cover. These results suggest that regenerating timber harvests promote abundant and diverse pollinator communities in the Appalachian Mountains, though pollinator abundance declined quickly as woody stems regenerated. Ultimately, our findings contribute to a growing body of literature suggesting that dynamic forest management producing a mix of age classes would benefit forest pollinator populations in the Central Appalachian Mountains.

1. Introduction

Insect pollinators, such as bees, are among the most beneficial invertebrates to human civilization. These insects provide critical pollination services valued as high as $34 billion/year in the United States (Jordan et al., 2021), and they act as ecological pillars in native terrestrial systems, pollinating over 85% of wild angiosperms (Ollerton et al., 2011) and over 75% of crop species (Klein et al., 2007). Widespread declines of insect pollinators across the globe have raised alarm among conservationists (Cameron et al., 2011; Hallmann et al., 2017;

Sánchez-Bayo and Wyckhuys, 2019; Wepprich et al., 2019), prompting the creation of conservation policies to slow declines (Byrne and Fitzpatrick, 2009) and necessitating research to inform these efforts. In North America, a recent index of predicted wild bee population densities (Koh et al., 2016) suggested that while native bees may be declining in much of the US, abundance of native bees remains unchanged in forested regions of the northeast. However, these estimates had high uncertainty, potentially resulting from a bias towards studies conducted in urban (*e.g.,* Lowenstein et al., 2015; Hall et al., 2017; Plascencia and Philpott, 2017) and agricultural (*e.g.,* Mandelik et al., 2012; Martins

---

et al., 2015; Buchanan et al., 2017) landscapes. Therefore, current scientific understanding of pollinator ecology remains largely based on assumptions made from observations in novel ecosystems such as agricultural landscapes (De Palma et al., 2016; Koh et al., 2016), despite the apparent value of forests for supporting abundant and diverse pollinator communities (King and Schlossberg, 2014; Hanula et al., 2016).

In the eastern United States, diverse, multi-aged forests are presumed to provide high-quality habitat for pollinators (Koh et al., 2016). Forests are the dominant land-cover type in this region (Albright et al., 2017), providing abundant forage and nest-site opportunities (Milam et al., 2018; Urban-Mead et al., 2021) and supporting many forest specialist species (Winfree et al., 2007). Heavily forested environments are expected to have lower managed honey bee (*Apis mellifera*) densities, which would reduce competition with native bees (Russo, 2016; Wignall et al., 2020) and lower disease transmission (Murray et al., 2019; Brettell et al., 2020; McNeil et al. 2020a). Moreover, forests likely provide pollinators with refugia from harmful mass-applied agricultural insecticides, such as neonicotinoids (Godfray et al., 2014), though this may not be the case immediately surrounding individual trees treated for the emerald ash borer (*Agrilus planipennis*) and hemlock woolly-adelgid (*Adelges tsugae*; Fortuin et al., 2020). Though pollinator communities in forests may seem removed from their economic benefits in agricultural landscapes, there is a growing body of literature that suggests that benefits to crop pollination occur via spillover from natural habitats (Watson et al., 2011; Blitzer et al., 2012; Garibaldi et al., 2014), particularly in heavily forested regions such as Pennsylvania (Kammerer et al., 2016). Therefore, a more holistic understanding of the factors associated with high-quality pollinator habitat within eastern North American forests is warranted.

Previous studies indicate that early successional forests such as those produced via silviculture serve as high-quality habitat for a wide variety of wildlife species (mammals: Litvaitis, 2001; birds: DeGraaf and Yamasaki, 2003) including bees (Roberts et al., 2017; Milam et al., 2018) and butterflies (Miller and Hammond, 2007; Fartmann et al., 2013). Indeed, young forests are frequently characterized by microclimatic conditions such as higher ambient temperature and light levels than surrounding mature forests that serve to benefit both insect pollinators and the flowers upon which they depend (Polatto et al., 2014). One study within a southern Appalachian forest community found that bee abundance was greater in younger forests, and particularly along logging roads, as compared to older forests (Jackson et al., 2014). However, this study compared mature forest (>90 years post-harvest) to 'younger' forests (20–40 years post-harvest), missing a potentially pivotal stage of forest succession for bees (early-successional; *i.e.*, prior to stem exclusion stage) that likely provides the most abundant floral and nesting resources throughout the entire growing season (Roberts et al., 2017; Milam et al., 2018). Throughout the eastern deciduous forests of North America, a lack of disturbance coupled with advancing ecological succession in many regions has led to landscapes dominated by even-aged sawtimber with very little in the early successional stage (<10%; Askins, 2001; Brooks, 2003; King and Schlossberg, 2014; Albright et al., 2017). As a direct result, many forest-dependent wildlife species have experienced steady population declines (King and Schlossberg, 2014; Sauer et al. 2017). Given the potential value of early seral stands to forest pollinator populations (Roberts et al., 2017; Milam et al., 2018), understanding the impacts of forest management on pollinator communities would provide critical insight to forest managers who wish to support landscapes with robust pollinator populations.

Eastern North America's forests were historically dynamic in structure and species composition, largely driven by natural disturbances like wildfire, beaver (*Castor canadensis*; Naiman et al., 1988; Butler and Malanson, 2005; Wohl, 2021), and old growth dynamics (Lorimer, 1980; Runkle, 1982; Whitney, 1994; Lovett et al., 2006). Today, stands of young regenerating forest have become increasingly rare as a result of anthropogenic suppression of natural disturbance agents such as wildfire (Askins, 2001; DeGraaf and Yamasaki, 2003). Many plant and animal populations dependent upon these early successional forests have declined with the loss of young forests (King and Schlossberg, 2014; Sauer et al., 2017). In 2011, an assessment of age distribution and disturbance legacy of North American forests found that only 8.6% of forest land in the northeastern United States was 0–20 years old (Pan et al., 2011). Professionals in forestry and wildlife conservation widely acknowledge that achieving healthy, balanced forest age-class distributions requires active forest management on public and private lands (Shifley et al., 2014), and efforts have been undertaken to balance forest age classes in the eastern United States (United States Department of Agriculture [USDA], 2014). Given that 75% of forestland in the northern United States is privately owned (Smith et al., 2009), private lands forest management has the potential to disproportionately affect landscape-level forest composition across the region (Shifley et al., 2014). Private lands conservation efforts such as U.S. Department of Agriculture Natural Resource Conservation Service's (NRCS) '*Working Lands for Wildlife*' (WLFW) partnership aim to improve forest health and restore habitat for at-risk wildlife populations (Ciuzio et al., 2013; USDA, 2014). One such target species within the eastern United States is the golden-winged warbler (*Vermivora chrysoptera*), a young forest- and shrubland-dependent songbird (McNeil et al., 2020b). Over 9000 ha of early successional forest has been created through NRCS-WLFW for nesting golden-winged warblers since the start of the partnership in 2012 (USDA, 2014; McNeil et al., 2020b; B. Costanzo, NRCS, oral communication, 2021). To this end, the increasing success of efforts such as NRCS-WLFW and similar efforts on publicly managed lands in creating early successional forest provides an unprecedented opportunity to assess the extent to which insect pollinators might benefit from much needed age class diversification in eastern forests (Shifley et al., 2014).

To improve the understanding of how regenerating stands benefit forest pollinators, we quantified bee and butterfly pollinator diversity and density within regenerating timber harvests of the central Appalachian Mountains. More specifically, our goals were to: 1) describe pollinator- and floral communities within regenerating timber harvests, and 2) determine how time since harvest, ownership type, vegetation structure, and floral resources are associated with bee and butterfly density and diversity. We discuss our results in the context of how regenerating hardwood stands may support insect pollinator communities within heavily forested landscapes.

2. Methods

2.1. Study area and experimental design

We studied pollinator communities in regenerating timber harvests on private and public forestlands across the state of Pennsylvania. Pennsylvania's forestlands exist primarily as privately-owned (>80%), mid-successional sawtimber (~40–80 years old) with only ~6% in the youngest age class (<20 years old; Albright et al., 2017). Across the state, we focused our efforts within four heavily forested regions: 1) Laurel Highlands, 2) Ridge-and-Valley, 3) Pennsylvania Wilds, and 4) Pocono Mountains (Fig. 1.A, Sevon, 2000; Albright et al., 2017). The Laurel Highlands region (n = 12 sites), in the southwestern portion of the state, is characterized by undulating hills (mean = 629 m ± 61.2; Sevon, 2000) dominated by oak (*Quercus* spp.) - hickory (*Carya* spp.) forests (Albright et al., 2017). The Ridge-and-Valley region (n = 30 sites), spanning across southcentral Pennsylvania, is characterized by moderate-elevation (mean = 359 m ± 35.4) oak-hickory ridges separated by lower-elevation agricultural valleys (Sevon, 2000; Albright et al., 2017). The Pennsylvania Wilds region (n = 39 sites) occurs across northcentral Pennsylvania and largely consists of high-elevation (mean = 551 m ± 31.4; Sevon, 2000) northern hardwood and mixed oak-hickory stands (Albright et al., 2017). Finally, the Pocono Mountains region (n = 62 sites) is characterized by rounded hills and valleys (Sevon, 2000) that support mixed-hardwood stands sparsely intermixed
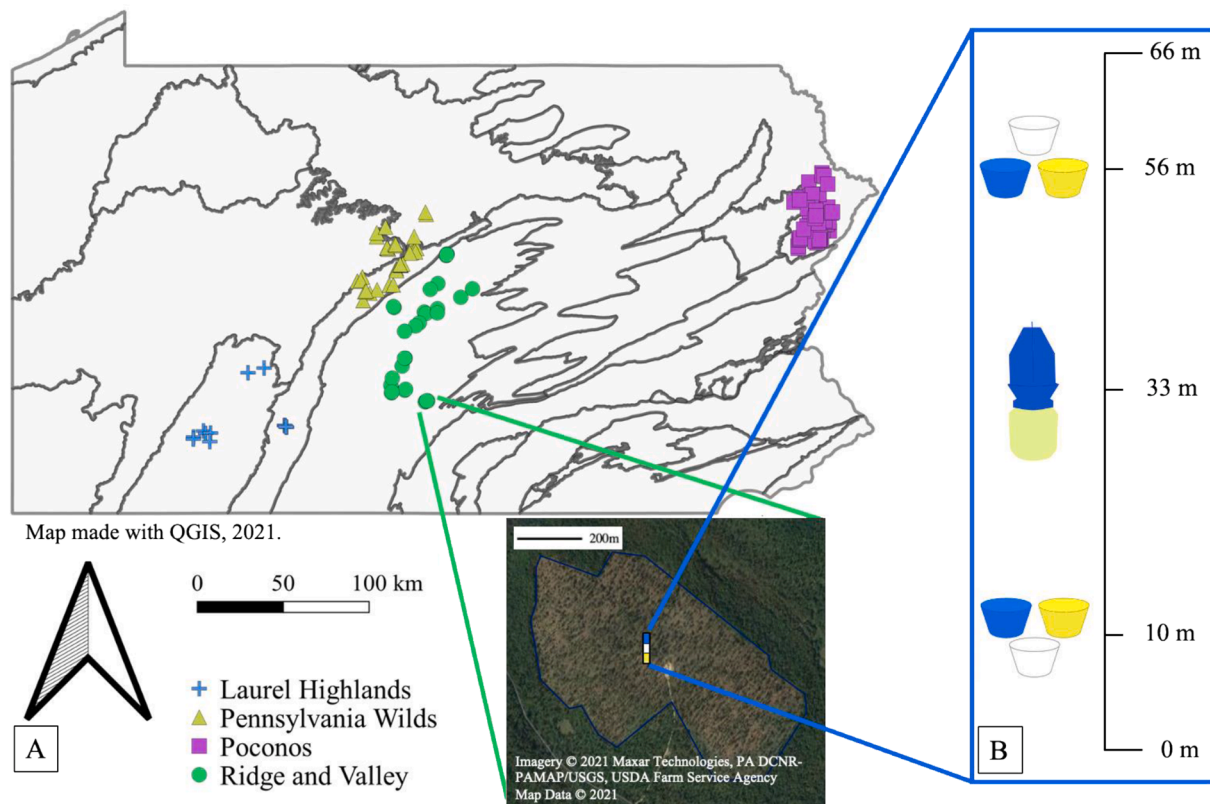
Fig. 1. A: Timber harvests that were surveyed in Pennsylvania in 2018 (n = 75) and 2019 (n = 100) to assess pollinator communities, floral resources, and vegetation structure. Inset is an example timber harvest with a 66-m survey transect. **B:** A representative graphic of a 66-m transect. Along the 66-m survey transect, we conducted pollinator visual surveys, floral resource surveys, and pollinator lethal sampling schemes. During lethal sampling (on a subset of our harvests), bee bowls were placed 10 m from the transect edge (10 and 56 m) and a blue-vane trap was hung from 1.5 m off the ground at the transect center (33 m). Illustrations created by C. Mathis. Note: Study site symbols have been randomly shifted within their respective ecoregion in order to protect landowner privacy. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with softwoods such as eastern hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobus*; Albright et al., 2017). The Pocono region is also the only portion of Pennsylvania that, in addition to upland woody communities, also supports many natural woody/emergent wetlands (Davis, 1993).

All private land sites in our study were enrolled in the NRCS – WLFW: Golden-winged Warbler habitat partnership. This conservation effort creates early successional forest via timber harvest across portions of the Appalachian Mountains by providing technical and financial assistance to private landowners to restore young forest nesting habitat for the golden-winged warbler. We also monitored comparable public land harvests on both State Game Lands and State Forests within each focal region. Regardless of ownership type, timber harvests were all regenerating 'overstory removals' <10 years post-harvest. To develop a candidate pool of *private* lands sites, we obtained ArcGIS shapefiles (ArcMap 10.2; ESRI 2011) for all WLFW management boundaries in our four focal regions. We obtained a candidate pool of *public* lands sites using the PA-DCNR State Forest Recent Timber Harvests database (newdata-dcnr.opendata.arcgis.com/datasets/pennsylvania-state-forest-recent-timber-harvests) and shapefiles provided by the Pennsylvania Game Commission, each stratified to only include overstory removal harvests completed after 2010.

To select private- and public timber harvest sites for monitoring in 2018, we first selected a random sample of private WLFW sites (n = 38) across our four regions and a nearly equal number of nearby public land sites (n = 37). In 2019, we followed a similar approach by monitoring 47 randomly selected timber harvests from the WLFW pool and 53 nearby public sites (2019; n = 100). In total, we surveyed 143 unique timber harvests (n = 32 monitored both years) that ranged in size from 0.42 ha

to 194.00 ha (mean = 19.37 ± 1.93). To establish survey locations within each harvest boundary, we centered a 66-m transect (N-S oriented; Ward et al., 2014) over a randomly generated point that was at least 80 m from the harvest edge. A more detailed account of the study area and site selection protocol can be found in Mathis (2020).

2.2. Pollinator community surveys: Visual surveys and specimen collection

To sample insect pollinator communities, we visited harvests every three weeks (2018; n = 5 bouts across the year; 15 May – 22 August) or every two weeks (2019; n = 9 bouts across the year; 15 May – 12 September). During each visit, we conducted a visual survey for bees and butterflies (hereafter, 'pollinators') using the Xerces Streamlined Bee Monitoring Protocol (Ward et al., 2014) as adapted by McNeil et al. (2019). This protocol involves a single observer walking each transect (described above) for 30 min searching for pollinators *in situ* (Ward et al., 2014; McNeil et al., 2019), taking care not to double-count individuals. For each pollinator observed, we recorded its behavior (*e.g.*, resting, flying, nectaring), plant interactions (if any), and estimated perpendicular distance from the transect upon initial detection (McNeil et al., 2019). Bees were categorized into one of six groups based on morphological features (Supplemental Fig. 1), though for data analyses we combined these morphogroups together. We took note of butterfly species identity whenever possible, though butterfly species identity data from transects are not presented here. Additionally, during each visit, we recorded ambient conditions relevant to pollinator detection probability (*e.g.*, wind, cloud cover, temperature; McNeil et al. 2019). Temperature was determined using weather data from the nearest

weather tower through Google Weather. Cloud cover was estimated at 0%, 25%, 50%, 75% or 100%. Wind intensity was estimated using the Beaufort Scale (World Meteorological Organization, 1970), which is a 0–5 scale with '0' representing 'no wind' and '5' being 'high wind'. We did not conduct surveys in high winds (≥4), during rain, or when the temperature was <15 °C, as these conditions inhibit pollinator activity (Ward et al., 2014; Dibble et al., 2018) and would severely impact detection probability (McNeil et al. 2019).

In addition to our non-lethal transect surveys, we trapped insect specimens at each site. More specifically, we collected insects during all sampling bouts on all public harvests in 2018 (n = 37) and randomly selected public and private lands in 2019 (n = 40). To obtain specimens from each site, we placed attractive pollinator traps (bee bowls/blue vane traps) at three locations along each transect (Fig. 1.B). Two trap locations, each set 10 m from the ends of the transect, each had a set of three bee bowls (white, blue, yellow) placed at ground-level (n = 6 bowls per transect). Between the two sets of bowls, we placed an elevated blue-vane trap (SpringStar) at the transect center, approximately 1.5 m above ground-level. All traps were filled ~2 cm deep with a solution consisting of Dawn (Procter & Gamble) 'Ultra Blue' dish soap + water and were collected approximately 24 h after being deployed. At the time of trap collection, we strained all captured insects through an aquarium net and placed each site's specimens in a labelled vial containing 15 mL of 70% ethanol until they could be pinned and labelled. We identified specimens to species using a digital microscope (Celestron Handheld Digital Pro, 200x magnification capacity) paired with identification guides for bees in the eastern United States (Gibbs, 2011; Gibbs et al., 2013; Mitchell, 1960, 1962) and the DiscoverLife website (discoverlife.org). We corroborated identifications with museum specimens from the Pennsylvania State University's Frost Entomological Museum and Cornell University's insect collection with the help of individuals with expertise in pollinator identification (see acknowledgements). Because traps were not placed under consistent weather conditions, we used weather data collected from the Weather Underground (wunderground.com) to characterize mean conditions for each trap's active period. Weather data included mean temperature, mean humidity, mean windspeed, mean atmospheric pressure, and total accumulated precipitation. These metrics were applied to all analyses that incorporated trap data.

2.3. Floral community and vegetation structure surveys

Floral resource abundance and diversity are well known to be among the most important components of pollinator habitat quality (Roulston and Goodell, 2011; Fowler et al., 2016). To this end, we quantified floral resource availability during the same visit as each visual pollinator survey. More specifically, we re-walked each transect and recorded the taxa and quantity of flowers actively blooming within 1-m on each side (Supplemental Fig. 1). To maintain floral counting efficiency, we tallied all individual flowers on each stem bearing <20 inflorescences and estimated counts for those with >20 inflorescences (to the nearest 10). Ultimately, this metric gave us an estimate of the absolute number of flowers for each taxon per unit area at the time of each pollinator survey (*i.e.*, flower density).

In addition to repeated measures of the floral community, we measured vegetation structure at each site once per year. Vegetation structure, such as floral resources, can be an important driver of pollinator habitat quality (McNeil et al., 2019). We conducted all vegetation surveys in July of each year and followed the same protocol as those conducted in McNeil et al., (2020b). Briefly, we collected vegetation data along 3 radial transects (0°, 120°, and 240°) that were each 50 m in length. We used an ocular tube (James and Shugart, 1970) to record the presence of various plant strata, where only the strata that were within the "crosshairs" of the ocular tube were considered present. We collected presence data of plant strata every 10 m (for a total of 15 sampling locations per harvest). Vegetation strata included canopy, saplings,

shrubs, brambles (*Rubus* spp.), ferns, forbs, 'grass' (including sedges), coarse woody debris, leaf litter, and/or bare ground. Distinctions between each vegetation class were chosen to represent those most important to insect pollinators within regenerating hardwood stands as per McNeil et al., (2019). Saplings and shrub strata were each further differentiated into "tall" (≥1 m in height) and "short" (<1 m in height).

2.4. Statistical analyses

2.4.1. Floral variables, data processing, and community composition

Preliminary observations indicated that pollinators did not use all floral resources equally; therefore, considering only the floral species that pollinators were observed using ("used" flowers) may be a better measure of site quality than a simple count of flowers blooming during each visit ("total" flowers). We determined "total" floral abundance by summing the flower counts for each harvest and then log-transforming the sums due to non-normality with $\ln(n + 1)$, and "total" floral diversity as the Shannon-Weiner Diversity Index modification for effective species unit (e^H; Jost, 2006). To create the "used" floral abundance and "used" floral diversity variables, we repeated the same procedure as above, but including only the subset of floral species we observed pollinators using during our visual surveys. These four floral variables (1. total floral abundance, 2. total floral diversity, 3. used floral abundance, 4. used floral diversity) were included in all subsequent analyses.

Prior to statistical modeling, we scaled all numerical independent variables, checked for pairwise correlations (Spearman's $\rho \geq 0.70$; Sokal and Rohlf, 1981), and removed outliers. All quantitative variables were scaled to have a mean of 0 and a standard deviation of 1 using the *scale* function in program R (R Core Team, 2020). Leaf litter and bare ground were the only pair of independent variables that were correlated. Because we expected bare ground to be more biologically relevant to ground-nesting bees (Danforth et al., 2019), we removed the leaf litter variable from further analyses. Finally, in 2019 we removed one outlier from analysis in sampling bouts 7 and 8, and 3 outliers in bout 9 because of disproportionately high pollinator counts during these sampling events that inhibited model convergence.

Because our timber harvests were grouped within four discrete regions across Pennsylvania (Fig. 1.A), it was important to determine if pollinator communities differed significantly among these landscapes, as such a finding would impact region-specific management recommendations. We used nonmetric multidimensional scaling (NMDS) to visually investigate differences in the pollinator community composition among regions and land ownership types (Clarke and Ainsworth, 1993; Borcard et al., 2011). We analyzed community composition using the R package *vegan* (Oksanen et al., 2019).

2.4.2. Habitat influences on pollinator density

To assess the impacts of habitat features on pollinator density, we specified hierarchical distance models (HDMs) using the package '*unmarked*' in R (Fiske and Chandler, 2011). Distance models allow independent estimation of detection (p) and abundance (λ) by fitting a distance function to animal observation data and using the relationship between 'count' and 'distance' to model the observation process (Buckland et al. 2015). Using this detection function to offset raw counts, distance models allow estimation of 'true' animal density, accounting for the confounding impacts of imperfect detection on the observation process (Buckland et al., 2015; Kéry and Royle, 2015). Distance models assume that taxa are identified correctly, are detected at their initial location from the transect with an accurate distance estimated, and that detections are independent (Thomas et al., 2010). For analyses, distances for pollinator observations were binned into 5 bins: 0–1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m. All observations past 5 m were excluded from analysis due to the low detection probability beyond this distance (Buckland et al., 2015; McNeil et al., 2019). We modeled bees and butterflies separately.

Using HDMs, we conducted two analyses: one examining *within-*

season patterns and another assessing *season-wide patterns*. To quantify how floral resources and harvest characteristics impact pollinator density *within* a single growing season, we created a candidate HDM set for each sampling bout independently (2018: n = 5 model sets; 2019: n = 9 model sets). In each model set, we first selected the appropriate key-function (hazard rate, half-normal, uniform, or exponential) and statistical distribution (Poisson or negative binomial; Kéry and Royle, 2015). Next, we modeled detection probability (p) as a function of survey covariates by specifying all possible univariate models constructed with our survey covariates (*e.g.,* wind index, temperature). Using the biologically meaningful (see below) survey covariates from our detection models, we next modeled density (λ) as a function of site covariates: floral resources (total floral abundance, total floral diversity, 'used' floral abundance, 'used' floral diversity), and harvest characteristics (ownership type [public or private] and stand age [number of growing seasons since harvest]). To rank and assess models, we used Akaike's Information Criterion adjusted for small sample size (AIC$_c$; Burnham and Anderson, 2002). Models were considered biologically meaningful if they had an AIC$_c$ > 2.00 ΔAIC$_c$ from an intercept-only (null) model and β 95% confidence intervals not including zero (Burnham and Anderson, 2002; Arnold, 2010). We ran a goodness-of-fit test using the *fitstats* function (Kéry and Royle, 2015) on the top candidate model to test for overdispersion ($\hat{c}$ > 1.0 = overdispersed).

To quantify how harvest characteristics and vegetation structure impact pollinator density *across* a single growing season, we specified 'temporary emigration' HDMs (Kéry and Royle, 2015). These 'temporary emigration' HDMs behave similarly to the static HDMs described above, but they allow for relaxation of the 'closure' assumption (*i.e.,* allowing for repeated site visits) within sites and across a season. The modeling methodology was like that described above for static HDMs except that in addition to the abundance (λ) and detection (p) functions, a time-dependent function (Φ) was incorporated. This time-dependent function does not assume a closed population and allows for temporal variation in the density of an organism over the replicate samples; this variation may be due to "spatial temporary emigration", where an individual is not physically within the transect to be detected, or "random temporary emigration", where the individual is present but hidden from detection in some way (*i.e.,* bees within their nests; Kéry and Royle, 2015). In addition to site covariates used in the *within-season analyses*, we also modeled structural vegetation metrics: % canopy, % tall (>1m) saplings, % short (<1 m) saplings, % tall (>1 m) shrubs, % short (<1 m) shrubs, % brambles, % forbs, % ferns, % grass, % coarse woody debris, and % bare ground. For these analyses, we assumed that vegetation percent cover was constant within a single growing season (*e.g.,* percent cover of small saplings is constant from May to September). We ran temporary emigration HDMs independently for both survey years due to differing number of sampling bouts conducted each year.

2.4.3. Habitat influences on pollinator diversity

We created linear mixed-effects models in R (*lmer* function: Bates et al., 2015) to examine the effects of site characteristics (vegetation structure, harvest characteristics, and floral resources) on pollinator species diversity. We included 'year' and 'region' in these models as fixed effects and site ID as a random effect; all other variables were treated as fixed effects. First, we created 4 model tiers: 1) weather [wind speed, temperature, humidity, barometric pressure, accumulated precipitation, date of survey, and date of survey^2], 2) stand characteristics [stand age, landowner type], 3) floral resources [total floral diversity and total floral abundance], and 4) vegetation structure (listed above). Within each tier, we created every combination of univariate (only one covariate) and multivariate (two covariates) models. We created a 'global', multivariate model using all variables within each tiers' competing models as well as models containing all possible subset combinations of those variables. Models were assessed using the same information theoretic approach described above.

3. Results

3.1. Pollinator communities

Across both years, we conducted 1129 visual pollinator surveys and observed 7563 bees and 1493 butterflies. Across all surveys, the most abundant morphospecies of pollinator we observed were bumble bees (*Bombus*, n = 2761; 30.5%), small black bees (andrenids and halictids, n = 2087; 23%), and butterflies (n = 1493; 16.5%). Most pollinator observations occurred in late spring (late May/early June) and in late summer (late August).

Of the 220 unique flowering taxa identified during our survey efforts, 102 native and 31 exotic taxa were observed being used by pollinators. The most abundant floral families used by pollinators included Asteraceae (27% of taxa), Rosaceae (11%), and Ericaceae (9%). As the floral community turned over throughout the summer, pollinators were observed using different flower taxa as they became available (Table 1). Early in the growing season (May), pollinators were observed collecting pollen and nectar from florally abundant short shrubs (*i.e.,* blueberries [*Vaccinium* spp.] and black huckleberry [*Gaylussacia baccata*]). Mid-season, pollinators were observed using laurels (*Kalmia latifolia* and *K. angustifolia*) and brambles (*e.g., Rubus alleghaniensis*). Near the end of the season, we observed pollinators foraging on forbs including fireweed (*Erechtites hieraciifolius*), asters (flat-topped white aster and common blue wood aster) and goldenrods (*Solidago* spp.).

Our nonmetric multidimensional scaling analysis indicated that pollinator community composition did not differ among regions or with ownership type (Supplemental Fig. 2), though it did vary across the growing season (Supplemental Fig. 3). In total, we collected 2072 individual bees and 203 individual butterflies, with peaks in specimen counts occurring in June (2018 & 2019) and September (2019). The

Table 1

Flowering plants with the most nectaring observations by pollinators in regenerating timber harvests across the central Appalachian region of Pennsylvania in 2018 and 2019. Associated percent is the proportion of observations with the floral species during each sampling bout.

2018		2019	
Bout 1 (May 14 – May 30)		**May 14 – May 30**	
Vaccinium angustifolium	45%	*Vaccinium* spp.	23%
Gaylussacia baccata	15%	*Rubus* spp.	23%
Vaccinium corymbosum	10%	*Potentilla simplex*	13%
Bout 2 (May 31 – June 22)		**May 31 – June 22**	
Rubus spp.	61%	*Rubus* spp.	54%
Kalmia angustifolia	11%	*Vaccinium stamineum*	10%
Kalmia latifolia	8%	*Rosa multiflora*	5%
Bout 3 (June 23 - July 13)		**June 23 – July 13**	
Actaea racemose	36%	*Rubus flagellaris*	35%
Fragaria vesca	24%	*Gaylussacia baccata*	18%
Rubus spp.	8%	*Asclepias syriaca*	11%
Bout 4 (July 14 - Aug 1)		**July 14 – Aug 1**	
Aralia spinosa	41%	*Lobelia inflata*	19%
Agastache nepetoides	14%	*Erechtites hieraciifolius*	8%
Lobelia inflata	7%	*Phytolacca americana*	6%
Bout 5 (Aug 2 - Aug 22)		**Aug 2 – Aug 22**	
Aralia spinosa	54%	*Erechtites hieraciifolius*	54%
Ageratina altissima	13%	*Solidago juncea*	11%
Eurybia sp.	6%	*Euthamia graminifolia*	8%
No Survey (Aug 23 – Sept 13)		**Aug 23 – Sept 13**	
–	–	*Erechtites hieraciifolius*	34%
–	–	*Solidago rugosa*	20%
–	–	*Euthamia graminifolia*	11%

Note. Rounds are grouped into 3-week intervals based on the timing of the 2018 sampling bouts.

bees represented 28 genera and 123 species, with the most common genera detected being *Lasioglossum (Dialictus)* (n = 485), *Ceratina* (n = 451), *Bombus* (n = 314) and *Augochlorella* (n = 154). When compared to the most up-to-date species checklist for Pennsylvania (Kilpatrick et al., 2020), over half of our collected bee species included new county-level records, with three species awaiting further validation that would be new published records for the state: *Osmia michiganensis, Lasioglossum (Hemihalictus) sopinci,* and *Andrena canadensis* (Supplemental Table 1). Additionally, we collected a worker *Bombus terricola*, a species of concern that has very few published records in the state in the past decade, with range-wide declines exceeding 30% of historic records (Hatfield et al., 2015; Kilpatrick et al., 2020). We also collected a rare oligolectic bee, *Macropis nuda*, that relies on *Lysimachia* floral oils (Mitchell, 1960); whorled loosestrife (*Lysimachia quadrifolia*) was a frequently observed plant within our harvests. Butterflies represented 20 genera and 29 species, with the most common genera collected being *Papilio* (n = 57) and *Poanes* (n = 72) (Supplemental Table 2). All observed and collected butterfly species are those presently considered common in Pennsylvania.

3.1.1. Factors associated with pollinator density – within season models

Within a growing season, pollinator density within timber harvests was largely associated with floral abundance and diversity. Bee density was consistently positively associated with floral abundance and diversity across the entire growing season, except for surveys conducted during the known floral dearth in late June through July (ordinal dates 163 – 195; gray squares in Fig. 2). Coincident with this floral dearth, bee density was positively associated with private lands (Fig. 2); this association was not observed at any other point throughout the growing season. Butterfly density was consistently positively associated with floral abundance, but only sometimes with floral diversity (Fig. 2). Models from August 2018 predicted that timber harvests with seven times as many floral species had pollinator densities four times greater, for both bees and butterflies (*e.g.*, Fig. 3). "Used" and "total" floral covariate sets were often competing in top candidate models across the sampling bouts, with neither consistently performing better than the other (Supplemental Table 3).

Stand age (number of years post-harvest) had a strong negative relationship with bee and butterfly density in late summer (Fig. 2), with older harvests supporting lower densities of pollinators than younger harvests. For example, in August 2018, our models predicted that a one-year-old harvest hosted five times the density of bees (β = -0.282 ±

0.221) than a nine-year old site. In contrast, bee density was constant across stand ages (0–9 years) early in the growing season (*i.e.*, May & June; 2nd bout, β = -0.235 ± 0.245). Our 2019 analysis, which focused on timber harvests 1 to 6 years post-harvest, showed no relationship between pollinator density and stand age from May through July and September. However, in early August (sampling bout 7), stand age was negatively associated with both bee and butterfly density (Fig. 2). Models of this bout estimated bee (β = −0.418 ± 0.267) and butterfly (β = −0.409 ± 0.345) densities were eight and six times higher in 1-year old harvest units than 6-year-old harvest units, respectively.

### 3.1.2. Factors associated with pollinator density – across season models

Model selection revealed strong support for HDMs with covariates for stand age, % short shrub cover, % forb cover, and % tall sapling cover in 2018 (AIC$_c$ weight = 0.83; Supplemental Table 4), and % grass, % brambles and stand age in 2019 (AIC$_c$ weight = 0.36; Supplemental Table 4). Models including a covariate for stand age accounted for the majority of AIC$_c$ weight (2018 cumulative AIC$_c$ weight = 0.83; 2019 = 1.00) suggesting that older harvests had the lowest bee densities; bee densities were 4.6 times higher in one-year old harvests compared to nine-year old harvests (Fig. 4). Additionally, percent cover of short shrub was also included in the top two models in 2018 suggesting a negative relationship between short shrub cover and bee density. For both bees and butterflies, densities were positively associated with characteristics suggestive of the earliest stages of succession (*i.e.,* high forb cover, brambles cover, and grass cover), whereas conditions characteristic of later successional stages (high fern cover and short shrub cover) showed the reverse pattern (Fig. 4; Supplemental Table 4).

### 3.2. Factors associated with pollinator diversity

Pollinator diversity was non-linear within the growing season with overall fewer pollinators observed as the season progressed (Fig. 5). In addition, fewer pollinators were active in humid conditions. Pollinator diversity was positively associated with floral diversity and forb cover, and negatively associated with tall (>1m) sapling cover and stand age (Fig. 5).

4. Discussion

Given the abundance of floral and nesting resources available during the stand initiation stage of regenerating timber harvests (Hanula et al.,
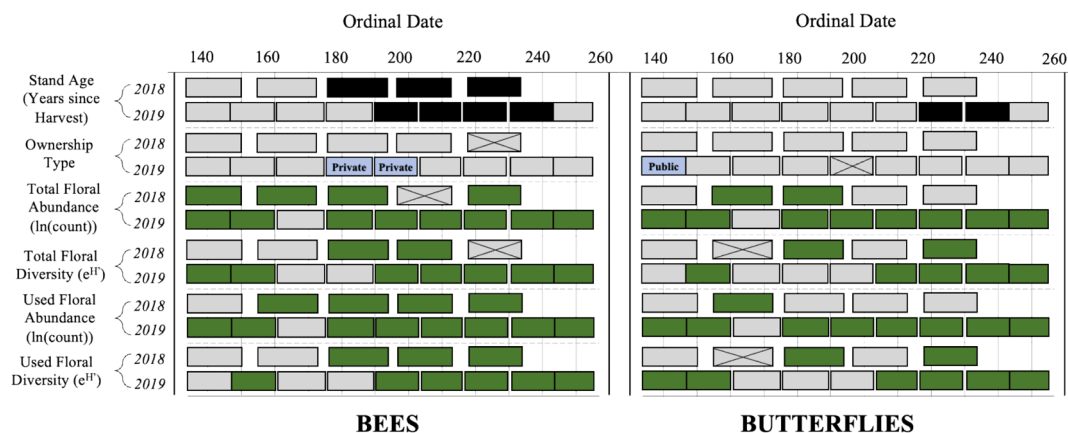
Fig. 2. Associations between pollinator densities (left: bees [Anthophila]; right: butterflies [Lepidoptera]) with time since management, ownership type, and floral community characteristics in regenerating timber harvests across the growing season in Pennsylvania in 2018 (five sampling bouts) and 2019 (nine sampling bouts). Results illustrated are from univariate hierarchical distance models, where models were determined to show biologically meaningful associations when they had an AICc > 2.00 ΔAIC$_c$ from an intercept-only (null) model and β 95% confidence intervals not including zero. Colors within the squares denote associations: light gray is no association, green is positive association, black is negative association, and blue is a difference in association between categorical variables with the variable that is positively associated with pollinator density stated. Crossed-out squares denote models that failed to converge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
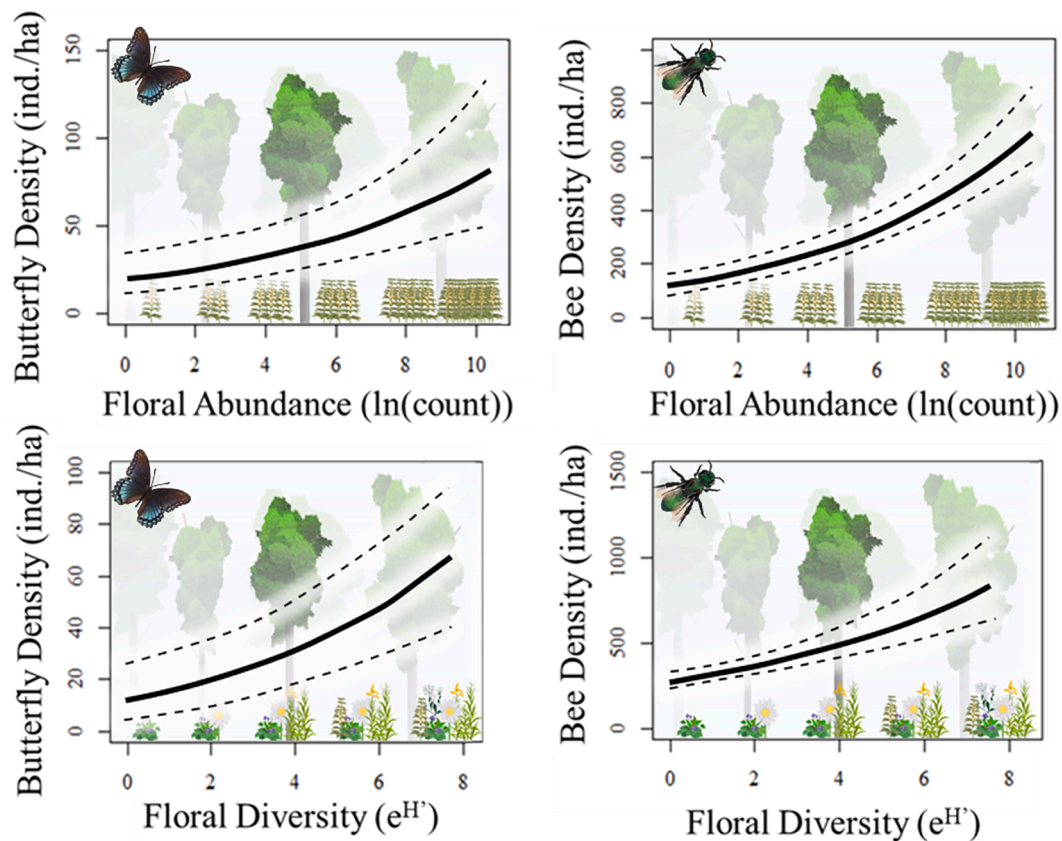
Fig. 3. Estimated pollinator densities (individuals per hectare; butterflies on the left, bees on the right) by the average floral abundance on a site (log-transformed; above) or average floral diversity (effective species: $e^{H'}$). Data are derived from observations of bees (Anthophila), butterflies (Papilionoidea), and flowers in regenerating timber harvests across Pennsylvania. Floral variables are from the total floral resource variable set. Models were created through hierarchical distance models in the package '*unmarked*' in program R. The solid line shows model predictions, and the dashed lines depict 95% confidence intervals. The models are fit to data from the fifth round of sampling in 2018 (Aug 2–22, 2018). Illustrations created by C. Mathis and D. J. McNeil.

2016; Roberts et al., 2017; Breland et al., 2018; Dibble et al., 2018; Milam et al., 2018), these early-successional communities are likely a key component of a healthy forest landscape for pollinators. Our study illustrates that timber harvests can support diverse and abundant pollinator communities, though their ability to do so is ephemeral and heavily reliant on the floral community these harvests support. Our study is among the first to use hierarchical distance models to show how vegetation characteristics, and thus the available floral community, drive variation in pollinator communities across growing seasons. Moreover, we found that stand age is an important factor that affects pollinator communities, meaning that the period over which pollinators are most abundant in a regenerating harvest is relatively short-lived (~6 growing seasons post-harvest), lasting only until the start of the stem exclusion stage when dense saplings outcompete short-stature herbaceous plants in the understory.

Younger stands had more diverse and abundant pollinator communities than older ones consistent with younger stands exhibiting microhabitat conditions (*i.e.,* temperature, light availability) well-suited for ectotherm activity and robust floral communities across an entire growing season (Taki et al., 2013; Hahn et al., 2015; Turley and Brudvig, 2016). Indeed, across our sites, younger harvests often supported more abundant and diverse floral communities (Mathis, 2020), though this relationship was dynamic throughout the growing season. In spring (May-June), older stands supported more flowers, but this relationship reversed after leaf-out of residual canopy and sapling trees (Proctor et al., 2012; Mathis, 2020). Although older regenerating timber harvests in our study area can support higher understory floral abundance in the early spring (Mathis, 2020), our results demonstrate that they never consistently host more abundant or diverse pollinator communities

(Figs. 2, 4). Indeed, during July and August when more floral resources are available in younger harvests (Mathis, 2020), our models predict that bee abundance is five times higher in younger regenerating stands (as compared to older regenerating stands). While previous studies have suggested that there may be a relatively short time window during which early successional forests are most beneficial for supporting pollinators (Taki et al., 2013; Heil and Burkle, 2018; Milam et al., 2018), our study is the first to demonstrate that this window in hardwood forests is quite brief – only about six years before woody regeneration advances beyond the point to support abundant pollinators. Ultimately, our results suggest that forest bee communities benefit from the creation and active management of young forest patches for vertebrate wildlife by increasing the availability of these ephemeral (<6 years post-harvest) conditions. As always, land managers will need to consider other management objectives when considering the creation of early seral forest stands and determine if a higher proportion of early successional forests is consistent with their regional forest management plans.

Within regenerating timber harvests in Pennsylvania, structural vegetation conditions, particularly regenerating woody stems, appear to be an indirect driver of pollinator abundance and diversity via their impact on floral resources. Canopy trees and high woody/fern cover not only limit light availability and interfere with seedling germination (deCalesta, 1994; Fredericksen et al., 1999; McKinney and Goodell, 2010), but these vegetation classes infrequently, or never, provide season-long floral resources to pollinators. Although short shrubs may provide high-quality forage during their brief bloom periods (*i.e., Vaccinium* bloom in the spring; McNeil et al., 2019), we found that short shrub cover was a negative predictor for pollinator density *across a growing season*. This pattern is likely driven by shrubs outcompeting
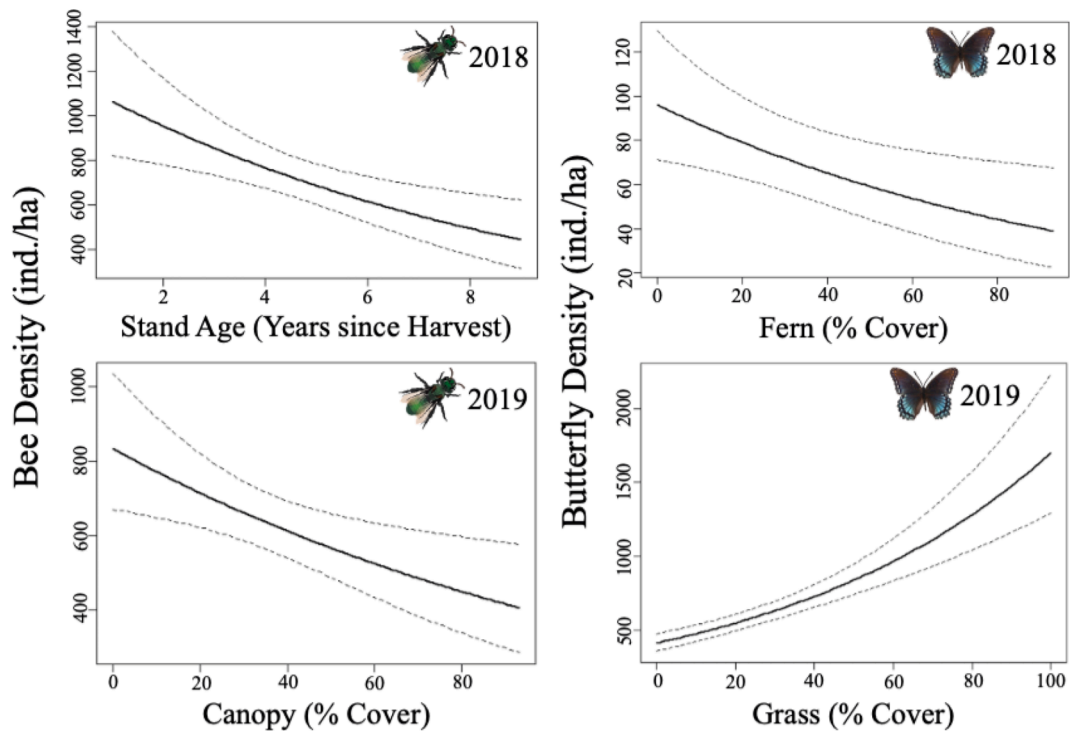
Fig. 4. Models of bee (left) and butterfly (right) density (individuals per hectare) as a function of stand age (# growing seasons since harvest) and vegetation structure (grass, fern, canopy; % cover) across the entire growing season in regenerating timber harvests in Pennsylvania in 2018 (top) and 2019 (bottom). All graphs shown were derived from top candidate hierarchical distance models accounting for temporary emigration with the package 'unmarked' in program R. The solid line shows model predictions, and the dashed lines depict 95% confidence intervals. Illustrations created by C. Mathis and D. J. McNeil.
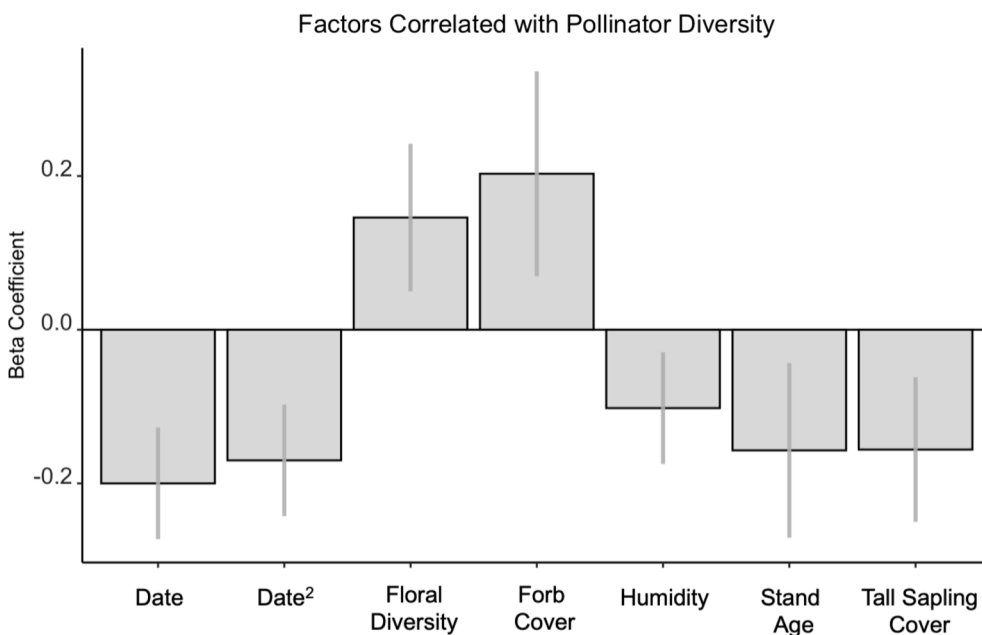
Fig. 5. Variables correlated with pollinator diversity and detectability within regenerating timber harvests in Pennsylvania in 2018 and 2019. Pollinator diversity (effective species: $e^{H'}$) is calculated from bee bowl and blue-vane trap collection data across both years. Beta coefficients were determined by linear-mixed effects regression models (function *lmer* in program R). Beta coefficients are taken from a univariate model for stand age, and from the multivariate top model for the remaining variables. Average humidity is recorded in the average relative humidity during the deployment of the traps, date is the ordinal date of survey (treated as a linear and quadratic term), tall (>1 m) sapling cover and forb cover are percent cover estimates from vegetation surveys, stand age is the number of growing seasons post-harvest, and floral diversity is the effective species unit ($e^{H'}$) calculated from floral community surveys. Error bars are the 95% confidence intervals.

other sources of floral resources (*e.g.*, herbaceous wildflowers; Hanula and Horn, 2011). Analyses of floral dynamics within our study area have suggested that sites with dense short shrub cover hosted very few flowers later in the growing season (Mathis, 2020); our finding of a positive relationship between pollinator density and vegetation structure indicative of early successional conditions seems to echo this work. Another study that investigated pollinator communities in cleared forests and mixed-pine forests of the southeastern United States found that

bee abundance was highest in areas with less canopy and reduced shrub cover (Hanula et al., 2015). However, this study also showed numbers of bee abundance and richness were highest in cleared forest and open-mature pine forests with an herbaceous understory when compared to other forest types. Thus, the underlying herbaceous plant community may be a more important determinant of value to pollinators than canopy or shrub cover alone. All of these results suggest that regenerating timber harvests are most beneficial to native pollinators when they

have diverse understory plant communities, preferably ones that promote floral abundance and diversity.

The pollen and nectar provided by flowers are important nourishment for pollinators and, for bees, also essential for provisioning young (Roulston and Goodell, 2011; Fowler et al., 2016). Many of our findings are explained by this floral-dependent life history; for instance, our models suggested that bee and butterfly density was heavily driven by flower density, though, this pattern was weaker for butterflies (Fig. 3; Supplemental Table 3). The reduced reliance of butterflies on flowers may be because they routinely feed on a variety of non-floral foods including rotting fruit and animal scat (Preston-Mafham and Preston-Mafham, 1988) and are instead seeking larval host plants across a suite of forest age classes (*e.g.*, trees). While not measured in this study, adult butterfly abundance may be better predicted by the density of larval host plants (Curtis et al., 2015), though this may not be true for migratory species (Fartmann et al., 2013). Many bees, on the other hand, rely almost exclusively on pollen/nectar as food for both themselves *and* their developing young (Michener, 2007), and use these foraging resources often within 1 km of their nesting sites (though many bee species are restricted to smaller radii; Zurbuchen et al., 2010). Although our work is among the first to draw a quantitative connection between forest pollinators and the rich floral communities present within regenerating hardwood stands in eastern North America, analogous connections have been drawn in many other plant-pollinator networks including grasslands in Germany (Steffan-Dewenter and Tscharntke, 2000), pine-forests post-fire in Israel (Potts et al., 2003), and forests in Japan (Taki et al., 2013). Ultimately, our finding that pollinator and floral communities are intimately interconnected within early successional forest highlights the need for abundant young forest within otherwise homogenous eastern forested landscapes (Shifley et al., 2014).

Our study suggests that a diverse assemblage of forest ages across a landscape will support more diverse and abundant pollinator communities, at least at the scale of a regenerating stand (Mallinger et al., 2016; Milam et al., 2018; Rivers et al., 2018; Odanaka and Rehan, 2020). We observed not only more diverse pollinator communities in younger harvests (Fig. 5), but also documented a vulnerable species that is known to be experiencing population declines across large portions of its' historic range (*Bombus terricola*), and a rare oligolectic bee (*Macropis nuda*) that specializes on plants in the genus *Lytimachia*, which were found in great abundance in our young harvests. Results of our study suggest that the creation and management of young regenerating forest that is being conducted for early-successional dependent wildlife species (such as the golden-winged warbler) would also indirectly promote pollinator communities, whether they are created through overstory removal (as in our study), group selection harvest (Proctor et al., 2012; Roberts et al., 2017) or other forest management practices such as open oak woodlands (Hanberry et al., 2020). Particularly, floral and pollinator communities may benefit from improving understory diversity through active management of invasive shrub and fern cover (Hanula and Horn, 2011), which is often compatible with habitat restoration for other wildlife and plant species (Hanula et al., 2015). As timber harvests regenerate, they advance from the 'stand initiation' (or 'seedling') phase characterized by a mosaic of herbaceous and woody vegetation into the 'stem exclusion' (or 'sapling') phase which is dominated by a dense canopy of saplings. During the stem exclusion phase, forest managers commonly implement treatments such as crop tree release (Ward, 2009) and prescribed fire (Dey and Schweitzer, 2018) to improve stand health and future economic potential. Such treatments ultimately create gaps in the regenerating sapling layer that can promote understory floral diversity (as in Proctor et al., 2012; Roberts et al., 2017) and thus can prolong the use of regenerating stands by diverse and abundant pollinator communities. However, it is important to note that sites that receive management treatments should be monitored post-treatment for invasive species colonization, particularly invasive shrubs, which are harmful to the pollinator communities (Hanula et al., 2016). Collectively, our results clearly indicate that efforts to diversify forest age classes in the name of

imperiled wildlife and forest health (*e.g.*, NRCS – WLFW) will also benefit native bee and butterfly populations.

Our study suggests additional research opportunities to better understand the value of forest management to insect pollinators. Models presented here suggest that overstory removal harvests on public and private lands indirectly create important habitat for pollinators throughout the growing season. Future work should examine pollinator response to additional forest conservation practices such as open woodland restorations (Hanberry and Thompson, 2019) and prescribed fire (Brown et al., 2017; Carbone et al., 2019), as well as the comparative value of these young forests and adjacent mature forests. In addition, the investigation of the impact of forest management to the native flower seed bank, as well as the response of pollinators to enhancing the native seed bank with pollinator-friendly native wildflower mixes within- and adjacent to harvests, is needed. Our study, and many before it, focused on bees and butterflies as insect pollinators; however, flies, beetles, and many other insects can also be important pollinators (Dunn et al., 2020) and work assessing how these insects respond to forest management would prove valuable. Additionally, while our study focused on timber harvest *interiors*, woody vegetation is often sparse in adjacent retired log *landings and skid trails*. Research examining how forest pollinators might benefit from log landing management would improve our understanding of the influence of forest management practices on pollinator conservation (Jackson et al., 2014; Hanula et al., 2016). Although previous studies have found that some nesting resources were positive predictors of bee abundance (*e.g.,* bare ground cover: Odanaka et al., 2020; coarse woody debris: Rivers et al., 2018), nesting resources were not predictive of bee density or diversity in this study. Given the importance of nesting resources to native bees, further investigation into the limitation of these resources in regenerating timber harvests is warranted. Finally, a recent study has documented vertical stratification of bee communities during canopy bloom (early spring; Urban-Mead et al., 2021), suggesting that understory surveys may be under-sampling bees at this time. In addition, our surveys began in mid-May, missing not only bloom of canopy trees but also some spring ephemeral flowers (*e.g.,* spring beauty, *Claytonia virginica*). Future research should incorporate vertical sampling stratification through understory- and canopy-surveys across the entire growing season to assess the difference in stratification between young (<6 years post-harvest) and old (>6 years post-harvest) regenerating overstory removal harvests.

CRediT authorship contribution statement

Codey L. Mathis: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Darin J. McNeil:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing, Visualization, Supervision. **Monica R. Lee:** Investigation, Data curation, Writing - review & editing. **Christina M. Grozinger:** Writing - review & editing, Supervision. **David I. King:** Conceptualization, Writing - review & editing. **Clint R.V. Otto:** Conceptualization, Methodology, Writing - review & editing. **Jeffery L. Larkin:** Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that influenced the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119373.

References

Albright, T.A., McWilliams, W.H., Widmann, R.H., Butler, B.J., Crocker, S.J., Kurtz, C.M., Lehman, S., Lister, T.W., Miles, P.D., Morin, R.S., Riemann, R., and Smith, J.E., 2017. Pennsylvania forests 2014 (NRS-RB-111; p. NRS-RB-111). U.S. Department of Agriculture, Forest Service, Northern Research Station. https://doi.org/10.2737/NRS-RB-111.

Arnold, T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J. Wildl. Manage. 74, 1175–1178.

Askins, R.A., 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildl. Soc. Bull. 29 (2), 407–412.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agric. Ecosyst. Environ. 146, 34–43.

Borcard, D., Legendre, P., Gillet, F., 2011. Numerical Ecology in R. Springer, New York.

Buckland, S.T., Rexstad, E.A., Marques, T.A., Oedekoven, C.S., 2015. Distance sampling: methods and applications, Vol. 431. Springer, New York, NY, USA.

Breland, S., Turley, N.E., Gibbs, J., Isaacs, R., Brudvig, L.A., 2018. Restoration increases bee abundance and richness but not pollination in remnant and post-agricultural woodlands. Ecosphere 9 (9), e02435. https://doi.org/10.1002/ecs2.2435.

Brettell, L.E., Riegler, M., O'Brien, C., Cook, J.M., 2020. Occurrence of honey bee-associated pathogens in *Varroa*-free pollinator communities. J. Invertebr. Pathol. 171, 107344. https://doi.org/10.1016/j.jip.2020.107344.

Brooks, R.T., 2003. Abundance, distribution, trends, and ownership patterns of early-successional forests in the northeastern United States. For. Ecol. Manage. 185 (1-2), 65–74. https://doi.org/10.1016/S0378-1127(03)00246-9.

Brown, J., York, A., Christie, F., McCarthy, M., James, J., 2017. Effects of fire on pollinators and pollination. J. Appl. Ecol. 54 (1), 313–322.

Buchanan, A., Gibbs, J., Komondy, L., Szendrei, Z., 2017. Bee community of commercial potato fields in Michigan and *Bombus impatiens* visitation to neonicotinoid-treated potato plants. Insects 8 (1), 30. https://doi.org/10.3390/insects8010030.

Burnham, K.P., Anderson, D.R., 2002. A practical information-theoretic approach. Model selection and multimodel inference, second ed. Springer, New York.

Butler, D.R., Malanson, G.P., 2005. The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71 (1-2), 48–60.

Byrne, A., Fitzpatrick, U., 2009. Bee conservation policy at the global, regional and national levels. Apidologie 40 (3), 194–210. https://doi.org/10.1051/apido/2009017.

Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F., Griswold, T.L., 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. 108 (2), 662–667.

Carbone, L.M., Tavella, J., Pausas, J.G., Aguilar, R., Mayfield, M., 2019. A global synthesis of fire effects on pollinators. Glob. Ecol. Biogeogr. 28 (10), 1487–1498.

Ciuzio, E., Hohman, W.L., Martin, B., Smith, M.D., Stephens, S., Strong, A.M., Vercauteren, T., 2013. Opportunities and challenges to implementing bird conservation on private lands. Wildl. Soc. Bull. 37 (2), 267–277.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology-Progress Series 92, 205–219.

Curtis, R.J., Brereton, T.M., Dennis, R.L.H., Carbone, C., Isaac, N.J.B., Diamond, S., 2015. Butterfly abundance is determined by food availability and is mediated by species traits. J. Appl. Ecol. 52 (6), 1676–1684.

Danforth, B.N., Minckley, R.L., Neff, J.L., Fawcett, F., 2019. The Solitary Bees: Biology, Evolution, and Conservation. Princeton University Press.

Davis, A.F., 1993. Rare wetland plants and their habitats in Pennsylvania. In: Proceedings of the Academy of Natural Sciences of Philadelphia, pp. 254-262.

De Palma, A., Abrahamczyk, S., Aizen, M.A., Albrecht, M., Basset, Y., Bates, A., Blake, R. J., Boutin, S., Bugter, R., Connop, S., Cruz-López, L., Cunningham, S.A., Darvill, B., Diekötter, T., Dorn, S., Downing, N., Entling, M.H., Farwig, N., Felicioli, A., Fonte, S. J., Fowler, R., Franzén, M., Goulson, D., Grass, I., Hanley, M.E., Hendrix, S.D., Herrmann, F., Herzog, F., Holzschuh, A., Jauker, B., Kessler, M., Knight, M.E., Kruess, A., Lavelle, P., Le Féon, V., Lentini, P., Malone, L.A., Marshall, J., Pachón, E. M., McFrederick, Q.S., Morales, C.L., Mudri-Stojnic, S., Nates-Parra, G., Nilsson, S.G., Öckinger, E., Osgathorpe, L., Parra-H, A., Peres, C.A., Persson, A.S., Petanidou, T., Poveda, K., Power, E.F., Quaranta, M., Quintero, C., Rader, R., Richards, M.H., Roulston, T'ai, Rousseau, L., Sadler, J.P., Samnegård, U., Schellhorn, N.A., Schüepp, C., Schweiger, O., Smith-Pardo, A.H., Steffan-Dewenter, I., Stout, J.C., Tonietto, R.K., Tscharntke, T., Tylianakis, J.M., Verboven, H.A.F., Vergara, C.H., Verhulst, J., Westphal, C., Yoon, H.J., Purvis, A., 2016. Predicting bee community responses to land-use changes: Effects of geographic and taxonomic biases. Sci. Rep. 6 (1) https://doi.org/10.1038/srep31153.

deCalesta, D.S., 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manag. 58 (4), 711. https://doi.org/10.2307/3809685.

DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. For. Ecol. Manage. 185 (1–2), 179–191. https://doi.org/10.1016/S0378-1127(03)00254-8.

Dey, D.C., Schweitzer, C.J., 2018. A review on the dynamics of prescribed fire, tree mortality, and injury in managing oak natural communities to minimize economic loss in North America. Forests 9 (8), 461.

Dibble, A.C., Drummond, F.A., Averill, A.L., Bickerman-Martens, K., Bosworth, S.C., Bushmann, S.L., Hoshide, A.K., Leach, M.E., Skyrm, K., Venturini, E., and White, A., 2018. Bees and Their Habitats in Four New England States (Misc. Report No. 448; Maine Agricultural and Forest Experiment Station, p. 58). The University of Maine.

Dunn, L., Lequerica, M., Reid, C.R., Latty, T., 2020. Dual ecosystem services of syrphid flies (Diptera: Syrphidae): pollinators and biological control agents. Pest Manag. Sci. 76 (6), 1973–1979.

ESRI, 2011. Release 10. Documentation Manual. Redlands, CA, Environmental Systems Research Institute.

Fartmann, T., Müller, C., Poniatowski, D., 2013. Effects of coppicing on butterfly communities of woodlands. Biol. Conserv. 159, 396–404, 0.1016/j.biocon.2012.11.024.

Fiske, I.J., Chandler, R.B., 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43 (10), 1–23. https://doi.org/10.18637/jss.v043.i10.

Fortuin, C.C., McCarty, E., Gandhi, K.J., 2020. Acute contact with imidacloprid in soil affects the nesting and survival success of a solitary wild bee, *Osmia lignaria* (Hymenoptera: Megachilidae). Chemosphere 264, 128572.

Fowler, R.E., Rotheray, E.L., Goulson, D., Schonrogge, K., Heard, M., 2016. Floral abundance and resource quality influence pollinator choice. Insect Conserv. Diversity 9 (6), 481–494.

Fredericksen, T.S., Ross, B.D., Hoffman, W., Morrison, M.L., Beyea, J., Johnson, B.N., Lester, M.B., Ross, E., 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For. Ecol. Manage. 116 (1-3), 129–139. https://doi.org/10.1016/S0378-1127(98)00452-6.

Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Kremen, C., Morandin, L., Scheper, J., Winfree, R., 2014. From research to action: enhancing crop yield through wild pollinators. Front. Ecol. Environ. 12 (8), 439–447. https://doi.org/10.1890/130330.

Gibbs, Jason, 2011. Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). Zootaxa 3073 (1), 1. https://doi.org/10.11646/zootaxa.3073.1.1.

Gibbs, J., Packer, L., Dumesh, S., Danforth, B.N., 2013. Revision and reclassification of *Lasioglossum* (*Evylaeus*), L. (*Hemihalictus*) and L. (*Sphecodogastra*) in eastern North America (Hymenoptera: Apoidea: Halictidae). Zootaxa 3672, 1–117.

Godfray, H.C.J., Blacquière, T., Field, L.M., Hails, R.S., Petrokofsky, G., Potts, S.G., Raine, N.E., Vanbergen, A.J., McLean, A.R., 2014. A restatement of the natural science evidence base concerning neonicotinoid insecticides and insect pollinators. Proc. Royal Society B: Biol. Sci. 281 (1786), 20140558. https://doi.org/10.1098/rspb.2014.0558.

Hahn, P.G., Orrock, J.L., Peters, D.P.C., 2015. Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. Ecosphere 6 (10), 1–16. https://doi.org/10.1890/ES15-00036.1.

Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J.S., Baldock, K.C.R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.I., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G.N., Threlfall, C.G., 2017. The city as a refuge for insect pollinators: Insect Pollinators. Conserv. Biol. 31 (1), 24–29. https://doi.org/10.1111/cobi.12840.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., Lamb, E. G., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12 (10), e0185809. https://doi.org/10.1371/journal.pone.

Hanberry, B.B., Thompson, F.R., 2019. Open forest management for early successional birds. Wildl. Soc. Bull. 43 (1), 141–151.

Hanberry, B.B., Bragg, D.C., Alexander, H.D., 2020. Open forest ecosystems: An excluded state. For. Ecol. Manage. 472, 118256. https://doi.org/10.1016/j.foreco.2020.118256.

Hanula, J.L., Horn, S., 2011. Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the southeastern United

States. Insect Conservation and Diversity 4 (4), 275–283. https://doi.org/10.1111/j.1752-4598.2011.00131.x.

Hanula, J.L., Horn, S., O'Brien, J.J., 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? For. Ecol. Manage. 348, 142–152. https://doi.org/10.1016/j.foreco.2015.03.044.

Hanula, J.L., Ulyshen, M.D., Horn, S., 2016. Conserving pollinators in North American forests: a review. Natural Areas Journal 36 (4), 427–439.

Hatfield, R., Jepsen, S., Thorp, R., Richardson, L., and Colla, S., 2015. *Bombus terricola*. The IUCN Red List of Threatened Species 2015: e.T44937505A46440206. https://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T44937505A46440206.en.

Heil, L.J., Burkle, L.A., 2018. Recent post-wildfire salvage logging benefits local and landscape floral and bee communities. For. Ecol. Manage. 424, 267–275.

Jackson, M.M., Turner, M.G., Pearson, S.M., 2014. Logging legacies affect insect pollinator communities in southern Appalachian forests. Southeast. Nat. 13 (2), 317–336. https://doi.org/10.1656/058.013.0213.

James, F.C., Shugart Jr, H.H., 1970. A quantitative method of habitat description. Audubon Field Notes 24 (6), 727–736.

Jordan, A., Patch, H.M., Grozinger, C.M., Khanna, V., 2021. Economic Dependence and Vulnerability of United States Agricultural Sector on Insect-Mediated Pollination Service. Environ. Sci. Technol. 55 (4), 2243–2253. https://doi.org/10.1021/acs.est.0c0478610.1021/acs.est.0c04786.s00110.1021/acs.est.0c04786.s002.

Jost, L., 2006. Entropy and diversity. Oikos 113 (2), 363–375.

Kammerer, M.A., Biddinger, D.J., Rajotte, E.G., Mortensen, D.A., 2016. Local plant diversity across multiple habitats supports a diverse wild bee community in Pennsylvania apple orchards. Environ. Entomol. 45 (1), 32–38.

Kéry, M., and Royle, J.A., 2015. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models. Academic Press.

Kilpatrick, S.K., Gibbs, J., Mikulas, M.M., Spichiger, S.-E., Ostiguy, N., Biddinger, D.J., Lopez-Uribe, M.M., 2020. An updated checklist of the bees (Hymenoptera, Apoidea, Anthophila) of Pennsylvania, United States of America. J. Hymenoptera Res. 77, 1–86.

King, D.I., Schlossberg, S., 2014. Synthesis of the conservation value of the early-successional stage in forests of eastern North America. For. Ecol. Manage. 324, 186–195.

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. Royal Soc. B: Biol. Sci. 274 (1608), 303–313. https://doi.org/10.1098/rspb.2006.3721.

Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., Ricketts, T.H., 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl. Acad. Sci. 113 (1), 140–145.

Litvaitis, J.A., 2001. Importance of early successional habitats to mammals in eastern forests. Wildl. Soc. Bull. 29 (2), 466–473.

Lorimer, C.G., 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61 (5), 1169–1184. https://doi.org/10.2307/1936836.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56 (5), 395–405.

Lowenstein, D.M., Matteson, K.C., Minor, E.S., 2015. Diversity of wild bees supports pollination services in an urbanized landscape. Oecologia 179 (3), 811–821. https://doi.org/10.1007/s00442-015-3389-0.

Mallinger, R.E., Gibbs, J., Gratton, C., 2016. Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. Landscape Ecol. 31 (7), 1523–1535. https://doi.org/10.1007/s10980-015-0332-z.

Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. Ecol. Appl. 22 (5), 1535–1546.

Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2015. Pollination services are mediated by bee functional diversity and landscape context. Agric. Ecosyst. Environ. 200, 12–20. https://doi.org/10.1016/j.agee.2014.10.018.

Mathis, C.M., 2020. Habitat Ecology of Native Pollinator Communities Within Early Successional Deciduous Forests of the Central Appalachian Mountains of Pennsylvania (Master's thesis, Indiana University of Pennsylvania, Indiana, PA, USA). ProQuest UMI No. 28028167.

McKinney, A.M., Goodell, K., 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biol. Invasions 12 (8), 2751–2763. https://doi.org/10.1007/s10530-009-9680-4.

McNeil, D.J., Otto, C.R.V., Moser, E.L., Urban-Mead, K.R., King, D.E., Rodewald, A.D., Larkin, J.L., 2019. Distance models as a tool for modelling detection probability and density of native bumblebees. J. Appl. Entomol. 143 (3), 225–235.

McNeil, D.J., McCormick, E., Heimann, A., Kammerer, M., Douglas, M., Goslee, S., Grozinger, C.M., Hines, H., 2020a. Bumble Bees in Landscapes with Abundant Floral Resources Have Lower Pathogen Loads. Nature Scientific Reports 10, 22306. https://doi.org/10.1038/s41598-020-78119-2.

McNeil, D.J., Rodewald, A.D., Robinson, O.J., Fiss, C.J., Rosenberg, K.V., Ruiz-Gutierrez, V., Aldinger, K.R., Dhondt, A.A., Petzinger, S., Larkin, J.L., 2020b. Regional abundance and local breeding productivity explain occupancy of restored habitats in a migratory songbird. Biol. Conserv. 245, 108463. https://doi.org/10.1016/j.biocon.2020.108463.

Michener, C.D., 2007. The bees of the world (No. 595.799 M53/2007).

Milam, J.C., Litvaitis, J.A., Warren, A., Keirstead, D., King, D.I., 2018. Bee Assemblages in Managed Early-Successional Habitats in Southeastern New Hampshire. Northeastern Naturalist 25 (3), 437–459. https://doi.org/10.1656/045.025.0309.

Miller, J.C., Hammond, P.C., 2007. Butterflies and moths of Pacific Northwest forests and woodlands: rare, endangered, and management-sensitive species. Technology

Transfer / Forest Health Technology Enterprise Team., (2006–07), iii, 234 p. Retrieved from http://www.fs.fed.us/foresthealth/technology/pdfs/miller_lepidoptera_web.pdf.

Mitchell, T.B., 1960. Bees of the Eastern United States: Volume 1. Technical Bulletin of the North Carolina Agricultural Experiment Station.

Mitchell, T.B., 1962. Bees of the Eastern United States: Volume 2. Technical Bulletin of the North Carolina Agricultural Experiment Station.

Murray, E.A., Burand, J., Trikoz, N., Schnabel, J., Grab, H., Danforth, B.N., 2019. Viral transmission in honey bees and native bees, supported by a global black queen cell virus phylogeny. Environ. Microbiol. 21 (3), 972–983.

Naiman, R.J., Johnston, C.A., Kelley, J.C., 1988. Alteration of North American streams by beaver. Bioscience 38 (11), 753–762.

Odanaka, K.A., Rehan, S.M., 2020. Wild bee distribution near forested landscapes is dependent on successional state. Forest Ecosystems 7, 1–13.

Odanaka, K., Gibbs, J., Turley, N.E., Isaacs, R., Brudvig, L.A., 2020. Canopy thinning, not agricultural history, determines early responses of wild bees to longleaf pine savanna restoration. Restor. Ecol. 28 (1), 138–146. https://doi.org/10.1111/rec.v28.110.1111/rec.13043.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120 (3), 321–326. https://doi.org/10.1111/more.2010.120.issue-310.1111/j.1600-0706.2010.18644.x.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. M., Szoecs E., and Wagner, H., 2019. vegan: Community Ecology Package. R package version 2.5-6.

Pan, Y., Chen, J.M., Birdsey, R., McCullough, K., He, L., Deng, F., 2011. Age structure and disturbance legacy of North American forests. Biogeosciences. 8, 715–732.

Plascencia, M., Philpott, S.M., 2017. Floral abundance, richness, and spatial distribution drive urban garden bee communities. Bull. Entomol. Res. 107 (5), 658–667. https://doi.org/10.1017/S0007485317000153.

Polatto, L.P., Chaud-Netto, J., Alves-Junior, V.V., 2014. Influence of abiotic factors and floral resource availability on daily foraging activity of bees: influence of abiotic and biotic factors on bees. Journal of Insect Behavior 27 (5), 593–612. https://doi.org/10.1007/s10905-014-9452-6.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., Willmer, P., 2003. Response of plant-pollinator communities to fire: Changes in diversity, abundance and floral reward structure. Oikos 101 (1), 103–112. https://doi.org/10.1034/j.1600-0706.2003.12186.x.

Preston-Mafham, R., 1988. Butterflies of the World; Blandford Press: London, UK, 192 pages.

Proctor, E., Nol, E., Burke, D., Crins, W.J., 2012. Responses of insect pollinators and understory plants to silviculture in northern hardwood forests. Biodivers. Conserv. 21 (7), 1703–1740.

R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.

Rivers, J.W., Mathis, C.L., Moldenke, A.R., Betts, M.G., 2018. Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest. GCB Bioenergy 10 (10), 766–781.

Roberts, H.P., King, D.I., Milam, J., 2017. Factors affecting bee communities in forest openings and adjacent mature forest. For. Ecol. Manage. 394, 111–122. https://doi.org/10.1016/j.foreco.2017.03.027.

Roulston, T'ai.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. Annu. Rev. Entomol. 56 (1), 293–312.

Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63 (5), 1533–1546. https://doi.org/10.2307/1938878.

Russo, L., 2016. Positive and negative impacts of non-native bee species around the world. Insects 7 (4), 69.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr, K. L. Pardieck, J. E. Fallon, and W. A. Link, 2017. The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD.

Sevon, W.D., 2000. Physiographic Provinces of Pennsylvania, Map 13. Pennsylvania Geologic Survey, Harrisburg, PA.

Shifley, S.R., Moser, W.K., Nowak, D.J., Miles, P.D., Butler, B.J., Aguilar, F.X., DeSantis, R.D., Greenfield, E.J., 2014. Five Anthropogenic Factors That Will Radically Alter Forest Conditions and Management Needs in the Northern United States. Forest Science 60 (5), 914–925. https://doi.org/10.5849/forsci.13-153.

Smith, W.B., Miles, P.D., Perry, C.H., and Pugh, S.A., 2009. Forest resources of the United States, 2007. USDA For Serv., Gen. Tech. Rep. WO-78, Washington, DC. 336 p.

Sokal, R.R., Rohlf, F.J., 1981. Biometry: the principles and practice of statistics in biological research. W. H. Freeman & Company, San Francisco.

Steffan-Dewenter, I., Tscharntke, T., 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122 (2), 288–296. https://doi.org/10.1007/s004420050034.

Taki, H., Makihara, H., Matsumura, T., Hasegawa, M., Matsuura, T., Tanaka, H., Makino, S., Okabe, K., 2013. Evaluation of secondary forests as alternative habitats to primary forests for flower-visiting insects. J. Insect Conserv. 17 (3), 549–556. https://doi.org/10.1007/s10841-012-9539-3.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A., Burnham, K.P., 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. J. Appl. Ecol. 47 (1), 5–14. https://doi.org/10.1111/j.1365-2664.2009.01737.x.

Turley, N.E., Brudvig, L.A., 2016. Agricultural land-use history causes persistent loss of plant phylogenetic diversity. Ecology 97 (9), 2240–2247. https://doi.org/10.1002/ecy.1443.

United States Department of Agriculture, 2014. Working Lands for Wildlife Progress Report. Retrieved from http://goo.gl/mE74va.

Urban-Mead, K.R., Muñiz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M., McArt, S.H., Danforth, B.N., 2021. Bees in the trees: Diverse spring fauna in temperate forest edge canopies. For. Ecol. Manage. 482, 118903. https://doi.org/10.1016/j.foreco.2020.118903.

Ward, J.S., 2009. Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. Can. J. For. Res. 39 (1), 118–130.

Ward, K., Cariveau, D., May, E., Roswell, M., Vaughan, M., Williams, N., Winfree, R., Isaacs, R., and Gill, K., 2014. Streamlined Bee Monitoring Protocol for Assessing Pollinator Habitat. 16 pp. Portland, OR: The Xerces Society for Invertebrate Conservation.

Watson, J.C., Wolf, A.T., Ascher, J.S., 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. Environ. Entomol. 40 (3), 621–632.

Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J., Haddad, N.M., Kerby, J., 2019. Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. PLoS ONE 14 (7), e0216270.

Whitney, G.G., 1994. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present. Cambridge University Press.

Wignall, V.R., Brolly, M., Uthoff, C., Norton, K.E., Chipperfield, H.M., Balfour, N.J., Ratnieks, F.L., 2020. Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community. Behav. Ecol. Sociobiol. 74 (12), 1–15.

Winfree, R., Griswold, T.L., Kremen, C., 2007. Effects of human disturbance on bee communities in a forested ecosystem. Conserv. Biol. 21 (1), 213–223.

Wohl, E., 2021. Legacy effects of loss of beavers in the continental United States. Environ. Res. Lett. 16 (2), 025010. https://doi.org/10.1088/1748-9326/abd34e.

World Meteorological Organization, 1970. The Beaufort scale of wind force: technical and operational aspects.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. 143 (3), 669–676. https://doi.org/10.1016/j.biocon.2009.12.003.