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Pollinator Ecology and Management

Factors driving bumble bee (Hymenoptera: Apidae: *Bombus*) and butterfly (Lepidoptera: Rhopalocera) use of sheared shrubland and young forest communities of the western Great Lakes

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In the northern Great Lakes region, the creation and maintenance of early-successional woody communities as wildlife habitat have increasingly become a conservation priority. The extent to which insect pollinators use these systems remains largely anecdotal. In summer (June–August) of 2021, we surveyed 49 early-successional sites in the western Great Lakes region treated with either shrub-shearing or silviculture (young forest) for bumble bees, butterflies, and habitat components (i.e., structural vegetation and floral resources). Hierarchical distance models predicted pollinator densities ($\hat{\lambda}$) to be, on average, $\hat{\lambda} = 84$ bumble bees/ha and $\hat{\lambda} = 102$ butterflies/ha. Although sheared shrubland and young forest communities supported comparable densities of bumble bees and butterflies, density was not equal across all sites. At the microhabitat scale, butterfly density and morphospecies richness were negatively associated with tall shrub cover and butterfly morphospecies richness (but not density) was driven by floral richness. Similarly, bumble bee density was positively associated with metrics of floral resources, underscoring the importance of blooming plants within these woody systems. Landscape covariates explained variation in butterfly density/richness but not bumble bee density. Ultimately, our results demonstrate that blooming plant abundance is an important driver of bumble bee and butterfly densities within these managed early-successional communities. Because early-successional woody communities are dynamic and their herbaceous openings are ephemeral, routine management would ensure that a variety of successional conditions exist on the landscape to meet the needs of bumble bees, butterflies, and potentially other insect pollinators.

Key words: woody community, shrub-shearing, bumble bee, butterfly, timber harvest

Introduction

Insect pollinators (hereafter "pollinators") play key roles in ecosystem function and agricultural production (Potts et al. 2016). Due to widespread declines in wild pollinators (Koh et al. 2016, Sluijs and Vaage 2016), many natural and agricultural systems are at-risk. The causes of pollinator decline include, but are not limited to, disease and pathogens, pesticides, climate change, and most notably habitat loss and degradation (Potts et al. 2016). Pollinator conservation has become a U.S. national priority following the creation of the Pollinator Health Task Force in 2015 (Vilsack and McCarthy 2015). One strategy from this effort is restoring or enhancing

pollinator habitat via management practices, such as: increasing floral resources via sowing seed mixes or plantings, retaining nesting and overwintering resources (e.g., coarse woody debris and snags), controlling invasive nonnatives, and restoring natural disturbance regimes (Hudson et al. 2013, Lukens et al. 2020, Glenny et al. 2022). A second conservation strategy is the need for research to document pollinator communities in natural systems (Vilsack and McCarthy 2015). Thereby, research efforts that inform both of these efforts are expected to provide valuable insights to pollinator conservation.

Forests are the most common natural community-type within the eastern United States (Trani et al. 2001), warranting the need

to understand pollinator relationships within these systems (Koh et al. 2016). Within an eastern temperate deciduous forest, 32 and 31% of collected bee species were found to be forest-associated (i.e., requiring mature or extensive forests) and forest-generalist (i.e., prefers younger or more disturbed forests), respectively (Smith et al. 2021). Butterfly species are also known to have varying forest associations (Grundel et al. 2020). Forests provide resources during important life stages, such as coarse woody debris, leaf litter, and snags, for nesting and overwintering bumble bees (Mola et al. 2021a). For example, reproductive output of *B. impatiens* nests were greater in forests compared to meadows and hay fields (Pugesek and Crone 2021). Bee abundance and richness have been reported to be especially high in forests during the spring (Harrison et al. 2018), believed to be a result of these communities providing temporally distinct floral and nonfloral resources compared to other surrounding land cover types (e.g., spring ephemerals; Mola et al. 2021b and tree pollen; Requier and Leonhardt 2020, Urban-Mead et al. 2021). In mid- to late-summer young forests are especially abundant with floral resources from disturbance-dependent herbaceous plants (e.g., goldenrod [*Solidago* spp.]), whereas older forests at this time are floral resource poor (Romey et al. 2007, Roberts et al. 2017). Temperate forests comprised of diverse deciduous tree species are especially important for Lepidoptera given that certain tree species (especially oaks [*Quercus* spp.]) are larval host plants for hundreds of caterpillar species (Narango et al. 2020). In summary, the greatest pollinator diversity is supported by a healthy forested-landscape with a balance of age classes to support varying species specific and life cycle needs (Ulyshen et al. 2023).

Forest structure and composition in the eastern United States has been drastically altered since European settlement (Trani et al. 2001), which has influenced pollinator communities (Hanula et al. 2015, Smith et al. 2021, Ulyshen and Horn 2023). Prior to European arrival, eastern forests were dynamic. Natural disturbance regimes created/maintained early-successional communities via wildfire and Native American fire, insect outbreaks, high winds, flooding, beavers (*Castor canadensis*), and large ungulates (e.g., Bison [*Bison bison*]; DeGraaf and Yamasaki 2003, Abrams and Nowacki 2008, Swanson et al. 2011, McClain et al. 2021, Wohl 2021). In the 19th to early 20th centuries forests were widely cleared for wood and agriculture (Williams 1989), which was followed by a period of farm abandonment (Pimm and Askins 1995), and has resulted in today's regrowth of even-aged forests lacking a balance of age classes (Trani et al. 2001, King and Schlossberg 2014). Due to the suppression of natural disturbances (e.g., wildfire control), evidence suggests that the proportion of early-successional communities on the landscape has been declining approximately since the 1950's because these communities are naturally ephemeral (Trani et al. 2001, Swanson et al. 2011, King and Schlossberg 2014). As a result, populations of wildlife species adapted to these communities are at-risk (Confer et al. 2020, Litvaitis et al. 2021). To combat this, biologists increasingly call for conservation practices that emulate ecological disturbances to be implemented (e.g., prescribed fire, timber harvesting, and shrub-shearing; Askins 2001, Swanson et al. 2011). The benefits of these conservation practices to vertebrate animals has been documented widely (Artman et al. 2001, Zwolak 2009, Fontaine and Kennedy 2012, Hocking et al. 2013, McNeil et al. 2020, Hunter and Rostal 2021, Litvaitis et al. 2021, Powell et al. 2022) but remains relatively less studied for invertebrates (like pollinators; Campbell et al. 2007, Romey et al. 2007, Mathis et al. 2021).

Among the few studies that have investigated pollinator responses to early-successional community management, most focus on timber harvesting practices in deciduous (Romey et al. 2007, Roberts et al. 2017, Mathis et al. 2021) and coniferous (Korpela et al. 2015, Rivers et al. 2018) forests. Beyond timber harvesting, other conservation practices are recommended as alternatives for managing habitat for early-successional wildlife including shrub-shearing (Buckardt Thomas et al. 2023). The value of sheared shrubland communities is apparent for some vertebrate wildlife species (Kramer et al. 2019, Buckardt Thomas et al. 2023), but no studies have examined the value of this community-type for pollinators. Although some studies have been conducted on the benefits of invasive shrub removal (Fiedler et al. 2012, Hudson et al. 2013) and using shrub-shearing to enhance utility line corridors (Wagner et al. 2019), no studies to date have examined pollinator responses to shrub-shearing as a primary conservation practice in eastern North America (Fartmann et al. 2013). Herein, we developed a study to compare bumble bee and butterfly densities within woody communities treated with 2 alternative conservation practices intended to create early-successional habitat for vertebrate wildlife. Specifically, our objectives were to (i) compare bumble bee and butterfly density and butterfly morphospecies richness between sheared shrubland and young forest communities implemented to benefit golden-winged warblers (*Vermivora chrysoptera*, Passeriformes: Parulidae) through the United States Department of Agriculture (USDA) – Natural Resources Conservation Service's (NRCS) *Regional Conservation Partnership Program* (Golden-winged Warbler Working Group 2019, Roth et al. 2019) and (ii) identify within-site and landscape factors that drive variation in bumble bee and butterfly communities.

Methods

Study Area

We surveyed bumble bee and butterfly communities at 49 sites throughout northern Minnesota (*n* = 32) and Wisconsin (*n* = 17). Each site was visited 3 times, once in June (2–30 June), once in July (1–29 July), and once in August (30 July–26 August). Our survey period did not include early spring (i.e., before leaf-out), which is known to be especially beneficial to bees (Harrison et al. 2018, Mola et al. 2021a, 2021b). Most sites were privately owned (*n* = 39, public: *n* = 10) and enrolled in NRCS-*Regional Conservation Partnership Program* (*n* = 32). Other funding programs for private sites were U.S. Fish and Wildlife Service (USFWS) Partners Program (*n* = 2), NRCS's Environmental Quality Incentives Program (*n* = 3), and USFWS Great Lakes Restoration Initiative (*n* = 2). Public sites were located on lands managed by the state (Cloquet Area Forest) or counties in the region: Carlton, Aikin, Douglas, and Saint Louis. Both private and public lands followed standard golden-winged warbler best management practices (Golden-winged Warbler Working Group 2019).

Sampling occurred within 2 community-types (sheared shrubland and young forest) that were managed through NRCS-*Regional Conservation Partnership Program's* golden-winged warbler initiatives in northern Minnesota and Wisconsin (Roth et al. 2019, Litvaitis et al. 2021). Our study area was 44–49°N and 89–97°W and 249–540 m in elevation (Omernik and Griffith 2014; Fig. 1). Sheared shrubland sites were managed during the winter by shrub-shearing/brush-hogging blocks or strips of mature alder wetlands to create within-stand structural diversity. These sheared shrubland sites were wet lowlands dominated by alders (*Alnus* spp.), willows (*Salix* spp.), and dogwoods (*Cornus* spp.). Young forest sites were prescribed a standard clear-cut with residuals (i.e., leaving a portion of the original canopy intact), and were harvested during the winter or nongrowing season. The objectives of this silviculture treatment is to regenerate a new cohort of trees while retaining some mature and
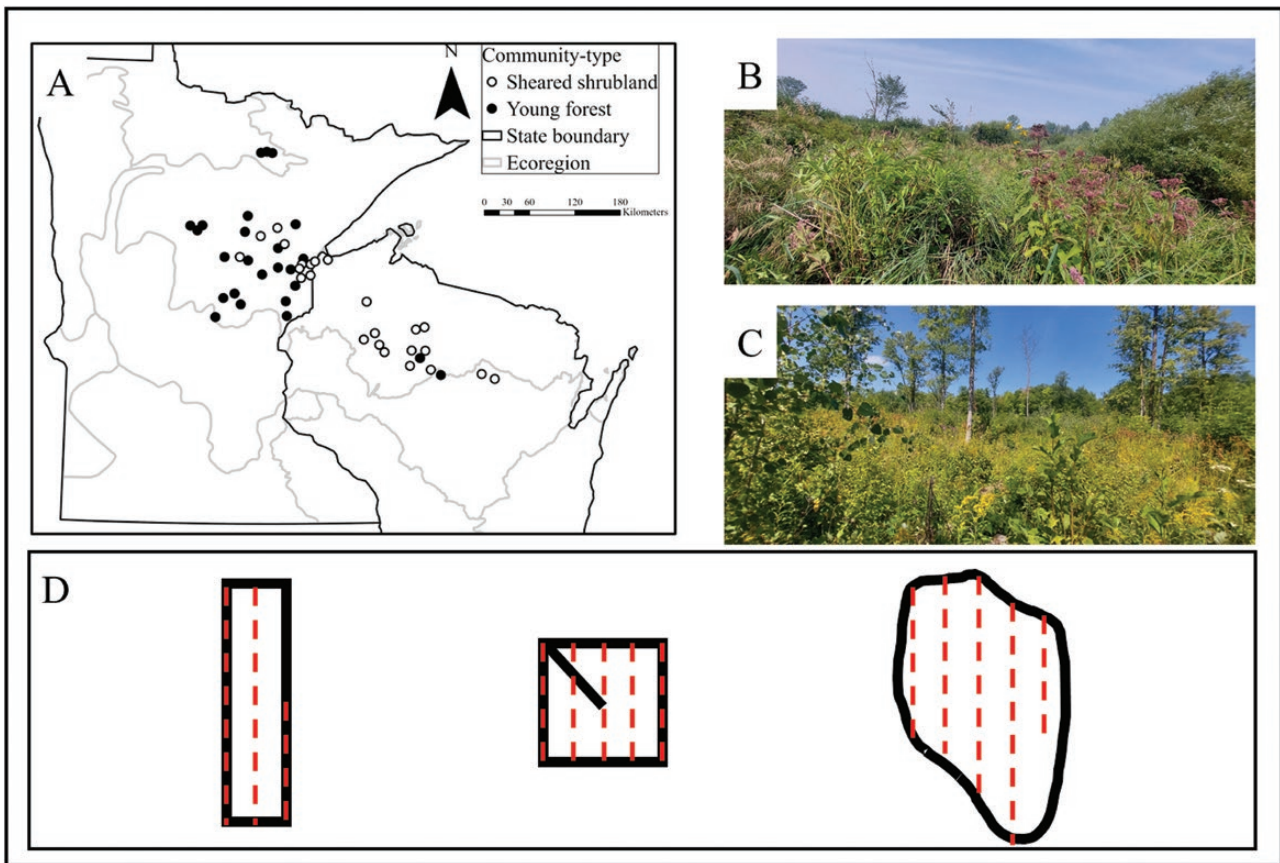
Fig. 1. Study map (A) of 49 sites in northern Minnesota and Wisconsin where bumble bee and butterfly communities were sampled within managed sheared shrubland (B; white) and young forest (C; black) communities. Each site was visited once in June, July, and August 2021. Field sampling efforts occurred within the 1 ha monitoring plots (D; 3 shape options), we estimated pollinator density (individuals/ha) by using visual distance sampling techniques along the monitoring plot perimeter (solid black line) and we quantified blooming nectar plant abundance by counting the number of flowers within 1 m² subplots along multiple transects (dashed lines).

overstory trees as a seed source (Nyland 2016). These communities were dominated by aspens (*Populus* spp.), maples (*Acer* spp.), and oaks (*Quercus* spp.). In general, management targets for these 2 community-types were to retain a basal area of 2.3–4.6 m²/ha with scattered patches of intermixed saplings/shrubs and grasses/forbs (Bakermans et al. 2015). More information about our study area and the 2 community-types can be found in McNeil et al. (2020) and Roth et al. (2019).

Study Design

We began our study site selection by obtaining a list of private land sites within 17 counties in northern Minnesota and Wisconsin (Fig. 1) enrolled within NRCS-*Regional Conservation Partnership Program* for golden-winged warbler habitat management. From this pool of candidate sites, we selected locations for monitoring based on the following criteria: i) sites were either sheared shrubland or young forest, ii) management implementation occurred 1–5 yr prior to monitoring, iii) managed area ≥ 2.6 ha (this is the minimum area needed to fit a 1 ha monitoring plot with a 30 m buffer, see below), and iv) sites of the same community-type were at least 700 m apart. This distance was chosen because it is greater than the average daily travel distance of a concurrent study's (Keele et al. 2023) focal species (monarch butterfly [*Danaus plexippus*]; Fisher and Bradbury 2021). This distance is slightly less than the average flight range of most bumble bee species (1,000 m; Greenleaf et al. 2007). In only 1 instance, 2 sites of different community-types were <700 m apart (413 m).

We selected 25 sheared shrublands and 24 young forests at random from the potential pool of candidate sites. The 49 sites ranged in size from 2.6 to 52.2 ha (*n* = 49, mean = 10.1 ha, median = 7.6 ha, SD = 8.6 ha). At each site, we created a 1 ha monitoring plot (hereafter "plot") where all sampling took place. This approach was adopted from the Monarch Joint Venture's Integrated Monarch Monitoring Program (MJV 2020). We used ArcGIS 10.7 (ESRI 2018) for placement of each plot within managed sites. First, we created a 30 m buffer extending inside the managed boundary, which was where the plot would be placed to avoid edge effects. We used 3 plot shapes (Fig. 1): rectangle (50 × 200 m), square (100 × 100 m), and irregular (dimensions variable). More information about the plot can be found within the Monarch Joint Venture's protocol (MJV 2020). Our priorities for each plot were: i) randomize placement within the managed area, ii) use regular shapes (rectangle first and square second) as it was easier for setting up in the field, and iii) place at least 30 m from managed boundary. Plot shape for each of the 49 sites was determined based on the size and geometry of the managed area (rectangle: *n* = 28, square: *n* = 5, irregular: *n* = 17). See Keele (2022) for additional details regarding the implementation of field transects (e.g., flagging procedure that was helpful for delineating transects during surveys).

Field Data Collection

Pollinator survey.

To quantify bumble bee and butterfly abundance during each site visit, we conducted a visual survey using distance sampling (Buckland

Table 1. Respective model sets with explanatory variables and definitions created for HDM and simple linear models. Each row represents a univariate model that was created for each explanatory variable. Pollinators, blooming plants, and vegetation characteristics were sampled at 49 sites within the western Great Lakes in 2021

Hierarchical distance models		Simple linear models		
Model set	Variable	Model set	Variable	Definition
1. Community-type	Community-type	1. Community-type	Community-type	Sheared shrubland and young forest are 2 community-types of early-successional habitat that are managed for disturbance-dependent wildlife in the Great Lakes.
2. Within-site characteristics	Years post management	2. Patch characteristics	Years post management	Number of growing seasons since early-successional habitat management
	Managed area		Managed area	Size of early-successional habitat managed area (ha)
	Floral frequency	3. Floral characteristics	Floral frequency	Average proportion of subplots with a blooming plant present per site
	Floral abundance		Floral abundance	Average number of flowering plants during a single visit by the number of subplots completed during that visit and log-transformed (ln[flowers/m² + 1])
	Floral richness		Floral richness	Average number of blooming plant species per site
	Floral diversity		Floral diversity	Shannon–Weiner Diversity Indices modified for effective species unit (Jost 2006)
	Basal area	4. Structural vegetation characteristics	Basal area	Cross-sectional area of all stems in a stand (m²/ha)
	Canopy		Canopy	A living tree (snags are not included) with a DBH ≥ 10 cm. Percent cover.
	Tall sapling		Tall sapling	A young tree (<10 cm DBH), woody and generally has 1 main stem, that is taller than 1 m. Percent cover.
	Short sapling		Short sapling	A young tree (<10 cm DBH), woody and generally has 1 main stem, that is shorter than 1 m. Percent cover.
	Tall shrub		Tall shrub	Woody and generally with multiple stems that branch at/below the soil, that is taller than 1 m. Percent cover.
	Short shrub		Short shrub	Woody and generally with multiple stems that branch at/below the soil, that is taller than 1 m. Percent cover.
	Rubus spp.		*Rubus* spp.	Any member of the genus *Rubus*. Percent cover.
	Forb		Forb	Broad-leaved, herbaceous flowering plants. Percent cover.
	Fern		Fern	Any seedless vascular plant. Percent cover.
	Grass		Grass	Any narrow-leaved sedge, grass, or rush. Percent cover.
	Coarse woody debris		Coarse woody debris	Any woody debris ≥ 10 cm diameter. Percent cover.
	Leaf litter		Leaf litter	Dead vegetation. Percent cover.
	Bare ground		Bare ground	Bare soil. Percent cover.
3. Landscape characteristics	Elevation	5. Landscape characteristics	Elevation	Height above sea level (m).
	Latitude		Latitude	Angular distance north or south of the equator (decimal degrees).
	Longitude		Longitude	Angular distance east or west of the prime meridian (decimal degrees).
	Grassland/herbaceous		Grassland/herbaceous	Model created for each spatial extent depending on bumble bee (100 m, 200 m, 500 m, 1 km) or butterfly models (100 m, 200 m, 500 m, 1 km, 5 km, 10 km). Same for other land cover types.
	Pasture/hay		Pasture/hay	See Grassland/herbaceous definition.
	Emergent herbaceous wetland		Emergent herbaceous wetland	See Grassland/herbaceous definition.
	Woody wetland		Woody wetland	See Grassland/herbaceous definition.
	Deciduous forest		Deciduous forest	See Grassland/herbaceous definition.
	Mixed forest		Mixed forest	See Grassland/herbaceous definition.

et al. 2005, McNeil et al. 2019). We walked transects at a consistent rate of 1 m/3 s, regardless of sampling scheme. For the rectangular plot, transects occurred around the perimeter of each site (500 m total walking distance). For square plots, transects were placed around the total perimeter plus a 100 m transect towards the center of the plot (500 m total). For irregular plots, we placed transects around the perimeter (total walking distance was variable; Fig. 1). At initial detection of a bumble bee or butterfly, we recorded the perpendicular distance from transect, associated plant species (if pollinator was observed foraging), and behavior (flying, foraging, resting) for each individual. When possible, we identified butterflies to lower taxonomic levels (e.g., subfamily, genus, species; Supplementary Table 2). We were not able to identify bumble bees to species as this is harder to do on-the-wing. We only conducted surveys during appropriate times (10:00–17:00) and weather conditions (no rain, low wind [Beaufort wind code ≤ 5], and ≥ 15.6 ℃). Although some bees and butterflies may engage in nonpollination activities (e.g., nectar robbing), for the purpose of this manuscript, we interpret bees and butterflies as "pollinators".

Blooming nectar plant survey.
To assess floral characteristics at each site, we conducted a blooming plant survey during each of the 3 visits. Regardless of plot shape, 500 m of total transects were marked for this survey (Fig. 1). We followed placement of blooming nectar plant transects from the Monarch Joint Venture's protocol (MJV 2020). A 1 m^2 subplot was placed every 5 or 10 m along transects for a total of 50 or 100 subplots (variation due to number of personnel available during each survey visit). Within each subplot, we counted the total number of flowers. We tallied individual flowers if < 20 flowers on a given stem and estimated to the nearest 10 if there were > 20 stems or flowers/stem (Mathis et al. 2021). Floral abundance was calculated as total number of flowers during a single visit by the number of subplots completed during that visit (flowers/m^2; Lee et al. 2021, Mathis et al. 2021).

Vegetation survey.
We conducted a woody vegetation survey during the second visit to each site in July. Surveys were designed to characterize each site's vegetation structure, modified from McNeil et al. (2018). We used an ocular tube (James and Shugart 1970) to quantify vegetation structure of 12 vegetation strata at 25 stops/site spaced 20 m apart. The 12 sampled vegetation strata were: tree canopy, sapling, shrub, *Rubus* spp., forb, fern, coarse woody debris, grass, leaf litter, and bare ground (McNeil et al. 2018). Saplings and shrubs were further broken down to short (<1 m) and tall (>1 m; see Table 1 for definitions). We took an ocular tube recording at every other or every fourth blooming nectar plant subplot and this was because availability of observers fluctuated between sampling visits. At each stop, we recorded those vegetation strata that intersected with the ocular tube crosshairs (James and Shugart 1970). We calculated percent occurrence for each of the 12 vegetation strata categories by dividing number of intersections by number of stops (25) and multiplying by 100. Hereafter, we interpreted percent occurrence as percent cover to be comparable with other studies (Lee et al. 2021, Mathis et al. 2021) and it is a more meaningful interpretation of the results. We also used a 10-factor basal area prism at the corners and center of the monitoring plot (*n* = 5) to calculate site basal area.

Landscape variables.
We assessed if the surrounding landscape influenced the density of bumble bees and butterflies at sheared shrubland and young forest sites. We calculated the percent area of 6 land cover categories extracted from the 2019 National Land Cover Database (Homer et al. 2012; 30 m resolution) within several buffer extents. We selected the primary landcover types in our study region: deciduous forest, mixed forest, woody wetlands, grassland/herbaceous, pasture/hay, and emergent herbaceous wetlands (Tavernia et al. 2016). We used the *extract* function within the *raster* package in R (Hijmans 2021, R Core Team 2021) to extract percent area within each spatial extent from the centroid of the plot. For bumble bee analysis, we used 4 spatial extents (100 m, 200 m, 500 m, 1 km; Zurbuchen et al. 2010, Roberts et al. 2017, Lanterman et al. 2019) and for butterfly analysis, we used 6 spatial extents (100 m, 200 m, 500 m, 1 km, 5 km, 10 km; Davis et al. 2007).

Statistical Analyses
To prepare data on floral characteristics for analysis, we only included blooming plant genera with evidence of being foraged on by bumble bees or butterflies (Mathis et al. 2021). We did this because we observed that 71 and 74% of blooming plant genera (117 total genera) had no foraging observations for bumble bees and butterflies, respectively. Our inclusion criteria were: i) observed being foraged on at least once by a bumble bee or butterfly during our study or ii) reported being foraged on in another study. We conducted a literature review (Supplementary Table 1) separately for bumble bees and butterflies to determine plant genera used by these 2 groups outside of our study. The spatial limit for the literature review was within the Xerces Society's Great Lakes Region: Illinois, Indiana, Iowa, Michigan, Minnesota, New York, Ontario, Pennsylvania, and Wisconsin. As a result, we included 56 blooming plant genera (this study: 30, other studies: 26, excluded: 61) and 72 blooming plant genera (this study: 34, other studies: 38, excluded: 45) for butterfly and bumble bee analyses, respectively. We calculated the following variables for all future analyses: floral frequency (proportion of subplots with a blooming plant present), floral abundance (flowers/m^2), floral richness (number of blooming plant species per site), and floral diversity (Shannon–Weiner Diversity Index modified for effective species unit [Jost 2006]; functional *diversity* in *vegan* package). To compare structural vegetation and landscape characteristics between sheared shrubland and young forest sites, we used Mann–Whitney-*U* tests (*wilcox.test* function *stats* package [R Core Team 2021]), due to nonnormality. We also did this to compare floral characteristics and we used blooming plant genera used by both bumble bees and butterflies (*n* = 79) for this comparison and calculating summary statistics. Floral abundance was log-transformed (*ln*[flowers/m^2 + 1]) for all modeling, due to nonnormality. All continuous variables were scaled to have a standard deviation of 1 and mean of 0 to improve model performance.

Hierarchical Distance Model Analysis
To estimate bumble bee and butterfly density we used Hierarchical Distance Models (HDM) using the *gdistsamp* function in the *unmarked* package in R (Fiske and Chandler 2011). HDMs incorporate count data along with distance estimates to create detection-adjusted estimates of organism density (Kéry and Royle 2015). HDMs allow for a more accurate estimate of the number of individuals in a given area at that time by accounting for imperfect detection. Accounting for detection is important because raw counts underestimate density due to imperfect detection (Buckland et al. 2015). Additionally, many factors (detection covariates) influence if an individual that is truly present will be detected by the observer (e.g., temperature, wind speed, cloud cover). For example, ordinal date as an influential detection covariate would be interpreted as date meaningfully

impacting the number of individuals detected (e.g., early vs. late June). Using these density estimates, we can incorporate within-site and landscape explanatory variables to evaluate what factors predict variation in bumble bee or butterfly density at a given time. Models for bumble bee and butterfly data were run separately. Due to detections being inconsistent at the furthest distances, the outer 10% of pollinator observations were excluded from our models, as is recommended for distance analyses (Buckland et al. 2005). Bumble bee observations were placed into 5 bins with 1 m widths (0–1, 1–2, 2–3, 3–4, 4–5 m) and butterfly observations were placed into 5 bins with 2 m width (0–2, 2–4, 4–6, 6–8, 8–10 m).

Season-Wide Analysis

To assess bumble bee and butterfly density *season-wide*, we created dynamic HDMs that allowed temporary emigration and included a time dependent function (Φ; Kéry and Royle 2015p). We used a 4-step model building process. First, we created univariate models to determine the best detection function (hazard rate, half-normal, exponential) and statistical distribution (Poisson or negative binomial). Second, we added a time dependent function (Φ), to determine if density varied among the 3 survey visits (June, July, August). Third, we created univariate models to determine the covariates (cloud cover, survey start time, temperature, Beaufort wind index, ordinal date, observer ID, and vegetation characteristics) that most influenced detection probability (p). Fourth, we created 3 model sets to test whether community-type (model set 1), within-site characteristics (model set 2), or landscape characteristics (model set 3) influenced bumble bee or butterfly density ($λ$). Within each model set we created univariate models for each explanatory variable and a null (intercept-only) model (Table 1). We did not have enough statistical power to create multivariate models and explore relationships between within-site and landscape explanatory variables. We compared models using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2015). We ran a goodness-of-fit test on the top model to assess overdispersion ($ĉ ≤ 1.0$). For overdispersed models ($ĉ > 1$), we used quasi-AIC_c ($ΔQAIC_c$) as an adjustment for this (Kéry and Royle 2015). We considered a variable to be meaningful for pollinator density if the AIC_c value for its model was at least 2.00 AIC_c values lower than that of the null model and β 85% confidence intervals did not include zero (Arnold 2010, Burnham and Anderson 2015).

Within-Season Analysis

To assess within-site and landscape habitat associations *within-season*, we created static HDMs to quantify bumble bee and butterfly densities during each of the 3 survey visits (June, July, August; Kéry and Royle 2015). These models do not include a time dependent function (ϕ) and assume that sites are closed to changes in density within each "season" (i.e., the closure assumption; Kéry and Royle 2015). Therefore, models were run separately for bumble bees and butterflies during each of the 3 survey visits. In contrast with the dynamic models, as described above, we used a 3-step model building process which excluded the time dependent function step and landscape variables. As before, within each model set we created univariate models for each explanatory variable and a null (intercept-only) model (included model sets 1 and 2; Table 1). The model selection and assessment process were the same as described above.

Simple Linear Models—Butterfly Morphospecies Richness

To assess the within-site and landscape characteristics that influence butterfly morphospecies richness, we created simple linear models using the *lm* function in R. We used morphospecies as a proxy for species richness because butterfly observations were identified to either subfamily, genus, or species (e.g., Coliadinae, *Boloria* spp., *Danaus plexippus*; Supplementary Table 2). For linear models, we used the same variables as the HDM, but variables were divided into 5 model sets (Table 1). Within each model set we created univariate models for each explanatory variable and a null (intercept-only) model. We considered a variable to be meaningful for butterfly morphospecies richness if the AIC_c value for its model was at least 2.00 AIC_c values lower than that of the null model (Burnham and Anderson 2015). We calculated R^2 values for the top-ranked model within each tier to assess model fit.

Results

Raw Pollinator Counts

During 147 site visits from 02 June–26 August 2021, we observed a total of 1,064 bumble bees. Average bumble bees per site visit increased throughout the summer (June = 1.18 ± 2.26, July = 2.41 ± 3.01, August = 18.12 ± 19.03). Our observations of behaviors for bumble bees were nectaring ($n = 865$, 81%), flying ($n = 180$, 17%) and resting ($n = 19$, 2%). The most common blooming plants that bumble bees were observed foraging on varied for each sampling visit (June [18 obs.]: *Rubus* spp. [$n = 16$; 89% obs.] and *Rosa* spp. [$n = 1$; 6% obs.], July [75 obs.]: *Rubus* spp. [$n = 27$, 36% obs.] and joe-pye weed [*Eutrochium* spp., $n = 7$, 9% obs.], August [771 obs.]: goldenrod [$n = 291$, 38% obs.] and flat-topped white aster [*Doellingeria umbellata*, $n = 113$, 15% obs.]).

We observed a total of 1,590 butterflies from 22 species or groups (Supplementary Table 2). Average butterflies per site visit decreased throughout the summer (June = 15.35 ± 10.54, July = 11.43 ± 11.86, August = 5.67 ± 8.26). Our observations of behaviors for butterflies were flying ($n = 1,237$, 78%), nectaring ($n = 182$, 11%), and resting ($n = 171$, 11%). The most common morphospecies of butterflies observed throughout our survey period varied temporally (June: skippers [subfamily: *Pyrginae* or *Hesperiinae*, 21% obs.], satyrs [subfamily: *Satyrinae*, 17% obs.], checkerspots [*Chlosyne* spp., 14% obs.], July: large fritillaries [*Speyeria* spp., 27% obs.], skippers [21% obs.], satyrs [12% obs.], and August: large fritillaries [44% obs.], small fritillaries [*Boloria* spp., 17% obs.], hairstreaks [subfamily: *Theclinae*, 8% obs.]). The most common blooming plants with nectaring observations varied for each sampling visit (June [41 obs.]: geraniums [*Geranium* spp., $n = 6$, 15% obs.] and *Rubus* spp., [$n = 6$, 15% observations], July [67 obs.]: Canada thistle [*Cirsium arvense*, $n = 13$, 19% obs.] and Northern blue flag iris [*Iris versicolor*, $n = 7$, 10% obs.], and August [74 obs.]: bull thistle [*Cirsium vulgare*, $n = 24$, 32% obs.] and swamp thistle [*Cirsium muticum*, $n = 21$, 28% obs.]).

Comparison of Within Site and Landscape Characteristics Between Community Types

Sheared shrublands and young forests differed in multiple ways with respect to floral, structural vegetation, and landscape characteristics. Young forests hosted on average greater floral richness (8.33 ± 2.99 species vs 5.75 ± 2.82 species; $P < 0.001$) and floral diversity (4.34 ± 1.30 $e^{H'}$ vs 3.26 ± 1.27 $e^{H'}$; $P < 0.001$) than sheared shrublands (Table 2). Floral frequency ($P = 0.70$) and floral abundance ($P = 0.70$) were similar between the 2 communities (Table 2). Average floral abundance increased throughout the summer in sheared shrubland (June: 10.79 ± 23.80 flowers/m², July: 10.48 ± 34.78 flowers/m², August: 48.58 ± 116.22 flowers/m²) and young forest (June: 11.75 ± 14.99, July: 25.61 ± 34.37, August: 33.82 ± 28.86) communities.

Table 2. Summary statistics and Mann–Whitney-*U* results from comparing floral characteristics between the 2 managed community-types. See Table 1 for variable definitions. Significant (*P* < 0.05) comparisons are bolded. Floral resources were sampled during 3 visits in 2021 for each of the 49 sites in the western Great Lakes

Variable	Community-type	Mean	St. Dev.	Min	Max	*W*	*P*
Floral frequency	Sheared shrubland	0.33	0.17	0.12	0.68	280.00	0.70
	Young forest	0.33	0.12	0.16	0.65		
Floral abundance	Sheared shrubland	23.29	41.15	1.89	198.12	210.00	0.70
	Young forest	23.73	18.19	3.23	74.67		
Floral richness	Sheared shrubland	5.75	2.82	2.67	15.67	**124.50**	**<0.001**
	Young forest	8.33	2.99	3.67	16.33		
Floral diversity	Sheared shrubland	3.26	1.27	1.79	8.28	**121.00**	**<0.001**
	Young forest	4.34	1.30	1.74	8.34		

Young forests had greater percent cover of forbs (55% ± 14 cover vs 38% ± 16 cover; *P* < 0.001) compared to sheared shrublands (Fig. 2). Additionally, young forests had lower tall shrub, *Rubus* spp., grass, and leaf litter percent cover but higher tall and short sapling and coarse woody debris percent cover compared to sheared shrublands (Fig. 2). The average basal area was similar (sheared shrubland = 4.33 ± 3.81 m²/ha, young forest = 3.68 ± 2.38 m²/ha) between both community-types (*P* = 0.83). At the land-scape scale, dominant land covers surrounding the 2 community-types varied by spatial extent. Both the percent area of deciduous forest and grassland/herbaceous were greater around young forests at the smallest spatial extents (100 m–1 km; *P* < 0.05), but both community-types were similar at larger spatial extents (5 and 10 km; *P* > 0.05; Supplementary Table 3). The percentage of emergent herbaceous wetlands had the opposite relationship, whereas it was higher around young forests at the largest spatial extents (1–10 km; *P* < 0.05), but both community-types were similar at smaller spatial extents (100–500 m; *P* > 0.05; Supplementary Table 3). The only land cover type that was greater around sheared shrubland sites was woody wetlands and only at the smaller spatial extents (100 m–1 km; *P* < 0.05; Supplementary Table 3). Both the percent area of pasture/hay and mixed forest were similar around both community-types at all spatial extents (*P* > 0.05; Supplementary Table 3).

Pollinator Habitat Associations—Season Wide

Both bumble bee and butterfly density models were best fit by a hazard rate function with negative binomial mixture with ob-server as the most influential detection covariate. In addition, the time dependent function (ϕ) was a significant predictor of bumble bee density, but not butterfly density. Throughout the summer, our models predicted mean bumble bee and mean butterfly densities to be 83.93 individuals/ha (95% CI: 66.39–106.11) and 101.53 individuals/ha (95% CI: 84.62–121.82), respectively. Community-type (sheared shrubland or young forest) did not predict density for either bumble bees or butterflies because the null model was the top model (Supplementary Table 4). As a result, sheared shrublands and young forests sites were pooled together for all following model sets. Floral frequency and floral abundance were both within-site characteristics that were positively associated with bumble bee density, but no landscape characteristics explained bumble bee density (Supplementary Table 4, Table 3, Fig. 3). Percent cover of tall shrubs was the top model in the within-site characteristics model set for butterfly density, but the null model was competing (Supplementary Table 4, Table 3). The landscape model set for butterflies suggested that density was negatively related with elevation and longitude but positively associated with percentage of pasture/hay within 10 km (Supplementary Table 4, Table 3, Fig. 4).
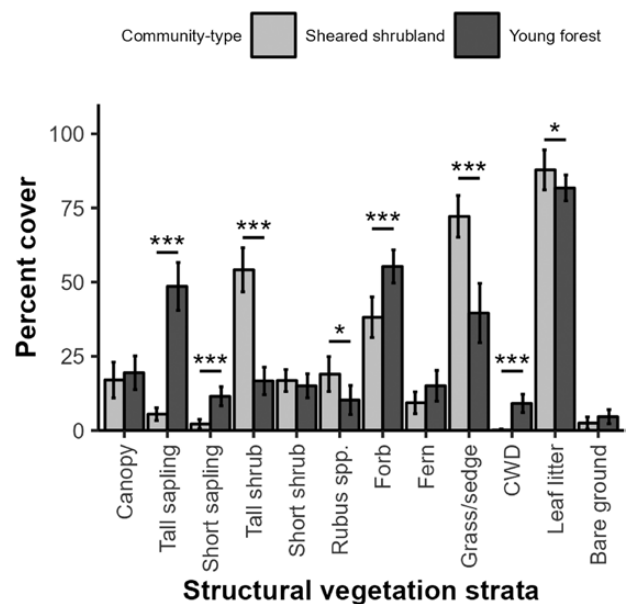

Fig. 2. Comparisons of percent cover among 12 structural vegetation strata between managed community-types (sheared shrubland and young forest). *P* value results from Mann–Whitney-*U* tests are represented as follows: *P < 0.05, **P < 0.01, ***P < 0.001. Error bars represent 95% confidence intervals. Vegetation strata were measured using an ocular tube and sampled once in July 2021 for each of the 49 sites in the western Great Lakes.

Pollinator Habitat Associations—Within Season

A hazard rate function with negative binomial mixture was the best fit for both bumble bee and butterfly data for the *within-season* models. For bumble bees, ordinal date and observer were the most influential detection covariates during June and July and August, respectively. For butterflies, observer, ordinal date, and temperature were the most influential detection covariates during June, July, and August, respectively. Our models predicted mean bumble bee density increased during each sampling visit: June (36.51 individuals/ha [95% CI: 15.36–86.79]), July (50.14 individuals/ha [95% CI: 26.59–94.54]), and August (68.81 individuals/ha [95% CI: 51.86–91.29]). Conversely, our models predicted butterfly density to de-crease during each sampling visit: June (96.26 individuals/ha [95% CI: 81.25–114.04], July (79.34 individuals/ha [95% CI: 60.58–103.91], and August (32.20 individuals/ha [95% CI: 22.00–47.13]).

Within the community-type model set, the null model was ei-ther the top-ranked model or was competing for both bumble bee and butterfly models, indicating that community-type was not influ-ential for either group and therefore the 2 community-types were

Table 3. Summary of the results from HDM *season-wide* and *within-season* to assess associations with bumble bee and butterfly densities. The 3 survey visits were June (2–30 June), July (1–25 July), and August (30 July–26 Aug). Landscape variables were not assessed for the *within-season* analyses, therefore marked by NA. Lastly, included are results from simple linear models assessing associations with butterfly morphospecies richness. The symbols "+" and "−" are used to represent positive and negative relationships, respectively. An asterisk (*) represents that the model was determined to be influential of density when AIC_c values were at least 2.00 AIC_c values lower than that of the null model and β 85% confidence intervals did not include zero. The same AIC_c comparisons, but not β 85% confidence intervals, were used to determine if models were influential of butterfly morphospecies richness (indicated by an asterisk). Models without an asterisk indicate it was the top model, but the null model was competing. Bumble bee and butterfly densities were estimated within 2 managed community-types (sheared shrubland and young forest) during the summer of 2021 at 49 sites in the western Great Lakes

	Variable	Butterfly density	Butterfly morphospecies richness	June butterfly density	July butterfly density	August butterfly density	Bumble bee density	June bumble bee density	July bumble bee density	August bumble bee density
Within-site characteristics	Managed size (ha)							−*		
	Floral frequency						+*	+*	+*	
	Floral abundance (log-transformed)						+*			+*
	Floral richness		+*							
	% *Rubus* spp. cover							+*		
	% Short shrub cover									−*
	% Tall shrub cover	−	−*			−				
	Basal area			+*						
Landscape characteristics	Elevation (m)	−*		NA	NA	NA		NA	NA	NA
	Longitude	−*	−*	NA	NA	NA		NA	NA	NA
	Pasture/hay (10 km)	+*		NA	NA	NA		NA	NA	NA

pooled together for following model sets, as for our *season-wide* analyses (Supplementary Table 5). Measures of floral characteristics (i.e., floral frequency, floral abundance, *Rubus* spp.) were consistent positive predictors for bumble bee density during each visit (Supplementary Table 5, Table 3). Also, bumble bee density was negatively associated with managed area in June and with short shrub percent cover in August (Supplementary Table 5, Table 3). Butterfly density was positively associated with basal area in June (Supplementary Table 5, Table 3). Additionally, in July, the percent cover of tall shrubs was the top model, but the null model was within the competing set (Supplementary Table 5, Table 3).

Butterfly Morphospecies Richness

The community-type did not influence butterfly morphospecies richness, as the null model was the top model (Supplementary Table 6) and therefore both community-types were pooled together for following model sets. Influential relationships that our models detected with butterfly morphospecies richness were with floral richness (positive), percent cover of tall shrubs (negative), and longitude (negative; Supplementary Table 6, Table 3).

Discussion

Our study is the first to compare bumble bee and butterfly densities between sheared shrubland and young forest communities in the western Great Lakes region. Despite a series of analyses spanning insect taxa and survey period, we found no evidence, for any subset of data, that sheared shrublands and young forests differed in summer bumble bee or butterfly density 1–5 yr post management, indicating both conservation practices "performed" equally. Although the 2 managed community-types did differ for some within-site habitat components and the surrounding percentage of dominant land cover types, they both provided important habitat

requisites for summer adult foraging bumble bees and butterflies (e.g., abundant wildflowers). Shrubland communities are common in the northern Great Lakes (Tavernia et al. 2016) and the implementation of mechanical management practices that create early-successional communities has provided habitat for at-risk vertebrate wildlife species (e.g., golden-winged warbler; McNeil et al. 2020, Buckardt Thomas et al. 2023). For example, from 2015 to 2022 approximately 10,964 ha of sheared shrubland and young forest communities have been managed for golden-winged warblers on private and public lands in Minnesota, Wisconsin, and Michigan (L. Rowse and P. Dieser, personal communication). Our findings as well as others inform how insect pollinators may benefit from early-successional habitat management for vertebrate wildlife (Lee et al. 2021, Mathis et al. 2021, Keele et al. 2023).

The within-site level habitat associations we observed in sheared shrubland communities in the Great Lakes mirror similar trends presented in other studies that investigated different types of shrubland management. Removal of nonnative invasive shrubs within riparian forests and prairie fen wetlands has been shown to improve the herbaceous blooming plant community by reducing aggressive and competing woody vegetation and therefore increase bee and butterfly abundance and richness (Fiedler et al. 2012, Hudson et al. 2013). In Europe, butterfly species richness increased at sites with greater nectar resources and host plants in broadleaf woodlands managed recently (1–2 yr) via cutting and thinning of small trees and shrubs (Fartmann et al. 2013). Lastly, mowing and herbicide treatments that suppressed tall woody vegetation within transmission line corridors increased bee richness and abundance (Wagner et al. 2019). These studies, along with our findings that both bumble bee and butterfly densities showed frequent positive relationships with multiple floral characteristics at sites with low levels of tall and dense woody vegetation provide evidence that managing shrubland communities for habitat requisites (e.g., abundant floral resources) will benefit bumble bee and butterfly communities.
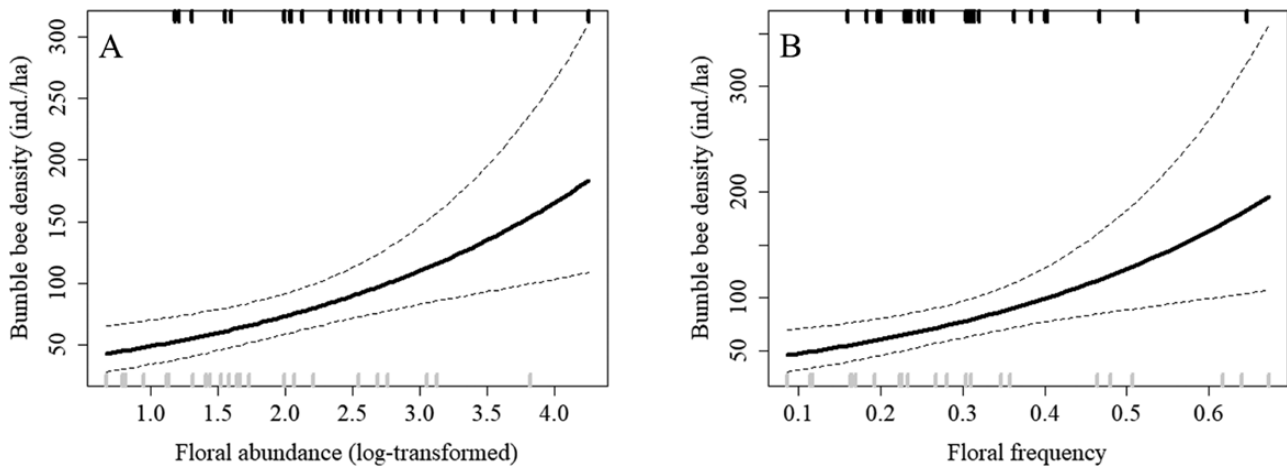
Fig. 3. Hierarchical distance model results of within-site characteristics that meaningfully predicted bumble bee density *season-wide*. Our models indicated bumble bee density increased with floral abundance (A; log-transformed) and floral frequency (B; proportion of subplots with a blooming plant present). Bumble bees and floral resources were sampled during 3 visits (June, July, August) in 2021 at 49 sites in the western Great Lakes. The dark middle line shows the model prediction, and the dashed lines are 95% confidence intervals. Rug marks show the distribution of our x-axis values (gray = sheared shrublands, black = young forests).

Differences among our density estimates of bumble bees and butterflies with other studies may provide insights into how resources in our sampled early-successional communities compare with others. During approximately the same time (July), average bumble bee density within Pennsylvania young forests (192 individuals/ha; McNeil et al. 2019) was nearly 4 times as dense compared to our sites in the western Great Lakes (50 individuals/ha). Average butterfly density between our study (102 butterflies/ha) and another in Pennsylvania young forests was relatively similar (88 butterflies/ha; Lee et al. 2021). When comparing all blooming species recorded, the same study (Lee et al. 2021) documented on average 128 flowers/m² (early June–early September), which is about 5× greater compared to our sites (28 flowers/m²). This large difference between bumble bee density and negligible difference between butterfly density, may be because bumble bees are strongly associated with floral resources, whereas butterflies are less so (Alanen et al. 2011). Within herbaceous-dominated communities in the Midwest multiple studies reported about 100–200 butterflies/ha for individual species (Moranz et al. 2012, Bendel et al. 2018, Cutter et al. 2022). The stark difference in butterfly density between our sites and aforementioned studies is likely due to less woody vegetation cover in herbaceous-dominated landscapes, which can lead to greater floral resources (Lett and Knapp 2005). Although density estimates allow for standard comparisons, caution should be exercised interpreting the magnitude of difference given these compared studies had slightly different survey times and were not done during the same year as our study, which both are known to greatly influence pollinator and blooming plant communities (Alarcón et al. 2008). With this in mind, although density estimates are informative, they are not the sole measure of habitat value for wildlife (Van Horne 1983) and our findings are most informative of what factors are most likely to influence pollinator densities within sheared shrubland and young forest communities.

Our *season-wide* and *within-season* models consistently detected summer bumble bees to be driven by the availability of floral resources and this has similarly been observed in other early-successional communities (Lee et al. 2021, Mathis et al. 2021). We observed a positive relationship between bumble bee density and *Rubus* spp. cover only in June, likely because this was an abundant

floral resources during this time and is known to be heavily visited by queens (Lanterman et al. 2019). Our observation that bumble bee density increased throughout our sampling period (June–August) is likely due to workers increasing throughout the summer (Mola et al. 2021b) and this was in conjunction with floral resource abundance peaking in late-summer within our sites (e.g., goldenrod). Other studies within early-successional communities have similarly reported high floral abundance in late-summer and early-fall (Romey et al. 2007, Roberts et al. 2017, Lee et al. 2021, Mathis et al. 2021). Nonfloral habitat attributes (e.g., woody vegetation cover) are drivers of floral resources and therefore also drivers of pollinator density (Mathis et al. 2022), explaining the negative relationship we observed between short shrub cover and bumble bee density in August. This relationship is due to woody vegetation obstructing sunlight from shade-intolerant wildflower species (Hanula and Horn 2011a, Mathis et al. 2022).

Although numerous studies have reported landscape scale patterns to drive bumble bee densities (Lanterman et al. 2019, Liczner and Colla 2020, Novotny et al. 2021, Pugesek and Crone 2021), our results did not suggest landscape variables to be important predictors of bumble bee density within our sites. Weak landscape patterns may be driven by biased site selection by conservation practitioners implementing NRCS-*Regional Conservation Partnership Program* golden-winged warbler habitat management. Indeed, golden-winged warbler best management practices require that managed sites meet landscape criteria (>50% forest cover within 2.4 km; Roth et al. 2019), which likely minimized variation in land cover that may have otherwise driven variation in bumble bee density. For example, at 1 km, average (±SD) percent forest cover (deciduous forest + mixed forest + woody wetlands) around our sites was 78.37% (±15.07%). Therefore, our sites likely lacked the variation in landscape conditions that would have influenced bumble bee density and other studies may have had enough variation to detect relationships. Importantly, this likely does not mean that bumble bee density in our system is not dependent upon landscape characteristics, but, rather, that our site selection precluded the sampling of landscapes that contained extensive nonforest land cover.

Previous studies have reported that butterfly communities are influenced by site level (Hanula and Horn 2011b, Mathis et al. 2021)
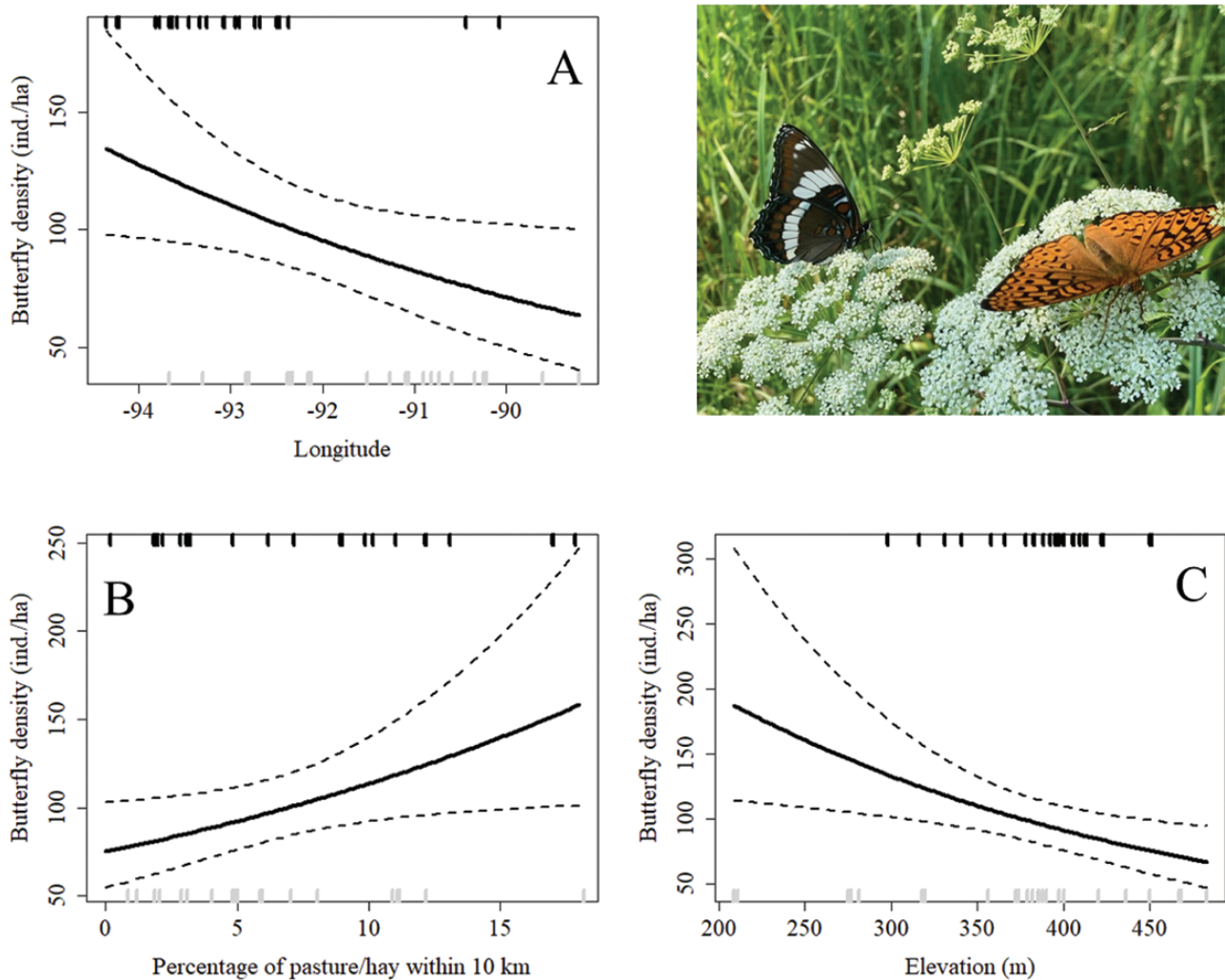
Fig. 4. Hierarchical distance model results of landscape characteristics that meaningfully predicted butterfly density *season-wide*. Our models indicated butterfly density decreased with longitude (A), and elevation (C) but increased with the percentage of pasture/hay within 10 km of the site (B). Butterflies were sampled during 3 visits (June, July, August) in 2021 at 49 sites in the western Great Lakes and cover data were extracted from the 2019 National Landcover Database. The dark middle line shows the model prediction, and the dashed lines are 95% confidence intervals. Rug marks show the distribution of our x-axis values (gray = sheared shrublands, black = young forests).

and landscape-level habitat characteristics (Davis et al. 2007, Moranz et al. 2012); although we did not observe all of these patterns as our models detected butterfly density to not be driven by within-site factors but were so by landscape variables. Our finding of weak or few within-site associations with butterfly density and morphospecies richness is likely because butterflies are noncentral place foragers, use nonnectar resources (Bodri 2018), and are also driven by host plant availability, which we did not measure (Fartmann et al. 2013). The one exception with woody vegetation relationships we observed was a positive association with basal area and butterfly density in June. Although we were not able to run species specific models this was likely driven by satyrs (a woodland associated group; Brock et al. 2003) being the second most common morphospecies (16% of observations) during this time. The *across-season* landscape-level relationships our models detected is likely because we most commonly observed open-habitat associated morphospecies throughout our survey period (e.g., fritillaries) that are known to travel long and linear distances throughout the landscape while searching for food and host plants (Haddad and Baum 1999, Townsend and Levey 2005, Kuefler and Haddad 2006). Other studies have similarly found

elevation and proportion of semi-natural herbaceous land covers (e.g., pasture/hay) to be drivers of open-habitat associated butterfly communities as sites at high elevation tend to have high soil pH (Grigal et al. 1991), leading to less diverse herbaceous understory (Brosofske et al. 2001, Barbier et al. 2008) and these semi-natural herbaceous land cover types can serve as movement corridors in a forested-landscape (Haddad 1999, Öckinger and Smith 2008). With this in mind, we recommend managers maintain diverse forest age classes on the landscape, not only for vertebrate wildlife (Gutowsky et al. 2020, Buckardt Thomas et al. 2023), but also for pollinators as ephemeral semi-natural herbaceous land cover can periodically increase butterfly abundance, likely leading to greater dispersal on the landscape (Haddad and Baum 1999).

In summary, our study provides empirical evidence of what factors drive variation in bumble bee and butterfly density within sheared shrubland and young forest communities in the western Great Lakes. Our models, as well as other studies (Romey et al. 2007, Proctor et al. 2012, Roberts et al. 2017, Lee et al. 2021, Mathis et al. 2022), support that low cover of woody vegetation and abundant and rich floral resources are essential habitat requisites for pollinators within

managed early-successional woody communities. Our study includes several limitations worth mentioning. Although we can compare our density estimates with other studies, we are not able to assess the relative beneficial value of our surveyed communities because we did not sample a control/unmanaged group. Secondly, our study precluded any spring sampling, which woody communities provide many valuable resources for bumble bees during this time (e.g., nesting habtiat; Mola et al. 2021a, Pugesek and Crone 2021) and spring ephemerals are an important floral resource during this time (Harrison et al. 2018, Mola et al. 2021b). Lastly, we did not have a large enough sample size to run species specific models and identifying bumble bees without capturing them is difficult. Therefore, although our findings follow similar trends reported by other studies for these 2 groups (Alanen et al. 2011, Mathis et al. 2021), varying forest habitat associations have been reported for different bumble bee (Mola et al. 2021a) and butterfly species (Meehan et al. 2013). We believe, future work investigating how less studied pollinators groups (e.g., flies, beetles, and moths) respond to early-successional management practices is needed, especially since the few studies that have, support contrasting habitat associations from bees and butterflies (Summerville 2013, Westby-Gibson Jr. et al. 2017).

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions

Emma Keele (Formal analysis [Lead], Investigation [Lead], Methodology [Lead], Project administration [Equal], Validation [Lead], Visualization [Lead], Writing—original draft [Lead]), Darin McNeil (Conceptualization [Equal], Formal analysis [Supporting], Methodology [Supporting], Supervision [Equal], Validation [Equal], Writing—review & editing [Lead]), Joseph Duchamp (Formal analysis [Supporting], Methodology [Supporting], Validation [Equal], Writing—review & editing [Supporting]), and Jeffery Larkin (Conceptualization [Lead], Funding acquisition [Lead], Methodology [Supporting], Project administration [Equal], Supervision [Lead], Validation [Equal], Writing—review & editing [Equal])

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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