

RESEARCH ARTICLE

Spatiotemporal patterns of forest pollinator diversity across the southeastern United States

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Abstract

Aim: Efforts to understand how pollinating insect diversity is distributed across large geographic areas are rare despite the importance of such work for conserving regional diversity. We sought to relate the diversity of bees (Hymenoptera: Apoidea), hover flies (Diptera: Syrphidae), and butterflies (Lepidoptera) to ecoregion, landscape context, canopy openness, and forest composition across southeastern U.S. forests.

Location: Nineteen experimental forests across nine states in the southeastern U.S.

Methods: We established 5–7 plots on each experimental forest. In each, we sampled pollinators monthly (March–September) using coloured pan traps, and collected data on local forest characteristics. We used the National Land Cover Database (NLCD) to quantify surrounding landcover at different spatial scales.

Results: Bee richness was negatively correlated with both the amount of conifer (pine) forest and the extent of wetlands in the surrounding landscape but was positively correlated with canopy openness. Hover flies and butterflies were less sensitive to landscape context and stand conditions. Pollinator communities differed considerably among ecoregions, with those of the Central Appalachian and Coastal Plain ecoregions being particularly distinct. Bee richness and abundance peaked 2 months earlier in Central Appalachia than in the Coastal Plain and Southeastern Mixed Forest ecoregions.

For affiliations refer to page 10.

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Main Conclusions: Our findings reveal ecoregional differences in pollinator communities across the southeastern U.S. and highlight the importance of landscape context and local forest conditions to this diverse fauna. The closed broadleaf forests of Appalachia and the open conifer-dominated forests of the Coastal Plain support particularly distinct pollinator communities with contrasting seasonality. Our results suggest pine forests may reduce pollinator diversity in regions historically dominated by broadleaf forests. However, efforts to create more open canopies can help improve conditions for pollinators in planted pine forests. Research exploring associations between forest pollinators and different broadleaf tree taxa is needed to better anticipate the impacts of various management activities.

KEYWORDS

Experimental Forest Network, flooding, plantation forests, seasonality, survey, tree composition

1 | INTRODUCTION

Despite growing concerns over declines in pollinating insects (Barendregt et al., 2022; Forister et al., 2021; Powney et al., 2019; Ulyshen & Horn, 2023), there is surprisingly little information on how the diversity of these organisms is distributed across time and space, especially at transregional scales. For conservation efforts to be effective over large areas, it is critical to understand how different ecoregions contribute to regional pollinator diversity, and how local diversity is influenced by landscape context and local conditions. Unfortunately, such fundamental information is lacking for many parts of the world, and even knowing which pollinator species are present remains a major knowledge gap for many land managers (Rivers et al., 2018). While museum records provide valuable insights into the distribution of species, such data are typically from specimens collected over many years using a variety of methods and rarely include detailed information on local habitat conditions (Orr et al., 2021). Furthermore, because pollinator populations exhibit strong inter-annual variation (Williams et al., 2001) and all sampling methods are more effective for some taxa than others (Cane et al., 2000; Joshi et al., 2015), there is a strong need for coordinated efforts to simultaneously and consistently sample pollinators over large geographic areas.

There is increasing awareness that forests play key roles in supporting pollinator diversity, which in turn provides pollination services to adjacent habitats, including crops (Ulyshen, Robertson, et al., 2023; Ulyshen, Urban-Mead, et al., 2023). However, many questions remain about how forest composition and structure shape these communities. A growing number of studies indicate that pollinators are active within the canopies of temperate forests (Allen & Davies, 2023; Cunningham-Minnick et al., 2024; Ulyshen et al., 2010; Urban-Mead et al., 2021, 2023) and utilize abundant pollen and nectar from flowering trees. Even wind-pollinated taxa, such as oaks (*Quercus* spp.), can serve as important pollen sources for many bees (Kraemer & Favi, 2005; Saunders, 2018; Urban-Mead et al., 2023). By contrast, conifer pollen is thought to be a less suitable resource (Pernal & Currie, 2000),

possibly resulting in less favourable conditions for pollinators in the canopy. This is significant, as conifer forests are favoured throughout the world for timber and pulp production (Kanninen, 2010). For example, the forests of the southeastern U.S. are the largest producer of industrial roundwood in the world and most of that production comes from densely stocked – often planted – stands of intensively managed pines native to the region (Prestemon & Abt, 2002).

Forests of the southeastern U.S. were historically far more open than many are today (Carroll et al., 2002; Van Lear et al., 2004). Pine dominance was greatest on the Coastal Plain where the frequent occurrence of fires played a key role in sustaining savanna-like conditions over large areas. Such open conditions support a high abundance and diversity of flowering plants in the herbaceous layer (Carr et al., 2010) which, in turn, benefit pollinator communities (Hanula et al., 2015; Moylett et al., 2019; Odanaka et al., 2020). Closed-canopy conditions, by contrast, often result in suppressed floral availability or concentrate flowering to the early spring months prior to canopy closure (Peterson & Reich, 2008; Taki et al., 2007; Watson et al., 2011). Despite strong interest in restoring open woodlands for a wide range of benefits including conserving endangered vertebrates and reducing the risk of bark beetle outbreaks (Dixon et al., 2022; Oluoch et al., 2021; Van Lear et al., 2004), relatively few of the region's pine and oak-dominated forests currently have open stand structures (Gilliam & Platt, 1999). Those that do typically arose from mechanical thinning, wind damage, low initial stocking levels, or the application of prescribed fire (Hanberry et al., 2020). Previous researchers suggested that the closure of southeastern U.S. forests over the past century may have contributed to pollinator declines (Hanula et al., 2015).

To address some of these concerns, we sampled bees, hover flies, and butterflies on 19 U.S. Forest Service experimental forests which together provide a good representation of major forest types typical of the southeastern U.S. Our objectives were to (1) collect baseline information on the diversity of these pollinators across the region, (2) determine how the diversity and composition of pollinator

communities differ among major ecoregions, (3) explore the relationship between pollinator diversity and landscape context (e.g., amount of surrounding conifer forest and wetland), and (4) compare pollinator seasonality among ecoregions.

2 | METHODS

2.1 | Study sites

The U.S. Forest Service Southern Research Station's (SRS) experimental forest network (EFN) consists of 19 units (Table 1) across the southeastern U.S. (Figure 1). Established decades ago, these experimental forests were intended to address a variety of research needs, from silviculture to naval stores production to forest genetics, erosion control, and hydrology. The SRS EFN covers seven of the nine distinct southeastern ecoregions as defined by Bailey (2016), including the Central Appalachian Forest, Southeastern Mixed Forest, Outer Coastal Plain Mixed Forest, Eastern Broadleaf Forest, Lower Mississippi Riverine Forest, Ouachita Mixed Forest, and Ozark Broadleaf Forest. The first three of these were the most sampled in this study (including three or more experimental forests) and correspond to the Southern Appalachians, Piedmont, and Coastal Plain physiographic regions, respectively.

In 2018–2019, a series of plots (coordinates) were systematically established on all experimental forests in the SRS EFN to provide a standardized and uniform framework for large-scale studies. The ultimate goal is to collect long-term forest data at these locations following the Forest Service's Forest Inventory and Analysis (FIA) protocol (Bechtold & Patterson, 2005). However, such data have not yet been collected at most of the plots sampled in this study, and were thus not available for the current analysis. From this collection of plots, we randomly selected five from each experimental forest for use in this study. We selected two additional plots at Chipola EF because there was a possibility that some would be disturbed by planned management operations, and would therefore need to be dropped from the study. However, this did not happen, resulting in a total of 97 plots across the network. The distance between plots within experimental forests was at least 500m while the distance between experimental forests ranged from ~20 to 1400km (Figure 1). All plots were forested, although canopy openness and successional stage differed considerably depending on recent disturbance events (e.g., Hurricane Michael) or management activities (e.g., mechanical thinning or prescribed burning). Based on National Land Cover Data from 2021, the mean and median percent forest cover within 500m of the plots were 86.8% and 91.0%, respectively, with a range of 31.3%–100%.

2.2 | Pollinator sampling and identification

Pollinators were sampled on all 19 experimental forests using coloured pan traps. Although pan traps provide a standardized, simple, and effective method for sampling pollinators in forests (Ulyshen

et al., 2022) they are known to be more effective at collecting some taxa than others (Baum & Wallen, 2011; Cane et al., 2000) and can also under-sample pollinators in areas with an abundance of flowers (Baum & Wallen, 2011). While netting off flowers would have improved the study (Roulston et al., 2007), we limited sampling to pan trapping given the limits of time and personnel as well as the logistical challenges inherent to visiting remote sites across such a large geographic area. Although we did not conduct floral surveys in this study, we did measure canopy openness (see Section 2.3, below) which correlates with flower availability (Chase et al., 2023) and include this term in models of pollinator richness (see Section 2.4, below). Sampling involved placing two sets of three pan traps at each plot, with the traps filled with soapy water during operation. Each set was situated 5m to the north or south of plot centre and consisted of a yellow, a blue and a white plastic bowl (15.5cm opening, ~400mL capacity) suspended 20–30cm above the ground on wire stands. Sets were oriented east–west with a 5m separation between traps. The traps were used as they were manufactured and were not painted.

Traps were operated once a month for 3 days at a time from March to September 2021. Target dates for sampling were established at the beginning of the study. However, because weather conditions differed considerably across our study region, the exact dates of sampling varied somewhat (Table S1) to ensure that trapping took place at all locations during periods of clear weather when pollinators would be most active. All bees, hover flies, and butterflies were pinned and identified by Ulyshen (bees and butterflies), Reynolds, and Young (hover flies) to species (or rarely to morphospecies) using online (discoverlife.org) and printed resources (Gibbs, 2011; Gibbs et al., 2013; Glassberg et al., 2000; Mitchell, 1960, 1962; Skevington et al., 2019). Voucher specimens have been deposited in the senior author's reference collection. Data were pooled by plot and sampling period for analysis.

2.3 | Plot measurements

We used a convex densiometer to measure canopy openness at the centre of each plot (Lemmon, 1956). Measurements were made while facing each cardinal direction in May, June, and July and we used the average of these readings as the percent canopy openness for each plot. Measurements at these times of year captured the maximum shade condition of overstorey trees across our study area. We also collected information on stand basal area and overstorey composition by recording the diameter and species of all trees (>20cm at 1.4m above the ground) within a 0.1 ha circular area centred on each plot.

2.4 | Statistical analysis

Our analysis, performed in R (R Core Team, 2022) and ArcGis Pro, consisted of two parts. First, we related the alpha diversity (i.e.,

Experimental forest					
Name	State	Estab. date	Size (ha)	Bailey's ecoregions (code)	Number of pollinator plots
Alum Creek	AR	1959	1885	Ouachita Mixed Forest (M231)	5
Bent Creek	NC	1925	2550	Central Appalachian Forest (M221)	5
Blue Valley	NC	1964	526	Central Appalachian Forest (M221)	5
Calhoun	SC	1947	2078	Southeastern Mixed Forest (231)	5
Chipola	FL	1952	1117	Outer Coastal Plain Mixed Forest (232)	7
Coweeta	NC	1934	1600	Central Appalachian Forest (M221)	5
Crossett	AR	1934	678	Southeastern Mixed Forest (231)	5
Delta	MS	1945	1044	Lower Mississippi Riverine Forest (234)	5
Escambia	AL	1947	1214	Outer Coastal Plain Mixed Forest (232)	5
Harrison	MS	1934	1662	Outer Coastal Plain Mixed Forest (232)	5
Hitchiti	GA	1946	1916	Southeastern Mixed Forest (231)	5
Koen	AR	1950	291	Ozark Broadleaf Forest (M222)	5
Olustee	FL	1931	3135	Outer Coastal Plain Mixed Forest (232)	5
Palustris	LA	1935	3035	Outer Coastal Plain Mixed Forest (232)	5
Santee	SC	1937	2469	Outer Coastal Plain Mixed Forest (232)	5
Scull Shoals	GA	1959	1816	Southeastern Mixed Forest (231)	5
Stephen F. Austin	TX	1945	1072	Southeastern Mixed Forest (231)	5
Sylamore	AR	1934	1737	Eastern Broadleaf Forest (222)	5
Tallahatchie	MS	1950	1416	Southeastern Mixed Forest (231)	5

TABLE 1 Characteristics of experimental forests in the USDA Forest Service, Southern Research Station's experimental forest network, adapted from Adams et al. (2008).

local species richness at the plot level) and community composition of pollinators to land cover data and stand metrics across all plots. We then tested for differences in community composition, pollinator diversity (alpha, beta, and gamma as defined below), and seasonal patterns of alpha diversity and abundance among the most-sampled ecoregions (i.e., those represented by three or more experimental forests: Central Appalachian, Coastal Plain, and Southeastern Mixed, Figure 1). Whereas alpha diversity is defined as the number of species observed in a plot, beta diversity represents the dissimilarity in diversity among plots within each experimental forest and consists of turnover (species replacement) and nestedness (species loss) components (Baselga, 2010).

Finally, gamma diversity refers to the total diversity within each ecoregion.

We used NLCD (National Land Cover Database, <https://www.usgs.gov/centers/eros/science/national-land-cover-database>) data from 2021 (Dewitz, 2023), with a resolution of 30×30m, to calculate the percentage of each land cover category surrounding our plots. This was done at five spatial scales (radii of 250m, 500m, 1km, 2km, and 4km). Land cover metrics tested for multicollinearity at each spatial scale were percentages of: non-wetland forest (i.e., deciduous forest+evergreen forest+mixed forest), non-wetland open land (i.e., grassland/herbaceous+shrub/scrub+pasture/hay+barren land+cultivated crops+developed high, medium, and low

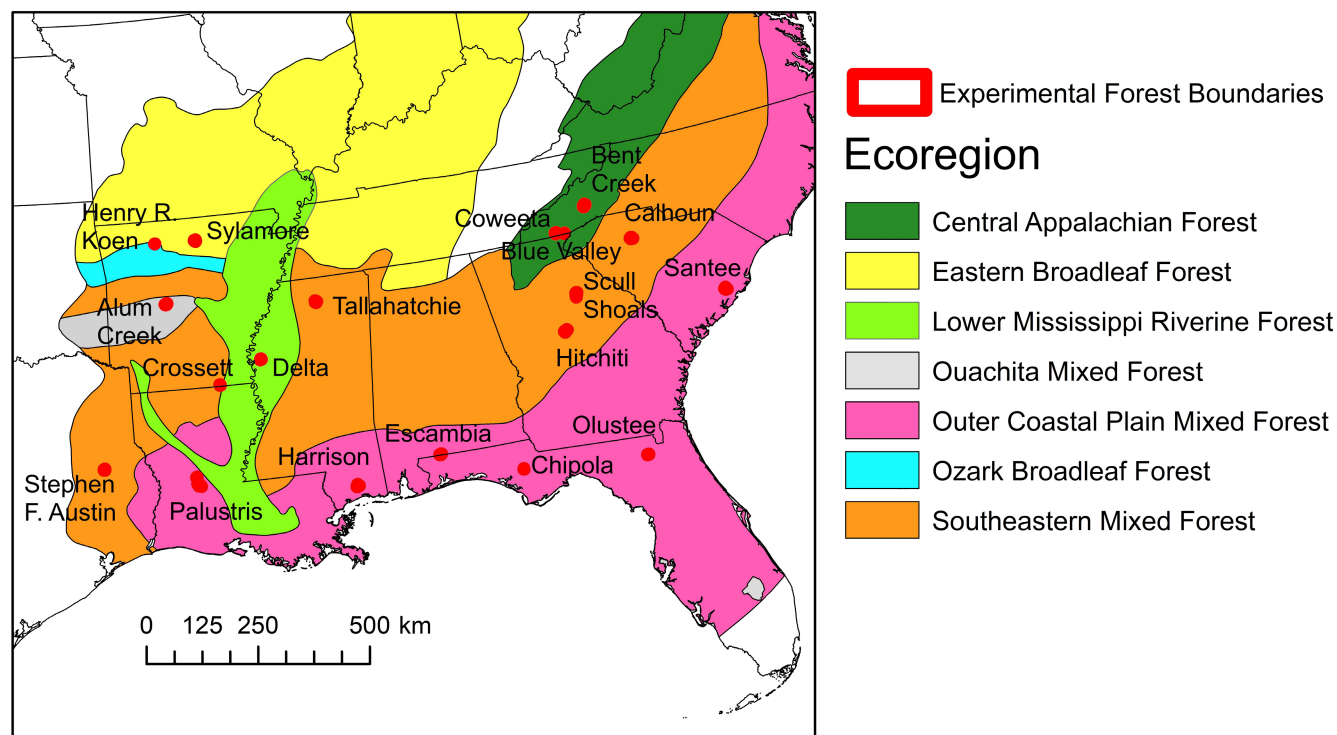


FIGURE 1 Locations of the studied Experimental Forests (red dots) in relation to Bailey's ecoregions across the southeastern U.S.

intensities+developed_open), wetland (i.e., woody wetlands+emergent herbaceous wetlands), and evergreen forest (hereafter referred to as conifer forest). Of these, non-wetland forest was dropped based on a high variance inflation factor (VIF) value, and non-wetland open land was dropped based on subsequent problems with model convergence.

After confirming a lack of spatial autocorrelation for any of the response variables among experimental forests based on Moran's *I* using the package *ape* (Paradis & Schliep, 2019), we used the *lme4* package (Bates et al., 2015) to produce negative binomial regression models (*glmer.nb*) of pollinator richness. To determine which spatial scale to use in the final models of pollinator diversity, we first tested separate models for each of the five spatial scales mentioned above and compared the *R*-squared values, using the *rsq.glm* function of the *rsq* package (Zhang & Zhang, 2022), i.e., the scale of effect (Holland et al., 2004). This was done separately for the richness of bees, hover flies, butterflies, and all pollinators combined. Based on this analysis, we determined landscape metrics to be most informative at the scale of 500m for bee, butterfly, and total pollinator richness, and at the scale of 2km for hover fly richness (Figure S1), so these were the scales used in the corresponding models.

Our final model of pollinator richness included canopy openness, wetland, and conifer forest as fixed effects (all scaled to have a mean of 0 and a standard deviation of 1) and experimental forest as a random effect to account for the lack of independence among plots within each experimental forest. Additional terms for the number of tree genera and basal area were not included due to multicollinearity. Given our study's large sample size, we used the default Wald Z-test to assess significance. However, to confirm these conclusions, we also conducted

likelihood ratio tests by dropping predictors one at a time (*drop1*) and using the chi-square test to assess significance. Using the same methods as described above, we calculated *R*-squared for each model and the contributions of fixed and random terms to the total.

To further explore how the relationship between bee richness and conifer forest may vary among ecoregions, we re-ran the model after limiting to the Southeastern Mixed or Coastal Plain ecoregions. We did not examine this relationship for other ecoregions due to either low replication (e.g., some ecoregions were represented by just one experimental forest) or, as for the Central Appalachian ecoregion, a low coverage of conifer forests. Moreover, we did not repeat these analyses for hover flies or butterflies because conifer forest was not a significant predictor in the main models for those groups.

For comparisons of pollinator community composition (all groups combined) among plots, we performed non-metric multidimensional scaling (NMDS) on a Bray-Curtis distance matrix using the *vegan* package (Oksanen et al., 2007). This was based on Hellinger-transformed abundance data which involves dividing each count by the sample total and taking the square root of each resulting proportion. We then conducted *envfit* tests for significant correlations between the resulting axes and the following variables of interest: canopy openness, wetlands within 500m, conifer forests within 500m, basal area, and the number of tree genera. Then we used the *adonis2* function of the *vegan* package (Oksanen et al., 2007) to test for pairwise differences (PERMANOVA) in pollinator composition among the three most-sampled ecoregions. Finally, to determine if any taxa were strongly associated with one or more of the ecoregions, we performed indicator species analysis using the *multipatt* function in the package

TABLE 2 Results from negative binomial models relating the richness of bees, hover flies, or butterflies to canopy openness and the amount of wetland and conifer forest on the landscape.

Taxon	Canopy openness		Percent wetland		Percent conifer		R-squared (fixed, random)
	Est. $\pm$ SE	z	Est. $\pm$ SE	z	Est. $\pm$ SE	z	
Bee (all)	0.25 $\pm$ 0.07	3.85***	-0.31 $\pm$ 0.07	-4.29***	-0.23 $\pm$ 0.07	-3.39***	0.58 (0.36, 0.21)
Bee (below-ground nesters)	0.33 $\pm$ 0.07	4.70***	-0.32 $\pm$ 0.08	-3.80***	-0.21 $\pm$ 0.08	-2.63**	0.58 (0.38, 0.20)
Bee (above-ground nesters)	0.02 $\pm$ 0.09	0.19	-0.28 $\pm$ 0.09	-2.94**	-0.27 $\pm$ 0.09	-2.90**	0.46 (0.19, 0.27)
Bee (Southeastern Mixed)	0.74 $\pm$ 0.20	3.60***	-0.30 $\pm$ 0.15	-1.92	-0.36 $\pm$ 0.11	-3.36***	0.44 (0.44, 0.00)
Bee (Coastal Plain)	0.28 $\pm$ 0.08	3.61***	-0.37 $\pm$ 0.14	-2.58**	-0.13 $\pm$ 0.12	-1.08	0.52 (0.52, 0.00)
Hover Fly	0.01 $\pm$ 0.07	0.07	0.01 $\pm$ 0.07	0.12	0.13 $\pm$ 0.07	1.81	0.22 (0.05, 0.17)
Butterfly	0.06 $\pm$ 0.09	0.703	-0.07 $\pm$ 0.11	-0.65	0.19 $\pm$ 0.11	1.66	0.46 (0.04, 0.43)
All Taxa	0.17 $\pm$ 0.06	2.88**	-0.17 $\pm$ 0.06	-2.84**	-0.08 $\pm$ 0.06	-1.31	0.44 (0.18, 0.26)

Note: The spatial scale used in these models was 500m for bees, butterflies, and all taxa and 2km for hover flies. Results for bee richness for all ecoregions combined and when limited to Southeastern Mixed and Coastal Plain are provided separately. Asterisks denote significance based on the following p -values: <.01**, <.001***. The total R-squared for each model is also provided as well as that for the fixed and random effects.

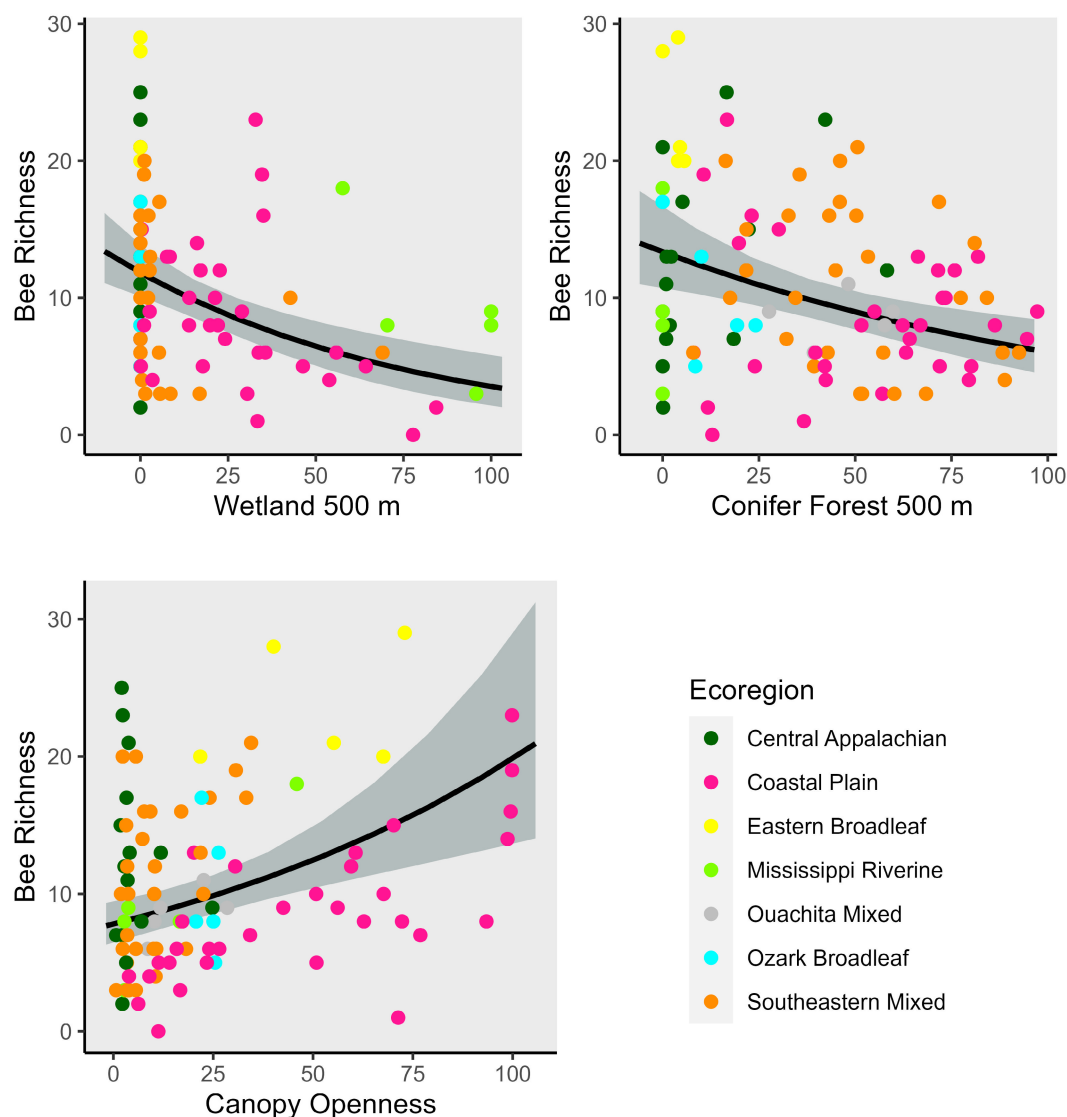


FIGURE 2 Relationships between bee richness and significant predictors across the southeastern U.S.

indicspecies (De Caceres et al., 2016). This test produces values ranging from 0 (no association) to 1 (complete association).

To compare the alpha (plot-level) diversity of bees, hover flies, butterflies, and all pollinators among the most-sampled ecoregions, we ran negative binomial models consisting of ecoregion and experimental forest as fixed and random effects, respectively. Total beta diversity, along with its individual turnover and nestedness components, were calculated for each experimental forest using the `beta.div.comp` function of the `adespatial` package (Dray et al., 2023). These metrics were then compared among the most-sampled ecoregions using generalized linear models. To compare gamma diversity among the most-sampled ecoregions, we used the `iNext` package (Hsieh et al., 2022) to produce rarefaction and extrapolation curves for richness ($q=0$), with statistical significance indicated by non-overlapping confidence intervals at the maximum reference sample size (Chao et al., 2014).

To better understand how landscape and stand metrics differed among the most-sampled ecoregions, and how these differences might help explain patterns in pollinator diversity, we tested linear mixed effects models (`lmer`) relating wetland, conifer forest, and canopy openness to ecoregion. Canopy openness was square-root transformed to meet assumptions of normality. Because assumptions could not be met for wetland data, we made pairwise comparisons between ecoregions using the non-parametric Wilcoxon signed-rank tests using the `pairwise.wilcox.test` function of the `stats` package.

To test whether pollinator seasonality differed among ecoregions, we compared when the richness and abundance of bees, butterflies, and hover flies peaked among the most-sampled ecoregions. First, for each sampled plot, we calculated the richness or abundance of each taxon by month relative to that taxon's highest monthly richness or abundance from the same plot, resulting in a standardized value ranging from 0 to 1. We then plotted the mean $\pm$ SE of these values by ecoregion and month to visualize differences in seasonality among ecoregions. We used pairwise Wilcoxon signed-rank tests to determine if the peak month of response varied among the most-sampled ecoregions.

Finally, we used the Chao1 estimator to estimate the richness of bees, butterflies, hover flies, and all pollinators combined that could be collected using pan traps across our studied forests. These calculations were made for the entire region as well as for each of the three most-sampled ecoregions using the `rareNMtests` package (Cayuela & Gotelli, 2014). The estimates are based on the corresponding lists of collected species and their abundances.

3 | RESULTS

3.1 | Diversity patterns

We collected 266 pollinator species, including 172 bee species, 50 hover fly species, and 44 butterfly species (Table S2). Based on the Chao1 estimator, this represents about 71% of the species that

could have been captured in this study using the same traps and sampling locations (Table S3). Across the entire region, bee richness was negatively correlated with the extent of both conifer forests and wetlands in the surrounding landscape and was positively correlated with canopy openness (Table 2, Figure 2). These patterns held mostly true for above- and below-ground nesting bee richness with the exception of there being no significant correlation between the richness of above-ground nesters and canopy openness (Table 2). When bee richness data from the Southeastern Mixed or Coastal Plain ecoregions were analysed separately, the negative relationship with conifer forests was only significant among Southeastern Mixed forests while the negative correlation with wetlands was only significant among forests of the Coastal Plain (Table 2). No factor in our models was a significant predictor of hover fly or butterfly diversity (Table 2). Overall, total pollinator richness was positively correlated with canopy openness, negatively correlated with wetlands, and not significantly related to conifer forests (Table 2). Likelihood ratio tests largely corroborated determinations of statistical significance from our models, with the only discrepancy being the detection of a weakly significant negative correlation between bee richness in the Southeastern Mixed ecoregion and the extent of wetlands (Table S4). There was no significant spatial autocorrelation in the richness of bees ($I = -0.10$, $p = .48$), hover flies ($I = -0.06$, $p = .99$), butterflies ($I = 0.06$, $p = .12$), or overall pollinator richness ($I = -0.11$, $p = .39$) among experimental forests.

Alpha diversity differed among the most-sampled ecoregions (Figure S3). Butterfly richness was significantly lower in Central Appalachian plots than in the other ecoregions. Moreover, hover fly richness was significantly lower in Central Appalachian plots than in those from the Southeastern Mixed ecoregion (Figure S3). Total beta diversity did not differ among the three most-sampled ecoregions: Central Appalachian versus Coastal Plain (Estimate = -0.04 , $t = -0.965$, $p = .35$); Central Appalachian versus Southeastern Mixed (Estimate = -0.06 , $t = -1.43$, $p = .18$); and Coastal Plain versus Southeastern Mixed (Estimate = -0.02 , $t = -0.57$, $p = .58$). The turnover and nestedness components of beta diversity also did not differ among these ecoregions (results not shown). Finally, butterfly gamma diversity differed significantly among the most-sampled ecoregions, with the Coastal Plain and Southeastern Mixed ecoregions having 2–3 times more species than Central Appalachia (Figure S2). However, no differences in gamma diversity among these three ecoregions were detected for bees, hover flies, or all pollinators combined (Figure S2). For estimates of bee, butterfly, and hover fly richness by ecoregion, see Table S3.

3.2 | Community composition

NMDS ordination (stress = 0.18) revealed a particularly distinct separation between the Central Appalachian and Coastal Plain ecoregions, with the other ecoregions being intermediate in composition (Figure 3). All of our landscape and stand variables, except

for the extent of wetlands, were significantly correlated with the NMDS axes (Table S5). PERMANOVA comparisons among the three most-sampled ecoregions revealed significant differences in pollinator composition among ecoregions ($F_{2,62} = 14.5135$, $p < .001$, $R^2 = 0.21$) and experimental forests ($F_{12,62} = 3.7352$, $p < .001$, $R^2 = 0.33$). All pairwise comparisons were significant: Central Appalachian versus Coastal Plain ($F_{1,45} = 11.041$, $p < .001$); Central Appalachian versus Southeastern Mixed ($F_{1,43} = 11.508$, $p < .001$); and Coastal Plain versus Southeastern Mixed ($F_{1,60} = 8.2707$, $p < .001$). Based on indicator species analysis, 72 taxa were associated with one or more of the most-sampled ecoregions (Table S6). Nearly half of these (33) were associated with the Central Appalachian ecoregion while a further six were associated with both the Central Appalachian and Southeastern Mixed ecoregions. Sixteen and 13 species were associated with the Coastal Plain and Southeastern Mixed ecoregions, respectively, and a further four were associated with both of those ecoregions (Table S6). No species was found to be associated with both the Central Appalachian and Coastal Plain ecoregions.

3.3 | Landscape and stand metrics

Significant differences in landscape and stand metrics were detected among the most-sampled ecoregions (Figure S4). Canopy openness was 2–3 times higher in Coastal Plain forests than in those from the other two ecoregions. Similarly, the extent of wetlands on the Coastal Plain was over five times greater than in the Southeastern Mixed ecoregion and far greater than in Central Appalachia where wetlands were essentially absent (Figure S4). We also found Central Appalachia to have about a fifth as much conifer forest on the surrounding landscape as compared to the other two ecoregions (Figure S4). However, there was no difference in conifer forest cover between the Coastal Plain and Southeastern Mixed ecoregions.

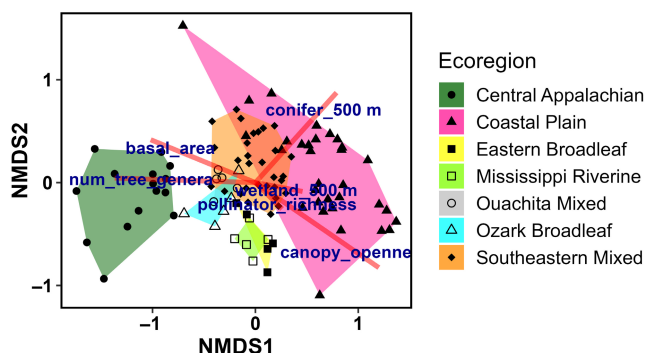


FIGURE 3 NMDS ordination reflecting differences in pollinator communities (bees, butterflies, and hover flies combined) among ecoregions and in relation to significantly correlated landscape and stand metrics. The symbols represent the 97 plots from which pollinators were collected.

3.4 | Seasonality patterns

We detected notable differences in the seasonality of pollinators among ecoregions (Figure 4 and Figure S5). Most notably, bee richness and abundance peaked about 2 months earlier in the Central Appalachian ecoregion than in the Coastal Plain or Southeastern Mixed ecoregions (Figure 4), and these differences were statistically significant (Figure S6). The only other significant difference in seasonality concerned butterfly abundance which peaked later in the season in the Southeastern Mixed than in the two other most-sampled ecoregions (Figure S6).

4 | DISCUSSION

We sought to better understand how forest pollinators are distributed across the southeastern U.S. and how they are affected by landscape context and local forest conditions. We detected strong differences in composition among the most-sampled ecoregions. Pollinator communities collected from the Central Appalachian and Coastal Plain ecoregions were particularly distinct, underscoring the value of these ecoregions to regional biodiversity, whereas those from the Southeastern Mixed and other ecoregions were roughly intermediate in composition. In addition, we found striking differences in pollinator seasonality among ecoregions, with bee richness peaking about 2 months earlier in Central Appalachian forests than in other ecoregions.

Differences in forest structure and composition likely drove many of the observed differences in pollinator composition and seasonality among ecoregions. For example, the combination of broadleaf-dominance and closed canopy conditions likely explains the distinct and spring-seasonal bee fauna collected from Central Appalachian forests. Floral availability in both the canopies and understories of temperate deciduous forests is known to peak in early spring and to decline rapidly following leaf expansion and canopy closure, with many bees exhibiting similar seasonal patterns (Chase et al., 2023; Harrison et al., 2018; Urban-Mead et al., 2021). By contrast, the largely pine-dominated forests of the Coastal Plain tend to be more open (Figure S4) and provide flowers throughout the growing season (Ulyshen, Robertson, et al., 2023; Ulyshen, Urban-Mead, et al., 2023). The abundance and variety of flowers peak later in the year (Platt et al., 1988), which likely explains the mid-summer peak in bee richness in Coastal Plain forests. However, recent work suggests bee richness in Coastal Plain pine savannas may peak in October when late-season aster specialists are active (Ulyshen et al., 2024). Thus, it is possible that we stopped sampling too early in the current study to fully capture bee diversity in many Coastal Plain forests. Interestingly, the seasonality of bees in the Southeastern Mixed ecoregion shared similarities with both of the other ecosystems. There was a main summer peak coinciding with that observed on the Coastal Plain as well as a smaller spring peak coinciding with that seen in Central Appalachian forests. It is clear from our results that pollinator activity is not confined to the spring months in most

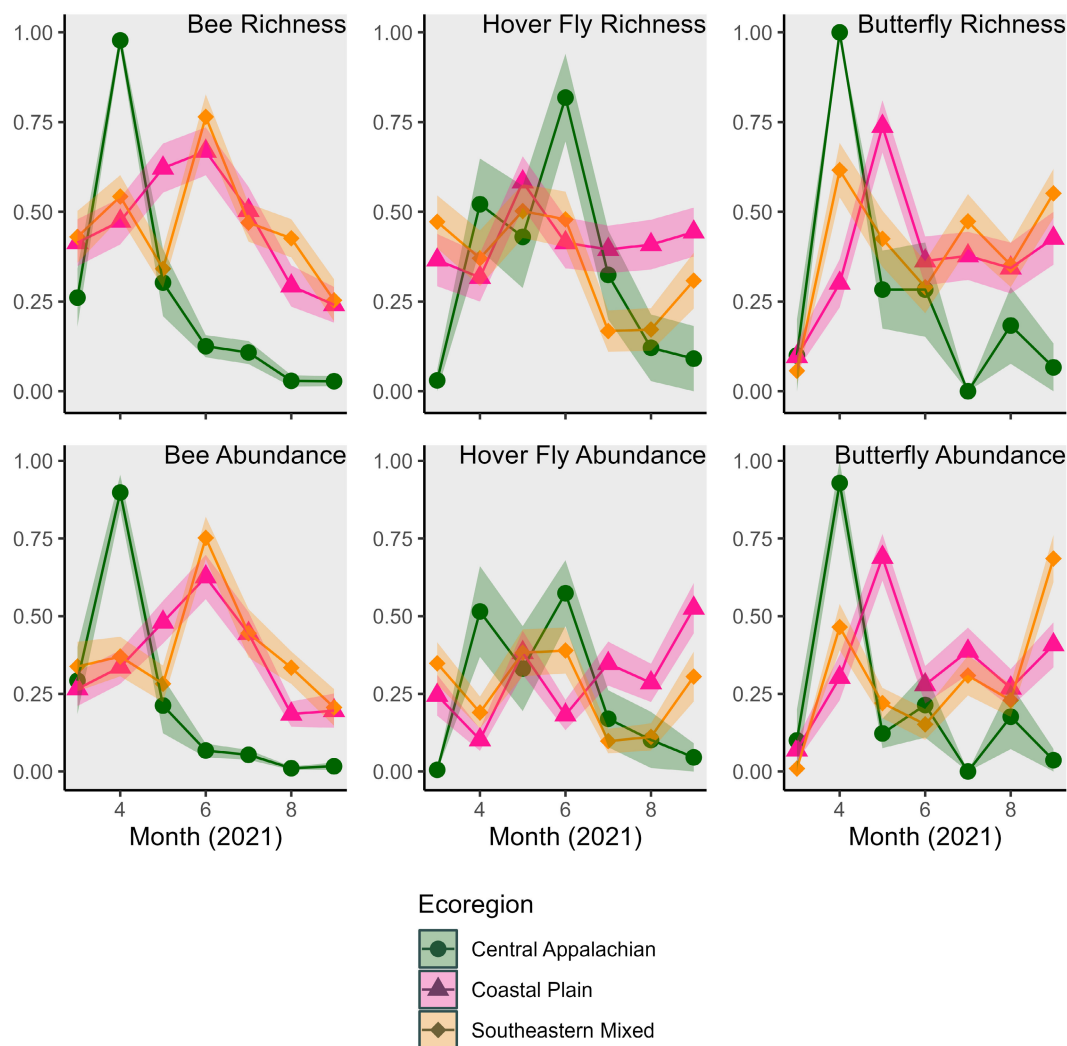


FIGURE 4 Mean $\pm$ SE richness and abundance of bees, hoverflies, and butterflies by ecoregion and month. Values were relativized by the maximum observed monthly value for each plot.

forests of the southeastern U.S. Only Central Appalachian forests exhibited the springtime peak in bee diversity reported from forests of the northeastern U.S. (Harrison et al., 2018).

We detected a negative relationship between bee richness and conifer forest cover across the southeastern U.S. However, this pattern was stronger within the Southeastern Mixed ecoregion, an area historically dominated by mixed broadleaf forests, than on the Coastal Plain where it was not statistically significant. This discrepancy may reflect conifer-dominated areas in the Southeastern Mixed region being primarily high-density, closed-canopy pine plantations. By contrast, conifer-dominated areas on the Coastal Plain are a mix of high-density pine plantations and open-canopy pine stands, the latter often maintained with prescribed fire (Cummins et al., 2023). It is well established that bee diversity increases as pine stands become more open with age and with certain natural or anthropogenic disturbances (Dixon et al., 2022; Hanula et al., 2015), and it is likely that such conditions differ between ecoregions given the relatively frequent occurrence of fire in open forests on the Coastal Plain (Pyne, 1982). Moreover, because bee diversity in Coastal Plain

pine savannas appears to peak in the fall (Ulyshen et al., 2024, the current study likely underestimates bee diversity in Coastal Plain forests. However, the conclusion that broadleaf-dominated areas play an important role in supporting bee diversity across the southeastern U.S. is supported by work documenting the value of flowering trees, including even wind-pollinated taxa such as oaks, to many bees (Kraemer & Favi, 2005; Saunders, 2018; Urban-Mead et al., 2023). Further support comes from T aylor et al. (2022, 2024) who reported positive relationships between bees and the diversity of insect-pollinated broadleaf trees in Georgia.

Despite the negative effects of conifer forest cover on bee richness, no such patterns were observed for hover flies or butterflies. In fact, we detected positive, though non-significant, correlations between conifer cover and the richness of both taxa. These patterns may help explain why butterfly alpha and gamma diversities appear to be lower in Central Appalachian forests than in those from the Southeastern Mixed or Coastal Plain ecosystems (Figures S2 and S3). The alpha diversity of hover flies was also significantly lower in Central Appalachian than in Southeastern Mixed forests.

One possible explanation for the observed patterns in butterfly diversity concerns skippers (Hesperiidae) which feed primarily on grasses which are less available in closed forests than in the more open stands typical of the Coastal Plain (Dixon et al., 2022; Knapp et al., 2014). Indeed, over half of the skippers found to be significantly associated with one or more ecoregions in this study were associated with Coastal Plain forests (Table S6).

We detected a negative correlation between bee richness and the extent of surrounding wetlands. This pattern held true for all bees combined as well as for both below- and above-ground nesting bees. Although these results are consistent with past work that also trapped fewer pollinator species in wetlands than in upland habitats (Begosh et al., 2020), other studies report a positive effect of wetlands on the abundance and richness of bees (Evans et al., 2018). Wetlands may be perceived to be more important when compared to highly disturbed habitats, such as row crops, than when compared to other semi-natural areas. The negative effect of wetlands on below-ground nesting bees reported in the current study is perhaps not surprising given that most species prefer to nest in well-drained soils (Harmon-Threatt, 2020) and are likely to be negatively affected by saturated or flooded conditions. However, this cannot fully explain our results given that the richness of above-ground nesting bees was similarly, though less strongly, negatively correlated with wetlands. The possibility that wetlands provide fewer floral resources than other habitats and therefore support a lower diversity of bees regardless of nesting substrate is not well supported given that hover flies and butterflies were unaffected by wetlands in the surrounding landscape (discussed below). Moreover, Begosh et al. (2020) found hymenopteran pollinators to forage more in wetlands at certain times of the year than in upland habitats in Nebraska. It could be that wetland conditions reduce nesting success even for bees that nest above ground (but see Simanonok et al., 2022).

The fact that no negative relationship was observed between wetland cover and hover fly or butterfly richness is not surprising given that these groups are generally less dependent on soil conditions than are bees for their reproductive success. In fact, some common species of hover flies have aquatic larval stages and may be associated with wetlands (Skevington et al., 2019). In Nebraska, Begosh et al. (2020) reported higher hover fly abundance from wetland habitats than from uplands. It is clear from our results that habitat requirements vary among major pollinator taxa and that, as a group, these insects will benefit most from a diverse mix of forest types.

As shown in previous work (Chase et al., 2023), we found a strong positive correlation between both total bee richness and the richness of below-ground nesting bees and canopy openness. While this may relate in part to a greater availability of floral resources in more open forests (Hanula et al., 2016; Platt et al., 2006), the fact that above-ground nesting bees were unaffected by canopy openness requires a different explanation. Frequent disturbances such as fire that maintain open canopies and patches of relatively bare ground are known to benefit ground-nesting bees in the region (Ulyshen

et al., 2021) but this benefit may not extend to other groups of bees including above-ground nesters and forest-dependent bees in general. More work is needed to understand the relative importance of different flowering tree taxa to bees and other pollinators in order to best guide conservation efforts. For example, the results from this and previous work suggest efforts to create more open conditions in Central Appalachian forests may benefit bees and other pollinators (Campbell et al., 2018; Ulyshen et al., 2022), especially later in the season. However, it is important to understand how the spring-active bee fauna will be impacted by such interventions. The utilization of fire, for instance, can be expected to alter tree composition by disadvantaging diffuse-porous taxa such as *Acer* and *Prunus* in favour of ring-porous, fire-hardy, taxa such as *Quercus* and *Carya* (Alexander et al., 2021; Krey et al., 2013; Nowacki & Abrams, 2008). The implications of such changes for pollinators remain unknown.

Similarly, it is important to consider the distinction between forest-dependent pollinators and habitat generalists. Research from the northeastern U.S. suggests about a third of the bee fauna native to that region is forest-associated and that those species are more sensitive to forest cover than other species (Smith et al., 2021). Given these findings, it is necessary to take community composition and species-level responses into account rather than simply looking at differences in the total richness or abundance of all pollinators between habitats. Otherwise, there is a risk of managing for generalists at the expense of forest specialists, which may ultimately reduce the total diversity of pollinators across the region.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

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The data and code used in the analyses are publicly available at: <https://doi.org/doi:10.5061/dryad.j0zpc86n6>.

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BIOSKETCH

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Author contributions Conceived of and coordinated the study: MU. Field work: CA, JA, SBA, MB, DCB, CB, MC, RC, GC, PC, CD, JF, PJ, TK, RM, VM, BM, KR, NS, BS, JS, MS, MKT, MU, JLW. Pollinator identification: MU (bees and butterflies), KO (Nomada spp.), SR and ADY (hover flies). Data curation and analysis: MU. Wrote the first draft of the paper: MU. Approved final version: all co-authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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