Received: 21 December 2023 | Revised: 29 June 2024 | Accepted: 2 August 2024

DOI: 10.1111/csp2.13231

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access
WILEY

CONTRIBUTED PAPER

Best management practices for bee conservation in forest openings

Michael J. Cunningham-Minnick[1,2] | **Joan Milam**[2] | **Aliza Fassler**[2] | **David I. King**[3]

[1]Department of Biology, Hiram College, Hiram, Ohio, USA

[2]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, Massachusetts, USA

[3]USDA Forest Service, Northern Research Station, Amherst, Massachusetts, USA

Correspondence
Michael J. Cunningham-Minnick, Department of Biology, Hiram College, 11715 Garfield Rd, P.O. Box 67, Hiram, OH, USA.
Email: cunninghammj@hiram.edu

Funding information
Environmental Protection Agency's Great Lakes Restoration Initiative

Abstract

Native bees are an ecologically diverse group of pollinators in global decline due at least in part to invasive species, pesticides, and habitat loss. Although guidelines exist for land managers to restore pollinator habitat, these "best management practices" (BMPs) include other pollinator taxa that may have different requirements than bees, do not give particular attention to rare bee species, or describe practices that are impractical for land managers. Using co-production science, our team of land managers and researchers sampled bee communities in 100 wildlife openings on six National Forests (NF) within the Great Lakes Basin of the United States during 2017–2019. We found that bee communities responded to site factors and management practices, including prescribed fire, mechanical methods (e.g., felling, brushhogging, mowing), herbicides, and pollinator plantings. Bee abundance, diversity, and rarity were strongly related to soil properties, landscape context, and the plant community, including small-statured woody species, which collectively informed our BMPs. For instance, mechanical treatments were most beneficial for openings with clayey or organic soils while prescribed fire was most effective in openings with well-drained soils. Our BMPs highlight effects of treatment combinations, including negative effects on rare species when herbicides were combined with plantings and positive effects on abundance and rare species when prescribed fire was combined with mechanical treatments. Since our BMPs were generated in collaboration with land managers, they better conform to their needs and constraints, contributing to more effective native bee conservation.

KEYWORDS

BMPs, co-production, Great Lakes Basin, INLA-SPDE, National Forest Service, native bee, SpORtI, treatments

1 | INTRODUCTION

Bees (Hymenoptera: Apoidea: Anthophila), the primary pollinators of angiosperms, are a diverse taxon of roughly 20,000 species worldwide with over 4,000 species in the United States (Gallai et al., 2009; Klein et al., 2007; Michener, 2007). Bees are globally in decline due to changes in land-use, invasive species, climate change, pesticides, pathogens, and other anthropogenic activities (Bartomeus et al., 2013; Dicks et al., 2021; Goulson et al., 2015; Potts et al., 2010). Recent initiatives have focused conservation efforts and recommendations on bee communities of forest openings following findings of abundant and diverse bee communities (Hanula et al., 2016; Johansson et al., 2020; Milam et al., 2020; Milberg et al., 2021; Roberts et al., 2017). Flowering plants and nesting substrate in small openings and near forest edges may supplement bee species within adjacent forests by providing additional resources (Roberts et al., 2017), but many studies have discovered bee communities of forest openings to have a composition distinct from those of the adjacent forests (Milam et al., 2020; Ulyshen et al., 2023). While overlap in species use of open-canopy (herein "open") and forest habitat is well documented (e.g., Harrison et al., 2018; Milam et al., 2020) there is strong evidence of both forest- and open-associated bee communities within forested landscapes (reviewed in part in Ulyshen et al., 2023). For instance, many plant and invertebrate species require resources only found in open habitats and are therefore open-habitat specialists (Fowler, 2016a & 2016b; Milam et al., 2020), including many bumblebee species with declining populations (Bartomeus et al., 2013; Cameron et al., 2011). In the United States, even the federally endangered *Bombus affinis* relies on open habitat for foraging and possibly nesting resources, especially after spring ephemerals of adjacent forests have senesced (Hepner et al., 2023; Mola et al., 2021; USFWS, 2018). Open habitats are therefore an important component of the landscape required to maintain a taxonomically and functionally diverse bee community in forested landscapes of the eastern United States.

Contemporary forests lack the dense shrubby and herbaceous habitat characteristics of forest openings required by many bee species due to recent anthropogenic disruptions of historical disturbance regimes (Fettig et al., 2022; Nowacki & Abrams, 2008). Precolonial forests of the eastern United States, for instance, were characterized by a heterogeneous mix of closed- and open-canopy habitat (Hanberry & Abrams, 2018; Hanberry et al., 2020). Forests within this region are now predominantly characterized by closed-canopy conditions with open-canopy communities like barrens, grasslands, wetlands, and sand dunes scarce and restricted in extent (Banaszak & Twerd, 2018; Exeler et al., 2009; Fettig et al., 2022; Kalhorn et al., 2003; Milam et al., 2020; Nowacki & Abrams, 2008; Tucker & Rehan, 2019). Thus, habitat restoration for forest-opening bee communities to correct this deficit will enhance regional bee conservation outcomes (Lettow et al., 2018; Mathis et al., 2021; Proctor et al., 2012; Roberts et al., 2017).

Current management recommendations for native bees in open habitats are often based on studies of multiple pollinator taxa including birds, butterflies, and flies, or non-native or domesticated bee species (e.g., honeybee (*Apis mellifera*) or blue orchard bee (*Osmia lignaria*), respectively) that may not reflect the conservation needs of wild bee communities (Iwasaki & Hogendoorn, 2021; USDA-USFS, 2015). While conservation efforts that promote a broad breadth of pollinator taxa are important to restore and sustain ecosystem processes and function, the unique yet diverse life history attributes of native bees require a unique set of management practices focused on foraging and nesting resources (Harmon-Threatt, 2020; Müller et al., 2006). For instance, 83% of nonparasitic native bees in North America use soil as a nesting substrate (Harmon-Threatt, 2020), yet most other pollinators, including most domesticated bees, typically do not depend on soil properties as a nesting substrate for developing offspring. Consequently, there is a need for best management practices (BMPs) for forest openings specific to native bees to improve the collective conservation outcome for pollinator communities.

The ambiguity on how to evaluate bee community health may add to the confusion of what management strategies to implement. The USDA states that pollinator health, including that of native bees "... should be assessed as a comprehensive multilevel measure of the vigor, resilience, and ecological functionality..." (López-Uribe et al., 2020; USDA, 2022). However, most reviews on the topic demonstrate that studies typically only consider simple metrics of the bee community, such as abundance and species richness (Glenny et al., 2022; Hanula et al., 2016; Kral-O'Brien et al., 2021; Ulyshen et al., 2023). These metrics ignore the species composition of bee communities, thus conferring equal weight to both common generalists and rare specialists. As a result, the management recommendations for native bees may identify practices that promote high richness of common and widespread species yet fail to support rare species that are geographically scarce and often have distinctive ecological characteristics (Violle et al., 2017). This can be a difficult task as the qualities of a "rare" species are still being defined (Kondratyeva et al., 2019). In the context of conservation, "rarity" should ideally identify those species with populations more vulnerable than other species,

and thus deserve the highest priority for management intervention to ensure their persistence (Flather & Sieg, 2007). Many characteristics are associated with the vulnerability of species, including specialized behaviors (e.g., clepto-parasitism, preferred nest substrate and forage species), which collectively may be indicative of greater functionality within the bee community and broader ecosystem (Sheffield et al., 2013; Simpson et al., 2022). Phylogenetic uniqueness may not be correlated with recorded specialized behaviors, yet clearly indicate species vulnerability through the apparent loss of closely related species (Cadotte & Davies, 2010). Thus, including a comprehensive metric that identifies species that are the most different, or unique, of such characteristics and weighs them to emphasize unique trait combinations should be considered in addition to abundance and diversity metrics to evaluate the overall health of bee communities (Cunningham-Minnick et al., 2022; Kondratyeva et al., 2019).

There is also a lack of information on how multiple management practices affect native bees, as studies typically only evaluate one, and uncommonly two, bee community metrics including bee species richness and abundance (Glenny et al., 2022; Hanula et al., 2016; Kral-O'Brien et al., 2021; Ulyshen et al., 2023). For example, gap creation due to logging results in more bees in gaps (Hanula et al., 2016) and pollinator plantings generally support higher bee species richness (Kral-O'Brien et al., 2021). Prescribed burning typically increases bee community abundance and species richness, but these effects may be site dependent (Glenny et al., 2022; Hanula et al., 2016; Tonietto & Larkin, 2018). Alternatively, mowing and grazing often produce negative effects (Glenny et al., 2022; Hanula et al., 2016; Tonietto & Larkin, 2018). Fewer studies incorporate the entire suite of management practices employed for habitat management, or even consider combinations of management practices. For instance, invasive shrub removal combined with pollinator plantings consistently increased bee abundance and diversity (Glenny et al., 2022), and many studies suggest a positive and potentially synergistic interaction between burning and mechanical (e.g., logging/thinning) practices (Glenny et al., 2022; Hanula et al., 2016). Collectively, there is much support throughout the literature that bee communities, or at least bee abundance and species richness, respond positively to most management practices employed to create (logging), maintain (prescribed fire, mechanical or hand removal of invasive shrubs), or enhance (pollinator plantings) forest openings, yet data on their interactions is lacking. Land managers often employ a variety of practices sequentially, such as herbicides followed by planting, on sites restored for conserve pollinator habitat (USDA-USFS, 2015).

Management recommendations may further misalign with the implementation of conservation practices due to the science-practice gap, or a lack of communication and understanding between researchers and land managers regarding region-specific approaches to habitat restoration, appropriate metrics or spatial scales, or available funds and labor, whereby findings and recommendations from the research community cannot be readily converted into management practices (Bertuol-Garcia et al., 2018; Lott et al., 2021; Vane-Wright et al., 1991). Therefore, to achieve the most applicable BMPs for the conservation of native bee communities in forest openings within our study region, we adopted a co-production approach whereby "managers, policy makers, scientists, and other stakeholders first identify specific decisions to be informed by science, and then jointly define the scope and context of the problem, research questions, methods, and outputs, make scientific inferences, and develop strategies for the appropriate use of science" (Beier et al., 2017). This approach is intended to increase the conformity of research findings to the needs of resource managers through building a partnership on shared interests for a conservation outcome that is feasible and most appropriate to the invested land managers and their ongoing management regimes (Beier et al., 2017; Caro et al., 2023; Fazey et al., 2013; Naugle et al., 2020). We employed this co-production framework to yield collected bee samples that were then analyzed in terms of abundance, diversity, and species rarity (a metric of support for rare species as defined by an index we developed separately in Cunningham-Minnick et al., 2022) to determine how prescribed fire, herbicide, mechanical and planting treatments, individually and in combination, affected the bee community. From these results, we developed spatially explicit BMPs for the conservation of native bee communities in forest openings of the Great Lakes Basin, a region comprising 760,000 km^2 land area (Figure 1).

2 | METHODS

In this project, the co-production science partners included conservation practitioners within Region 9 of the United States Department of Agriculture—Forest Service (USFS), as well as six National Forests within USFS Region 9 (Chequamegon-Nicolet, Finger Lakes, Hiawatha, Huron-Manistee, Ottawa, Superior), herein referred to collectively as "Region 9." The other parties in this co-production effort were academic researchers with the USDA Forest Service Northern Research Station (NRS) and the Department of Environmental Conservation at the University of Massachusetts-Amherst (UMass). The

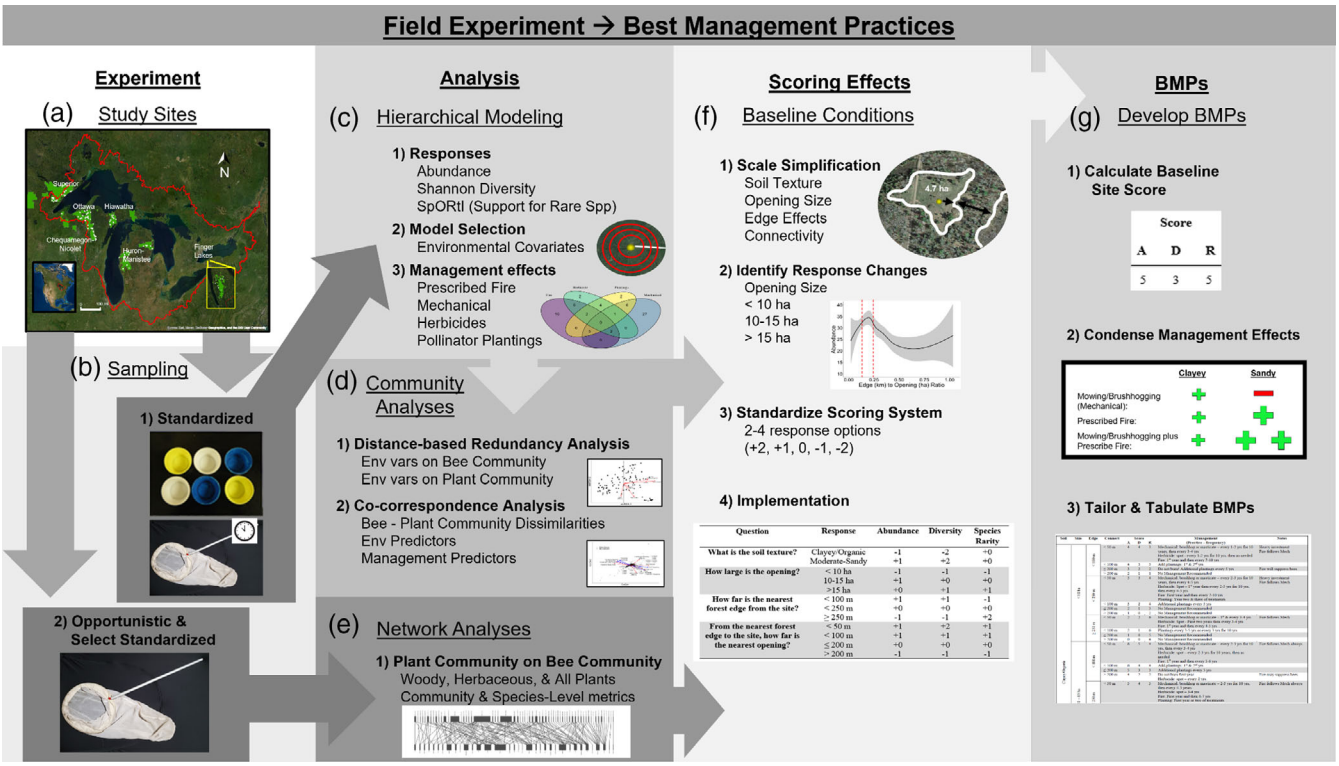

FIGURE 1 Paper workflow beginning from study sites to the final best management practices (BMPs) document. Staff of the six National Forests (NF) within the Great Lakes Basin (a) sampled bees at 100 established sites with timed netting and colored pan traps (bee bowls) using a standardized protocol (b1) and netted bees on flowers opportunistically throughout the study period (b2). We analyzed data collected from the standardized protocol by evaluating the abundance, diversity, and support for rare species of the bee community with hierarchical models that incorporated group-level information to identify dependencies and differences among groups (c1). Initially, we fit environmental covariates at multiple scales (c2). Then, we individually tested the addition of four categories of experimental treatments (prescribed fire; herbicide; pollinator plantings; mechanical; any management) in addition to variables representing any treatment, each in four different formats: If applied in the last 20 years; if it was the last treatment applied; years since a treatment was applied (also considered nonlinear effects); frequency of a treatment category applied in the last 20 years (also considering nonlinear effects), as well as two-way interactions (c3). We then evaluated the effects of environmental covariates on the composition of the bee, as well as plant, communities with distance-based redundancy analyses (d1). With knowledge on how the bee community composition changed along environmental gradients, we then determined which of these effects were most likely due to environmental effects on the plant community while inferring the role of management practices on bee and plant communities through a co-correspondence analysis that considered experimental treatments (d2). Recorded bee-flower occurrences from opportunistically netted bees, along with bees recorded on flowering plants from standardized netting events (b2), were included in network analyses to describe the role of woody plants within openings (e1). We simplified our collective results into four categories based on relationships at the plot (i.e., soil texture), opening (i.e., opening size), and landscape (i.e., distance to forest edge, connectivity) scales (f1) and identified ranges for each category that represented different environmental–environmental or environmental-management relationships (f2). We then scored bee responses to environmental and experimental treatment variables from $+2$ to -2 (f3) and summed these scores across the four categories (f4) yielding a standardized site score between 0 and 8 for each metric: abundance—A, diversity—D, rarity—R (g1). Now knowing the expected deficiencies of the bee community at any given site, we condensed statistically significant patterns of treatment effects and their interactions from models of improved fit (g2) to tailor best management practices for bees of forest openings (g3).

need and basic study design of the project was conceived by Region 9, who also secured funds from the Environmental Protection Agency (EPA) Great Lakes Restoration Initiative (GLRI). Staff at the NRS and UMass provided suggestions for the study design, drafted sampling procedures for bees and vegetation, and then traveled to each National Forest to provide trainings on bee ecology and conservation and field sampling. During these trainings, Region 9 staff provided comments on the draft protocols and recommended changes to working copies of field data forms drafted by NRS and UMass, which were finalized by the last field training. Researchers at NRS and UMass helped troubleshoot issues with field sampling, and later Region 9 staff assisted with identifying relevant site metrics and management practices to include in the analyses. This back-and-forth collaboration was

facilitated by emails, conference calls, and webinars, and led to the development of a standardized sampling protocol that was directed at a range of conditions and management practices relevant to the study sites.

2.1 | Study design

2.1.1 | Study system

The study system of the Great Lakes States Pollinator Project included 100 openings ranging 0.3—>900 ha in size located between 42.5 and 47.8° N, −92.1 and −76.7° W and represented a variety of habitats including wetlands, barrens, grasslands, pasture, and scrublands within a matrix dominated by coniferous, deciduous, or mixed forests that varied in composition depending on the geographic location of the site within the six National Forests of the Great Lakes Basin (Figure 2). Personnel at each National Forest selected up to 10 openings each year (2017–2019) to include in the study that either had a history (prior 20 years) of being unmanaged (reference) or encompassed a range of land management practices (herein "experimental treatments") of interest and relevance to them, such as prescribed fire, herbicide (spot, blanket), mechanical methods (mowing, brushhogging, mastication, felling, logging), pollinator plantings (seeding or transplants of pollinator-friendly plants), or combinations of these treatments (Figure 3). To ensure the results of this study were responsive to the needs of the participating National Forests, each of which has different restoration and conservation goals and challenges for the opening and larger landscape, we did not restrict the selection of openings, the specific sampled location chosen within each opening, nor the management practices (experimental treatments) employed at candidate openings. We employed appropriate statistical approaches to address the unbalanced design, sampling, and ongoing

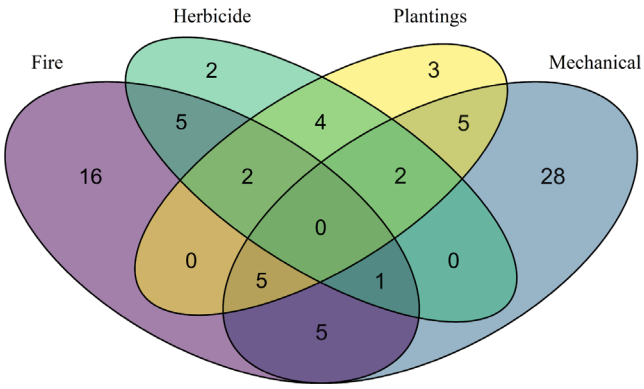

FIGURE 3 Venn diagram of experimental treatment combinations of the 78 managed openings (100 openings total) in the last 20 years, where each ellipse represents a different treatment category and overlapping ellipses represent treatment combinations. Due to active management during the 3-year study period, some sites had multiple combinations of experimental treatments depending on the sample, which is reflected here. The 22 reference (unmanaged) openings are not included.

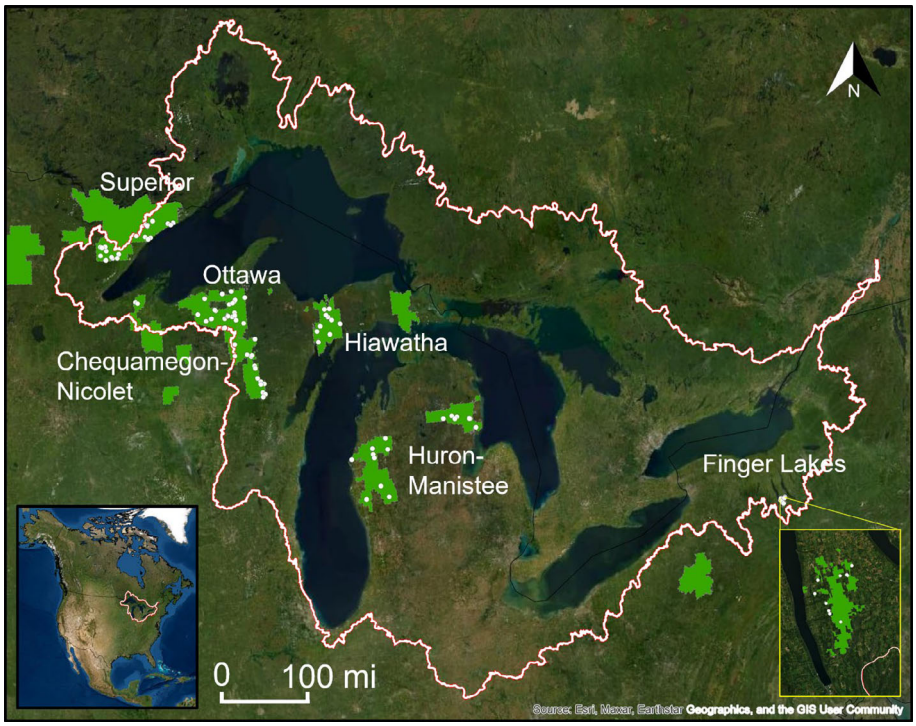

FIGURE 2 Sites (white circles) within National Forests (green polygons) of the Great Lakes Basin (red line), including Finger Lakes National Forest magnified (yellow inset).

management regimes (Table S1) within and across National Forests, which we discuss at great depth in the Analysis section. Though some of these inconsistencies allowed us to better describe responses of the bee communities to features in the landscape. For instance, since National Forest personnel were free to sample the bee community close or far from the forest-opening edge, we were able to address how distance from the forest edge affected the bee community depending on opening size and other opening conditions. Slightly different locations of site centers at the same site across sampling points, which were accounted for in our statistical analysis, further provided more variation within a site that strengthened the understanding of these spatial relationships in models.

2.1.2 | Sampling

The bee community was sampled within each opening up to three times per year (late spring, summer, and fall) for 3 years (2017–2019) using standardized methods including 21 evenly spaced pan traps (96 ml) that alternated in colors of blue, yellow, or left white (herein "bee bowls") and timed netting for a total of 492 combined samples of bee bowls and netting. A sampling event therefore consisted of a set of bee bowls deployed for 24 h as well as netting for 30 min during bee bowl deployment within the 15-m radius circular plot within the forest opening (Droege et al., 2010; Figure S1). National Forest personnel also opportunistically netted bees outside of timed netting events, which we analyzed separately from timed netting and bee bowl sampling data. During opportunistic netting, netters were suggested to target plant genera in bloom with known or suspected specialist relationships with bees unlikely to be included in the standardized sampling, including *Apocynum*, *Ceanothus*, *Chelone*, *Geranium*, *Ilex*, *Kalmia*, *Lysimachia*, *Monarda*, *Pontederia*, *Physalis*, *Salix*, and *Zizia*. All captured bees were returned to UMass, then washed, pinned, and identified to species by Michael Arduser, Robert Jean, and JM using published keys (e.g., Gibbs, 2011; Gibbs et al., 2013; LaBerge, 1973, 1980, 1986; Mitchell, 1960, 1962; Onuferko, 2018; Oram, 2018) and the online source Discoverlife.org (Ascher & Pickering, 2020). Specimens were deposited in museum collections in the state in which they were encountered: Michigan—A.J. Cook Arthropod Research Collection at Michigan State University, Minnesota—University of Minnesota Insect Collection, New York—Native Bee Biology & Systematics Lab at Cornell University, Wisconsin—University of Wisconsin Green Bay.

2.2 | Analysis

2.2.1 | Bayesian hierarchical models

To determine how management practices affected different aspects of bee communities in forest openings, we built generalized additive mixed effects models relating environmental variables at multiple scales, as well as experimental treatment variables, to three responses of the bee community derived from standardized sampling data. All analyses were conducted in the R statistical language (R Core Team, 2021).

Modeling framework

All models were conducted using a Bayesian approach to infer model coefficients while accounting for the spatial and temporal clumpiness of our data. Specifically, we performed analyses in an Integrated Nested Laplace Approximation with Stochastic Partial Differential Equation (INLA-SPDE) framework with the *inla* function in the *INLA* package (Lindgren & Rue, 2015; Martins et al., 2013; Rue et al., 2017), which employs graph theory in the creation of mesh surfaces of triangles to produce spatially-explicit models that can account for spatiotemporal autocorrelation in the data (Huang et al., 2017). Few ecological studies have incorporated hierarchical Bayesian models with spatiotemporal autocorrelation terms in their analyses due to excessive computation, but the INLA-SPDE framework allows for the non-Gaussian likelihood families typical of ecological responses and requires much less processing time compared to other Bayesian methods such as Monte Carlo Markov Chains (Engel et al., 2022; Huang et al., 2017; Lezama-Ochoa et al., 2020). Models of each response employed negative binomial error distributions and non-informative priors.

Bee response variables

To ensure our findings were comprehensive, we included three metrics to characterize bee responses to environmental variables: bee abundance, species diversity, and species rarity. We considered bee abundance to broadly represent the quantity of pollination services, as more bees are generally associated with more pollination services (Blaauw & Isaacs, 2014). To address the range of support provided by habitat at sites to different bee species, we evaluated Shannon's diversity, a metric which represents the effective number of species within the community (Jost, 2006). Finally, we modeled bee species rarity to ensure that the response variables included the conservation importance of individual bee species. We employed the Species Originality and Rarity Index (SpORtI; Cunningham-Minnick et al., 2022) which is the

most comprehensive rarity index developed to date due to its inclusion of numeric rarity, geographic rarity, phenological rarity, phylogenetic originality, and functional originality as weights for each species in the dataset (Cunningham-Minnick et al., 2022). Employing SpORtI, we generated a rarity score for each sample that represented how well that site supported rare bee species (Table S2).

Environmental covariates

Bees are highly mobile animals with diverse life-history requirements that are relevant to their habitat needs and conservation. Therefore, we generated a suite of environmental variables that represented the availability of different nesting and food resources at scales of the plot (15-m radius circle), opening (0.3–900 ha), and landscape (100–1000 m radius circles centered on plot) (Table 1). We did not have information on the exact size or configuration of the managed portion of the opening for every experimental treatment, and thus did not include it in our analyses. At the plot scale, National Forest personnel recorded the presence of exposed soil and woody debris within 1 m of each bee bowl at each sampling event (Figure S1), which were then converted into variables representing the proportion of the plot with exposed soil or wood nesting substrates, respectively. Similarly, the abundance and species of flowering stems within 1 m of bowls ($N = 21$) were recorded per sampling event to represent potential local food sources. Due to some cases of uncertain identification, we used plant genus (160 genera were identified across plots) to derive six variables representing different aspects of the flowering plant

TABLE 1 Environmental and management variables included in INLA-SPDE models for model selection in determining best fit for describing bee abundance, diversity, and species rarity. The Contiguity Index (LaGro, 1991) and Contagion Index (O'Neill et al., 1988) were calculated as CONTIG and CONTAG, respectively, in the FRAGSTATS software version 4.2.1 (Ene & McGarigal, 2023; McGarigal & Marks, 1995) on the geospatial data layer created representing opening habitat.

Plot	Opening	Landscape[a]	Management
Flower Coverage	Area	Deciduous Forest Cov	Opening Managed
Flower Richness	Edge Length	Evergreen Forest Cov	Plot Managed[c]
Flower Diversity (Shannon)	Edge Length:Area	Herbaceous Cov	Management Frequency[c]
Flower Diversity (Simpson)	Distance To Edge	Wetlands Cov	Yrs Since Last Management[c]
Flower Community (NMDS 1)	Average % Sand Top 25 cm (100 m)	Roads Length	Last Management[d]
Flower Community (NMDS 2)	Stand. Dev. Sand Top 25 cm (100 m)	Landscape Diversity	
Total Basal Area		Proportion Opening	
Trees Present		Opening Edge Density	
Proportion Exposed Soil		Contiguity of Open Area[b]	
Proportion Dead Wood		Contagion (Aggregation of Open Area)	
Proportion Top 25 cm Sand			
Soil Texture Rating by Teams			
Soil Drainage Class			
Weather—Time of Day (PCA 1)			
Weather—Temp and Wind (PCA 2)			

[a]All cover predictors were relative cover. All landscape variables included linear predictors at 100, 250, 500, 750, and 1000 m. Deciduous Forest Cov, Evergreen Forest Cov, Herbaceous Cov, and Wetlands Cov also included quadratic predictors with the exception of Evergreen Forest at 100 m which did not meet the criterium of ≥5% total cover.

[b]All CONTIG predictors included MN (mean), AM (area-weighted mean), RA (range), and CV (coefficient of variation) at the class and landscape scales.

[c]Plot Managed, Management Frequency, and Yrs Since Last Management each represent five predictors that describe any, prescribed fire, mechanical, herbicide, and planting management.

[d]Last Management included if the last management practice was prescribed fire, mechanical, herbicide, planting, or the union of combinations of two or three management practices at the plot scale. The union of all four management practices was not included since this is the equivalent to the Plot Managed predictor.

community, including plot coverage, genus richness, Shannon diversity, and Simpson diversity. We also included the loadings of each of the two axes in a non-metric multi-scaling ordination fit in two dimensions ($k = 2$) from Bray–Curtis dissimilarities applied to a square-rooted matrix of genus cover as two variables to represent composition dissimilarity among sites. Flowering trees are an important food source for native bees near forest edges early in the year (Cunningham-Minnick & Crist, 2020; Urban-Mead et al., 2021), or may conversely depress food availability by suppressing herbaceous flowering plants (Proctor et al., 2012). Therefore, species identity and diameter at breast height (DBH) were recorded of trees with DBH greater than 12.5 cm within the boundaries of the 15-m radius circular plot. Unsurprisingly, large mature trees were not common in managed openings, so we created covariates that addressed the presence or absence of trees in the plot, as well as their total basal area.

We used outside databases and the expertise of NF personnel to identify environmental covariates from remote-sensed data at scales up to 1 km from the center of the plot, which includes the typical foraging distance of most bees (Zurbuchen et al., 2010). These included plot-scaled conditions such as the soil drainage and proportion of the top 25 cm of soil that was sand (texture) extracted from the Soil Survey Geographic Database (SSURGO; USDA-NRCS, 2020). Ranked categories of soil drainage in the SSURGO database (very poorly, poorly, somewhat poorly, moderately well, well, somewhat excessively, and excessively drained) were transformed into ordinal data (0–6, respectively) and treated as a continuous variable. Though highly correlated, soil texture and soil drainage may indicate different properties relevant to use by bees. For instance, different bee species are reported to exhibit soil texture preferences for nesting, and different drainage properties may foster different plant communities, which in turn provide specific food resources (Harmon-Threatt, 2020). We focused on the properties of the top 25 cm of soil since this depth likely includes the nesting depth of most bee species (Cane & Neff, 2011). We included soil variation at the opening level by also considering soil characteristics within 100 m of the plot center weighted by area of each soil type, as well as its standard deviation. However, the value generated by SSURGO is an expected value, and thus subject to model uncertainty. For this reason we created an additional soil texture variable based on the detailed field knowledge of the sites, including soil maps and databases for each sampled plot, queried from Region 9.

Patch-scale variables, including the size (area) and shape (total edge length in kilometers; edge length to area in hectares ratio) of the opening, as well as landscape variables (diversity and composition of deciduous forest, evergreen forest, wetland, and herbaceous vegetation) were characterized using aerial imagery and Land-Use Land-Cover data layers from 2016 (layers freely available as .img files at https://www.mrlc.gov/data), respectively, in ArcGIS v10.8.2. Finally, we calculated two metrics representing the connectivity of open habitat: contiguity, which describes the spatial connectedness of landscape elements (Contiguity Index; LaGro, 1991) and aggregation (Contagion Index; O'Neill et al., 1988), which describes the degree of clumping of attributes by evaluating the dispersion and interspersion of open patches within a landscape with the software FRAGSTATS v4.2.1 (McGarigal & Marks, 1995). To generate these metrics we created a data layer to map forest openings in the landscape by overlaying the LULC data layers, specifically tree canopy cover, impervious surface, and road length. We cross-validated the accuracy of our resulting layer with digitized openings on the Hiawatha NF, centrally located among our study sites and, we reasoned, more likely to exhibit representative values. We estimated the opening metric using natural breaks in the canopy cover values (32, 57, 67, and 77%) and selected 67% canopy cover by comparing 95% confidence intervals of prediction accuracy among the natural breaks. This validation process suggested our opening data layer, used herein to describe properties of "open area" within the landscape, had an accuracy of 84 ± 3%. We calculated all landscape metrics within 100, 250, 500, 750, and 1,000 m of plot centers.

Treatment variables

Region 9 personnel provided information on all experimental treatments applied to each opening within the last 20 years. To account for multiple treatment types, we divided practices into four broad categories and developed variables describing treatment frequency (prescribed fire: ≤5, herbicide: ≤8, mechanical: ≤9, plantings: ≤6, combined: ≤10), the most recent treatment, if the treatment had been applied, and the years since the most recent treatment. We included both linear and nonlinear predictors for treatment frequency and years since the last application of each treatment using natural splines with up to six knots in the mgcv package (Wood, 2011). We chose natural splines, rather than for instance B-splines, because of their lower tendencies for the curve to oscillate between data points, which can overfit the data, and thus artificially amplify treatment effects (Hastie, 1992).

Non targeted variation

To increase precision in the estimated effects of experimental treatments and their interactions with

environmental factors on the bee community, we also included fixed covariates describing the local weather conditions, an offset term to account for differences in sampling effort, random effects to address repeated as well as unbalanced sampling, and a spatiotemporal autocorrelation term to account for similarities in metrics due to sampled locations being closer in space and time. Weather influences bee foraging activity and thus captures, so we used the first two axes of a principal components analysis on variables known to characterize or influence weather (latitude and longitude, temperature, cloudiness, relative wind speed, time of day, and day of year; Table S3). Measurements of temperature, cloud cover, and wind speed were missing from 29%, 24%, and 19% of sample points, respectively. We imputed missing values by deriving predicted values of generalized additive models of extracted data from nearby weather stations (Tables S4–S6; Horel et al., 2002). Fitted relationships from each of the three models (temperature, cloud, and wind responses) were then used to predict the missing values within our dataset.

Similarly, since variation in sampling effort may affect our estimates, we included an offset term for sampling effort (E) in all models that accounted for the number of netters, minutes netted, total hours bee bowls were deployed, and number of bowls tipped over (lost) with the following formula:

$$E_i = [T_b/24(1\text{-}B/21) + (N \times T_n/30)]/2$$

where B is the number of bee bowls that were not active at the time of collection, T_b is the length of time (hours) bowls remained active, N is the number of netters, and T_n is the length of time (minutes) that a single netter was collecting bees. Since the protocol called for 21 bee bowls to be deployed for 24 h and total netting time of 30 min within each plot, this simple formula allowed sampling effort to be greater than (>1) or less than (<1) expected while ensuring that effort between bowls and netting were weighted equally in the calculation of sampling effort E_i per sample i. Thus, $E = 0$ if all bee bowls were lost and no netting took place, $E = 1$ if all bowls were active for 24 h and a total of 30 min of netting occurred.

We allowed the intercept of all models to vary with year and site (opening) to account for repeated sampling at each site and within different years. We nested the random effect of site within National Forest to also account for legacy (management regimes, biogeography, etc.) differences among National Forests. This error structure also addressed the unbalanced design of the resultant data as previously described. Finally, we included a spatiotemporal autocorrelation term within all models to account for the fact that any two samples closer in space and time (via month) than any two other samples are likely to be more similar due to, for instance, foraging distances (geographic space) of bee species or the co-presence and turnover of local bee-plant communities.

Model selection

Models were built in a two-step process. First, we modeled the influence of site, landscape, and weather variables on bee community metrics; once these were constructed, we added experimental treatment variables using a similar variable screening process described below, since informing management was a key objective of our study. To model the influence of site and weather characteristics, we successively added terms and evaluated them based on the Deviance Information Criterion score (DIC), a common Bayesian model comparison method (Lezama-Ochoa et al., 2020). Once the addition of a term did not increase model fit by >2.00 DIC units, no more terms were added to that model. We limited models to eight terms to reduce risk of overfitting models in later phases of the model building process.

Models were initially fit with a coarse SPDE mesh to reduce computation time, and then all models ≥4.00 DIC units of the top model were refitted with a SPDE mesh of finer resolution (Figure S2) to decrease computation time of the model selection process. Each refitted model took 15–20 min of computation time with an AMD Ryzen 95900HX CPU @ 3.3 GHz and RAM of 32.00 GB run in parallel across 12 threads using the "num.threads" option in the *inla.setOption* function. New DIC scores were then calculated on refitted models, and Widely Applicable Information Criterion (WAIC) scores were calculated for the best model of each response (Vehtari et al., 2017). Finally, we evaluated linear and nonlinear terms for each bee community metric, including all potential two-way interactions with environmental and other management terms. The strength of relationships was designated as strong, moderate, or weak if the probability of the magnitude of the mean posterior distribution being greater than zero was ≥95%, ≥90%, or <90%, respectively. We considered only strongly and moderately supported relationships, with the addition of weakly supported terms if there was a strongly supported interaction term with another covariate. Finally, terms of top models were evaluated for multicollinearity with the *check. collinearity* function in the performance package (Lüdecke et al., 2021) on generalized additive mixed models (GAMMs) using the glmmTMB package without the spatiotemporal autocorrelation term, since inla-type models are not supported.

Experimental treatment variables were added individually to the best model of each response, along with two-

way interactions with environmental covariates and other treatment variables in a different experimental treatment category, and DIC and WAIC scores were calculated. Up to 20 models with strongly or moderately supported terms, as before, with a better fit (ΔDIC and ΔWAIC <0 compared to best model of only environmental covariates) were retained and considered in the development of the BMPs.

2.2.2 | Multivariate analysis of bee and plant community composition

Relationships between bee species composition, the plant community, and predictor variables were analyzed using distance-based Redundancy Analyses (dbRDA) on a square-rooted relative abundance (bee) or cover (plant) matrix of Bray–Curtis dissimilarities using the *vegan* package (Oksanen et al., 2020). The abundance (bees) and flower cover (plant) matrices were standardized by site (divided by site total). Environmental and management terms that were moderately and strongly supported in INLA models were used to inform and build dbRDA models to each the bee and plant dissimilarity matrices separately in a stepwise fashion, where a term was not kept unless it was both significant to the model as determined by likelihood ratio tests with the *anova* function and improved model fit from the reduced model as evaluated by AIC.

We used co-correspondence analysis (CoCA) to determine how environmental factors and management practices structured bee and plant communities with the *coca* function in the *cocorresp* package while invoking the "predictive" option (Simpson, 2009) on the Bray–Curtis dissimilarity matrices. Significance of the first two axes was determined via 999 permutation tests with the *randtest.coca* function derived in Alric et al. (2020). We then regressed strongly supported covariates from the best INLA models across responses using the *env.fit* function in the *vegan* package on each CoCA axis. This process identified how environmental and management factors were affecting bee community composition irrespective of influences of the plant community on the bee community (Alric et al., 2020; Simpson, 2009).

2.2.3 | Plant-pollinator network analysis

Network analysis can be a useful tool for informing conservation and restoration decisions because it provides information on community function and stability in response to management (Fisogni et al., 2021; Kaiser-Bunbury & Blüthgen, 2015; Walton et al., 2021). We described the contribution of interactions between 4,115 bees (1,172 from standardized netting, 2,943 from opportunistic netting) of 188 species with 83 plant genera to investigate the role of small-statured shrubs and trees within forest openings by comparing networks that included the herbaceous, woody, or entire plant community. We used the *specieslevel* function with indices "species strength" (Bascompte et al., 2006), "weighted closeness" (González et al., 2010), "effective partners" (Bersier et al., 2002), and "d" (Blüthgen et al., 2006) to address the relevance, independence, generality, and specialization of species within the network, respectively, using the *bipartite* package (Dormann et al., 2008). We also compared five measures of network structure (*networklevel* function) among all three networks (Dormann et al., 2009), including "nestedness," "connectance," "interaction evenness," "links per species," and "H2" to describe the organization, observed versus possible, diversity of, specialist bee-generalist plant (Almeida-Neto et al., 2008; Dormann, 2011), and overall specialized (Blüthgen et al., 2006) interactions of each network, respectively. Significance of each metric describing networks was determined by calculating a Z-score and associated *p*-value from comparisons against 5,000 weighted null models randomly generated using the "r2dtable" method (function) from the *stats* package (R Core Team, 2021), which keeps margin totals of species-abundance matrices constant while randomizing matrix contents. Since networks serve the sole objective of establishing the general importance of woody plants within openings in supporting the bee community, we do not discuss in thorough detail the bee–plant relationships or implications associated with the findings of each considered metric.

3 | RESULTS

We collected 14,176 bees of 234 species in forest openings through standardized sampling (bee bowls and timed netting) in addition to 3,246 bees of 175 species by opportunistic netting, for a total of 17,422 bees representing 261 species sampled (Table S7). Abundance, diversity, and species rarity of bee communities differed by National Forest (Figure S3), though there were many general patterns of native bee responses to local and landscape factors, as well as treatments, across National Forests.

3.1 | Local and landscape effects

GAMMs demonstrated that bee abundance was positively affected by bare ground, flowering plant diversity, sandier soils, and edge to area ratio (Table 2; Table S8). Bee abundance was negatively affected by the amount of

TABLE 2 Summary statistics for posterior distributions of the regression coefficients for the fixed effects explaining bee abundance, diversity, and rarity in focal models, including basic range description, mean and Credible Interval, statistical significance of the term as the probability of the magnitude of the coefficient (β) being greater than zero and the corresponding support for the term (S—strong (≥ 0.95), M—moderate (≥ 0.90), or W—weak (< 0.90)) in the model. Model 0 represents the best model following model selection (lowest DIC) of environmental covariates. Experimental treatment variables were then individually added in separate models, where a term and its two-way interactions with other treatment and environmental covariates were considered. Thus, models with IDs greater than zero include the listed terms in addition to all terms within Model 0. Models are separated by shading. This table includes best-fitting models with experimental treatment terms from unique combinations of treatment categories (fire, mechanical, herbicide, pollinator planting). For example, Model 1 (Years Since Fire × Variability in Opening Habitat Contiguity) shares the treatment category but is a better fit (1.75 DIC and 3.4 WIAC units) than Model 5 (Fire Treatment × Variability in Opening Habitat Contiguity), although the interpretation of each treatment term within categories is different in some respects. See Table S8 for a full list of models that were incorporated into the best management practices document. All terms in models are accounted for by one degree of freedom.

Response	Covariate	Covariate range (low—high)	β (mean)	95% CrI	$P(\beta) > 0$	Support	Model ID	ΔDIC	ΔWAIC
Abundance	PCA2 weather (temperature/wind speed)	High/low—low/high	0.186	0.080–0.290	1.000	S	0	0.00	0.00
	PCA1 weather (time of day)	Late—early	0.096	0.009–0.184	0.985	S	0		
	Soil texture ranking (1–5)	Sandy—Clayey	−0.208	−0.316–−0.100	1.000	S	0		
	Proportion of soil exposed	Low—high	0.438	0.161–0.720	0.999	S	0		
	Edge length to opening area ratio	km:ha	0.455	−0.029–0.948	0.967	S	0		
	Variability in opening habitat contiguity (250 m)	Low—high	−0.161	−0.336–0.015	0.964	S	0		
	Flowering plant diversity (Shannon)	Low—high	0.072	−0.088–0.231	0.811	W	0		
	Years since fire		−0.023	−0.035–−0.011	1.000	S	1	−16.73	−17.93
	Variability in opening habitat contiguity (250 m) × years since fire		−0.127	−0.310–0.053	0.917	M	1		
			−0.033	−0.054–−0.012	0.999	S	1		
	Years since pollinator planting		−0.029	−0.043–−0.015	1.000	S	2	−15.80	−17.03
	Herbicide frequency × years since pollinator planting		0.034	−0.038–−0.108	0.820	W	2		
			0.011	0.004–0.018	0.998	S	2		
	Treatment applied to opening		0.007	−0.228–0.240	0.525	W	4	−15.04	−13.72
	Soil texture ranking × treatment applied to opening		−0.205	−0.322–−0.088	1.000	S	4		
			0.265	0.073–0.464	0.997	S	4		
	Last treatment mechanical		−0.207	−0.417–0.002	0.974	S	6	−14.55	−14.33
	Variability in opening habitat contiguity (250 m) × last treatment mechanical		−0.115	−0.309–0.077	0.880	W	6		
			−0.487	−0.866–−0.110	0.994	S	6		
	Soil texture ranking × last treatment mechanical		−0.237	−0.353–−0.122	1.000	S	6		
			0.191	0.015–0.373	0.983	S	6		
	Years since fire (d.f. = 5)		NA	NA	NA	NA	7	−13.60	−14.07

(Continues)

TABLE 2 (Continued)

Response	Covariate	Covariate range (low—high)	β (mean)	95% CrI	$P(\beta) > 0$	Support	Model ID	ΔDIC	ΔWAIC
	Last treatment herbicide		0.322	−0.009–0.664	0.972	S	10	−12.23	−11.99
	Soil texture ranking × last treatment herbicide		−0.202	−0.313–−0.090	1.000	S	10		
			0.614	0.240–0.996	0.999	S	10		
	Years since pollinator planting		−0.028	−0.041–−0.014	1.000	S	13	−10.47	−10.75
	Last treatment mechanical × years since pollinator planting		−0.124	−0.309–0.063	0.905	M	13		
			−0.032	−0.062–−0.002	0.982	S	13		
	Fire treatment		0.342	0.144–0.540	1.000	S	14	−10.04	−9.21
	Mechanical treatment × fire treatment		0.031	−0.140–0.204	0.635	W	14		
			0.718	0.330–1.105	1.000	S	14		
Diversity	PCA2 weather (temperature/wind speed)	High/low—low/high	0.095	0.030–0.159	0.998	S	0	0.00	0.00
	Soil drainage rank	Very poor—excessive	0.089	0.030–0.151	0.998	S	0		
	Total coverage of flowering plants	Low—high	−0.274	−0.438–−0.109	0.999	S	0		
	Contiguity of open habitat (100 m)	Low—high	−1.542	−2.546–−0.566	0.999	S	0		
	Deciduous forest cover (750 m) squared	Low—high	0.312	0.067–0.564	0.994	S	0		
	Proportion of landscape open habitat (250 m)	Low—high	0.614	0.204–1.036	0.998	S	0		
	Length of opening edge (km)	Short—long	−0.020	−0.045–0.004	0.948	M	0		
	Years since fire		−0.017	−0.026–−0.007	1.000	S	1	−7.97	−8.15
	Contiguity of open habitat (100 m) × years since fire		−1.167	−2.126–−0.232	0.993	S	1		
			0.117	0.029–0.205	0.995	S	1		
	Planting frequency		0.066	−0.030–0.161	0.913	M	8	−3.61	−3.50
	Contiguity of open habitat (100 m) × planting frequency		−1.521	−2.50–−0.560	0.999	S	8		
			−0.744	−1.590 to 0.083	0.961	S	8		
	Treatment frequency (d.f. = 1)		0.290	0.100–0.481	0.998	S	9	−3.26	−3.39
	Last treatment mechanical		−0.158	−0.313–−0.005	0.979	S	10	−2.73	−2.85
	Mechanical treatment		−0.062	−0.212–0.086	0.795	W	11	−1.80	−2.19
	Soil drainage rank × mechanical treatment		0.094	0.035–0.156	0.999	S	11		
			−0.131	−0.235–−0.028	0.993	S	11		
Rarity	PCA2 weather (temperature/wind speed)	High/low—Low/high	0.217	0.102–0.331	1.000	S	0	0.00	0.00
	PCA1 weather (time of day)	Late—early	0.043	−0.054–0.140	0.807	W	0		

TABLE 2 (Continued)

Response	Covariate	Covariate range (low—high)	β (mean)	95% CrI	$P(\beta) > 0$	Support	Model ID	ΔDIC	ΔWAIC
	Flowering plant diversity	Low—high	0.209	0.036–0.382	0.991	S	0		
	Landscape cover diversity (100 m)	Low—high	0.339	0.085–0.594	0.996	S	0		
	Edge length (km) to opening area (ha) ratio × landscape cover diversity (100 m)	Low—high	0.678	0.045–1.316	0.982	S	0		
			−1.613	−3.137–−0.107	0.982	S	0		
	Herbaceous cover (250 m) ^2	Low—high	0.564	0.254–0.873	1.000	S	0		
	Years since fire		−0.021	−0.033–−0.009	1.000	S	1	−13.31	−12.03
	Mechanical frequency × years since fire		0.043	−0.044–0.129	0.833	W	1		
			−0.027	−0.039–−0.014	1.000	S	1		
	Planting frequency		0.052	−0.072 to 0.176	0.792	W	5	−5.56	−5.86
	Herbicide frequency × planting frequency		−0.007	−0.078–0.065	0.578	W	5		
			−0.174	−0.289–−0.059	0.998	S	5		
	Last treatment fire or planting		0.290	0.085–0.496	0.997	S	8	−4.39	−4.23
	Mechanical frequency × last treatment fire or planting		0.042	−0.146–0.130	0.825	W	8		
			0.386	0.159–0.610	0.999	S	8		
	Mechanical frequency		−0.008	−0.099–0.082	0.571	W	12	−3.11	−3.16
	Edge length (km) to opening area (ha) ratio × mechanical frequency		0.441	−0.217–1.102	0.905	M	12		
			−0.856	−1.434–−0.291	0.999	S	12		
	Years since planting		−0.006	−0.021–0.009	0.797	W	14	−2.68	−2.46
	Landscape diversity (100 m) × years since planting		0.374	0.120–0.630	0.998	S	14		
			−0.050	−0.089–−0.011	0.994	S	14		

variability in the connectivity of open habitat within 250 m of the plot. However, we will discuss this relationship in terms of contiguity of openings within 250 m of the plot ($r = -0$—.91; Figure S4) herein for simplicity and practicality reasons while recognizing that the variability variable was a better fit. Modeling also showed that bee diversity was higher in sites with the following conditions: sandy excessively drained soils, lesser contiguity of open area within 100 m, more open area within 250 m, and more deciduous forest cover within 750 m. There was lower bee diversity at sites with high coverage of flowering plants and openings with greater edge to area ratio. Finally, modeling with SpORtI indicated that rare bees were positively associated with sites of high flowering plant diversity and more herbaceous and sparsely vegetated natural land cover within 250 m. Rare bees were negatively associated with high edge to area ratio of openings, except for openings with low landscape diversity, where rarity scores increased with high edge to area ratio (Figure 4).

dbRDA showed that bee community composition was primarily structured by interactions between soil texture and the flowering plant community composition on the first axis and interactions between soil texture and herbaceous and sparsely vegetated land cover on the second axis ($\chi^2(6) = 7.45$, p-value < 0.001; Figure 5a). The best model explaining composition of the plant community in bloom was total length of the opening edge and soil texture ($\chi^2(2) = 1.87$, p-value < 0.001; Figure 5b). The CoCA further demonstrated that soil texture, bare ground, coverage of flowering plants, and flowering plant diversity were also associated with

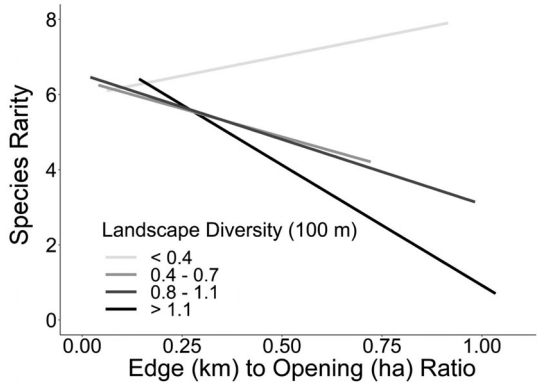

FIGURE 4 Support for rare bees was negatively associated with less round sites (high edge to area ratio), except for sites in low-diversity landscapes, where the opposite pattern was observed.

the covariation of the plant and bee communities (F-ratio = 0.53, $p < 0.001$; Figure 6).

3.2 | Management effects

Overall, we found positive effects of fire, herbicide, and pollinator planting treatments, including their frequency and more recent applications, and negative effects of mechanical treatments on bee abundance, diversity, and species rarity model responses with exceptions due to interactions (Table 2). All metrics of the bee community were generally higher in experimental sites than reference sites. The CoCA indicated that management frequency structured the plant community, and in turn, the bee community within openings ($r^2 = 0.19$, $p < 0.005$; Figure 6).

3.2.1 | Prescribed fire

Models showed that prescribed fire resulted in a time-dependent pattern of higher bee abundance, diversity, and rare species (Table 2). Bee abundance was higher at 1 year, as well as more than 4 years, following treatment (Figure 7). Bee diversity and support for rare species was highest immediately following treatment and monotonically declined to pre-burn conditions 20 years later. However, the magnitude of the positive relationship between bee abundance, or species rarity, and fire was greater with the addition of mechanical treatments (Table 2). More generally, bee diversity and rarity model responses were higher if the last experimental treatment was prescribed fire or pollinator planting (Table 2; Table S8). Prescribed fire was also associated with high bee abundance in openings with greater contiguity within 250 m,

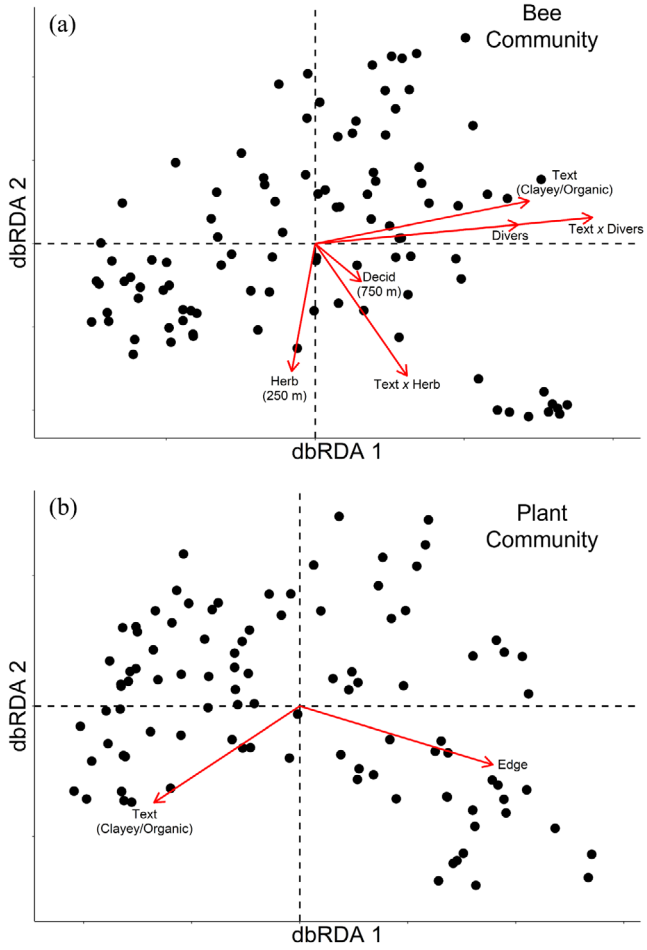

FIGURE 5 Bee communities (dots) were structured by soil texture (Text), diversity of flowering plants (Divers), herbaceous and sparsely vegetated cover (Herb), and deciduous forests (Decid) (a) while flowering plant communities were structured by soil texture and the amount of edge (Edge) of an opening (b).

as well as higher bee diversity in sites with more contiguity of open area within 100 m (Table 2). The CoCA indicated that the influence of prescribed fire on bee community composition was mediated through changes in the plant community and diminished with time since treatment ($r^2 = .23$, $p < 0.005$; Figure 6).

3.2.2 | Herbicides

Modeling showed that herbicide treatments generally affected bee abundance and diversity positively, but these effects were often weakly supported unless performed with high frequency in combination with other treatments (abundance) or in sites with more moderately textured soil (Table 2; Table S8). However, herbicide application in addition to plantings had negative effects on the bee community, particularly rare species (Table 2;

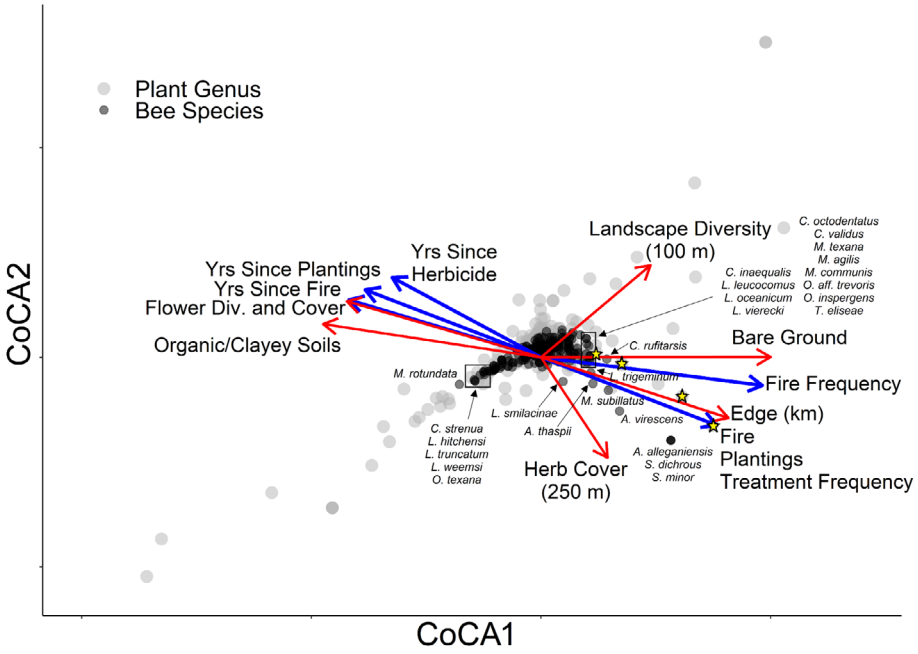

FIGURE 6 Co-correspondence analysis of the plant and bee communities in a predictive framework and fitted with environmental (red arrows) and management (blue arrows) variables. Select bee species (black dots) are labeled along important gradients. Nonnative weedy plant species associated management practices are indicated by yellow stars and include *Berteroa incana*, *Centaurea stroebe*, *Hypericum perforatum*, and *Rumex acetosella*.

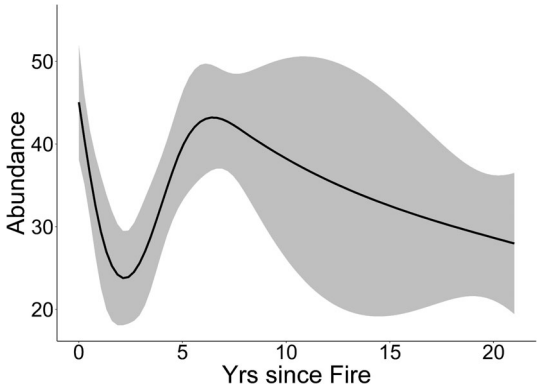

FIGURE 7 Bee abundance initially decreases following prescribed fires but recovers.

Table S8). Herbicide treatments altered plant community composition that changed bee community composition ($r^2 = 0.11$, $p < 0.05$; Figure 6).

3.2.3 | Mechanical

Modeling demonstrated that mechanical management on clayey or organic soils resulted in higher bee abundance and diversity while these practices in moderate to more sandy soils resulted in less bee abundance and diversity (Table 2). However, negative effects of mechanical treatments on bee abundance and rarity were reversed by prescribed fire (Table 2; Table S8). Mechanical treatments also interacted with pollinator planting treatments and resulted in higher bee abundance (Table 2; Table S8). Support for rare species was also higher due to an interaction between mechanical and herbicide treatments, offering an alternative to the negative effect observed when herbicides were combined with pollinator plantings (Table S8).

3.2.4 | Pollinator plantings

Pollinator plantings generally resulted in greater bee abundance and diversity according to models (Table 2; Table S8), though this effect decreased for at least 20 years (Table 2). Effects of pollinator planting were more pronounced when combined with other treatments as previously described. Species rarity was lower in sites that were managed with pollinator plantings when there was low to moderate landscape diversity within 100 m (Table 2; Figure 4). Similar to other treatments, pollinator planting treatments were identified to restructure the bee community by altering the composition of the plant community according to the CoCA (Pollinator planting Treatment: $r^2 = 0.18$, $p < 0.005$; Figure 6).

3.3 | Network structure

We found that 73 bee species visited both herbaceous and woody plants, while 89 bee species were only encountered on herbaceous plants and 26 bee species were only netted on woody plants (Figure S5). Thus, 14 genera of woody plants (17%) provided support for 99 bee species (52% of the community considered). Network structure analyses indicated that the bee-woody plant network had

Index	Network	Value	z-Score	*P*-Value
Nestedness	Woody	10.95	−0.304	.761
	Herbaceous	2.70	−0.098	.922
	Combined	2.55	−1.090	.276
Links per species	Woody	2.07	−14.64	1.65×10^{-48}
	Herbaceous	3.29	−37.58	$<1.00 \times 10^{-323}$
	Combined	3.66	−44.09	$<1.00 \times 10^{-323}$
Shannon's evenness	Woody	0.68	−26.09	4.52×10^{-150}
	Herbaceous	0.62	−79.71	$<1.00 \times 10^{-323}$
	Combined	0.63	−92.72	$<1.00 \times 10^{-323}$
Connectedness	Woody	0.17	−14.64	1.65×10^{-48}
	Herbaceous	0.07	−37.58	$<1.00 \times 10^{-323}$
	Combined	0.06	−44.09	$<1.00 \times 10^{-323}$
Specialization (H2)	Woody	0.45	26.09	4.69×10^{-150}
	Herbaceous	0.33	79.72	$<1.00 \times 10^{-323}$
	Combined	0.34	92.73	$<1.00 \times 10^{-323}$

TABLE 3 Calculated values and associated P-values for indices of nestedness, links per species, evenness, and specialization (H2) of bee species-plant genera interactions within the woody, herbaceous, and woody-herbaceous combined networks. P-values derived from the comparison of observed values against 5,000 null models, in which contents of rows and columns are randomized for each model while column and row (margin) totals remain constant.

Rank	Species strength		Effective partners		*d*	
1	*Rubus*	29.8	*Rubus*	47.5	*Anemone*	0.82
2	***Salix***	**28.5**	***Salix***	**39.1**	*Hydrophyllum*	0.74
3	*Monarda*	17.8	***Prunus***	**28.0**	*Physalis*	0.70
4	*Solidago*	16.0	*Apocynum*	27.0	*Heracleum*	0.67
5	*Rudbeckia*	11.4	*Solidago*	25.5	***Cornus***	**0.65**
6	*Apocynum*	8.8	*Rudbeckia*	23.6	***Elaegnus***	**0.61**
7	***Prunus***	**6.8**	*Monarda*	19.2	***Salix***	**0.57**
8	*Lysimachia*	5.8	***Vaccinium***	**18.5**	*Ranunculus*	0.57
9	*Euthamia*	4.4	***Ilex***	**18.1**	*Claytonia*	0.56
10	*Hieracium*	4.1	***Amelanchier***	**17.5**	*Lysimachia*	0.53

TABLE 4 Woody plants of forest openings support the bee community in multiple ways. Scores of the top 10 plant genera with the most species strength (higher value means greater influence network importance), effective number of partners (higher value means more generalized), and *d* (higher value means more specialized). Woody plant genera are emboldened.

greater nestedness (represented by a lower value), less links per species, higher evenness and connectedness, and more specialized interactions than the herbaceous network (Table 3). Addition of interactions between bees and the woody plant community resulted in 12% more links per species in the entire network than the herbaceous network (Table 3). The woody network was also important at the species (genus) level. The seven woody plant genera that were collectively identified within the top 10 plant genera for species strength, effective number of partners, and specialized relationships interacted with 94 bee species (Table 4). For example, *Salix* was the second most important plant genus in the entire bee-plant network, acting both as a pollinator hub and forming specialized relationships with bee species. Alternatively, *Prunus* provided strong support to the network but primarily served the native bee community as a floral resource hub, while *Cornus* was not important for the overall network but exhibited specialized relationships with native bee species (Table 4).

4 | DISCUSSION AND BMPs

Findings of The Great Lakes States Pollinator Project showed that ongoing management within forest openings of the Great Lakes Basin supports an abundant and diverse bee community including rare species. However, our findings also highlight that there is room for improvement. For example, the positive effects of forest-opening management were both ephemeral, and in some cases delayed, suggesting openings need additional management treatments to properly maintain opening conditions favorable to native bees. By considering how management practices influence bee abundance, diversity, and species rarity independently and in combination

throughout open areas in different environmental contexts, we developed specific BMPs that consist of a 20 year planning horizon to promote bee conservation in forest openings of the Great Lakes Basin (Table 5).

4.1 | The important role of soil

Our findings demonstrated that the structure and composition of bee communities in forest openings were fundamentally influenced by soil properties. Our findings identified sites in clayey soils resulted in fewer ground-nesting bees compared to sandy sites, a guild that comprises about 80% of bee species (Figure S6; Antoine & Forrest, 2021; Harmon-Threatt, 2020). This may be a byproduct of the fact that ground-nesting guilds comprised different species. Different species assemblages suggest different life histories that may in part reflect a compensatory balance with colony size due to a greater effort needed to excavate clayey soils, though this area of research is currently understudied (Tschanz et al., 2023). Nonetheless, we infer that a number of soil-nesting species, including rare species, prefer clayey soils for nesting, which is not often described in the literature but aligns with other work (Lybrand et al., 2020).

Separately, our study results indicated that the bee community was structured by soil conditions mediated through the plant community. Soil texture was an important predictor of plant community structure and composition. In turn, the plant communities associated with these soil conditions led to alternative resources available to the bee community (Schaffers et al., 2008), including floral resources and nesting substrates. For example, flowering vegetation on clayey and organic soils was denser and more diverse with lower amounts of exposed soil, leading to a less abundant bee community. The paradoxical finding that bee captures decrease with increased floral resources has been explained as the result of a threshold in attractiveness of passive traps or simply a reduction in trap visibility (e.g., Baum & Wallen, 2011; Portman et al., 2020). Since our analyses pooled specimens from active and passive trapping methods, these potential biases are unlikely to cause our findings. For example, we would expect that netting at sites that were clayey and had more open blooms would result in more bees than sandy sites with fewer blooms if bees were more attracted to the open flowers and less to bee bowls at clayey sites. However, we found no difference in the total number of bees netted at clayey sites (mean ± se net total: 26.7 ± 3.7) compared to sandy sites (mean ± se net total: 24.7 ± 2.6; Table S9). A reduction in trap visibility could explain an overall lower abundance of bees but of course does not explain why different ground nesting bee species were sampled at clayey versus sandy sites. We therefore suggest an alternative hypothesis that dense growth of flowering plants and vegetation debris limits access to nesting substrates for some soil-nesting bee species in more clayey or organic soils (Cunningham-Minnick et al., 2019; Gardein et al., 2022; Twerd et al., 2021), resulting in a different, less speciose, and less abundant assemblage of ground-nesting bees than those of sandy soils. These findings do not imply that habitat of forest openings with clayey or organic soils should not be considered for bee conservation; the bee and plant community composition are different, and the lack of a response by our rare bee response metric to soil properties in models suggest that clayey and sandy sites have their own distinct subsets of rare opening-associated bees.

Differences in bee and plant communities associated with soil conditions were also reflected in bee responses to management practices. For example, the positive effects of herbicide application on bee abundance and diversity were greater in moderately sandy sites than sites with very sandy soils. The mechanism is unclear but could reflect a larger environmental impact following control measures on invasive plants, which may grow at greater density in soils with better water retention (Bansal et al., 2014). Similarly, mechanical treatments led to greater bee abundance and diversity in clayey/organic sites, but lower abundance and diversity at moderately and very sandy sites. Most of the mechanical treatments applied in this region (mowing, brushhogging, mastication) result in accumulated organic debris on the ground. Therefore, the debris from mechanical treatments likely increased ideal nesting conditions for some species, such as *Lasioglossum hitchensi*, Gibbs 2012, *L. truncatum* (*Robertson*, *1901*), and *L. weemsi* (Mitchell, 1960) which were associated with the densely vegetated sites of low exposed soil cover and clayey/organic soils. The associations between these species and soil characteristics may be due to moisture content, temperature, shade, organic matter content, soil particulate size, and so forth but are not well understood (Harmon-Threatt, 2020). The plant communities at sites with sandy soils were more sparsely distributed and associated with dryer conditions, more exposed bare ground, and a different composition of bee species, collectively suggestive of a fire-driven system (Antoine & Forrest, 2021). The finding that mechanical treatments negatively impacted the bee community of sandy soils, yet mechanical treatment followed by fire increased bee abundance and diversity more than fire alone (see also Campbell et al., 2018; Glenny et al., 2022; Lettow et al., 2018; Ulyshen et al., 2022) supports the notion that in fire-adapted systems debris from mechanical treatments restricts bees access to preferred nesting substrates. Mechanical treatments reduce the vegetation structure (height), but accumulated organic debris from the action still covers the soil surface. Subsequent burning removes that debris while

TABLE 5 Bee best management practices document ("BeeMPs"). Management treatments (prescribed fire, mechanical, herbicide, pollinator planting) for a proposed restoration site conditionally based on soil properties (clayey/organic or moderate-sandy/well-drained), opening size (<10 ha, 10–15 ha, >15 ha) and edge effects (distance from site center to forest edge), and configuration and connectivity with other openings (distance from nearest forest edge to edge of neighboring opening) of the proposed restoration site. Management regimes are further tailored to provide additional support for aspects of the bee community that are anticipated to be low in abundance (A), diversity (D), or species rarity (R) as indicated by their scores from 0 to 8 where an "8" is considered high. Lower scores imply a greater need for management intervention; however, we suggest that no management be applied in situations in which the mean score across metrics of the bee community is a "2" or lower, as the resources required to restore and maintain that site for bee conservation are not likely feasible. Best management practices are based on 20 year planning horizon.

Soil	Size	Edge	Connect	Score			Management (Practice—frequency)	Notes
				A	D	R		
Clayey/ Organic	<10 ha	<100 m	<50 m	4	4	3	Mechanical (e.g., brushhog, masticate): every 1–2 yrs for 10 yrs, then every 3–4 yrs Herbicide (e.g., spot): every 1–2 yrs for 10 yrs, then as needed Fire: first yr, then every 7–10 yrs	Heavy investment Fire follows Mech
			<100 m	4	3	3	Add Pollinator Planting: first and second yrs	
			≤200 m	3	2	2	Increase Planting frequency to every 5 yrs. Do not burn!	Fire will suppress bees
			>200 m	2	1	1	No Management Suggested	
		<250 m	<50 m	3	3	4	Mechanical (e.g., brushhog, masticate): every 2–3 yrs for 10 yrs, then every 4–5 yrs Herbicide (e.g., spot): first yr, then every 2–3 yrs for 10 yrs, then every 4–5 yrs Fire: first yr, then every 7–10 yrs Pollinator Planting: second and third yrs	Heavy investment Fire follows Mech
			<100 m	3	2	4	Increase Planting frequency to every 5 yrs	
			≤200 m	2	1	3	No Management Suggested	
			>200 m	1	0	2	No Management Suggested	
		≥250 m	<50 m	2	2	6	Mechanical (e.g., brushhog, masticate): first yr, then every 3–4 yrs Herbicide (e.g., spot): first and second yr, then every 3–4 yrs Fire: first yr, then every 4–5 yrs	Fire follows Mech
			<100 m	2	1	6	Add Pollinator Planting: every 3–5 yrs for 10 yrs	
			≤200 m	1	0	5	No Management Suggested	
			>200 m	0	0	4	No Management Suggested	
	10–15 ha	<100 m	<50 m	6	5	4	Mechanical (ie., brushhog, masticate): every 2–3 yrs for 10 yrs, then every 3–4 yrs Herbicide (e.g., spot): every 2–3 yrs for 10 years, then as needed Fire: first yr, then every 5–6 yrs	Fire follows Mech always
			<100 m	6	4	4	Add Pollinator Planting: first and second yrs	
			≤200 m	5	3	3	Add Planting at 5th, 10th, 15th, and 20th yrs	
			>200 m	4	2	2	Do not burn first yr Increase Herbicide frequency to every 2 yrs	Fire may suppress bees
		<250 m	<50 m	5	4	5	Mechanical (e.g., brushhog, masticate): every 2–3 yrs for 10 yrs, then every 4–5 yrs Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then 6–7 yrs Pollinator Planting: first yr OR first and second yrs	Fire follows Mech always

TABLE 5 (Continued)

Soil	Size	Edge	Connect	Score			Management (Practice—frequency)	Notes
				A	D	R		
			<100 m	5	3	5	Add Planting at 5th, 10th, 15th, and 20th yrs	
			≤200 m	4	2	4	Increase Herbicide frequency to every 2–3 yrs for 10 yrs	
			>200 m	3	1	3	Same as above	May not be worth restoring
		≥250 m	<50 m	4	3	7	Mechanical (e.g., brushhog, masticate): first yr, then every 3–5 yrs Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then every 6–7 yrs Pollinator Planting: first yr OR first and second yrs	Fire follows Mech always
			<100 m	4	2	7	Increase Mechanical frequency to first yr, then every 2–3 yrs Add Planting at 5th, 10th, 15th, and 20th yrs	
			≤200 m	3	1	6	Same as above	
			>200 m	2	0	5	No Management Suggested.	
	>15 ha	<100 m	<50 m	5	6	5	Mechanical (e.g., brushhog, masticate): first yr, then every 2–3 yrs—re-evaluate after 10 years Herbicide (e.g., spot)—every 2–3 yrs Fire: first yr, then every 5–6 yrs	Fire follows Mech always
			<100 m	5	5	5	Add Pollinator Planting: first and second yrs	
			≤200 m	4	4	4	Add Planting at 5th, 10th, 15th, and 20th yrs	
			>200 m	3	3	3	Same as above	
		<250 m	<50 m	4	5	6	Mechanical (e.g., brushhog, masticate): first yr, then every 3–4 yrs Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then every 6–7 yrs Pollinator Planting: first yr OR first and second yrs	Fire follows Mech always
			<100 m	4	4	6	Same as above	
			≤200 m	3	3	5	Add Planting at 5th, 10th, 15th, and 20th yrs Increase Herbicide frequency to every 2–3 yrs	
			>200 m	2	2	4	Same as above	
		≥250 m	<50 m	3	4	8	Mechanical (e.g., brushhog, masticate): every 4–5 yrs Herbicide (ie., spot): every 3–4 yrs Fire: first yr, then every 5 yrs Pollinator Planting: first yr OR first and second yrs	Fire follows Mech always
			<100 m	3	3	8	Same as above	
			≤200 m	2	2	7	Add Planting at 5th, 10th, 15th, and 20th yrs Increase Herbicide frequency to every 2–3 yrs Increase Mechanical frequency to every 3–4 yrs	
			>200 m	1	1	6	Increase Mechanical frequency to every 2–3 yrs	May not be worth restoring

(Continues)

TABLE 5 (Continued)

Soil	Size	Edge	Connect	Score			Management (Practice—frequency)	Notes
				A	D	R		
Moderate—Sandy	<10 ha	<100 m	<50 m	6	8	3	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 1–2 yrs for 10 yrs, then every 2–3 yrs Fire: every 2–3 yrs	Heavy investment
			<100 m	6	7	3	Add Pollinator Planting: 1st, 2nd, and 3rd yrs	
			≤200 m	5	6	2	Decrease Fire Frequency to first yr, then sixth yr, then every 2–3 yrs Add Mechanical (e.g., brushhog) early in sixth yr before burn	Fire benefit to rarity realized at post-year 5.
			>200 m	4	5	1	Same as above	
		<250 m	<50 m	5	7	4	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 2–3 yrs for 10 yrs, then every 4–5 yrs Fire: every 3–4 yrs Pollinator Planting: first and second yrs	
			<100 m	5	6	4	Same as above	
			≤200 m	4	5	3	Same as above	
			>200 m	3	4	2	Change Fire: first yr, then sixth yr, then every 2–3 yrs Add Mechanical (e.g., brushhog) early in sixth yr before burn	Fire benefit to rarity realized at post-year 5.
		≥250 m	<50 m	4	6	6	Mechanical (i.e., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 3–4 yrs for 10 yrs, then every 4–6 yrs Fire: first yr, then every 4–5 yrs Pollinator Planting: first and second years	
			<100 m	4	5	6	Same as above	
			≤200 m	3	4	5	Add Planting at 5th, 10th, 15th, and 20th yrs Add Mechanical (e.g., brushhog) in yr fifth or sixth yr before burn	
			>200 m	2	3	4	Increase Fire frequency to first yr, then every 3–4 yrs	
	10–15 ha	<100 m	<50 m	8	8	4	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then every 5–7 yrs	
			<100 m	8	8	4	Same as above	
			≤200 m	7	7	3	Increase Fire frequency to first yr, then every 3–4 yrs Add Mechanical (e.g. brushhog) prior to every other burn	
			>200 m	6	6	2	Add Pollinator Planting: first and second yrs	
		<250 m	<50 m	7	8	5	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 4–5 yrs Fire: first yr, then every 5–7 yrs	
			<100 m	7	7	5	Same as above	
			≤200 m	6	6	4	Add Pollinator Planting: 1st and 2nd yrs	
			>200 m	5	5	3	Increase Fire frequency to first yr, then every 3–4 yrs	

TABLE 5 (Continued)

Soil	Size	Edge	Connect	Score			Management (Practice—frequency)	Notes
				A	D	R		
		≥250 m	<50 m	6	7	7	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 4–5 yrs Fire: first yr, then every 5–7 yrs	
			<100 m	6	6	7	Same as above	
			≤200 m	5	5	6	Increase Fire frequency to first yr, then every 4–5 yrs	
			>200 m	4	4	5	Same as above	
	>15 ha	<100 m	<50 m	7	8	5	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then every 5–7 yrs	
			<100 m	7	8	5	Same as above	
			≤200 m	6	8	4	Add Pollinator Plantings: first and second yrs	
			>200 m	5	7	3	Increase Fire frequency to first yr, then every 4–5 yrs	
		<250 m	<50 m	6	8	6	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then every 5–7 yrs	
			<100 m	6	8	6	Same as above	
			≤200 m	5	7	5	Same as above	
			>200 m	4	6	4	Add Pollinator Planting: first and second yrs Increase Fire frequency to first yr, then every 4–5 yrs	
		≥250 m	<50 m	5	8	8	Mechanical (e.g., masticate, girdle/fell): first yr Herbicide (e.g., spot): every 3–4 yrs Fire: first yr, then every 5–7 yrs	
			<100 m	5	7	8	Same as above	
			≤200 m	4	6	7	Same as above	
			>200 m	3	5	6	Add Pollinator Planting: first and second yrs Increase Fire frequency to first yr, then every 4–5 yrs Increase Herbicide to every 2–3 yrs for 10 yrs, then every 3–4 yrs	

further reducing vegetation structure, a one to two punch. Our findings that soil conditions influence the effects of treatments make it clear that BMPs for bee conservation should include consideration of soil properties.

4.2 | Bee community metrics are determined by landscape context

Bee abundance, diversity, and support for rare bee species were influenced by the surrounding landscape, as well as conditions within the openings. Though we a priori restricted environmental covariates to linear model fits, visual inspection of edge to area ratio showed a nonlinear relationship with bee abundance where highest values were in openings 10–15 ha in size (e.g., Figure 8). Since an opening 10–15 ha corresponds to a circular opening with a radius 178–219 m, our model fit that highest bee abundance occurred at sites with high open-area contiguity within 250 m supports this nonlinear relationship and suggests an association of bees with intermediate patch sizes. Ecologically, this may represent a tradeoff between preference for larger patches that enhance recolonization following management, and smaller patches that encompass a larger proportion of edge, which provides enhanced floral resources.

The positive association of bee diversity with greater forest cover in the landscape and negative association with open-area contiguity within 100 m, and thus

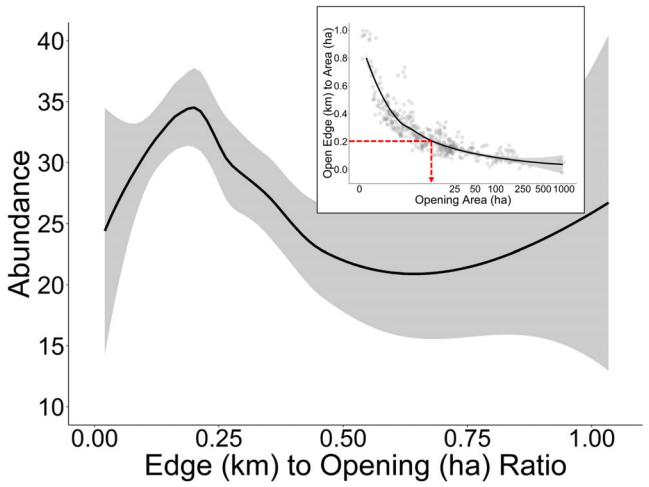

FIGURE 8 Bee abundance was greatest in openings with a relatively low edge length (km) to opening area (ha) ratio, the peak of which corresponded to openings 10–15 ha in size.

positive association with nearby forest edge, is consistent with the findings of others who suggest bees benefit from resources in the surrounding forest and forest edge (reviewed in Ulyshen et al., 2023). Because of the multi-scale approach we employed in models, our findings further suggest higher bee diversity when the nearby edge has a complex configuration (i.e., edge habitat that is not oriented in a straight line and is of thin width), which would still allow a high proportion of the land area within 250 m to be open. Combined with our findings that openings with comparatively less overall edge length leads to higher bee diversity, our results collectively suggest that land managers consider managing for smaller and irregularly shaped openings to enhance bee diversity (Roberts et al., 2017).

Our bee-plant network analysis further indicated that floral resources of short trees and shrubs typical of early-successional habitat (e.g., *Amelanchier canadensis* (L.) Medik, *Ilex verticilata* (L.) Gray, *Salix discolor* Muhl.) play an important role in supporting the foundation of the bee community within openings. Though we did not analyze relationships describing how bee communities change within a season, the floral phenology of these woody species emphasizes their potential to enhance support for early spring bee communities of openings in addition to the typically considered floral resources of late-season flowering forbs. Our network analyses identified some woody species (e.g., *Cornus* spp.) exhibiting specialized relationships with bee species, which is consistent with reviews of oligolects in nearby regions (Fowler, 2016a, 2016b) and collectively suggest that land managers may want to selectively include shrubs and tree species identified in Table 4 in openings to conserve these often uncommon bee species. The higher specialization of the bee-woody plant network within openings (compared to the herbaceous community) combined with their high nestedness suggest that including these woody species in openings may increase resiliency of the opening bee community to future changes in environmental conditions (Song et al., 2017).

Our finding that rare bee species favor opening interiors suggests forest encroachment into the opening via vegetational succession is not supportive of rare species associated with open areas. Though pollinator plantings did not elicit a negative effect on rare bee species directly, the lack of an anticipated positive effect could be due to poor correspondence between seed mixes and the requirements of rare native bees (Lane et al., 2022; Menz et al., 2011; Williams & Lonsdorf, 2018). For instance, many species that ranked high in our rarity index are identified oligolects that require specific species or genera of foraging plants (Fowler, 2016a, 2016b). Since the National Forests have managed many of these openings for purposes other than native bee conservation, hence the need for this study, it is sensible that this sensitive subset of bees did not respond positively to the pollinator plantings. Rather, rare bees responded negatively to the disturbance and removal of established plants that previously occupied that space in preparation for the pollinator planting treatment, as explained by the interactive effects of the models. Alternatively, our CoCA models indicated that the results of management actions were associated with the occurrence of some invasive or weedy plant species that contributed to changes in bee community structure, including *Berteroa incana* L., *Centaurea stoebe* L., *Hypericum perforatum* L., and *Rumex acetosella* L. The spread of unwanted plant species by large equipment and the establishment of weedy pioneer species in newly disturbed areas are common, which likely place additional pressure on rare bee species by outcompeting preferred host plants (Kost et al., 2007; Mortensen et al., 2009). Therefore, our findings collectively suggest that pollinator planting treatments be reserved for restoration areas <250 m from the forest edge to minimize forest-encroachment effects, including negative interactions with rare bee species, and that precautions be put in place to mitigate the introduction or spread of invasive species such as washing apparel and machinery between sites.

Finally, our findings demonstrate that herbicide application in combination with plantings is especially detrimental to rare bees, perhaps because herbicides kill plants preferred by rare bees, preferred plants are not in conventional seed mixes, or some combination thereof. Though most herbicide applications were less than 20% of the site, there were a few cases of large (90% of site) applications in the summer followed by expansive (15%) seeding events in the fall. Species rarity scores in these

sites were extremely low, and our results suggest it will take more than 20 years for rare bee populations at these sites to recover. Thus, our findings collectively illustrate that forest-edge effects are beneficial to most of the forest-opening bee community, with exception of rare open-associated species, which are a sensitive subset of the community that rely on resources specific to opening interiors.

4.3 | Translating results to BMPs

4.3.1 | Scoring baseline conditions

The contrasting effects of management treatments and environmental factors on bee abundance, diversity, and rare species suggest practitioners may be faced with tradeoffs in respect to management practices. For example, forest-edges increase bee abundance and diversity, but potentially at the expense of rare species. To resolve this issue, we created a scoring system that identifies how management practices can increase bee abundance, diversity, and conditions favorable for rare species by taking into account the current characteristics of the site and its management history. The scoring system ranges from 0 to 8 for each bee community metric, where 0 indicates very poor conditions for bees and a score of 8 indicates conditions that support the maximum level of bee abundance, diversity, or rarity. All sites start with an initial neutral value of 4 points for each metric. Based on the statistical relationships we described above and the practitioner's answers to the questions below, points are then added or subtracted to determine the relative baseline value for each bee community metric at a given site. This scoring system resembles the Habitat Suitability Index approach, which is an effective means to simplify and apply complex and continuous relationships between organisms and their environment for the purpose of gauging their value relative to other sites or conditions (Schamberger & O'Neil, 1986). The following questions should be assessed to establish the baseline community metrics for a site:

1. Is the soil at the site clayey/organic or moderate to sandy textured?
2. Is the target opening <10 ha, 10–15 ha, or >15 ha in size?
3. From the center of the treatment area, is the nearest forest edge <100 m, <250 m, or ≥250 m?
4. From the nearest edge to the center of the treatment area, is the nearest opening <50 m, <100 m, ≤200 m, or >200 m?

Potential responses to these questions were numerically scored from −2 to +2 depending on if our results indicated the effect would be strongly negative (−2), somewhat negative (−1), no effect (0), somewhat positive (+1), or strongly positive (+2) to bee abundance, diversity, or rare species comparatively (Table 6).

4.3.2 | Deriving baseline questions and value ranges

The four questions employed to establish baseline site conditions collectively represent a simplified understanding of the variables of importance at varying scales. These questions address local (soil), patch (opening size and edge effects), and landscape (connectivity) factors that were found to affect bee abundance, diversity, and rare species. The values provided as potential answers act as effect ranges which further address the fitted and interpolated nonlinear relationships and potential interactions with different experimental treatments and are presented in a simplified format to facilitate practitioner adoption and interpretation. We describe the justification for each question and its value range below and provide detailed information in supplementary documents.

The first question reflects our findings that bee communities on clayey and organic soils are less abundant and diverse than that of sandy soils and their unique species respond best when the sites are managed with mechanical means that leave behind organic debris, while in contrast, bees on sandy sites benefit from mechanical treatments only when prescribed fires are performed. Since soil conditions were not an important predictor of species rarity, the score of this bee community metric did not differ with soil type. The values of the soil variable most fitting in models was a direct reflection of expert knowledge by NFS staff with a bimodal distribution (Table S9); therefore, we provided simple answers of sandy or clayey.

The second question primarily reflects our finding that bee abundance is highest in openings of intermediate size with an edge length (km) to open area (ha) ratio of 0.19–0.21, which corresponded to openings between 10 and 15 ha. Visual inspection of the data identified a nonlinear relationship with maximum abundance occurring in openings between 12 and 13 ha in size. Therefore, we decided to interpolate three relationships representative of smaller, moderate, and larger openings that affected bees differently based on three criteria focused on this maximum value as it relates to site edge length to open area ratios: (1) equidistance from the maximum fitted value; (2) as hectares for simplicity of

TABLE 6 Scoring system to establish expected bee community abundance, diversity, and species rarity prior to management, which will determine which management practices to employ. Expected bee community metrics are each based on four questions (alternate shading) derived from important soil conditions, opening properties, and landscape context. Bee communities respond differently to management practices based on these starting criteria. We transformed study findings into a numeric ranking system ranging from 0 to 8, where "8" represents a high value for a metric. Each site receives an initial value of "4" and points are added or subtracted based on which option best describes the site, defined as center of the treatment area.

Question	Response	Abundance	Diversity	Species rarity
What is the soil texture?	Clayey/organic	−1	−2	+0
	Moderate—Sandy	+1	+2	+0
How large is the opening?	<10 ha	−1	−1	−1
	10–15 ha	+1	+0	+0
	>15 ha	+0	+1	+1
How far is the nearest forest edge from the site?	<100 m	+1	+1	−1
	<250 m	+0	+0	+0
	≥250 m	−1	−1	+2
From the nearest forest edge to the site, how far is the nearest opening?	<50 m	+1	+2	+1
	<100 m	+1	+1	+1
	≤200 m	+0	+0	+0
	>200 m	−1	−1	−1

implementation; and (3) have a standard error that does not overlap that of the smaller or larger openings outside of the sizes for which there was the highest abundance. We found that openings with range boundaries of 9 and 16 ha did not meet the third criteria, and thus used 10 and 15 ha to represent these three ranges (Table S10).

Although it may be expected that bee diversity should receive a positive score for small (<10 ha) openings since the proportion of edge habitat in an opening increased inversely with patch area, we instead assigned this answer a "−1" based on the influences of patch area and scored edge effects separately, since it is also influenced by opening shape via the edge length to open area ratio variable. As previously discussed, proximity (<100 m) of a site to the forest edge resulted in greater bee diversity. This relationship for sites <250 m from the forest edge was similar, but with less magnitude and less certainty and thus, not as good of a model fit (data not shown). We therefore chose 100 and 250 m to represent the spatial boundaries of edge effects in question 3. The second and third questions will thus collectively assign a neutral score (+0) on bee diversity to a very small opening when the center of the target management area is close (<100 m) to the forest edge, while a larger opening with the center of a target management area close to the forest edge will receive a positive score (+1). Conversely, support for rare species receives a greater negative score of "−2" when the opening is small, reflecting the results of our analyses that support for rare species within any but the largest of openings is dependent on a lack of landscape diversity within 100 m, with a strong preference of sparsely vegetated and grassy/herbaceous cover 250 m from sites; proximity to any other land cover leads to decreased support for these bees (Figure 4). Rare bee species of forest openings thus have the highest probability of inhabiting large openings in sites away from edges and thus receive a "+3" score for this combination of replies to questions two and three.

The fourth question reflects the influence of opening connectivity and configuration within the landscape. The scale at which connectivity and configuration of open area affected bee metrics was 100 m (abundance) and 250 m (all metrics). Therefore, we made 200 m a range boundary rather than 250 m to accommodate this imbalance of response distances. We did not specifically address the variability of connectivity (variable in the best model explaining abundance) for simplicity, practicality, and the tight relationship between the connectivity (contiguity) and its variability (Figure S4). Finally, in order to further accommodate our collective findings that bees in open areas are functioning primarily at small scales, we interpolated two additional range boundaries to provide guidance on openings with greater connectivity. These include 50 m to reflect inferred bee diversity responses to narrow widths of forest, as well as 100 m to represent high connectivity without very narrow forest widths. Thus, these values (<50, 50–99, 100–199, >199) represent

distances that our results collectively suggest bees will respond to differently. Sites of high connectivity (50 and 100 m) are consequently assigned a score of "+1" for bee abundance and species rarity, while bee diversity is assigned a score of "+2" for sites with the highest connectivity (50 m).

4.3.3 | Application of scores for management

Collectively, different combinations of response values for these four questions generate a set of scores that identify the conditions under which conservation intervention is beneficial. For instance, a proposed treatment area with a score of "7" (abundance), "7" (diversity), "3" (species rarity) indicates that land managers should focus their resources on managing for rare species. Sites that score an average of "2" or less across metrics will be extremely resource-intensive for land managers to restore and maintain, and it may be advisable to target another site to implement management for native bees. For example, a site with clayey soils that is <10 ha in size, <100 m from an edge, and isolated from other openings by at least 200 m will be scored as "2," "1," "1" because it likely has limited resources, very slow recolonization ability, unlikely rescue effects for most populations following a disturbance, and yet will require a high management frequency to maintain opening conditions. Considering the anticipated negative effects that initial management treatments incur (i.e., prescribed fire), the very small populations at these types of openings will take much longer to recover. There also exist a few possible response combinations for the bee diversity metric to result in scores outside of the 0–8 range (Table S11). In the most extreme case, a very large sandy site close to the forest edge and with high connectivity would result in a diversity score of "10." In this uncommon instance, the diversity score should be treated as an "8."

The tabulated BMP content (Table 5) is conveniently organized to fit on the front and back of a single sheet of paper. Congruent with the order of the four questions, they depict four columns that are hierarchically organized and easy to follow. For instance, the front of the page is dedicated to a reply of "clayey/organic" soils to the first question. The second question addressing opening size is the next column and has all responses contained within the vertical spatial extent covered by the response "clayey/organic"; this process continues through all four questions and will lead to a single set of scores for abundance "A," diversity "D," and species rarity "R" associated with the management area proposed.

4.3.4 | Best management practices

The translation of abundance, diversity, and rarity scores into suggested practices involves a balanced incorporation of our results on the effects of opening management. For instance, our findings clearly indicate that sandy sites should be burned instead of mechanically treated. Rather than suggest sites with moderate to sandy soils be only burned, we suggest that all moderate to sandy soiled sites be mechanically treated in the first year followed by a fire treatment. This provides land managers the opportunity to, for instance, masticate persistent woody shrubs and then burn the residue to acquire the synergistic benefit of the treatment combination for bee abundance and species rarity, as well as the benefit of fire to bee diversity. The BMPs are designed to then maintain this fire-driven system without future mechanical treatments.

The baseline scores of abundance, diversity, and rarity are based on the assumption that the target site has not been managed in the previous 20 years. Since lower scores imply a greater need for management intervention, we adjusted management intensity by modifying treatment frequencies needed for bee conservation within alternately shaded, black-outlined boxes in the BMPs. The "Management" column is organized such that greater connectivity among openings will always support the most robust bee community given replies to the first, second, and third questions. Thus, a site with the nearest opening <50 m away will require the least amount of management intervention and its BMPs include only the treatments listed next to it. Alternatively, sites isolated by more than 200 m will require the most intervention and their BMPs will include the treatments, or their modifications, listed at the "<50 m," "<100 m," "≤200 m," and ">200 m" responses in a cumulative manner.

For an example, suppose the target conservation site is sandy, <10 ha in size, >250 m from the forest edge, and with a connectivity value of >200 m. This scenario results in A, D, and R scores of "2," "3," and "4," respectively. If the opening was highly connected, the entire BMP plan would first include a mechanical treatment immediately followed by a prescribed burn to remove aboveground woody vegetation, retard invasive herbaceous growth, and encourage the fire-tolerant seed bank to germinate while creating more exposed soil for the bee community, followed by seedings and pollinator plantings in the first year to take advantage of the newly exposed soil substrate, followed by another round of pollinator plantings the second year. The site is expected to be maintained for the purposes of bee conservation through prescribed fire every 4–5 years with a similar frequency of spot herbicide application to control invasive or weedy plants. Since the target opening is isolated in the landscape, the BMP plan is modified to include

(1) additional pollinator plantings every 5 years to further support bee abundance and diversity, (2) an additional mechanical treatment followed by a regularly scheduled burn to support bee abundance and rare species, and (3) an increase in fire frequency to support all aspects of the bee community. This organization allows BMPs to differentially address properties of a site while providing land managers with a compact and easy-to-follow document.

4.4 | Flexibility and limitations

Our BMPs are unique in that they are address sites based on local and landscape properties, simultaneously address multiple aspects of the bee community including rare species, are easy to understand, and directly incorporate landscape context, soil conditions, and differential effects of management practice (treatment) combinations. Though highly relevant to the Great Lakes Region, their precision may limit application to other regions and systems. For instance, other temperate systems may require the implementation of different restoration practices (e.g., grazing, scarification, biochar) or include openings within a matrix of forest cover with different resources available to the bee community (e.g., Rivers & Betts, 2021). Since the evaluated management practices were employed for a variety of restoration objectives focused on restoring or maintaining the opening, our findings do not directly address management of habitats intermediate between open- and closed-canopy (Odanaka & Rehan, 2020; Zitomer et al., 2023). Further, all prescribed fire dates were in April or May and predominantly of moderate intensity, which may influence bee responses (Galbraith et al., 2019). We also did not request high-resolution information from NF personnel such as environmental conditions in which treatments were applied (e.g., cloudiness, time of day, wind speed). Since we did not have details on the size or configuration of the managed area within an opening for every treatment, we could not include this information in our analyses. Though this information would surely increase the precision of our results, our study instead included the differences in these details as variation in the models, some of which may have been accounted for with the random effect of National Forest. Furthermore, the main objective of this project was the production of BMPs, which are not quantitative predictions but rather derived from simplified quantified patterns (Shamberger and O'niel, 1986).

Abundance and Shannon diversity are common metrics employed to understand the complexities of community structure, though the use of other diversity metrics or weights, such as mass (Müller et al., 2006) may have influenced our results. To fulfill this need for a species-specific index that included life history traits, we developed SpORtI (Cunningham-Minnick et al., 2022). Modeled rarity scores from SpORtI indicated that rare bee species in open habitat are a subset of the broader open-habitat community and are very sensitive to changes in community composition of plants within opening interiors. As the first application of the index, additional studies will be needed to validate its general reliability for bees or other taxa. We emphasize that SpORtI's ranking system takes advantage of the fact that "rarity" is a relative measure and restricts its application to species of the dataset and is representative of relative support that a site provides to rare species. Therefore, SpORtI output in this study provided great insight to regionally rare species of openings within a forest matrix, but does not address rare species in the surrounding forest since all bees were sampled within openings (Cunningham-Minnick et al., 2022).

This study did not sample the bee or plant community within the forest matrix and thus, our results and derived BMPs cannot be applied to forested areas. Further, these openings are large and not representative of small canopy gaps. Many studies have demonstrated the important role of forests in supporting bee communities (reviewed in Ulyshen et al., 2023). While our findings support the conclusions of others that forest cover is important in supporting aspects of opening bee communities within a forested landscape, details of the surrounding forests were not controlled for, nor considered in the analyses of this study. Thus, our approach applied to future studies that include sampling in open- and closed-canopied sites across forest-dominated landscapes would provide further insights on appropriate management actions to enhance and conserve bee communities of open- and closed-canopy habitat across the landscape.

5 | CONCLUSION

Soil conditions within forest openings play a key role structuring plant and bee communities as well as the appropriate management actions for native bee conservation (notably, for moderate—sandy soils, there is no combination of factors that results in an opening not worth managing). Opening and landscape configuration and composition play an important role in supporting native bee communities, and these factors can help inform land managers which opening should be a conservation priority. Rare species, abundance, and diversity of the native bee community can be simultaneously managed for in

forest openings through strategic employment of individual and combined practices already in place throughout the Great Lakes Basin.

ACKNOWLEDGMENTS

The authors are grateful to Sierra Dawkins, Greg Flood, Tracy Grazia, Jack Greenlee, Phil Huber, Janet Kudell-Ekstrum, Matt Lark, Eric North, Linda Parker, Nicole Shutt, Dana Smith, Paul Thompson, and Sue Truell, of the United States Forest Service for managing bee surveys throughout the National Forests of the Great Lakes Basin. The authors thank Mike Arduser, Sam Droege, Jason Gibbs, Rob Jean, and Michael Veit for verifying, and assisting in, the identification of specimens. We also thank the USFS Northern Research Station and University of Massachusetts—Amherst for hosting the research, and Chris Buelow for helpful comments on an earlier draft. Funding was provided by the Environmental Protection Agency's Great Lakes Restoration Initiative. Finally, the authors express gratitude to the six anonymous reviewers for their helpful comments.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code used in analyses are freely available upon request.

ORCID

Michael J. Cunningham-Minnick https://orcid.org/0000-0002-4478-4113
Joan Milam https://orcid.org/0000-0002-8056-1304
David I. King https://orcid.org/0000-0001-6827-0398

REFERENCES

Almeida-Neto, M., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. *Oikos*, *117*, 1227–1239.

Alric, B., ter Braak, C. J. K., Desdives, Y., Lebredonchel, H., & Dray, S. (2020). Investigating microbial associations from sequencing survey data with co-correspondence analysis. *Molecular Ecology Resources*, *20*(2), 468–480.

Antoine, C. M., & Forrest, J. R. K. (2021). Nesting habitat of ground-nesting bees: A review. *Ecological Entomology*, *46*, 143–159.

Ascher, J. S., & Pickering, J. (2020). Discover life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Retrieved from http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Banaszak, J., & Twerd, L. (2018). Importance of thermophilous habitats for protection of wild bees (Apiformes). *Community Ecology*, *19*(3), 239–247.

Bansal, S., James, J. J., & Sheley, R. L. (2014). The effects of precipitation and soil type on three invasive annual grasses in the western United States. *Journal of Arid Environments*, *104*, 38–42.

Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., & Hedtke, S. M. (2013). Historical changes in northeastern US bee pollinators related to shared ecological traits. *PNAS*, *110*(12), 4656–4660.

Bascompte, J., Jorando, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*, 431–433.

Baum, K. A., & Wallen, K. E. (2011). Potential bias in pan trapping as a function of floral abundance. *Journal of the Kansas Entomological Society*, *84*(2), 155–159.

Beier, P., Hansen, L. J., Helbrecht, L., & Behar, D. (2017). A how-to guide for co-production of actionable science. *Conservation Letters*, *10*(3), 288–296.

Bersier, L.-F., Banašek-Richter, C., & Cattin, M.-F. (2002). Quantitative descriptors of food-web matrices. *Ecology*, *83*(9), 2394–2407.

Bertuol-Garcia, D., Morsello, C., El-Hani, C. N., & Pardini, R. (2018). A conceptual framework for understanding the perspectives on the causes of the science-practice gap in ecology and conservation. *Biological Reviews*, *93*(2), 1032–1055.

Blaauw, B. R., & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, *51*, 890–898.

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 9.

Cadotte, M. W., & Davies, T. J. (2010). Rarest of the rare: Advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, *16*(3), 376–385.

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

Campbell, J. W., Vigueira, P. A., Viguierra, C. C., & Greenberg, C. H. (2018). The effects of repeated prescribed fire and thinning on bees, wasps, and other flower visitors in the understory and midstory of a temperate forest in North Carolina. *Forest Science*, *64*(3), 299–306.

Cane, J. H., & Neff, J. L. (2011). Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation*, *144*(11), 2631–2636.

Caro, T., Andrews, J., Clark, M., & Mulder, M. B. (2023). Practical guide to coproduction in conservation science. *Conservation Biology*, *37*, e14011.

Cunningham-Minnick, M. J., & Crist, T. O. (2020). Floral resources of an invasive shrub alter native bee communities at different vertical strata in forest-edge habitat. *Biological Invasions*, *22*, 2283–2298.

Cunningham-Minnick, M. J., Milam, J., & King, D. I. (2022). SpORtI: The species originality and rarity index combines phylogenetic and functional originality with rarity metrics to provide a new perspective on species rarity. *Ecological Indicators*, *143*, 109339.

Cunningham-Minnick, M. J., Peters, V. E., & Crist, T. O. (2019). Nesting habitat enhancement for wild bees within soybean fields increases crop production. *Apidologie*, *50*, 833–844.

Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L. A., Gemmill-Herren, B., Howlett, B. G., Imperatriz-Fonseca, V. L., Johnson, S. D., Kovács-Hostyánszki, A., Kwon, Y. J., Lattorff, H. M. G., Lungharwo, T., Seymour, C. L., … Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, *5*, 1462.

Dormann, C. F. (2011). How to be a specialist? Quantifying specialization in pollination networks. *Network Biology*, *1*, 1–20.

Dormann, C. F., Fruend, J., Bluethgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*, 7–24.

Dormann, C. F., Gruber, B., & Fruend, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, *8*(2), 8–11.

Droege, S., Tepedino, V. J., LeBuhn, G., Link, W., Minckley, R. L., Chen, Q., & Conrad, C. (2010). Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conservation and Diversity*, *3*, 15–23.

Ene, E., & McGarigal, K. (2023). FragStats. Retrieved from ttps://www.fragstats.org/index.php/documentation

Engel, M., Mette, T., & Falk, W. (2022). Spatial species distribution models: Using Bayes inference with INLA and SPDE to improve the tree species choice for important European tree species. *Forest Ecology and Management*, *507*, 119983.

Exeler, N., Kratochwil, A., & Hochkirch, A. (2009). Restoration of riverine inland sand dune complexes: Implications for the conservation of wild bees. *Journal of Applied Ecology*, *46*, 1097–1105.

Fazey, I., Evely, A. C., Reed, M. S., Stringer, L. C., Kruijsen, J., White, P. C. L., Newsham, A., Jin, L., Cortazzi, M., Phillipson, J., Blackstock, K., Entwistle, N., Sheate, W., Armstrong, F., Blackmore, C., Fazey, J., Ingram, J., Gregson, J., Lowe, P., … Trevitt, C. (2013). Knowledge exchange: A review and research agenda for environmental management. *Environmental Conservation*, *40*(1), 19–36.

Fettig, C. J., Runyon, J. B., Homicz, C. S., James, P. M. A., & Ulyshen, M. D. (2022). Fire and insect interactions in North. *American Forests*, *8*, 301–316.

Fisogni, A., Massol, F., de Manincor, N., Quaranta, M., Bogo, G., Bortolotti, L., & Galloni, M. (2021). Network analysis highlights increased generalisation and evenness of plant-pollinator interactions after conservation measures. *Acta Oecologica*, *110*, 103689.

Flather, C. H., & Sieg, C. (2007). Species rarity: Definition, causes, and classification. In *Conservation of rare or little-known species: Biological, social, and economic considerations*. Island Press.

Fowler, J. (2016a). Specialist bees of the northeast. *Northeastern Naturalist*, *23*(2), 305–320.

Fowler, J. (2016b). Specialist bees of the mid-Atlantic: Host plants and habitat conservation. *The Maryland Entomologist*, *6*(4), 2–40.

Galbraith, S. M., Cane, J. H., Moldenke, A. R., & Rivers, J. W. (2019). Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere*, *10*(4), e02668.

Gallai, N., Salles, J. M., Settele, J., & Vaissiére, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, *68*, 810–821.

Gardein, H., Fabian, Y., Westphal, C., Tscharntke, T., & Hass, A. (2022). Ground-nesting bees prefer bare ground areas on calcareous grasslands. *Global Ecology and Conservation*, *39*, e02289.

Gibbs, J. (2011). Revision of the metallic Lasioglossum (Dialictus) of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa*, *3073*, 1–216.

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

Glenny, W., Runyon, J. B., & Burkle, L. A. (2022). A review of management actions on insect pollinators on public lands in the United States. *Biodiversity and Conservation*, *31*, 1995–2016.

González, A. M. M., Dalsgaard, B., & Olesen, J. M. (2010). Centrality measures and the importance of generalist species in pollination networks. *Ecological Complexity*, *7*, 36–43.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.

Hanberry, B. B., & Abrams, M. D. (2018). Recognizing loss of open forest ecosystems by tree densification and land use intensification in the Midwestern USA. *Regional Environmental Change*, *18*, 1731–1740.

Hanberry, B. B., Bragg, D. C., & Alexander, H. D. (2020). Open forest ecosystems: An excluded state. *Forest Ecology and Management*, *472*, 118256.

Hanula, J. L., Ulyshen, M. D., & Scott, H. (2016). Conserving pollinators in North American forests: A review. *Natural Areas Journal*, *36*(4), 427–439.

Harmon-Threatt, A. (2020). Influence of nesting characteristics on health of wild bee communities. *Annual Review of Entomology*, *65*, 39–56.

Harrison, T., Gibbs, J., & Winfree, R. (2018). Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology*, *24*, 287–296.

Hastie, T. J. (1992). In J. M. Chambers & T. J. Hastie (Eds.), *Generalized additive models*. Wadsworth & Brooks/Cole.

Hepner, M. J., Orcutt, E., Price, K., Goodell, K., Roulston, T., Jean, R. P., & Richardson, R. T. (2023). Montane central Appalachian forests provide refuge for the critically endangered rusty patched bumble bee (*Bombus affinis*). bioRxiv. https://doi.org/10.1101/2023.10.19.563135

Horel, J., Split, M., Dunn, L., Pechmann, J., White, B., Ciliberti, C., Lazarus, S., Slemmer, J., Zaff, D., & Burks, J. (2002). MesoWest: Cooperative mesonets in the western United States. *Bulletin of the American Meteorological Society*, *83*, 211–225.

Huang, J., Malone, B. P., Minasny, B., McBratney, A. B., & Triantafilis, J. (2017). Evaluating a Bayesian modelling approach (INLA-SPDE) for environmental mapping. *Science of the Total Environment*, *609*, 621–632.

Iwasaki, J. M., & Hogendoorn, K. (2021). How protection of honey bees can help and hinder bee conservation. *Current Opinion in Insect Science*, *46*, 112–118.

Johansson, V., Gustafsson, L., Adersson, P., & Hylander, K. (2020). Fewer butterflies and a different composition of bees, wasps and hoverflies on recently burned compared to unburned clear-cuts, regardless of burn severity. *Forest Ecology and Management*, *463*, 118033.

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

Kaiser-Bunbury, C. N., & Blüthgen, N. (2015). Integrating network ecology with applied conservation: A synthesis and guide to implementation. *AoB Plants*, *7*, plv076.

Kalhorn, K. D., Barrows, E. M., & LaBerge, W. E. (2003). Bee (Hymenoptera: Apoidea: Apiformes) diversity in an Appalachian shale barrens. *Journal of the Kansas Entomological Society*, *76*(3), 455–468.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, *274*, 303–313.

Kondratyeva, A., Grandcolas, P., & Pavoine, S. (2019). Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution. *Biological Reviews*, *94*, 1317–1337.

Kost, M. A., Albert, D. A., Cohen, J. G., Slaughter, B. S., Schillo, R. K., Weber, C. R., & Chapman, K. A. (2007). Natural communities of Michigan: Classification and description. Michigan Natural Features Inventory. Report No. 2007-21, Lansing, MI. Retrieved from https://mnfi.anr.msu.edu/reports/MNFI-Report-2007-21.pdf

Kral-O'Brien, K., O'Brien, P. L., Hovick, T. J., & Harmon, J. P. (2021). Meta-analysis: Higher plant richness supports higher pollinator richness across many land use types. *Annals of the Entomological Society of America*, *114*(2), 267–275.

LaBerge, W. E. (1973). A revision of the bees of the genus *Andrena* of the Western hemisphere. Part VI. Subgenus *Trachandrena*. *Transactions of the American Entomological Society*, *99*, 235–371.

LaBerge, W. E. (1980). A revision of the bees of the genus Andrena of the Western hemisphere. Part X. Subgenus Andrena. *Transactions of the American Entomological Society*, *106*, 395–525.

LaBerge, W. E. (1986). A revision of the bees of the genus *Andrena* of the Western hemisphere. Part XII. Subgenera *Leucandrena*, *Ptilandrena*, *Scoliandrena*, and *Melandrena*. *Transactions of the American Entomological Society*, *112*, 191–248.

LaGro, J., Jr. (1991). Assessing patch shape in landscape mosaics. *Photogrammetric Engineering and Remote Sensing*, *57*, 285–293.

Lane, I. G., Portman, Z. M., Herron-Sweet, C. H., Pardee, G. L., & Cariveau, D. P. (2022). Differences in bee community composition between restored and remnant prairies are more strongly linked to forb community differences than landscape differences. *Journal of Applied Ecology*, *59*, 129–140.

Lettow, M. C., Brudvig, L. A., Bahlai, C. A., Gibbs, J., Jean, R. P., & Landis, D. A. (2018). Bee community responses to a gradient of oak savanna restoration practices. *Restoration Ecology*, *26*(5), 882–890.

Lezama-Ochoa, N., Pennino, M. G., Hall, M. A., Lopez, J., & Murua, H. (2020). Using a Bayesian modelling approach (INLA-SPDE) to predict the occurrence of the Spinetail Devil Ray (*Mobular mobular*). *Scientific Reports*, *10*(1), 18822.

Lindgren, F., & Rue, H. (2015). Bayesian spatial modelling with R-INLA. *Journal of Statistical Software*, *63*(19), 1–25.

López-Uribe, M. M., Ricigliano, V. A., & Simone-Finstrom, M. (2020). Defining pollinator health: A holistic approach based on ecological, genetic, and physiological factors. *Annual Review of Animal Biosciences*, *8*, 269–294.

Lott, C. A., Akresh, M. E., Costanzo, B. E., D'Amato, A. W., Duan, S., Fiss, C. J., Fraser, J. S., He, H. S., King, D. I., McNeil, D. J., & Stoleson, S. H. (2021). Do review papers on bird-vegetation relationships provide actionable information to forest managers in the eastern United States? *Forests*, *12*(8), 990.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *The Journal of Open Source Software*, *6*(60), 3139.

Lybrand, R. A., Fedenko, J., Tfaily, M., & Rao, S. (2020). Soil properties and biochemical composition of ground-dwelling bee nests in agricultural settings. *Soil Biology & Chemistry*, *84*(4), 1139–1152.

Martins, T. G., Simpson, D., Lindgren, F., & Rue, H. (2013). Bayesian computing with INLA: New features. *Computational Statistics and Data Analysis*, *67*, 68–83.

Mathis, C. L., McNeil, D. J., Jr., Lee, M. R., Grozinger, C. M., King, D. I., Otto, C. R. V., & Larkin, J. L. (2021). Pollinator communities var with vegetation structure and time since management within regenerating timber harvests of the central Appalachian Mountains. *Forest Ecology and Management*, *496*, 119373.

McGarigal, K., & Marks, B. J. (1995). FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 122.

Menz, M. H. M., Phillips, R. D., Winfree, R., Kremen, C., Aizen, M. A., Johnson, S. D., & Dixon, K. W. (2011). Reconnecting plants and pollinators: Challenges in the restoration of pollination mutualisms. *Trends in Plant Science*, *16*(1), 4–12.

Michener, C. D. (2007). *The bees of the world* (2nd ed.). The Johns Hopkins University Press.

Milam, J., Johnson, D. E., Andersen, J. C., Fassler, A. B., Narango, D. L., & Elkinton, J. S. (2020). Validating morphometrics with DNA barcoding to reliably separate three cryptic species of *Bombus* Cresson (Hymenoptera: Apidae). *Insects*, *11*, 669.

Milberg, P., Eriksson, V., & Bergman, K. O. (2021). Assemblages of flower-visiting insects in clear-cuts are rich and dynamic. *European Journal of Entomology*, *118*, 182–191.

Mitchell, T. B. (1960). *Bees of the eastern United States* (Vol. 1). North Carolina Agricultural Experiment Station.

Mitchell, T. B. (1962). *Bees of the eastern United States* (Vol. 2). North Carolina Agricultural Experiment Station.

Mola, J. M., Hemberger, J., Kochanski, J., Richardson, L. L., & Pearse, I. S. (2021). The importance of forests in bumble bee biology and conservation. *Bioscience*, *71*(12), 1234–1248.

Mortensen, D. A., Rauschert, E. S. J., Nord, A. N., & Jones, B. P. (2009). Forest roads facilitate the spread of invasive plants. *Invasive Plant Science and Management*, *2*(3), 191–199.

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., & Dorn, S. (2006). Quantitative pollen requirements of solitary bees:

Implications for bee conservation and the evolution of bee-flower relationships. *Biological Conservation*, *130*, 604–615.

Naugle, D. E., Allred, B. W., Jones, M. O., Twidwell, D., & Maestas, J. D. (2020). Coproducing science to inform working lands: The next frontier in nature conservation. *Bioscience*, *70*(1), 90–96.

Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and "mesophication" of forests in the Eastern United States. *Bioscience*, *58*(2), 123–138.

Odanaka, K. A., & Rehan, S. M. (2020). Wild bee distribution near forested landscapes is dependent on successional state. *Forest Ecosystems*, *7*, 26.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). Vegan: Community ecology package. Retrieved from https://CRAN.R-project.org/package=vegan

O'Neill, R. V., Krummel, J. R., Gardner, R. H., Sugihara, G., Jackson, B., DeAngelis, D. L., Milne, B. T., Turner, M. G., Zygmunt, B., Christensen, S. W., Dale, V. H., & Graham, R. L. (1988). Indices of landscape pattern. *Landscape Ecology*, *1*, 153–162.

Onuferko, T. M. (2018). A revision of the cleptoparasitic bee genus Epeolus Latreille for Nearctic species, north of Mexico (Hymenoptera, Apidae). *ZooKeys*, *755*, 1–185. https://doi.org/10.3897/zookeys.755.23939

Oram, R. J. (2018). Revision of the genus Hylaeus Fabricius (Hymenoptera: Colletidae) in Canada. MSc Thesis, University of Regina, Regina, 165.

Portman, Z. M., Bruninga-Socolar, B., & Cariveau, D. P. (2020). The state of bee monitoring in the United States: A call to refocus away from bowl traps and towards more effective methods. *Annals of the Entomological Society of America*, *113*(5), 337–342.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution*, *25*(6), 345–353.

Proctor, E., Nol, E., Burke, D., & Cribs, W. J. (2012). Responses of insect pollinators and understory plants to silviculture in northern hardwood forests. *Biodiversity and Conservation*, *21*, 1703–1740.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rivers, J. W., & Betts, M. G. (2021). Postharvest bee diversity is high but declines rapidly with stand age in regenerating douglas-fir forest. *Forest Science*, *67*, 275–285.

Roberts, H. P., King, D. I., & Milam, J. (2017). Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management*, *394*, 111–122.

Rue, H., Riebler, A., Sorbye, S. H., Illian, J. B., Simpson, D. P., & Lindgren, F. K. (2017). Bayesian computing with INLA: A review. *Annual Reviews of Statistics and Its Applications*, *4*-(March), 395–421.

Schaffers, A. P., Raemakers, I. P., Sýkora, K. V., & ter Braak, C. J. F. (2008). Arthropod assemblages are best predicted by plant species composition. *Ecology*, *89*(3), 782–794.

Schamberger, M., & O'Neil, J. (1986). Concepts and constraints of habitat model testing. In J. Verner, M. L. Morrison, & C. J. Ralph (Eds.), *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates* (pp. 5–10). University of Wisconsin Press.

Sheffield, C., Pindar, A., Packer, L., & Kevan, P. (2013). The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. *Apidologie*, *44*(5), 501–510.

Simpson, D. T., Weinman, L. R., Genung, M. A., Roswell, M., MacLeod, M., & Winfree, R. (2022). Many bee species, including rare species, are important for function of entire plant-pollinator networks. *Proceedings of the Royal Society B*, *289*, 20212689.

Simpson, G. L. (2009). Cocorresp: Co-correspondence analysis ordination methods. (R package version 0.4-3). Retrieved from http://cran.r-project.org/package=analogue

Song, C., Rohr, R. P., & Saavedra, S. (2017). Why are some plant-pollinator networks more nested than others? *Journal of Animal Ecology*, *86*(6), 1417–1424.

Tonietto, R. K., & Larkin, D. J. (2018). Habitat restoration benefits wild bees: A meta-analysis. *Journal of Applied Ecology*, *55*, 582–590.

Tschanz, P., Koestel, J., Volpe, V., Albrecht, M., & Keller, T. (2023). Morphology and temporal evolution of ground-nesting bee burrows created by solitary and social species quantified through X-ray imaging. *Geoderma*, *438*, 116655.

Tucker, E. M., & Rehan, S. M. (2019). Wild bees (Hymenoptera: Apoidea) of the Ossipee Pine Barrens. *Northeastern Naturalist*, *26*(2), 379–391.

Twerd, L., Sobieraj-Betlińska, A., & Szefer, P. (2021). Roads, railways, and power lines: Are they crucial for bees in urban woodlands? *Urban Forestry & Urban Greening*, *61*, 127120.

Ulyshen, M. D., Elliott, K., Scott, J., Horn, S., Clinton, P., Liu, N., Miniat, C. F., Caldwell, P., Oishi, C., Knoepp, J., & Bolstad, P. (2022). Effects of *Rhododendron* removal and prescribed fire on bees and plants in the southern Appalachians. *Ecology and Evolution*, *12*, e8677.

Ulyshen, M. D., Urban-Mead, K. R., Dorey, J. B., & Rivers, J. W. (2023). Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops. *Biological Reviews*, *98*, 1118–1141.

Urban-Mead, K. R., Muñiz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M., McArt, S. H., & Danforth, B. N. (2021). Bees in the trees: Diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management*, *482*, 118903.

USDA. (2022). *USDA annual strategic pollinator priorities report* (p. 80). United States Department of Agriculture, Office of the Chief Scientist. Retrieved from https://www.usda.gov/sites/default/files/documents/annual-pollinator-report-2022.pdf

USDA-NRCS. (2020). *Soil survey staff*. Ratural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Retrieved from https://websoilsurvey.nrcs.usda.gov/

USDA-USFS. (2015). *Pollinator-friendly best management practices for federal lands* (p. 52). United States Department of Agriculture—United States Forest Service. Retrieved from https://www.fs.usda.gov/wildflowers/pollinators/BMPs/documents/PollinatorFriendlyBMPsFederalLands05152015

USFWS. (2018). Conservation management guidelines for the rusty patched bumble bee (*Bombus affinis*). United States Department of the Interior—U.S. Fish and Wildlife Service. Version

1.6, 18. Retrieved from https://www.fws.gov/sites/default/files/documents/ConservationGuidanceRPBBv1_27Feb2018_0.pdf

Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect—Systematics and the agony of choice. *Biological Conservation*, *55*, 235–254.

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validationa and WAIC. *Statistical Computing*, *27*, 1413–1432.

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional rarity: The ecology of outliers. *Trends in Ecology & Evolution*, *32*(5), 356–367.

Walton, R. E., Sayer, C. D., Bennion, H., & Axmacher, J. C. (2021). Improving the pollinator pantry: Restoration and management of open farmland ponds enhances the complexity of plant-pollinator networks. *Agriculture, Ecosystems and Environment*, *320*, 107611.

Williams, N. M., & Lonsdorf, E. V. (2018). Selecting cost-effective plant mixes to support pollinators. *Biological Conservation*, *217*, 195–202.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*, *73*(1), 3–36.

Zitomer, R. A., Galbraith, S. M., Betts, M. G., Moldenke, A. R., Progar, R. A., & Rivers, J. W. (2023). Bee diversity decreases rapidly with time since harvest in intensively managed conifer forests. *Ecological Applications*, *33*, e2855.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*(3), 669–676.

SUPPORTING INFORMATION

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

How to cite this article: Cunningham-Minnick, M. J., Milam, J., Fassler, A., & King, D. I. (2024). Best management practices for bee conservation in forest openings. *Conservation Science and Practice*, e13231. https://doi.org/10.1111/csp2.13231