

PERSPECTIVE

The contribution of canopy samples to assessments of forestry effects on native bees

Joan Milam¹  | Michael Cunningham-Minnick¹  | Henry Patrick Roberts¹  | Christopher Buelow² | David I. King³ 

¹Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, Massachusetts, USA

²Massachusetts Natural Heritage and Endangered Species Program, Westborough, Massachusetts, USA

³USDA Forest Service Northern Research Station, University of Massachusetts Amherst, Amherst, Massachusetts, USA

Correspondence

Joan Milam Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA 01003, USA.

Email: jmilam@umass.edu

Funding information

Massachusetts Division of Fisheries and Wildlife, Grant/Award Number: DFW-2018-018

Abstract

Forest management is often practiced to enhance conditions for wildlife, including native bees. Evaluations of the effects of forest management on bees have shown that abundance and diversity are higher in newly created early-successional conditions. To date, studies have restricted sampling to the forest understory; however, recent research finds that bee abundance is as high or higher in forest canopies than in understories, suggesting that previous observations of substantially greater bee abundance and diversity in recently managed areas could be an artifact of incomplete sampling of the vertical gradient within forests. To examine the potential implications of sampling biases associated with the failure of previous studies to include canopy samples in comparisons of managed and unmanaged forests, we sampled bees within a recently harvested forest as well as the understory and canopy of adjacent unmanaged forest. Bee abundance and diversity were an order of magnitude higher in managed areas compared to the unmanaged forest, even when understory and canopy samples were combined. These results suggest that not sampling the canopy is inconsequential with respect to the broadly reported conclusion that managed areas support more abundant and diverse bee communities than surrounding forest cover.

KEYWORDS

abundance, Apoidea, barrens, blue vane trap, canopy, forest, richness

1 | INTRODUCTION

Reports of declining bee populations (Bartomeus et al., 2013; Potts et al., 2010), specifically bumble bees (Cameron et al., 2011; Carrié et al., 2017; Kerr et al., 2015), have caused widespread concern among

researchers and conservationists. Understanding the habitat needs of native bees is key to developing measures to conserve their populations (Neumüller et al., 2020; Tonietto & Larkin, 2017; Williams et al., 2010). Studies have reported higher bee abundance and species richness in disturbed areas, including powerline rights-of-way (Russell et al., 2018; Wagner et al., 2014; Wagner et al., 2019), thinned or cleared forest (Campbell et al., 2018;

This article will be of interest to forest managers and conservationists.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Conservation Science and Practice* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

Hanula et al., 2015; Lee et al., 2021; Mathis et al., 2021; Roberts et al., 2017), and managed barrens (Bried & Dillion, 2012; Winfree et al., 2007), likely due to the increased floral resources and nesting substrates newly made available (Milam et al., 2018; Tonietto & Larkin, 2017). As a result, management for early-successional conditions is increasingly practiced with the intention of promoting more abundant and diverse bee communities (Natural Resources Conservation Service, 2017).

The assumption that forest management activities enhance bee communities is based on studies that compare samples from recently harvested areas with samples from forest understories (Campbell et al., 2018; Rivers et al., 2018; Roberts et al., 2017; Taki et al., 2013). However, recent findings suggest that the forest canopy may support a more abundant and diverse bee community than the forest understory. For instance, Ulyshen et al. (2010) found that diversity and abundance of the bee community was greater in the canopy than forest floor in the southeastern United States, with the abundance of one species reaching nearly 40 times that of the forest floor. Similarly, Campbell et al. (2018), Cunningham-Minnick and Crist (2020), Ulyshen et al. (2020), and Urban-Mead et al. (2021) reported diverse and abundant bee communities within forest canopies in the eastern United States. These studies emphasize the potential importance of the canopy for bees within temperate forests, which suggests that sampling the understory alone may not adequately reflect forest bee communities. If the current understanding that open-canopy habitats support more abundant and diverse bee communities than forests is simply an artifact of insufficient sampling of the vertical gradient in forests then efforts to promote bee communities through management practices that create open-canopy conditions may be misguided (Roberts et al., 2017).

The goal of this study was to examine whether sampling the forest canopy in addition to the understory could alter conclusions regarding the value of using forest management to enhance bee communities. Our specific objectives were to (a) compare bee communities between managed areas and adjacent unmanaged forest understories to illustrate the conventional approach researchers have used to gauge the relative value of management for bees and (b) sample bees in forest canopies to determine whether the addition of canopy bees changes the perceived value of unmanaged forest versus managed forest habitat for native bees. Because forest management activities are routinely challenged based on perceived deleterious impacts on biodiversity (King & Schlossberg, 2014), managers need robust scientific knowledge to guide their practices and defend them when necessary.

2 | METHODS

This study was conducted in 2018 within the Patrill Hollow section of the Muddy Brook Wildlife Management Area, in Hardwick, Massachusetts (Worcester Co.; 42.3°, −72.2°; Figure 1). The historic land use of the study site was timberland, which resulted in 60–80% of the land being harvested at any given time, as was typical with most of the forest in this region. The last major timber harvest occurred here in the early 1900s, at which point the land was left to regenerate to a typical mixed oak-pine forest. From 2014 to 2017, approximately one third of the 784 ha area was treated with whole-tree harvest and prescribed fire to reestablish barrens communities retaining mature tree oak (*Quercus* spp.), pitch pine (*Pinus rigida*), and scrub oak (*Quercus ilicifolia*). Prior to restoration, this site was a typical transition hardwood forest with a heavy influence of white pine (*Pinus strobus*) in all strata. After treatment, managed areas featured scattered pitch pine, retained tree oaks, scrub oaks, heaths (*Vaccinium* spp.), warm season grasses (e.g., *Schizachyrium scoparium*), and composites (e.g., *Aster* and *Solidago* spp.) and areas of bare mineral soil. The surrounding forest primarily consisted of red oak (*Q. rubra*), white oak (*Quercus alba*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), shagbark hickory (*Carya ovata*), white pine (*P. strobus*), and birch (*Betula* spp.).

We sampled bees at 20 points distributed throughout the study area that were established in 2015 prior to restoration, such that each point within a managed area was paired with a point in the forest (Figure 1). The mean distance of points in managed areas from edges was 83.7 m (SD = 41.4; range = 30.7 m–148.8 m), and the distance of points within forest to edge was on average 88.8 m (SD = 43.0; range = 41.4 m–58.7 m) from edges. Mean distance between neighboring points in managed areas was 231.1 m (SD = 25.0; range = 194.0 m–271.1 m) and the average distance between neighboring points within the forest was 278.6 m apart (SD = 92.11; range = 116.7–404.8 m). The distance between adjacent sample points was greater than the average flight distance of most bee species (Hofmann et al., 2020), and thus provided a reasonable level of independence among sample points.

At every point, we mounted a blue vane trap (SpringStar Inc., Woodinville, WA) on a 1-m tall wooden post and used propylene glycol diluted with soapy water to collect bees. Within the canopy of each forest point, we suspended a blue vane trap in the mid-to-lower canopy following the methods of Ulyshen et al. (2010). We selected blue vane traps because they sample a high diversity of bees (Gibbs et al., 2017), particularly in open and wooded habitats (Kimoto et al., 2012; Rao & Stephen, 2010; Stephen & Rao, 2007), and were relatively

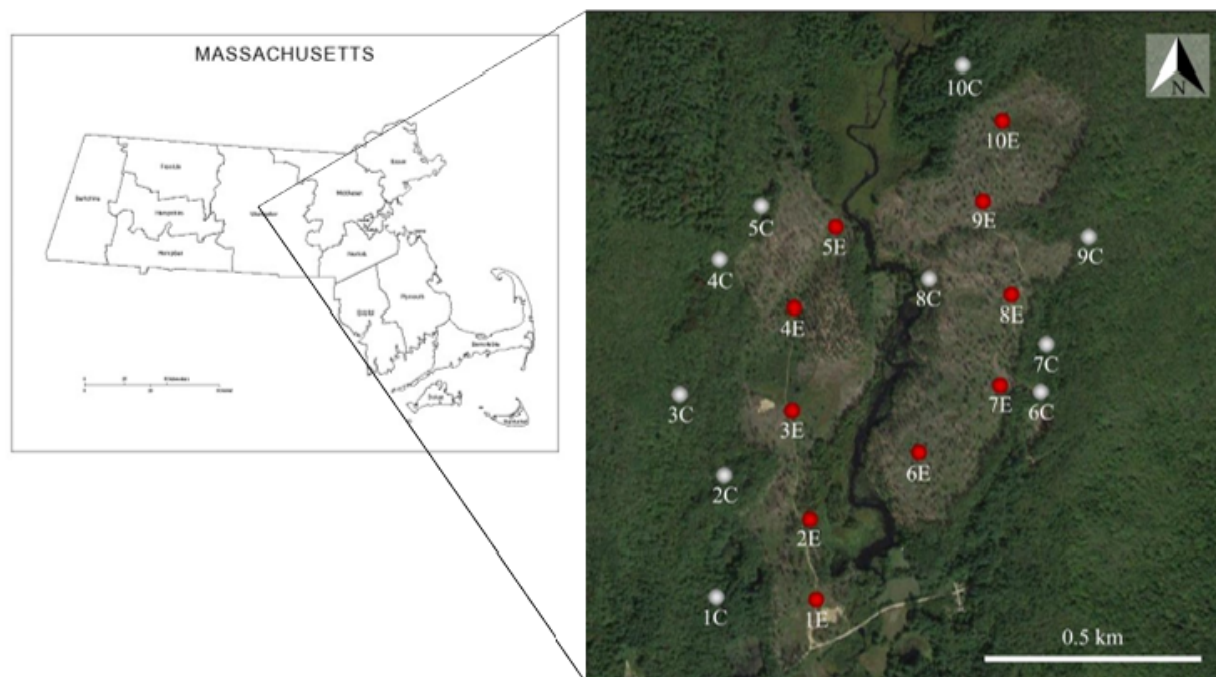


FIGURE 1 Map of the Patrill Hollow section of the Muddy Brook Wildlife Management Area (Worcester County, MA) in which experimental plots of forest management treatments and controls were sampled

efficient to deploy. Other canopy studies had used blue vane traps (Cunningham-Minnick & Crist, 2020), bucket traps (Ulyshen et al., 2010), bowl traps (Campbell et al., 2018), or a combination of methods (Urban-Mead et al. 2021). The choice of collecting method influences bee captures near the ground (Portman et al., 2020); however, there have been no comprehensive comparisons of bee captures among trapping methods, including blue vane traps, in prior canopy studies. Since we employed the same collection methods in all conditions, any biases would not affect the relative abundance of species, which is sufficient for our purposes, although they might affect comparisons of our results with other studies. Canopy traps were hung on average 8.63 m above the ground ($SD = 1.72$; range = 6–13 m).

The bee community was sampled in managed areas during three periods in 2018: May 23–28, July 11–16, and September 17–20. Forest canopy and understory traps remained deployed continuously from May 3 to September 20, and specimens were collected a total of nine times: May 23 and 28, June 12, July 11 and 16, August 10 and 31, and September 17 and 20. Canopy trees and spring ephemerals were both in flower during the May sampling period. Bees were identified by JM to species or morphospecies using published keys (Gibbs, 2011; Gibbs et al., 2013; LaBerge, 1973, 1980, 1987, 1989;

Mitchell, 1960, 1962) and the online source [Discoverlife.org](https://www.discoverlife.org) (Ascher & Pickering, 2020). Due to unresolved taxonomy, most bidentate specimens of the *Nomada* genus were lumped as *Nomada bidentate* group. Male *Hylaeus affinis* and *modestus* specimens were identified to species. Identification assistance was provided by M. F. Veit with *Nomada*, *Sphecodes*, and male *Andrena* identifications. Voucher specimens are currently held in the research collection of JM.

2.1 | Statistical analysis

We used generalized linear mixed effects models with the *glmmTMB* package (Brooks et al., 2017) to relate bee abundance, extrapolated species richness, and diversity (Shannon's diversity; Jost, 2006) to environmental covariates. We used a negative binomial error distribution to model bee abundance and a quasi-Poisson error for species richness and diversity. Extrapolated species richness was calculated using the *estimateR* function while correcting for small sample size with the *vegan* package (Okansen et al., 2019). Two sets of models were built: the first only included bees sampled within managed areas and the forest understory, while the second set of models included bees sampled within managed

TABLE 1 Number of bees included in analyses that compared the three overlapping sampling periods among managed, forest floor, and forest canopy habitats, as well as all bees captured throughout the year (nine sampling periods) on the forest floor and in the canopy at points

Species	Managed (3)	Floor (3)	Canopy (3)	Floor (9)	Canopy (9)
<i>Agapostemon sericeus</i>	1				
<i>Agapostemon texanus</i>	3			1	
<i>Agapostemon virescens</i>	2			4	1
<i>Andrena carolina</i>				1	1
<i>Andrena carlini</i> ^a		1		2	1
<i>Andrena mandibularis</i>					1
<i>Andrena miserabilis</i>					1
<i>Andrena nivalis</i>				1	
<i>Andrena rufosignata</i> ^a				2	
<i>Andrena rugosa</i> ^a				2	1
<i>Andrena thaspii</i>				1	1
<i>Andrena vicina</i>				1	
<i>Apis mellifera</i>	1				
<i>Augochlora pura</i> ^a	4	7	2	28	13
<i>Augochlorella aurata</i>	1	1		4	1
<i>Bombus bimaculatus</i> ^b	93	3	5	7	16
<i>Bombus fervidus</i>	1				
<i>Bombus griseocolis</i>				1	
<i>Bombus impatiens</i> ^a	68	5	5	51	42
<i>Bombus perplexus</i>		1		2	
<i>Bombus sandersoni</i>	24	1	1	2	3
<i>Bombus vagans</i> ^a	1			9	1
<i>Ceratina calcarata</i> ^b	2	1	1	5	4
<i>Ceratina dupla</i> ^b	2				
<i>Ceratina mikmaqi</i>				1	
<i>Colletes simulans armatus</i>					1
<i>Halictus ligatus</i>	2				
<i>Halictus rubicundus</i> ^b	5			4	2
<i>Hylaeus mesillae</i>	1				
<i>Hylaeus modestus</i>				1	
<i>Lasioglossum acuminatum</i>	2				1
<i>Lasioglossum birkmanni</i>				2	
<i>Lasioglossum bruneri</i> ^b	3			3	
<i>Lasioglossum coeruleum</i> ^a		6	1	15	9
<i>Lasioglossum coriaceum</i> ^a	1	2		21	9
<i>Lasioglossum cressonii</i> ^a	10			8	1
<i>Lasioglossum katherineae</i>				1	
<i>Lasioglossum leucomus</i>				1	
<i>Lasioglossum leucozonium</i>	3			1	
<i>Lasioglossum nelumbonis</i>	6			3	
<i>Lasioglossum nigroviride</i>	1			2	

TABLE 1 (Continued)

Species	Managed (3)	Floor (3)	Canopy (3)	Floor (9)	Canopy (9)
<i>Lasioglossum oblongum</i> ^a	1			3	
<i>Lasioglossum pectorale</i> ^b	2			4	
<i>Lasioglossum quebecense</i> ^a	1	2		15	6
<i>Lasioglossum subviridatum</i>				1	
<i>Lasioglossum versans</i> ^a			1	1	1
<i>Lasioglossum versatum</i>	14			4	2
<i>Megachile latimanus</i>	1				
<i>Megachile mendica</i> ^b					1
<i>Megachile relativa</i> ^b				2	
<i>Melissodes bimaculatus</i>	1			1	
<i>Melissodes desponsus</i>	1				
<i>Melissodes druriellus</i>				5	
<i>Nomada bidentate-group</i> ^a				3	
<i>Nomada maculata</i> ^a				1	
<i>Osmia atriventris</i> ^a	7			12	3
<i>Osmia cornifrons</i> ^a				4	
<i>Osmia pumila</i> ^a	1	1		13	6
<i>Osmia taurus</i> ^a				8	1
<i>Osmia virga</i> ^a				1	
<i>Peponapis pruinosa</i>	17			3	
Total	283	31	16	268	130

Note: Species are alphabetically listed.

^aForest associated bees.

^bHabitat generalist bees as designated by Smith et al. (2021).

areas, but pooled bees captured in the forest understory and the forest canopy. Only data from sampling periods shared between managed and forest points were used in models. We included habitat type (managed vs. unmanaged forest), distance to nearest water, distance to forest edge, and their interaction as fixed effects and used Akaike Information Criteria corrected for small sample sizes (AICc) for model selection with the *AICcmodavg* package (Mazerolle, 2020). We measured distance variables using aerial imagery (dated September 2017) in Google Earth Pro v. 7.3.3.7786 (© 2021 Google). We included a nested random effect of each unique point within a site in all models to address the paired-point design and account for the uneven sampling between points of each site. Models included an offset term to account for the differences in days between sampling periods. Marginal significance of habitat type was determined using likelihood ratio tests (*anova* function) models with and without the habitat type predictor and evaluated using the *r2_nakagawa* function in the *performance* package (Lüdtke et al., 2021). Only the best

model is discussed. Post-hoc Tukey tests were performed with the *glht* function in the *multcomp* package (Hothorn et al., 2008) with a “holm” correction to determine significance of each habitat type comparison.

To visualize differences in bee species composition among forest strata and habitat type, we created a non-metric multidimensional scaling (NMDS) plot of the Bray-Curtis dissimilarities of square-rooted transformed relative species abundances within each point using the *metaMDS* function in the *vegan* package. We then performed a PERMANOVA using the *pairwiseAdonis* function with the “bray” simulation method and Bonferroni correction in the *pairwiseAdonis* package (Arbizu, 2017) on the same standardized species matrix to determine significance. We also performed an NMDS and a PERMANOVA using data from all nine sample periods to compare bee communities between forest understory and canopy strata. All analyses were performed in the R programming language v. 4.0.3 (R Core Team, 2020) and all graphics were created with the *ggplot2* package (Wickam, 2016).

Response	Chi-squared	<i>p</i> -value	Marginal R^2	Conditional R^2
Abundance	35.8	<.0001	0.527	0.527
Abundance	32.5	<.0001	0.449	0.449
Extrap. species richness	29.4	<.0001	0.369	0.383
Extrap. species richness	25.9	<.0001	0.315	0.327
Shannon's diversity	33.1	<.0001	0.438	0.448
Shannon's diversity	31.6	<.0001	0.398	0.398

TABLE 2 Summary of best-fitting generalized linear mixed effects models, including Chi-squared statistic from likelihood ratio tests, associated *p*-value, and marginal and conditional pseudo- R^2 of the model with and without the “habitat type” predictor

Note: Models are listed by bee abundance, extrapolated species richness, and Shannon's diversity responses; shaded rows include canopy bees within the response while non-shaded rows do not include canopy bees.

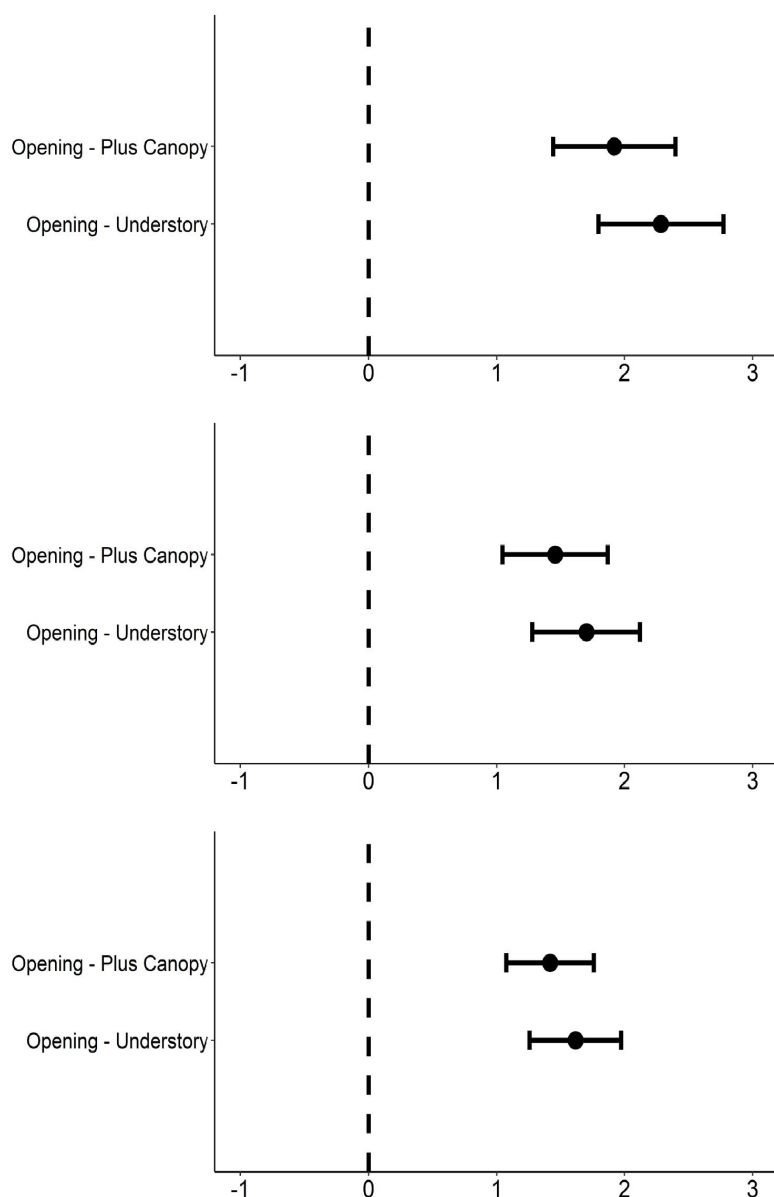


FIGURE 2 Means with 95% CI of post-hoc Tukey comparisons between shrubland (Opening) and forest bees with (Plus Canopy) and without (Understory) canopy samples for abundance (top), extrapolated species richness (middle) and Shannon's diversity (bottom) responses. The relationship between shrubland and forest bees is not significant if the 95% CI includes 0

3 | RESULTS

We captured a total of 681 individual bees representing 62 described species (Table 1). Six additional bees could

not be identified due to either body damage (five bees) or taxonomic difficulties (one; Table S1).

Best performing models for bee abundance, extrapolated species richness, and Shannon's diversity included

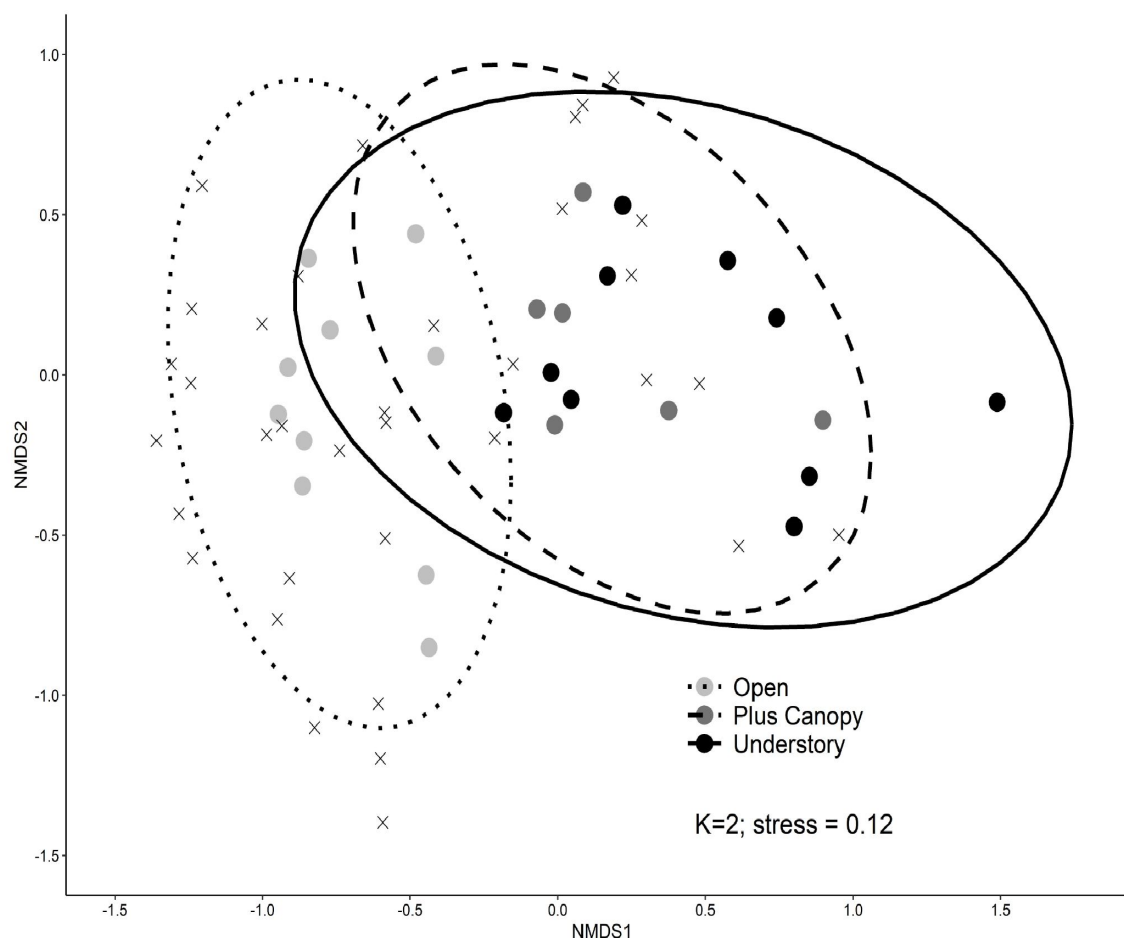


FIGURE 3 Non-metric multidimensional scaling and 95% confidence ellipses of Bray–Curtis dissimilarity matrix comparing bee assemblages standardized by site in shrubby openings (light gray circles; dotted lines), forest understory and canopy (dark gray circles; dashed lines), and forest understory (black circles; solid lines) habitat. Species scores are represented by “X”

only habitat type, which explained 32%–53% of the variation in the data (Table 2). Bee abundance, species richness, and Shannon's diversity were significantly greater in managed areas than in forest, and there was no change in these relationships when canopy bees were included or excluded (Figure 2; Table S2).

Species composition of the bee community differed between managed areas and forest with ($F_{\text{pseudo}}[1] = 9.49$, $p_{\text{adj}} < .005$) and without ($F_{\text{pseudo}}[1] = 7.81$, $p_{\text{adj}} < .005$) canopy samples (Figure 3). Bee species composition did not differ between the forest understory and the pooled assemblage of the forest understory and forest canopy ($F_{\text{pseudo}}[1] = 0.24$, $p_{\text{adj}} = .98$; Figure S1), though the composition of canopy and understory bees were different when considered separately ($F_{\text{pseudo}}[1] = 2.11$, $p_{\text{adj}} < .05$; Figure S2).

4 | DISCUSSION

Recent revelations of remarkably high bee abundance and diversity in temperate forest canopies (Cunningham-

Minnick & Crist, 2020; Ulyshen et al., 2010; Ulyshen et al., 2020; Urban-Mead et al., 2021) have raised critical questions about whether widespread biases in forest bee research—due to insufficient vertical sampling—have inaccurately portrayed forest bee communities as depauperate relative to other habitat types (e.g., Roberts et al., 2017). Our study showed that the general pattern of greater bee numbers in open-canopy, early-successional areas compared to forest was apparent whether or not forest canopies were sampled. These findings suggest that previous evaluations that reported greater bee abundance, species richness, and diversity in forest openings based on comparisons with forest understory bee communities are generally correct despite the omission of samples from the forest canopy. Thus, this study supports the widely held view that forest management enhances bee communities.

Differences in community composition indicated that the greater bee diversity in managed areas was driven by bee species associated with open habitats. These included open nesting sites in sun-exposed areas for solitary

ground-nesting species from genera including *Lasioglossum* and *Halictus* and stem nesting bees such as the *Ceratina*. Open sandy soils associated with sandplain communities also support several ground nesting genera such as *Andrena*, *Lasioglossum*, and *Halictus*. Forest-associated species including *Augochlora pura* (Smith), *Lasioglossum coeruleum* (Robertson), *Lasioglossum coriaceum* (Smith), and *Lasioglossum quebecense* (Crawford) were more abundant in traps within forest. Overall, the composition of the bee assemblage in the managed areas had transitioned into a distinct community that differed from the forest.

Although the inclusion of the canopy samples in the analyses did not alter the fact that bee abundance and extrapolated species richness were higher in harvested areas than forest, we did observe differences in bee communities between forest strata. The overall forest bee community was compositionally nested within that of the understory, suggesting that the differences we found in species composition between the forest canopy and understory were likely driven by species with low abundances that did not comprise much of the overall community. This finding contrasts with Ulyshen et al. (2010) and Cunningham-Minnick and Crist (2020) and Campbell et al. (2018), who found some species (i.e., *Augochlora pura*) in much higher numbers in the canopy. These differences could be explained by bees using resources within forest strata differently throughout the year as suggested by Cunningham-Minnick and Crist (2020). We did not measure temporal changes in resource availability since it was outside the scope of our question. However, addressing factors that may affect differences in vertical stratification of bee communities throughout the year would provide forest managers with a higher resolution perspective of how forest bees use canopy resources.

We suspended canopy traps “above the lowest leaf-bearing branch in each tree” following Ulyshen et al., (2010); however, the height of our traps was lower than other canopy studies (Cunningham-Minnick & Crist, 2020; Ulyshen et al., 2010; Ulyshen et al., 2020; Urban-Mead et al., 2021). Nevertheless, the traps were high enough to reveal a contrast with the forest floor samples, and reflected an assemblage of the bee community that was unsampled by the traps on the forest floor, which was the objective of our study. Moreover, Cunningham-Minnick and Crist (2020) reported no difference in species richness between traps suspended 7–10 m high (similar to the height of our traps) and canopy traps suspended 13–16 m high, further indicating that our sample heights were sufficient for sampling the canopy. Furthermore, our study was conducted on a restored barrens, and since barrens communities are known to support distinct bee communities (Bried & Dillion, 2012),

one could argue that our findings might not pertain to other forest systems. We maintain that these results are generally applicable since the pre-treatment forest consisted of a mixed hardwood forest typical of the region, which was oak-dominated, as were the forests where vertical stratification of bees was demonstrated by Ulyshen et al. (2010) and Campbell et al. (2018). Finally, we can only speculate what bees are doing in the canopy, however, others have suggested they are seeking forage from tree flowers and/or nesting opportunities in dead limbs or trunks (Cunningham-Minnick & Crist; Ulyshen et al., 2010; Urban-Mead et al., 2021).

5 | CONCLUSION

Concern for native bees is widespread, and many agencies and organizations are tasked with undertaking measures to promote bee abundance and diversity through habitat management, and to ensure that forest practices are undertaken to address that other objectives are consistent with bee conservation. Since evaluations of forest management effects on bees have been based on samples from forest understories, prior to this study it was uncertain whether high numbers of bees in managed forests relative to unmanaged forests were due to the failure of prior studies to account for bees in the forest canopy (Roberts et al., 2017). Thus, practitioners had reason to be uncertain about the effects of forest management on bees, and this uncertainty left forest management practices open to challenge and controversy. Our study demonstrates that comparisons of bee communities between managed and unmanaged forests based on samples from the forest understory accurately reflect the effects of management, despite reports that bee communities in forests are vertically stratified. Thus, managers are justified in implementing forest management to increase bee diversity and abundance, and can confidently evaluate their outcome by comparing samples of bee communities between managed areas and the forest understory.

ACKNOWLEDGMENTS

The authors thank three anonymous reviewers for their detailed comments that improved the manuscript. We also thank A. Fassler, A. Sroka-Rivera, P. Hynes, J. Day, K. King, B. Joyce for field assistance, to D. Blanton and K. Elowe for their help setting up traps in the canopy, to B. Hawthorne for his site knowledge, to A. Fassler for assistance with specimen preparation, and to M. F. Veit for assistance with species identification. Funding for this project was provided by the Massachusetts Division of Fisheries and Wildlife Project DFW-2018-019. This research was supported by the Massachusetts Division of

Fisheries and Wildlife Westborough, MA. Finally, we acknowledge that our field site is on unceded land belonging to the people of the Nipmuc Nation.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Joan Milam and David King: Conceived the idea, designed the research, and acquired the data. Michael Cunningham-Minnick: Analyzed the data, prepared figures and tables, and interpreted the analyses with input from all authors. Joan Milam and David King: Drafted the manuscript with input from all authors. All authors contributed to critically editing and revising the manuscript.

DATA AVAILABILITY STATEMENT

Data supporting the results of the study can be accessed upon reasonable request from the corresponding author.

ORCID

Joan Milam  <https://orcid.org/0000-0002-8056-1304>

Michael Cunningham-Minnick  <https://orcid.org/0000-0002-4478-4113>

Henry Patrick Roberts  <https://orcid.org/0000-0001-7846-6335>

David I. King  <https://orcid.org/0000-0001-6827-0398>

REFERENCES

- Arbizu, P. (2017). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0.1.
- Ascher, J. S., & Pickering, J. (2020). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Draft-55. Retrieved from http://www.discoverlife.org/mp/20q?guide=Apoidea_species.
- Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D., Hedtke, S. M., & Winfree, R. (2013). Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 4656–4660. <https://doi.org/10.1073/pnas.1218503110>
- Bried, J. T., & Dillion, A. (2012). Bee diversity in scrub oak patches 2 years after mow and herbicide treatment. *Insect Conservation and Diversity*, 5, 237–243. <https://doi.org/10.1111/j.1752-4598.2011.00154.x>
- Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400. <https://doi.org/10.5167/uzh-148918>
- 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. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 662–667.
- Campbell, J. W., Vigueira, P. A., Vigueira, 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, 299–306. <https://doi.org/10.1093/forsci/afx008>
- Carrié, R., Andrieu, E., Cunningham, S. A., Lentini, P. E., Loreau, M., & Ouin, A. (2017). Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. *Ecography*, 40, 85–97.
- 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.
- Gibbs, J. (2011). Revision of the metallic Lasioglossum (Dialictus) of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa*, 3073, 1–216.
- Gibbs, J., Joshi, N. K., Wilson, J. K., Rothwell, N. L., Powers, K., Haas, M., Gut, L., Biddinger, D. J., & Isaacs, R. (2017). Does passive sampling accurately reflect the bee (Apoidea: Anthophila) communities pollinating apple and sour cherry orchards? *Environmental Entomology*, 46, 579–588.
- Gibbs, J., Packer, L., Dumesh, S., & Danforth, B. N. (2013). Revision and reclassification of Lasioglossum (Evylaeus), L. (Hemihalictus) and L. (Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa*, 3672, 1–117.
- Hanula, J. L., Horn, S., & O'Brien, J. J. (2015). Have changing forests conditions contributed to pollinator decline in the south-eastern United States. *Forest Ecology and Management*, 348, 142–152.
- Hofmann, M. M., Fleischmann, A., & Renner, S. S. (2020). Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. *Journal of Hymenoptera Research*, 77, 105–117.
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375.
- Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., Rasmont, P., Schweiger, O., Colla, S. R., Richardson, L. L., Wagner, D. L., Gall, L. F., Sikes, D. S., & Pantoja, A. (2015). Climate change impacts on bumblebees converge across continents. *Science*, 349(6244), 177–180.
- Kimoto, C., DeBano, S. J., Thorp, R. W., Rao, S., Stephen, W. P., & Jeanne, R. (2012). Investigating temporal patterns of a native bee community in a remnant north American bunchgrass prairie using blue vane traps. *Journal of Insect Science*, 12, 1–23.
- King, D. I., & Schlossberg, S. (2014). Synthesis of the conservation value of the early-successional stage in forests of eastern North America. *Forest Ecology and Management*, 324, 186–195.
- 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. (1987). A revision of the bees of the genus *Andrena* of the Western hemisphere. Part XII. Subgenera *Leucandrena*, *Ptilandrena*, *Scoliadrena*, and *Melandrena*. *Transactions of the American Entomological Society*, 112, 191–248.
- LaBerge, W. E. (1989). A revision of the bees of the genus *Andrena* of the Western hemisphere. Part XIII. Subgenera *Simandrena* and *Taeniandrena*. *Transactions of the American Entomological Society*, 115, 1–56.
- Lee, M. R., McNeil, D. J., Jr., Mathis, C. L., Grozinger, C. M., & Larkin, J. L. (2021). Microhabitats created by log landings support abundant flowers and insect pollinators within regenerating mixed-oak stands in the central Appalachian Mountains. *Forest Ecology and Management*, 497, 119472.
- 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. *Journal of Open Source Software* 2021;6(60). <https://doi.org/10.31234/osf.io/vtq8f>.
- Mathis, C. L., McNeil, D. J., Jr., Lee, M. R., Grozinger, C. M., King, D. I., Otto, C. R., & Larkin, J. L. (2021). Pollinator communities vary with vegetation structure and time since management within regenerating timber harvests of the central Appalachian Mountains. *Forest Ecology and Management*, 496, 119373.
- Mazerolle, M. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.1. Retrieved from <https://cran.r-project.org/package=AICcmodavg>.
- Milam, J. C., Litvaitis, J. A., Warren, A., Keirstead, D., & King, D. I. (2018). Bee assemblages in managed early-successional habitats in southeastern New Hampshire. *Northeastern Naturalist*, 25, 437–459.
- 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.
- Natural Resources Conservation Service. (2017). Vermont—Biology Technical Note #4. Retrieved from https://www.nrcs.usda.gov/wps/PA_NRCSCConsumption/download?cid=nrcseprd1431219&ext=pdf.
- Neumüller, U., Burger, H., Krausch, S., Blüthgen, N., & Ayasse, M. (2020). Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities. *Landscape Ecology*, 35, 2209–2224.
- Okansen, 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. Wagner, H. (2019). Vegan: Community ecology package. R package version 2.5-6. Retrieved from <https://CRAN.R-project.org/package=vegan>.
- Portman, Z. M., Bruninga-Socular, 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, 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, 345–353.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Rao, S., & Stephen, W. P. (2010). Abundance and diversity of native bumble bees associated with agricultural crops: The Willamette Valley experience. *Psyche*, 2010, 9.
- Rivers, J. W., Mathis, C. L., Moldenke, A. R., & Betts, M. G. (2018). Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest. *Global Change Biology Bioenergy*, 10, 1757–1693.
- Roberts, H., King, D., & Milam, J. (2017). Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management*, 394, 111–122.
- Russell, K. N., Russell, G. J., Kaplan, K. L., Mian, S., & Kornbluth, S. (2018). Increasing the conservation value of powerline corridors for wild bees through vegetation management: An experimental approach. *Biodiversity and Conservation*, 27, 2541–2565.
- Smith, C., Harrison, T., Gardner, J., & Winfree, R. (2021). Forest-associated bee species persist amid forest loss and regrowth in eastern North America. *Biological Conservation*, 260, 109202.
- Stephen, W. P., & Rao, S. (2007). Sampling native bees in proximity to a highly competitive food resource (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society*, 80, 369–376.
- Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T., & Makino, S. I. (2013). Succession influences wild bees in a temperate forest landscape: The value of early successional stages in naturally regenerated and planted forests. *PLoS One*, 8, e56678.
- Tonietto, R. K., & Larkin, D. J. (2017). Habitat restoration benefits wild bees: A meta-analysis. *Journal of Applied Ecology*, 55, 582–590.
- Ulyshen, M. D., Horn, S., & Hanula, J. L. (2020). Effects of Chinese privet on bees and their vertical distribution in riparian forests. *Forest Science*, 66, 416–423.
- Ulyshen, M. D., Soon, V., & Hanula, J. (2010). On the vertical distribution of bees in a temperate deciduous forest. *Insect Conservation and Diversity*, 3, 222–228.
- 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. <https://doi.org/10.1016/j.foreco.2020.118903>
- Wagner, D. L., Ascher, J. S., & Bricker, N. K. (2014). A transmission right-of-way as habitat for wild bees (Hymenoptera: Apoidea: Anthophila) in Connecticut. *Annals of the Entomological Society of America*, 107, 1110–1120. <https://doi.org/10.1603/AN14001>
- Wagner, D. L., Metzler, K. J., & Frye, H. (2019). Importance of transmission line corridors for conservation of native bees and other wildlife. *Biological Conservation*, 235, 147–156. <https://doi.org/10.1016/j.biocon.2019.03.042>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143, 2280–2291. <https://doi.org/10.1016/j.biocon.2010.03.024>

Winfree, R., Griswold, T., & Kremen, C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, 21, 213–223.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Milam, J., Cunningham-Minnick, M., Roberts, H. P., Buelow, C., & King, D. I. (2022). The contribution of canopy samples to assessments of forestry effects on native bees. *Conservation Science and Practice*, 4(6), e12690. <https://doi.org/10.1111/csp2.12690>