# Abundant, distinct, and seasonally dynamic bee community in the canopy-aerosphere interface above a temperate forest

Michael Cunningham-Minnick[1], Milam J[1], Kane B[1], Henry Roberts[1], and King DI[2]

[1]University of Massachusetts Amherst
[2]USDA Forest Service Northern Research Station

September 20, 2022

## Abstract

1. Our understanding of how bees (Apoidea) use temperate forests is largely limited to sampling the understory and forest floor. Studies over the last decade have demonstrated that bee communities are vertically stratified within forests, yet the ecology of bee assemblages immediately above the canopy, the canopy-aerosphere interface, remains unexplored. 2. We sampled and compared bee communities above the canopy of a temperate forest to the understory (1 m), midstory (10 m), and canopy (20 m) on the campus of the University of Massachusetts, in Amherst, Massachusetts, USA from April – August, 2021. 3. Overall, we found that assemblages above the canopy had more bees than in the understory, were distinct in composition from all other strata, and included the greatest proportion of unique species. Bee abundance and species richness were highest in the understory throughout the spring (April and May) and decreased as the season progressed, while bee abundance and species richness at higher strata increased into the summer months. We also found that bees with preferences to nest in moist and rotting wood were largely restricted to canopy and midstory strata. 4. We conclude that bee assemblages occupying the space above the forest canopy are abundant and diverse, and their unique composition suggests that this canopy-aerosphere interface plays an additional role in the bee community of temperate forests. Alternatively, our findings question how forest bee communities should be defined while highlighting the need for research on fundamental processes governing species stratification in and above the canopy.

## Introduction

Studies examining bee communities within temperate forests have largely restricted sampling to the understory (Milam et al., 2022) with the presumption that most bees remain in this lower stratum. However, recent evidence indicates that bees are vertically distributed within temperate forests (e.g., Ulyshen et al., 2010; Urban-Mead et al., 2021), suggesting a potentially large knowledge gap in the ecological role of these important forest pollinators. Despite this revelation, research regarding the vertical distribution of bees and other pollinators within forests is further limited by the difficulty of sampling the high canopy (Cannon et al., 2021; Cunningham-Minnick et al., *in press* ). Current sampling methods reach into the canopy (e.g., Maguire et al., 2014; Ulyshen et al., 2010), but the canopy-aerosphere interface — a potentially ecologically important area for bees due to copious floral resources available — remains unexplored in temperate forests (Nakamura et al., 2017; Urban-Mead et al., 2021). Thus, our understanding of pollinator ecology within forests will remain incomplete until the distribution of forest bee communities along the entire vertical gradient of vegetation structure is documented. Moreover, if the current understanding of bee abundance and diversity patterns in forests are inaccurate, forest management recommendations for bee conservation may be biased or potentially misguided (Milam et al., 2022; Urban-Mead et al., 2021), further highlighting the importance of understanding the distribution of bee communities along the full vertical gradient of temperate forests, including the canopy-aerosphere interface.

Bees are expected to be spatially and temporally distributed throughout temperate forests in response to

local resource availability. Studies have demonstrated that forest bee communities are diverse and vertically stratified on sun-exposed edges (e.g., Cunningham-Minnick & Crist, 2020), within forests near edges (e.g., Urban-Mead et al., 2021), and within the forest interior (e.g., Campbell et al., 2018; Milam et al. 2022; Ulyshen et al., 2010) when floral resources of the forest are available, as well as when they are not. Inferences and observations further suggest that bees will both forage on floral resources and nest at different vertical strata within forests (Cunningham-Minnick & Crist, 2020; MacIvor et al 2014; Russo & Danforth, 2017; Smith et al., 2019; Sobek et al., 2009; Urban-Mead et al., 2021; Wood et al. 2018). For instance, Smith et al. (2019) and Wood et al. (2018) found support through pollen analyses that forest bee communities rely upon floral resources of dominant tree species. Yet floral resources of herbaceous and woody species within temperate forests are typically limited to a spring and early summer phenology, which has been correlated to fewer late-season bees in the forest understory (Cunningham-Minnick & Crist, 2020). Alternatively, studies have found more bees in the forest herbaceous layer during spring and more bees in the canopy during the summer (Cunningham-Minnick & Crist, 2020; Ulyshen et al., 2010), suggesting that the distribution of forest bees may also shift out of the understory and into the higher vertical strata of the forest as the year progresses. However, no studies have examined the bee fauna in the aerosphere above the forest canopy. Thus, we undertook this study to determine the extent to which bees occupy the open air above the forest canopy, how the bee assemblages of this canopy-aerosphere interface compare in abundance, species richness, and composition with assemblages at other strata, and how these patterns change with seasonal phenology.

## Material and Methods

We selected two trees 50 m apart in each of two forest patches on the campus of the University of Massachusetts-Amherst in Amherst, Mass., USA (Fig. A1); each pair of trees consisted of a northern red oak (*Quercus rubra* L.) and a red maple (*Acer rubrum* L.). Both sites were in USDA Hardiness Zone 5a and were characterized by an herbaceous stratum of ferns (e.g., *Dennstaedtia punctilobula* (Michx.) T.Moore, *Polystichum acrostichoides* (Michx.) Schott), wild sarsaparilla (*Aralia nudicaulis* L.), white wood aster (*Eurybia divaricata* (L.) G.L.Nesom), star flower (*Lysimachia borealis* (Raf.) U.Manns & Anderb), Canada mayflower (*Maianthemum canadense* Desf.), partridge berry (*Mitchella repens* L.), and Solomon's seal (*Polygonatum spp* .). The understory of these sites consisted of brambles (*Rubus spp.* ), poison ivy (*Toxicodendron radicans* (L.) Kuntze), maple-leaf viburnum (*Viburnum acerifolium* L.), witch hazel (*Hamamelis virginiana* L.), glossy buckthorn (*Rhamnus cathartica* L.), and seedlings of the dominant canopy trees (e.g., *A. rubrum, A. saccharum* Marshall*, Betula lenta* L., *B. papyrifera* Marshall, *Q. rubra* and *Q. alba* L.). We chose *A. rubrum* and *Q. rubra* because they are dominant species in forests of the area and represent different flowering systems and blooming times that span the duration of most available floral resources in these canopies. We chose these forest patches due to their accessibility and general representation of dominant species in forests of the area.

The bee community was sampled using blue vane traps in the understory, midstory, canopy, and above-canopy strata of the forests at each focal tree. Three traps were individually attached to a rope hung over a high branch in the canopy as in Cunningham-Minnick & Crist (2020). Traps were placed 1, 10, 20, and 30 meters above the ground (Table A1) to represent the following strata: understory, midstory, canopy and above canopy (Fig. 1). The trap above the canopy was set one meter above the tallest leaf bearing branch of each tree using a telescoping hanger attached to a vertical limb in the crown of the canopy as described in Cunningham-Minnick et al. (*in press* ). Traps were deployed on April 2, 2022, and checked every 1–3 weeks until August 21, 2022, for a total of 12 checks. Bees were sorted, pinned, and identified to species by JM using published keys (e.g., Gibbs, 2011; Gibbs et al., 2013; LaBerge, 1987, 1989; Mitchell, 1960, 1962) and the online source Discoverlife.org (Ascher & Pickering, 2020); voucher specimens are in the possession of MC-M. To distinguish differences in microclimate from other conditions among strata, Onset HOBO® Pendant data loggers (Part AU-002-64) were placed directly above each trap to record light intensity and temperature every 10 minutes June 7–21, 2022, to provide data of daily microclimate conditions and hourly from June 22–August 21, 2022, to represent seasonal change.

*Data Analysis* : To compare bee abundance and species richness across vertical strata throughout the samp-

ling season, we built generalized linear mixed effects models with negative binomial errors and created 95% confidence intervals of pairwise comparisons for each response across strata. Models were made using the glmmTMB function in the glmmTMB package (Brooks et al., 2017) with fixed effects of stratum (understory, midstory, canopy, above canopy), sample (1–12) as a continuous variable, and their interaction. We allowed the model intercept to vary by tree to account for tree-specific differences, and accounted for differences in sampling effort by including an offset term of the log of the trap deployment duration (days). Significance of interaction terms was evaluated by likelihood ratio tests; simulated model residuals through the DHARMa package were used to evaluate overall model fit (Hartig, 2020). Post-hoc comparisons were made using the confint and glht functions in the multcomp package (Hothorn et al., 2008). Differences in bee species composition among strata were visualized with non-metric multidimensional scaling ordinations performed on a species occurrence matrix of Sorensen distances using the metaMDS function in the vegan package (Oksanen et al., 2019); statistics and p-values were derived using the pairwiseAdonis function with a Bonferroni adjustment for multiple comparisons (Arbizu, 2017).

### Results

We collected 144 bees of 37 species in the understory, 170 bees of 31 species in the midstory, 198 bees of 36 species in the canopy, and 167 bees of 28 species in the aerosphere above the canopy, for a total of 679 bees of 75 species across strata (Table A2; full details in Data.xlsx of supporting information). Twelve specimens could not be identified to species due to body damage and were not included in species richness or composition analyses. After accounting for differences among individual trees, generalized linear mixed models found that there were significantly more bees and bee species in the understory than within, or above, the canopy (Fig. 2c & 2f). Interaction terms (abundance: $\chi^2(3) = 19.0$, P < 0.0005; richness: $\chi^2(3) = 16.4$, P < 0.001) demonstrated that bee abundance ($\chi^2(7) = 24.1$; P < 0.005) and species richness ($\chi^2(7) = 30.8$; P < 0.0001) changed among strata throughout the study period (Fig. 2b & 2e; Fig. A2). Specifically, bee abundance and species richness were highest within the understory during the spring months (April and May) and decreased as the season progressed, while more bees and more species were encountered in and above canopy layers during the summer months (Fig. 1, 2a & 2d). Species composition of the bee community above the canopy was significantly different from the understory, midstory, and canopy layers (Fig. 1) but there were no statistical differences among the lower strata (Table A3; Fig. A3). More generally, abundant species were collected across strata (Fig. A4), whereas 13 species occurred only above the canopy (Table 1).

### Discussion

Our study is the first to demonstrate that bees occupy the aerosphere immediately above the forest canopy; furthermore, the community above the canopy was compositionally distinct with similar abundances compared to lower strata (understory, midstory, canopy). These findings expand our understanding of forest bee communities and build on earlier research that revealed differences between understory and canopy bees (Cunningham-Minnick & Crist, 2020; Milam et al., 2022; Ulyshen et al., 2010; Urban-Mead et al., 2021). However, when attempting to characterize the forest bee community, the importance of sampling the canopy-aerosphere interface hinges upon the question of whether these bees should be considered as part of the forest community, or if they are transients moving among resources. The fact that the above-canopy assemblage was generally characterized by many species that were not observed at lower strata and were also associated with non-forested habitats (e.g., *Agapostemon texanus* Cresson, *Halictus parallelus* Say, *Peponapis pruinosa* (Say); Harrison et al., 2018) suggests that while some bees may forage on floral resources available at tree crowns in the spring, many others may be moving over the forest to access other habitat patches or resources throughout the season, as reported in other insect taxa (Wainwright et al., 2017). Nevertheless, the presence of an abundant and species rich bee assemblage at the canopy-aerosphere interface, which had not previously been considered, suggests that more studies are needed to address the extent to which these bees should be considered a subset of the forest bee community.

This study also demonstrated how the vertical stratification of forest bee communities changed throughout the flight season. Our observations confirm the findings of previous studies that have documented a positive relationship between day of year and bee abundance in the canopy (i.e., Cunningham-Minnick & Crist,

3

2020; Ulyshen et al., 2010; Urban-Mead et al., 2021). However, while this pattern may reflect a response to the depletion of floral resource availability near the ground in temperate forests (Proesman et al., 2019; Ulyshen et al., 2010), it remains unclear why bees moved to the canopy. It is possible that the canopy provides alternative foraging resources (Campbell et al., 2018; Ulyshen et al., 2010), nesting opportunities (Cunningham-Minnick & Crist, 2020), or favorable conditions associated with tree leaf phenology (Urban-Mead et al., 2021). Our results add a layer of complexity to the issue by demonstrating that this temporal pattern extends vertically beyond the forest canopy and involves a compositionally distinct subset of the bee community that may be responding to a mix of environmental cues. For example, the highest bee abundance across sampling points in the spring was at the canopy-aerosphere interface during the peak bloom of *A. rubrum* , suggesting that this stratum may provide access to floral resources of the forest canopy. However, it seems unlikely that summer bees above the canopy were foraging or nesting since forest floral resources were depleted and most were soil-nesting species. Vegetation height has been negatively associated with bee abundance and diversity (Roberts et al., 2017); therefore, bees may instead use the canopy-aerosphere interface for movement or dispersal since this space lacks the obstacles created by the vegetation structure of forest interiors. Alternatively, bees may be physiologically driven to take advantage of the greater light intensities and warmer temperatures above the canopy compared to other strata to forage earlier or later in the day (Fig. A5; Kebler et al., 2019; Roubik, 1993). It is also possible that some species were seeking mates above the canopy. For instance, groups of male *Apis mellifera* L. mate with females 10 – 40 m above the ground (Ruttner, 1966); similarly, male groups of some *Bombus* species will fly to higher elevations to mate with emerging females, a behavior known as 'hill-topping' (Goulson et al., 2011). Though *A. mellifera* and *Bombus* spp. comprised 56% of the overall abundance of bees above the canopy, these behaviors are unlikely to explain our findings because only three individuals of these species were males. Alternatively, males of two solitary soil-nesting species, *Andrena imitatrix* Cresson and *A. mandibularis* Robertson, comprised 57% of bee abundance above the canopy in the spring, though we are not aware of any studies addressing hill-topping behavior in these species or the *Andrena* genus. Thus, it appears that many of the species above the canopy were flying over the forest to unknown ends.

There were notable differences in bee assemblages among the other strata that may be best explained through life-history traits. For instance, bees in our study that nest in moist, decayed wood (e.g., *Augochlora pura* (Say), *Lasioglossum coeruleum* (Robertson), *L. cressoni* (Robertson), *L. subviridatum* (Cockerell)) or pithy twigs (e.g., *Hylaeus* spp., *Ceratina* spp.) were nearly absent above the canopy ($< 1\%$), while 77% were found in the canopy and midstory, and only 22% of bees from this guild were sampled from the understory. Our findings are consistent with other studies that demonstrated a high abundance of wood-nesting bees within the canopy (e.g., Urban-Mead et al., 2021; Cunningham-Minnick & Crist, 2020; Campbell et al., 2018; Ulyshen et al., 2010) and suggest that bees that nest in wood, including species that nest in moist decayed wood, or 'soft' wood, exhibit a preference for canopy strata within forests likely due to the availability of wood nesting substrates. Nesting substrate in the canopy has yet to be tested as a mechanism in explaining high abundances of wood-nesting bees within the higher strata of forests due to the known availability of dead and rotting wood on the forest floor, despite a lack of correlation between coarse woody debris on the ground and the abundance of this guild in the canopy (Urban-Mead, 2021; Campbell et al., 2018; Ulyshen et al., 2010). Therefore, studies that quantify potential nesting substrates for wood-nesting bees within the canopy, including those that nest in 'soft' wood, are clearly needed to resolve these discrepancies (Harmon-Threatt, 2020).

Milam et al. (2022) found that the inclusion of canopy sampling in addition to understory sampling did not influence their ability to characterize the forest bee community. Our study supports their conclusion when only considering bees below the maximum height of the canopy (i.e., understory, midstory, and canopy strata), but further demonstrates that the bee community above the canopy is distinct from lower strata. The existence of bees above the forest canopy is highly relevant to understanding pollinator ecology and may have additional implications for their conservation vis a vis our understanding of the effects of habitat fragmentation and isolation on bee movements and related population processes (Proesman et al., 2019; Roberts et al., 2017; Winfree et al., 2009). Though our study was limited in sampling intensity, it clearly

demonstrates the complexities of spatiotemporal bee dynamics within forests, suggests a new perspective on the role of forests in the surrounding landscape, and emphasizes caution when drawing conclusions about forest bee communities that were sampled with vertically or temporally restricted designs. Thus, our study supports the growing body of literature that asserts the need for additional baseline research of forest bee communities along the full vertical gradient to inform forest management and bee conservation.

## Acknowledgements

## Conflict of Interest

The authors declare no conflict of interest.

## References

Arbizu, P.M. (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). Retrieved from http://www.discoverlife.org/mp/20q?/guide=Apoidea_species.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9 (2), 378–400.

Campbell, J.W., Vigueira, P.A., Viguiera, 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.

Cannon, C. H., Borchetta, C., Anderson, D. L., Arellano, G., Barker, M., Charron, G., LaMontagne, J. M., Richards, J. H., Abercrombie, E., Banin, L. F., Casapia, X. T., Chen, X., Degtjarenko, P., Dell, J. E., Durden, D., Andino, J. E. G., Hernandez-Gutierrez, R., Hirons, A. D., Kua, C., Vigne, H. L., et al. (2021) Extending our scientific reach in arboreal ecosystems for research and management. *Frontiers in Forests and Global Change* , 4, 712165.

Cunningham-Minnick, M.J., Roberts, H.P., Kane, B., Milam, J., King, D.I. *in press.* A cost-effective method to passively sample communities at the forest canopy-aerosphere interface. Methods in Ecology and Evolution.

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., Paker, 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.

Goulson, D., Sangster, E.L., Young, J.C. (2011) Evidence for hilltopping in bumblebees? Ecological Entomology 36, 560–563.

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.

Hartig, F. (2020) DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa.

Hothorn, T., Bretz, F., Westfall, P. (2008) Simultaneous inference in general parametric models. Biometrical Journal 50 (3), 346–363.

Kebler, A., Somanathan, H. (2019) Spatial vision and visually guided behavior in Apidae. Insects 10, 418.

LaBerge, W.E. (1987) 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.

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, 116, 1–56.

MacIvor, J.S., Cabral, J.M., Packer, L. (2014) Pollen specialization by solitary bees in an urban landscape. Urban Ecosystems 17 (1), 139–47.

Maguire, D.Y., Robert, K., Brochu, K., Larrivee, M., Buddle, C.M., Wheeler, T.A. (2014) Vertical stratification of beetles (Coleoptera) and flies (Diptera) in temperate forest canopies. Environmental Entomology 43 (1), 9–17.

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, e12690.

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.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C.N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H., Ashton, L.A. (2017) Forests and their canopies: Achievements and horizons in canopy science. Trends in Ecology and Evolution 32 (6), 438–451.

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. (2019) vegan: Community ecology package. R package version 2.5-6.*https://CRAN.R-project.org/package=vegan*.

Proesman, W., Bonte, D., Smagghe, G., Meeus, I., Verheyen. (2019) Importance of forest fragments as pollinator habitat varies with season and guild. Basic and Applied Ecology 34, 95–107.

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.

Roubik, D.W. (1993) Tropical pollinators in the canopy and understory: field data and theory for stratum "Preferences". Journal of Insect Behavior 6 (6), 659–673.

Russo, L., Danforth, B. (2017) Pollen preferences among the bee species visiting apple (*Malus pumila*) in New York. Apidologie 48, 806–820.

Ruttner, F. (1966) The life and flight activity of drones. Bee World 47, 93–100.

Smith, C., Weinman, L., Gibbs, J., Winfree, R. (2019) Specialist foragers in forest bee communities are small, social or emerge early. Journal of Animal Ecology 88, 1158–1167.

Sobek, S., Tscharntke, T., Scherber, C., Schiele, S., Steffan-Dewenter, I. (2009) Canopy vs. understory: does tree diversity affect bee and wasp communities and their natural enemies across forest strata? Forest

Ecology and Management 258, 609–615.

Ulyshen, M.D., Soon, V., Hanula, J.L. (2010) On the vertical distribution of bees in a temperate deciduous forest. Insect Conservation and Diversity 3, 222–228.

Urban-Mead, K.R., Muniz, 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.

Wainwright, C.E., Stepanian, M., Reynolds, D.R., Reynolds, A.M. (2017) The movement of small insects in the convective boundary layer: linking patterns to processes. Scientific Reports 7, 5438.

Winfree, R., Aguilar, R., Vazquez, D., LeHuhn, G., Aizen, M. (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90 (8), 2068–2076.

Wood, T.J., Gibbs, J., Rothwell, N., Wilson, J.K., Gut, L., Brokaw, J., Isaacs, R. (2018) Limited phenological and dietary overlap between bee communities in spring flowering crops and herbaceous enhancements. Ecological Applications 28 (7), 1924–1934.

**Table 1:** Total bee abundance and species richness, as well as number of unique species, females, soil-nesting species, soil-nesting individuals, wood-nesting species that prefer moist and decayed ('soft') wood, and soft wood-nesting individuals at each stratum.

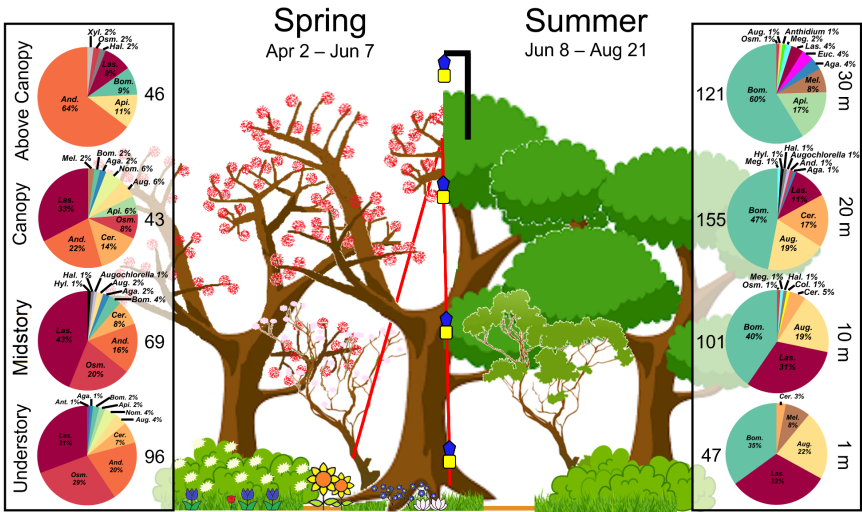|                              | Understory | Midstory | Canopy | Above Canopy |
|------------------------------|------------|----------|--------|--------------|
| Total Abundance              | 144        | 170      | 198    | 167          |
| Total Species Richness       | 37         | 31       | 36     | 28           |
| Unique Species               | 10         | 7        | 11     | 13           |
| Females                      | 78%        | 82%      | 88%    | 78%          |
| Soil Species                 | 35%        | 28%      | 32%    | 28%          |
| Soil Nester Abundance        | 59%        | 53%      | 55%    | 81%          |
| 'Soft' Wood Species          | 8%         | 10%      | 11%    | 4%           |
| 'Soft' Wood Nester Abundance | 14%        | 25%      | 26%    | 1%           |



**Fig. 1:** Sampling trap design and composition (first three letters of genus) for the bee community at 1, 10, 20, and 30 meters above the ground with blue vane traps to represent the understory, midstory, canopy, and

above the canopy of the forest, respectively, in the spring when floral resources were available and in the summer at full leaf-out when floral resources were depleted. Traps in the understory, midstory, and canopy were attached to a rope hung over a high branch in the canopy and anchored to a nearby stem for easy collection. The trap above the canopy was employed using a telescoping hanger designed as described in Cunningham-Minnick et al. (*in press*), which had a rope threaded through the hanger that was anchored to the stem in the understory to allow the trap to lowered along with another cord at the trap to aid in lowering (not depicted). Numbers next to pie charts represent total abundance across sites.
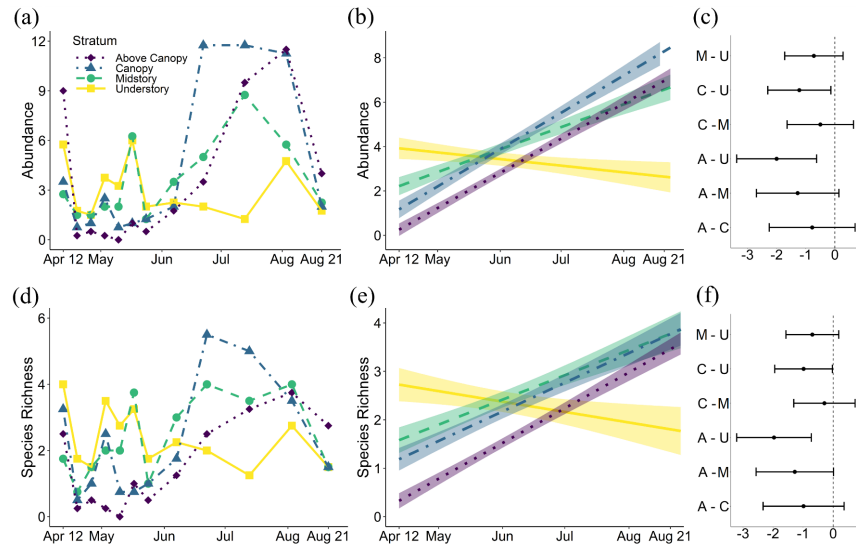


**Fig. 2:** Relationships between bee abundance (a-c) or species richness (d-f) and time of year among strata, including mean values of the data (a & d), fitted mixed effects models with 95% CI (b & e), and pairwise contrasts (logged response) between strata (c & f): Above canopy (A), Canopy (C), Midstory (M), and Understory (U).

## Appendix A

**Table A1:** Location, diameter at breast height (DBH) in centimeters and associated trap heights (m). Traps were hung 1 m above the tree canopy.

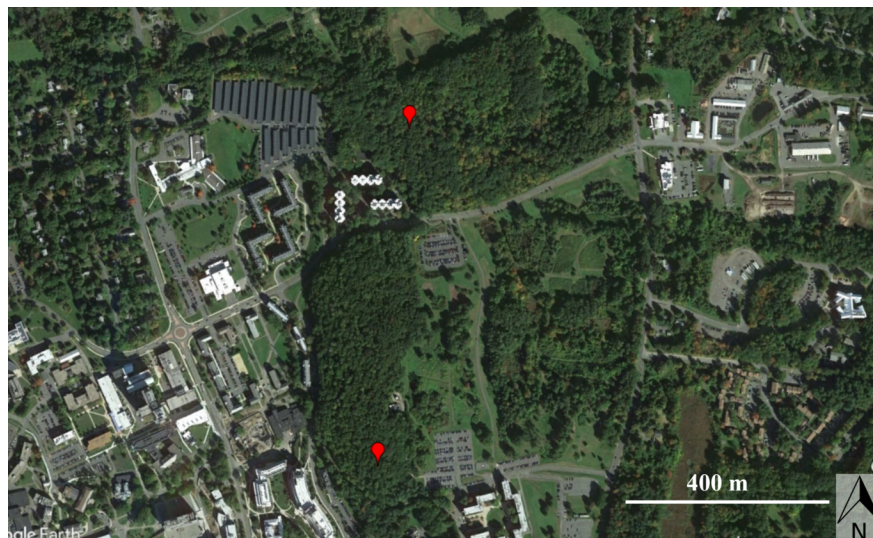| Site | Tree | Lat (°N) | Long (°W) | DBH | Understory | Midstory | Canopy | Above Canopy |
|---|---|---|---|---|---|---|---|---|
| 1 | *Q. rubra* | 42.39884 | -72.52118 | 89.2 | 1.3 | 11.8 | 20.9 | 28.9 |
| 1 | *A. rubrum* | 42.39870 | -72.52127 | 73.2 | 1.4 | 13.0 | 21.5 | 31.2 |
| 2 | *Q. rubra* | 42.39275 | -72.52200 | 51.6 | 1.4 | 9.0 | 18.8 | 30.8 |
| 2 | *A. rubrum* | 42.39297 | -72.52212 | 56.4 | 1.2 | 12.1 | 20.2 | 30.2 |

**Fig. A1:** Aerial photo of the two forest fragments within the study area. Red icons mark locations of sites. The bee community was sampled at one *Acer rubrum* and one *Quercus rubra* tree within each site.

**Table A2:** Total bees of each species found at each stratum within the forest. Number of females are in parentheses. Numbers do not include five *Bombus* , four *Lasioglossum* , and three *Melissodes* specimens that could not be identified to species due to body damage.

| Species | Understory | Midstory | Canopy | Above Canopy |
|---|---|---|---|---|
| *Agapostemon sericeus* | | 1(1) | 1(1) | |
| *Agapostemon texanus* | 1(1) | | | 2(2) |
| *Agapostemon virescens* | | 1(1) | 2(2) | 2(2) |
| *Andrena barbilabris* | | 1(1) | | |
| *Andrena bisalicis* | | | 1(1) | |
| *Andrena carlini* | 2(2) | | 1(1) | 3(3) |
| *Andrena cornelli* | 8(5) | 1(0) | 1(1) | |
| *Andrena frigida* | | | | 1(1) |
| *Andrena imitatrix* | 2(1) | 3(1) | | 28(0) |
| *Andrena mandibularis* | 2(1) | 3(0) | 2(0) | 2(0) |
| *Andrena milwaukeensis* | | 1(0) | 1(0) | |
| *Andrena miserabilis* | | | 2(0) | |
| *Andrena nasonii* | 3(2) | | | |
| *Andrena pruni* | 1(0) | 1(0) | | |
| *Andrena robertsonii* | | 1(0) | | |
| *Andrena rugosa* | 2(0) | 1(0) | 4(4) | |
| *Andrena tridens* | 1(1) | 1(0) | | |
| *Anthidium oblongatum* | | | | 1(1) |
| *Anthophora terminalis* | 1(0) | | | |
| *Apis mellifera* | 2(2) | | 3(3) | 24(24) |
| *Augochlora pura* | 12(11) | 18(17) | 31(29) | 1(1) |
| *Augochlorella aurata* | | 1(1) | 1(1) | |
| *Bombus bimaculatus* | 1(0) | 10(6) | 4(1) | 6(4) |
| *Bombus fervidus* | | | | 2(2) |
| *Bombus griseocollis* | | | | 7(7) |
| *Bombus impatiens* | 12(12) | 17(17) | 50(50) | 54(53) |

9

| | | | | |
|---|---|---|---|---|
| *Bombus perplexus* | 2(1) | 9(6) | 9(6) | 1(1) |
| *Bombus sandersoni* | | | 3(2) | |
| *Bombus vagans* | | | 4(3) | |
| *Ceratina calcarata* | 8(4) | 11(9) | 30(26) | |
| *Ceratina dupla* | | | 2(2) | |
| *Coelioxys modesta* | | 1(1) | | |
| *Peponapis pruinosa* | | | | 4(4) |
| *Halictus ligatus* | | 1(1) | | |
| *Halictus parallelus* | | | | 1(1) |
| *Halictus rubicundus* | | 1(1) | 1(0) | |
| *Hylaeus affinis/modestus* | | | 1(1) | |
| *Hylaeus sp. A/illinoiensis* | | 1(0) | | |
| *Lasioglossum bruneri* | 1(1) | 2(2) | | |
| *Lasioglossum cinctipes* | | | 1(1) | 1(1) |
| *Lasioglossum coeruleum* | 4(4) | 22(22) | 15(15) | |
| *Lasioglossum coriaceum* | 6(6) | 8(8) | 5(5) | |
| *Lasioglossum cressonii* | | 3(2) | 1(1) | |
| *Lasioglossum foxii* | 2(2) | | | |
| *Lasioglossum hitchensi* | 1(1) | | | |
| *Lasioglossum imitatum* | | | | 1(1) |
| *Lasioglossum lineatulum* | | | | 1(1) |
| *Lasioglossum nigroviride* | 2(2) | 2(2) | | |
| *Lasioglossum pectorale* | | | 1(1) | |
| *Lasioglossum pilosum* | | | | 5(5) |
| *Lasioglossum quebecense* | 20(20) | 24(22) | 5(4) | 1(1) |
| *Lasioglossum smilacinae* | | 1(1) | | |
| *Lasioglossum subviridatum* | 6(6) | | 5(5) | |
| *Lasioglossum versans* | 1(1) | | | |
| *Lasioglossum viridatum* | 1(1) | | | |
| *Lasioglossum weemsi* | 1(1) | | | |
| *Megachile campanulae* | | | 1(0) | |
| *Megachile mendica* | | 1(0) | | |
| *Megachile montivaga* | | | 1(1) | |
| *Megachile rotundata* | | | | 1(0) |
| *Megachile sculpturalis* | | | | 1(1) |
| *Melissodes bimaculata* | | | | 8(8) |
| *Melissodes desponsus* | 3(3) | | | 1(1) |
| *Melissodes trinodis* | | | 1(1) | |
| *Nomada armatella* | 1(0) | | | |
| *Nomada* (bidentate-group) | 2(2) | | 1(1) | |
| *Nomada composita* | | | 1(1) | |
| *Nomada luteoloides* | 1(1) | | 1(0) | |
| *Osmia atriventris* | 6(3) | 1(1) | | |
| *Osmia bucephala* | 1(1) | | | 1(1) |
| *Osmia cornifrons* | 9(1) | | 1(1) | |
| *Osmia pumila* | 12(10) | 17(14) | 3(3) | 1(0) |
| *Osmia sandhouseae* | 1(0) | | | |
| *Osmia taurus* | 1(1) | | | |
| *Xylocopa virginica* | | | | 1(1) |
| **TOTALS** | **142(110)** | **166(137)** | **197(174)** | **162(127)** |
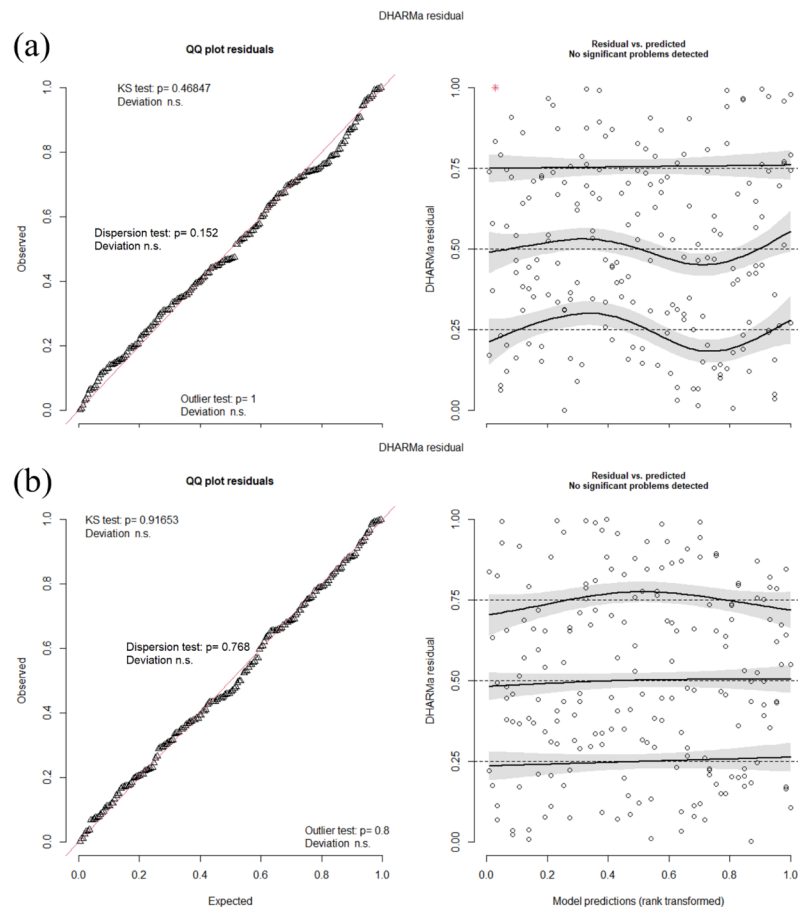
**Fig. A2** : Examination of residuals for proper model fit for bee abundance (a) and species richness (b). Output from the DHARMa package in R.

**Table A3:** Test statistic (Pseudo-F) on one degree of freedom from simulated contrasts of species composition between strata with associated p-value adjusted for multiple comparisons.

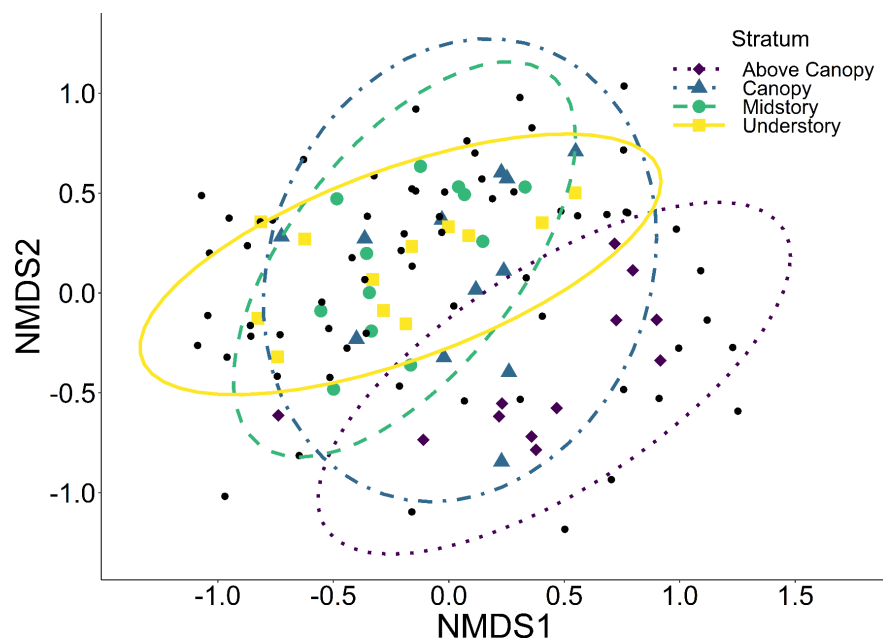| Comparison | Pseudo-F | P value |
|---|---|---|
| Understory - Midstory | 1.03 | NS |
| Understory - Canopy | 1.09 | NS |
| Understory - Above Canopy | 4.96 | < 0.01 |
| Midstory - Canopy | 1.36 | NS |
| Midstory - Above Canopy | 5.87 | < 0.01 |
| Canopy - Above Canopy | 3.34 | < 0.01 |

**Fig. A3:** Non-metric multidimensional scaling of bee community composition at each stratum, marked by colored dots and 95% Confidence Ellipses. Black dots represent species scores.
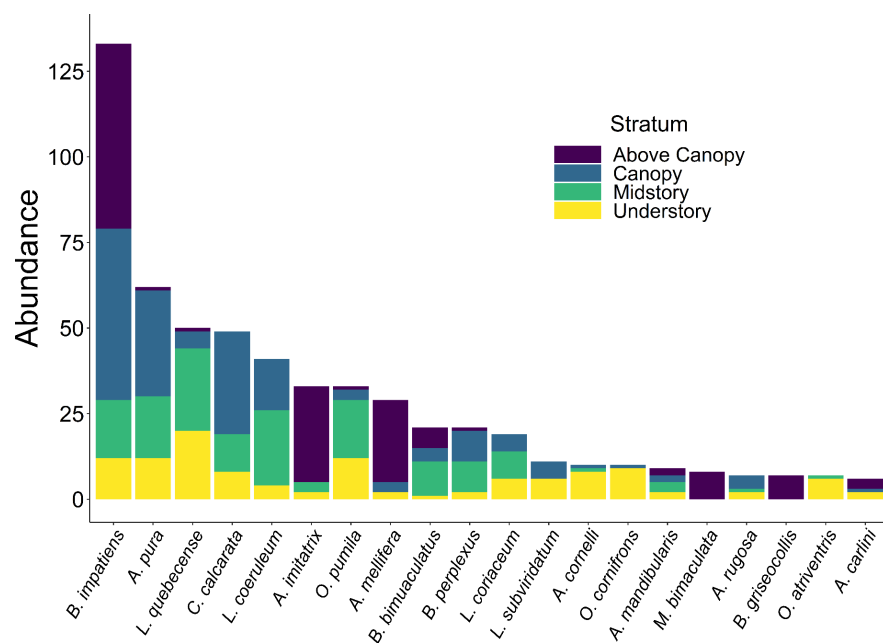


**Fig. A4:** Stacked bar plot of bee abundances among forest strata for all bee species with $> 5$ total individuals collected.
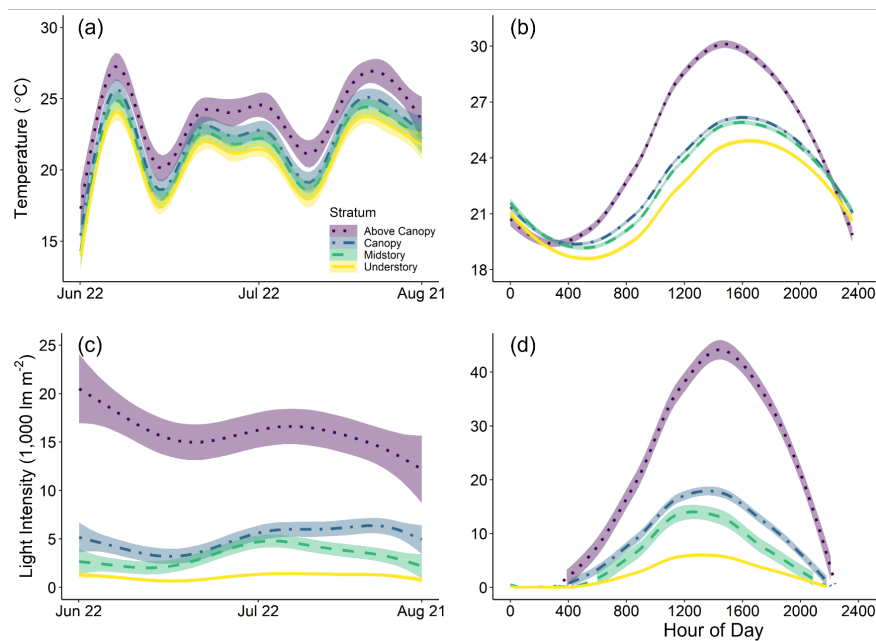
**Fig A5:** Generalized additive regressions of mean temperatures (a, b) and light intensities (c, d) of traps at each stratum with 95% CI. Readings were recorded in 60-minute intervals from June 22–August 21 (a, c). Records were taken at 10-min intervals (b, d) from June 7–21 to represent a typical 24-hr (x-axis) day.



13