DE GRUYTER Fla. Entomol. 2025; 108(1): 20240080

Research Article

Michael Ulyshen*, Doug Booher, Miriam Edelkind-Vealey, Scott Horn, Emilee Poole and Clayton Traylor

Missing jewels: the decline of a wood-nesting forest bee, *Augochlora pura* (Hymenoptera: Halictidae), in northern Georgia

https://doi.org/10.1515/flaent-2024-0080
Received October 15, 2024; accepted January 11, 2025;
published online March 27, 2025

Abstract: It is clear from research on pollinator declines that some taxa are more vulnerable than others. The sooner these more sensitive species are detected, and the cause(s) contributing to their decline are identified, the better the chance of developing effective conservation plans. Using data from nine studies conducted in northern Georgia, U.S., we present evidence that *Augochlora pura* (Say) (Hymenoptera: Halictidae), once one of the most abundant of all forest bee species in our study area, is becoming less common as a proportion of all bees collected and has experienced a 70 % decline in abundance over the past 18 years (2007–2024) at long-term monitoring sites. We hypothesize that *Brachyponera chinensis* (Emery) (Hymenoptera: Formicidae), the Asian needle ant, is contributing to the decline of *A. pura* and possibly other bee species within its invaded range.

Keywords: biodiversity; Halictidae; invasive species; saproxylic; wood-nesting

Resumen: De las investigaciones sobre la disminución de los polinizadores se desprende claramente que algunos taxones son más vulnerables que otros. Cuanto antes se detecten estas especies más sensibles y se identifiquen las causas que contribuyen a su disminución, mayores serán las posibilidades de desarrollar planes de conservación eficaces. Utilizando datos de nueve estudios realizados en el norte de Georgia, EE. UU., presentamos evidencia de que alguna vez *Augochlora pura* (Say) (Hymenoptera: Halictidae), fue una de las especies de abejas forestales más abundantes en nuestra área de estudio, de que se está volviendo menos común como proporción de todas las abejas recolectadas y de que ha experimentado una disminución en abundancia del 70 % en los últimos 18 años (2007–2024) en sitios de monitoreo a largo plazo. Nuestra hipótesis es que *Brachyponera chinensis* (Emery) (Hymenoptera: Formicidae), la hormiga aguja asiática, está contribuyendo a la disminución de *A. pura* y posiblemente de otras especies de abejas dentro de su área de distribución invadida.

Palabras clave: biodiversidad; Halictidae; especies invasoras; saproxílico; anidación de madera

1 Introduction

Evidence that native bees and other pollinating insects are in decline is mixed. While some studies report significant reductions in diversity (Barendregt et al. 2022; Forister et al. 2021; Grixti et al. 2009), others suggest no decline (Herrera 2019) or reach contrasting conclusions depending on how data are analyzed and on what length of time is considered (Aldercotte et al. 2022). Some of the strongest evidence comes from population trends of individual species, such as documented declines and even extinctions of certain well-studied bumble bee species over the past several decades (Cameron et al. 2011; Colla and Packer 2008). By contrast, populations of other species appear to be comparatively stable (Cameron et al. 2011; Roubik et al. 2021). Because bees vary widely in their resource requirements, seasonality, habitat associations, and other factors, it is not surprising that some are more sensitive to environmental stressors than others. Early indications that a species is in decline can help identify ongoing or emerging threats. However, there is a shortage of

Correction note: Correction effected after online publication on March 27, 2025: In the article title, original "Diptera" was replaced with "Hymenoptera".

***Corresponding author: Michael Ulyshen**, USDA Forest Service, Athens, GA 30602, USA, E-mail: michael.d.ulyshen@usda.gov
Doug Booher, Scott Horn and Emilee Poole, USDA Forest Service, Athens, GA 30602, USA, E-mail: douglas.booher@usda.gov (D. Booher), george.horn@usda.gov (S. Horn), emilee.poole@usda.gov (E. Poole)
Miriam Edelkind-Vealey, University of Georgia, Athens, GA 30602, USA, E-mail: miriam.edelkind@uga.edu
Clayton Traylor, Temple University, Philadelphia, PA, 19122, USA, E-mail: clayton.r.traylor@gmail.com

Open Access. © 2025 the author(s), published by De Gruyter on behalf of the Florida Entomological Society. This work is licensed under the Creative Commons Attribution 4.0 International License.

monitoring studies of sufficient duration to distinguish true population declines from normal inter-annual fluctuations (Aldercotte et al. 2022). Although recently initiated long-term monitoring campaigns will eventually provide much-needed information on the status of insect populations (Woodard et al. 2020), evaluations of existing data in the meantime can be informative. Even the impressions of scientists and other long-term observers of nature can be useful, though imperfect, early indicators of community-wide or species-specific changes (Janzen and Hallwachs 2021).

Semi-natural areas are understood to provide crucial refugia for numerous organisms in mixed-use landscapes, including pollinators. However, even some of these relatively undisturbed habitats are experiencing pollinator declines. For example, we recently documented significant declines in both bees and butterflies over 15 years at long-term monitoring sites in a National Forest in Georgia, U.S., even though the sampled forests experienced no major anthropogenic disturbances over that period (Ulyshen and Horn 2023). Interestingly, stronger declines were detected for above-ground nesting bees than for those that nest below ground. The current study was prompted by our observation that one of the most familiar forest bee species in our region, *Augochlora pura* (Say) (Hymenoptera: Halictidae), has become noticeably less common in recent trapping efforts compared to past studies (Ulyshen et al. 2010). To investigate this further, we conducted another year of sampling at the long-term monitoring plots mentioned above and explored changes in the abundance of *A. pura* relative to other bees over time based on past studies.

Augochlora pura is a strictly forest-dependent bee found throughout the deciduous forests of eastern North America. Although *A. pura* will visit flowers in non-forested habitats, it depends on hardwood forests for decomposing logs and stumps in which to nest and overwinter (Stockhammer 1966). It nests in abandoned insect galleries or other available openings in wood that has become soft from decay. Nest entrances are left open when females are foraging but are closed with a plug of sawdust when the bee returns for the night (Stockhammer 1966). While *A. pura* most commonly nests and overwinters within moist wood in close contact with the soil, it also has been observed nesting in dead limbs within the forest canopy (Urban-Mead et al. 2021). Although the dependence of *A. pura* on decomposing wood is shared by only a few other halictid species native to eastern North America, the species shares this resource with hundreds of other saproxylic invertebrates that also depend upon it for food, moisture, or shelter (Ulyshen 2018). Here we present evidence that *A. pura* populations have declined significantly in our study region. We also propose the hypothesis that an invasive species of wood-nesting ant, *Brachyponera chinensis* (Emery) (i.e., the Asian needle ant) (Hymenoptera: Formicidae), is driving the decline of this species.

2 Materials and methods

To document local changes in *A. pura* abundance, we synthesized data from nine separate bee sampling studies conducted over the past 20 years (2005–2024) in forests of Clarke County, Georgia (near the city of Athens), or about 30 km to the southeast on the Oconee National Forest in Oglethorpe and Greene counties (Table 1).

One of these studies involved 18 years (2007–2024) of sampling at three National Forest locations that originally served as reference sites in a Chinese privet eradication study (Ulyshen et al. 2022) but are now used for the long-term monitoring of pollinator populations (Ulyshen and Horn 2023). The same pan traps were used throughout the study and the forests experienced no noticeable changes in structure or composition over the entire study period. We established five subplots at each location and used a pair of colored bowls (blue and yellow) filled with soapy water to sample pollinators at ground level in each subplot for one week per month from March to October (September excluded). The 10 bowls per location were combined at the time of collection. We used the lme4 package (Bates et al. 2015) in R to test how the abundance of *A. pura* changed with time at these locations. We used a negative binomial generalized linear model (GLMM) with year (scaled) as the only fixed effect and location as a random term. A likelihood ratio test was performed to compare this model with a negative binomial model that did not include location as a random term.

All nine studies were used to describe how the abundance of *A. pura* has changed over time relative to all bees collected. Although initially designed to test different hypotheses, all of these studies involved sampling throughout the growing season within mature, closed-canopy hardwood forests. The studies either employed white bucket traps with plexiglass panels attached (WBT, see Traylor et al. (2024), blue vane traps (BVT, see Edelkind-Vealey et al. 2024), or pan traps (PT) consisting of colored plastic bowls (Ulyshen and Horn 2023) or cups coated with fluorescent paint (Fortuin and Gandhi 2021). Although WBT and BVT were consistent across studies, PT varied among studies in terms of size and color. Trap height also varied among studies, ranging from ≤1 m (ground) to 5–24 m (canopy). Although *A. pura* is usually more common in canopy traps than near the ground (Ulyshen et al. 2010), here we classify all traps ≥5 m as canopy traps as one study showed the abundance of *A. pura* to be similar between 5 and 15 m (Ulyshen et al. 2020a). The sampled forests also differed considerably, ranging from extensive floodplain forests adjacent to a major river to urban forests near smaller

Table 1: Chronology of efforts to sample *Augochlora pura* and other bee species in a variety of hardwood forests in or near Athens, Georgia. Sampling took place either in the canopy (≥5 m) or near the ground (<1 m) and involved white bucket traps (WBT), pan traps (PT), and blue vane traps (BVT).

Sampling year(s)	*A. pura*	All bees	% *A. pura*	Sampling method	Trap height	References
2005	5,919	6,300	94.0	WBT	Canopy	Study 1, Ulyshen et al. (2010)
2005	145	353	41.1	WBT	Ground	Study 1, Ulyshen et al. (2010)
2006	560	941	59.5	WBT	Canopy	Study 2, Ulyshen et al. (2020a, b)
2006	44	138	31.9	WBT	Ground	Study 2, Ulyshen et al. (2020a, b)
2006	580	2,509	23.1	PT	Ground	Study 3, Ulyshen et al. (2022)
2007	952	4,585	20.8	PT	Ground	[a]Study 3, Ulyshen et al. (2022)
2011	293	3,435	8.5	PT	Ground	[a]Study 3, Ulyshen et al. (2022)
2012	293	2,412	12.1	PT	Ground	[a]Study 3, Ulyshen et al. (2022)
2017–2018	16	160	10.0	PT	Ground	Study 4, Fortuin and Gandhi (2021)
2019	245	1,570	15.6	PT	Ground	[a]Study 3, Ulyshen et al. (2022)
2020	536	4,223	12.7	WBT	Canopy	Study 5, Traylor et al. (2024)
2021	15	294	5.1	PT	Ground	Study 6, Ulyshen et al. unpublished
2022	1	267	0.4	PT	Ground	Study 7, Edelkind-Vealey et al. (2024)
2022	49	1,173	4.2	BVT	Canopy	Study 7, Edelkind-Vealey et al. (2024)
2022	6	337	1.8	PT	Ground	[a]Study 8, Ulyshen and Horn (2023)
2023	2	148	1.4	WBT	Canopy	Study 9, Ulyshen et al. unpublished
2023	0	10	0	PT	Canopy	Study 9, Ulyshen et al. unpublished
2023	0	76	0	BVT	Canopy	Study 9, Ulyshen et al. unpublished
2023	0	45	0	WBT	Ground	Study 9, Ulyshen et al. unpublished
2023	0	6	0	PT	Ground	Study 9, Ulyshen et al. unpublished
2023	0	80	0	BVT	Ground	Study 9, Ulyshen et al. unpublished
2023	1	365	0.3	PT	Ground	Study 7, Edelkind-Vealey et al. (2024)
2023	17	1,971	0.9	BVT	Canopy	Study 7, Edelkind-Vealey et al. (2024)
2024	20	166	12.1	PT	Ground	[a]Study 8 (continued), unpublished

[a]Involved sampling at the long-term monitoring plots.

streams. Because trap type, height, and local forest conditions are all likely to influence the number of bees captured, it is not possible to isolate changes in *A. pura* numbers over time from these other parameters. We therefore did not attempt to analyze changes in the relative abundance of *A. pura* across studies. However, we can use these nine datasets to get a general sense of how the relative abundance of *A. pura* has changed over time. To do so, we calculated the proportion of bees consisting of *A. pura* in the different studies and made these calculations separately for canopy and ground traps.

3 Results

The number of *A. pura* collected declined by nearly 70 % over 18 years of consistent sampling at our three long-term monitoring sites, a significant negative relationship in models with (estimate = –0.45, $z = -2.92$, $p < 0.01$) and without (estimate = –0.45, $z = -2.88$, $p < 0.01$) location included as a random effect (Figure 1A). The likelihood ratio test showed no significant difference in fit between these two models ($\chi^2 = 0.21$, $p = 0.65$).

The relative abundance of *A. pura* varied greatly among the nine studies (Table 1, Figure 1B) depending on trap type, height, and study location. Despite this variability, substantial reductions in the relative abundance of *A. pura* over time are apparent. Since 2020, *A. pura* has accounted for a particularly low proportion of bee individuals, although this pattern reversed somewhat in 2024.

4 Discussion

As reported previously, total bee richness and abundance declined significantly at our long-term sampling locations between 2007 and 2022 (Ulyshen and Horn 2023). That previous analysis found stronger declines among above-ground-nesting bees than those that nest below ground. These declines were somewhat surprising given that all three locations remained essentially undisturbed over the entire study period. The only significant changes known to us include significant increases in mean annual minimum temperature and invasion by *B. chinensis*, a non-native species of ant from Asia (Ulyshen and Horn 2023). Because the native range of *A. pura* extends far into Florida where average temperatures are naturally higher, we feel invasion by *B. chinensis* poses the greater threat to *A. pura* and other wood-nesting bee species.

Brachyponera chinensis was first detected in North America in 1932 (Smith 1934) and has since spread widely across the eastern US from Florida to Connecticut and west

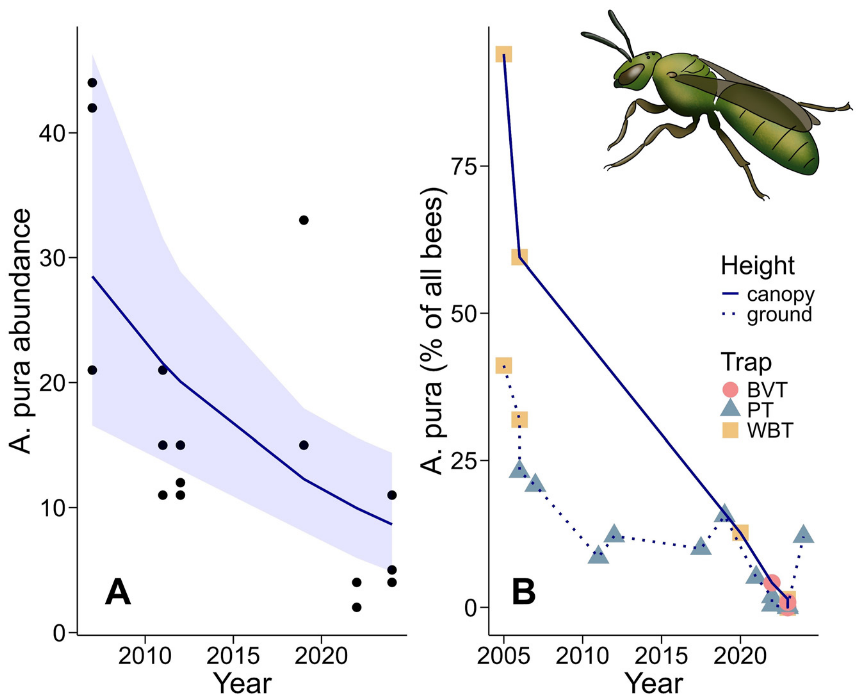

Figure 1: Changes in the number of *Augochlora pura* captured in pan traps over eighteen years (2007–2024) at three sites in Oconee National Forest, Georgia (A) and observed changes in the number of *A. pura* as a proportion of all bees captured over twenty years (2005–2024) near Athens, Georgia (B). The latter data come from nine studies using one of three trap types (WBT = white bucket traps, PT = pan traps, and BVT = blue vane traps) placed in the canopy (≥5 m, connected with a solid line) or near the ground (≤1 m, connected with a dashed line) (see Table 1 for more details).

to Arkansas with a disjunct population introduced to Washington. It is not clear when the species first reached our study area, but we do know that it was present in the Oconee National Forest by 2011 (Vogt et al. 2022). Repeated surveys of thirty-six 2,000 m^2 plots within a nature preserve in Clarke County Georgia found the incidence of *B. chinensis* to increase from 8.3 % in 2011 to 91.6 % in 2022 (Doug Booher, unpublished data). Similarly, in another Clarke County survey from 2020, *B. chinensis* was detected at 31 out of 40 widely-separated forested sites (Clayton Traylor, unpublished data). Unlike most invasive ants, *B. chinensis* readily colonizes undisturbed forests in addition to anthropogenic habitats (Guénard and Dunn 2010; Nelder et al. 2006) and can be found nesting or foraging within practically every piece of dead wood encountered in invaded forests (Doug Booher, personal observation). It is known to feed on termites and other invertebrates encountered in dead wood and on the forest floor (Bednar and Silverman 2011).

A wide variety of invertebrates inhabit dead wood in forests, and interactions among species remain poorly studied. A co-occurrence analysis of ant and beetle species inhabiting decomposing pine logs in Mississippi suggests that most associations between these taxa are neutral or positive, with only a small fraction of interactions being negative (Ulyshen et al. 2020b). However, *B. chinensis* was not part of that study and the impact of that species on the abundance and diversity of saproxylic insects in dead wood remains unknown. However, *A. pura* may be particularly vulnerable considering that their nests are left open and exposed while females are out foraging (Stockhammer 1966). Our local observations suggest a low chance of such nests going undiscovered given the ubiquity of *B. chinensis* in dead wood.

The spread of *B. chinensis* throughout southeastern U.S. forests may represent yet another threat to native bee populations, particularly those that nest within dead wood. Although this hypothesis remains untested, ants have been shown to negatively impact bee populations in previous studies. For instance, Plentovich et al. (2021) reported lower reproductive success by a *Hylaeus* species (Hymenoptera: Colletidae) due to predation by a species of invasive ant in Hawaii. Studies specifically designed to assess the impact of *B. chinensis* on *A. pura* and other wood-nesting bees are needed.

If *B. chinensis* is indeed contributing to the decline of *A. pura* and perhaps other bee species, research on the spatial distribution of nests and foragers may help develop conservation strategies. For example, if *B. chinensis* primarily nests and forages near the ground, dead wood within the canopy may represent comparatively safe nesting substrates for *A. pura*. Urban-Mead et al. (2021) reported observing active Augochlorini nests (most likely *A. pura*) in dead oak branches about 25 m above the ground, highlighting the potential value of old trees as nesting habitat. However, recent reports of *B. chinensis* nesting in oak trees 9.5–18 m above the ground in North Carolina (Kirchner et al. 2025) suggest that *A. pura* is likely to encounter this species even high within the forest canopy.

Acknowledgments: This paper was written and prepared in part by U.S. Government employees on official time, and therefore it is in the public domain and not subject to copyright. The findings and conclusions in this publication are those of the authors and should not be construed to represent an official USDA, Forest Service, or U.S. Government determination or policy.
Research ethics: Not applicable.
Informed consent: Not applicable.
Author contributions: Michael Ulyshen: Conceptualization; investigation; writing – original draft; formal analysis. Doug Booher: investigation; writing – review and editing. Miriam Edelkind-Vealey: investigation; writing – review and editing. Scott Horn: investigation; writing – review and editing. Emilee Poole: writing – review and editing. Clayton Traylor: investigation; writing – review and editing.
Use of Large Language Models, AI and Machine Learning Tools: None declared.
Conflict of interest: The authors state no conflict of interest.
Research funding: None declared.
Data availability: The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

References

Aldercotte, A.H., Simpson, D.T., and Winfree, R. (2022). Crop visitation by wild bees declines over an 8-year time series: a dramatic trend, or just dramatic between-year variation? *Ins. Conserv. Diversity* 15: 522–533.
Barendregt, A., Zeegers, T., van Steenis, W., and Jongejans, E. (2022). Forest hoverfly community collapse: abundance and species richness drop over four decades. *Ins. Conserv. Diversity* 15: 510–521.
Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67: 1–48.
Bednar, D.M. and Silverman, J. (2011). Use of termites, *Reticulitermes virginicus*, as a springboard in the invasion success of a predatory ant, *Pachycondyla* (=*Brachyponera*) *chinensis*. *Insectes Soc.* 58: 459–467.
Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F., and Griswold, T.L. (2011). Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci. U.S.A.* 108: 662–667.
Colla, S.R. and Packer, L. (2008). Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity Conserv.* 17: 1379–1391.
Edelkind-Vealey, M., Ulyshen, M.D., and Braman, S.K. (2024). Local factors influence the wild bee functional community at the urban-forest interface. *Front. Ecol. Evol.* 12: 1389619.
Forister, M.L., Halsch, C.A., Nice, C.C., Fordyce, J.A., Dilts, T.E., Oliver, J.C., Prudic, K.L., Shapiro, A.M., Wilson, J.K., and Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science* 371: 1042–1045.
Fortuin, C.C. and Gandhi, K. (2021). Functional traits and nesting habitats distinguish the structure of bee communities in clearcut and managed hardwood and pine forests in Southeastern USA. *Forest Ecol. Manag.* 496: 119351.
Grixti, J.C., Wong, L.T., Cameron, S.A., and Favret, C. (2009). Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol. Conserv.* 142: 75–84.
Guénard, B. and Dunn, R.R. (2010). A new (old), invasive ant in the hardwood forests of eastern North America and its potentially widespread impacts. *PLoS One* 5: e11614.
Herrera, C.M. (2019). Complex long-term dynamics of pollinator abundance in undisturbed Mediterranean montane habitats over two decades. *Ecol. Monogr.* 89: e01338.
Janzen, D.H. and Hallwachs, W. (2021). To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *Proc. Natl. Acad. Sci. U.S.A.* 118: e2002546117.
Kirchner, M., Sorenson, C., Blaimer, B.B., and Youngsteadt, E. (2025). Reaching new heights: arboreal ant diversity in a North American temperate forest system. *Insect Conserv. Divers.* 18: 95–106.
Nelder, M.P., Paysen, E.S., Zungoli, P.A., and Benson, E.P. (2006). Emergence of the introduced ant *Pachycondyla chinensis* (Formicidae: Ponerinae) as a public health threat in the southeastern United States. *J. Med. Entomol.* 43: 1094–1098.
Plentovich, S., Graham, J.R., Haines, W.P., and King, C.B.A. (2021). Invasive ants reduce nesting success of an endangered Hawaiian yellow-faced bee, *Hylaeus anthracinus*. *NeoBiota* 64: 137–154.
Roubik, D.W., Basset, Y., Lopez, Y., Bobadilla, R., Perez, F., and Ramírez, S., J.A. (2021). Long-term (1979–2019) dynamics of protected orchid bees in Panama. *Conserv. Sci. Prac.* 3: e543.
Smith, M.R. (1934). Ponerine ants of the genus *Euponera* in the United States. *Ann. Entomol. Soc. Am.* 27: 557–564.
Stockhammer, K.A. (1966). Nesting habits and life cycle of a sweat bee, *Augochlora pura* (Hymenoptera: Halictidae). *J. Kansas Entomol. Soc.* 39: 157–192.
Traylor, C.R., Ulyshen, M.D., Bragg, D.C., and McHugh, J.V. (2024). Forest bees benefit from compositionally diverse broadleaf canopies. *Forest Ecol. Manag.* 566: 122051.
Ulyshen, M.D. (Ed.) (2018). *Saproxylic insects: diversity, ecology and conservation*. Springer, Cham, Switzerland, pp. 904.
Ulyshen, M.D., Soon, V., and Hanula, J.L. (2010). On the vertical distribution of bees in a temperate deciduous forest. *Insect Conserv. Divers.* 3: 222–228.
Ulyshen, M.D., Horn, S., and Hanula, J.L. (2020a). Effects of Chinese privet on bees and their vertical distribution in riparian forests. *Insect Conserv. Divers. Forest Sci.* 66: 416–423.
Ulyshen, M.D., Lucky, A., and Work, T.T. (2020b). Effects of prescribed fire and social insects on saproxylic beetles in a subtropical forest. *Sci. Rep.* 10: 9630.
Ulyshen, M.D., Horn, S., and Hanula, J.L. (2022). Decadal patterns of forest and pollinator recovery following the eradication of an invasive shrub. *Front. Ecol. Evol.* 10: 832268.
Ulyshen, M.D. and Horn, S. (2023). Declines of bees and butterflies over 15 years in a forested landscape. *Curr. Biol.* 33: 1346–1350.
Urban-Mead, K.R., Muñiz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M., McArt, S.H., and Danforth, B.N. (2021). Bees in the trees: diverse spring fauna in temperate forest edge canopies. *Forest Ecol. Manag.* 482: 118903.
Vogt, J.T., MacGown, J.A., Lewis, J., Horn, S., and Ulyshen, M.D. (2022). Diversity and seasonal occurrence of native and nonnative ants (Hymenoptera: Formicidae) in long-term experimental Chinese privet (Lamiales: Oleaceae) plots in Georgia, USA. *J. Entomol. Sci.* 57: 297–309.
Woodard, S.H., Federman, S., James, R.R., Danforth, B.N., Griswold, T.L., Inouye, D., McFrederick, Q.S., Morandin, L., Paul, D.L., Sellers, E, et al. (2020). Towards a U.S. national program for monitoring native bees. *Biol. Conserv.* 252: 108821.