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ORIGINAL PAPER

Two for One: Canopy Gaps that Improve the Health of Adelgid-Infested Eastern Hemlock also Favor Bee Diversity and Abundance

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Abstract

Creation of small canopy gaps around understory eastern hemlocks (*Tsuga canadensis* (L.) Carrière) can increase resilience to hemlock woolly adelgid (*Adelges tsugae* Annand), an invasive insect pest in eastern North America. In this study, the diversity and community composition of bees were quantified by monitoring pan traps in canopy gaps (mean size 0.06 ha, created 2.5—3 yrs earlier) and paired control plots (mature, intact forest) in western North Carolina and Virginia. Mean bee richness and abundance were significantly greater in silvicultural gaps. There were significant compositional differences in bee communities between treatments (gap vs. control) and forest locations (North Carolina vs. Virginia), and three indicator bee species were detected, all of which were associated with gaps. The mean health index of residual hemlocks at gap center was maintained over time, whereas the health index of hemlocks in control plots declined. These results suggest that in mature mixed hardwood – hemlock stands of the southern Appalachians, small-scale canopy disturbances can be used as a tool in the conservation of both eastern hemlock and native bee communities.

Keywords Hemlock woolly adelgid · *Tsuga canadensis* · *Adelges tsugae* · Pollinators · Silviculture · Invasive species

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Human population growth generates an increasing demand on forests to provide for multiple uses, including timber and pulpwood, non-timber forest products, recreation, and ecological services such as clean air, water, carbon storage, and biodiversity (Baskent et al. 2020; Hovis et al. 2022). Foresters must frequently manage for many of these objectives simultaneously, particularly on public lands where agency priorities and societal expectations are diverse (D'Amato et al. 2018). Furthermore, accelerated rates of climate change, non-native invasive pest introductions, and biodiversity losses have generated a need to adapt traditional silvicultural approaches for application to novel conditions (D'Amato et al. 2018; Muzika 2017; Nagel et al. 2017). Given these challenges, silvicultural practices that address more than one management objective simultaneously should be particularly valuable to forest managers.

One of the most damaging invasive forest insects in the United States (US) has been the hemlock woolly adelgid, *Adelges tsugae* Annand (Fei et al. 2019). Native to east Asia and western North America where it is not considered a pest (Havill et al. 2006), *A. tsugae* was introduced from Japan to eastern North America prior to 1951 (Stoetzel 2002) and has spread from the southern Appalachian Mountains north to Maine and Nova Scotia, and west to Michigan (EDDMapS 2024). In its invaded range, *A. tsugae* is a serious pest of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelmann), on which it uses piercing-sucking mouthparts to extract carbohydrates from twigs, causing branch dieback and tree mortality (Limbu et al. 2018). The *A. tsugae* life cycle in eastern North America consists entirely of asexual stages, including a long sistens generation (summer through winter) and a short progrediens generation (spring) (Limbu et al. 2018; McClure 1989). Eastern hemlock is considered a foundation species (Ellison et al. 2005) and the ecological impacts of the adelgid on stand composition, nutrient and hydrologic cycling, and associated fauna have been substantial (Ellison et al. 2018). Although eastern hemlock is one of the most shade-tolerant tree species in the Northern Hemisphere (Niinemets and Valladares 2006), *A. tsugae* has functionally eliminated the ability of this species to survive in, and create, the deeply shaded environments that have commonly characterized its presence on forest landscapes (Ellison et al. 2005).

The pest management strategy for *A. tsugae* in eastern US forests has employed the integration of multiple tactics including chemical control, biological control, gene conservation, development of host resistance, and silviculture (USDA Forest Service et al. 2021). Historically, most operational efforts to reduce *A. tsugae* impacts in forests have involved systemic insecticide application to individual trees (McCarty and Addesso 2019), release of biological control agents (Mayfield et al. 2023a), or integration of the two (Mayfield et al. 2020). A number of studies, however, have shown that increasing the amount of sunlight available to understory and experimentally-shaded eastern hemlock trees improves their physiological performance and growth when infested with *A. tsugae* (Brantley et al. 2017; Mayfield et al. 2023b; McAvoy et al. 2017; Miniat et al. 2020). For example, cutting small gaps (0.02 – 0.06 ha) in the codominant canopy above adelgid-infested understory hemlocks increased their shoot and diameter growth over the following 3 years relative to shaded control plots (Mayfield et al. 2023b).

Silviculture has also been identified as a means of influencing the abundance and diversity of bees and other insect pollinators, declines of which have been recognized at local, regional and global scales (Graves et al. 2020; Dicks et al. 2021; Ulyshen and Horn 2023; Zattara and Aizen 2021). Canopy openness, as created by natural (e.g., wildfire) or anthropogenic disturbances (e.g., timber harvest), has been associated with increases in bee abundance and diversity in several North American forest types (Hanula et al. 2015, 2016; Mullally et al. 2019; Proctor et al. 2012; Roberts et al. 2017; Ulyshen et al. 2022, 2024b). However, forest disturbances can also result in conditions that have negative consequences for native pollinator populations, such as when they facilitate invasive plant introductions, or eliminate plants on which populations of rare pollinator species are dependent (Hanula et al. 2016). Wild forest pollinators are not only key sources of ecosystem services and biodiversity but also promote pollination of food crops on adjacent non-forest landscapes (Ulyshen et al. 2023). Thus, pollinator conservation has been a priority for government agencies like the US Department of Agriculture due to their role in food security and ecosystem health (USDA 2022), and a greater understanding of how forest management practices influence pollinator populations in specific forest types are needed to adequately address this priority.

Understanding how pest management strategies affect both pest populations and insect biodiversity was recently identified as an important knowledge gap in insect conservation research (Gazzea et al. (2024). Experiments demonstrating that bee abundance and diversity increase with the amount of forest canopy removed (Romey et al. 2007) may suggest that the effect of relatively small forest gaps (<0.1 ha) on pollinator populations is limited. The objective of this study was to determine if a silvicultural practice (creation of small canopy gaps) aimed at reducing impacts of an invasive forest pest (*A. tsugae*) is simultaneously useful in the effort to conserve pollinators, specifically forest bees. The study was conducted at a subset of sites used to evaluate the response of eastern hemlock trees and *A. tsugae* populations to silvicultural canopy gaps in mixed hardwood-hemlock stands in the southern Appalachians (Mayfield et al. 2023b). We evaluated the hypothesis that canopy gaps created to release understory hemlocks would result in higher abundance and richness in the localized bee species community when compared with plots in the adjacent, intact forest.

Methods

Sites and Treatments

The study utilized eight of the original 21 replicate sites used by Mayfield et al. (2023b), including five on the Jefferson National Forest (JNF) in southwestern Virginia (VA) and three on the Green River Game Lands (GRG) in western North Carolina (NC) (Fig. 1A, Table SI−1, supp. info.). Stands were mixed species with variable amounts of *Liriodendron tulipifera* L., *Quercus alba* L., *Quercus coccinea* Muenchh., and/or *Pinus strobus* L. dominating the overstory, with *T. canadensis*, *Acer rubrum* L., *Oxydendrum arboreum* (L.) DC. and *Betula lenta*

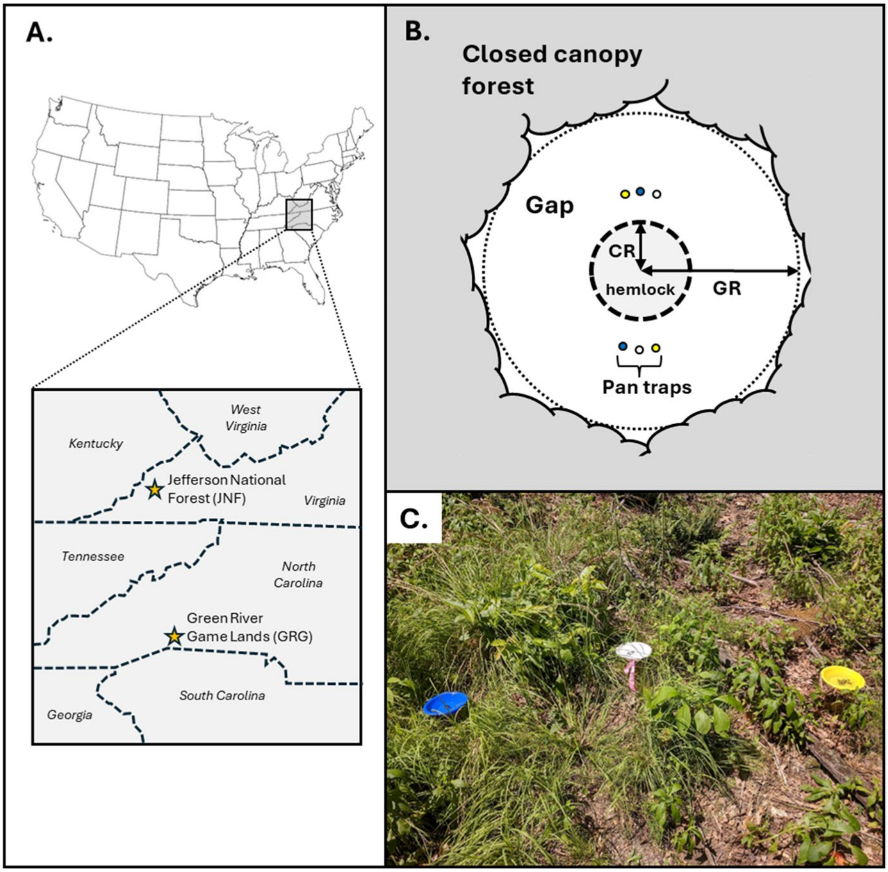

Fig. 1 **A**) Location of two forests in the southern Appalachian Mountains, USA, used to evaluate bee abundance and diversity in small silvicultural gaps. **B**) Illustration of silvicultural gaps used to release understory eastern hemlock trees, and pollinator traps installed three years after gap creation. CR = crown radius of the target hemlock, GR = gap radius = CR + 0.25 × dominant tree height. **C**) Plastic pan traps deployed to the north and south of each target hemlock (photo by A.E. Mayfield).

L. as common midstory and understory species. Mayfield et al. (2023b) evaluated hemlock response to four canopy gap treatments and an untreated control in each replicate, but in the present study, each replicate was limited to the two silvicultural treatments representing the greatest contrast in canopy disturbance: "large fell" (hereafter called "gap") and "control" treatments. Silvicultural treatments were implemented between Jun-Nov 2017 in mature, closed-canopy, mixed-species stands. Gap treatments were applied by locating an understory or midstory eastern hemlock (minimum diameter at breast height (DBH) 10 cm), determining its maximum crown radius, extending this radius by a horizontal distance equal to 25 percent of the dominant tree height, and felling all trees that touched an imaginary cylinder of this radius (Fig. 1B) (Mayfield et al. 2023b). Mean (SE) gap size for the 8 sites used in the pollinator study was 0.06 (0.007) ha. Felled trees were left on the ground. In some cases, hemlock trees other than the target hemlock were retained in the gap for hemlock conservation purposes, but this was rare and did not typically occur within 10 m of the target hemlock. In the control treatment, no trees were felled around the target hemlock.

Pollinator Trapping

At each gap and control plot, two sets of three pollinator pan traps (six traps total) were deployed 3 m beyond the crown edge of the target hemlock, with one set to the north and one set to the south of the tree (Fig. 1B, C). Each set consisted of a yellow, a blue and a white plastic bowl (15.5 cm opening, ~ 400 mL capacity), with bowls spaced 1 m from each other and suspended 20–30 cm above the ground on wire stands (Ulyshen and Horn 2023). Traps were filled with soapy water and were operated during the following periods in 2020: 27 – 30 Apr, 30 Apr – 4 May, 11 – 14 May, and 1 – 4 June. Bees were transferred to 95 percent ethanol prior to identification to species by M.D. Ulyshen and were added to the USDA Forest Service Southern Research Station reference collection in Athens, GA.

Hemlock Health Index

In association with the study reported by Mayfield et al (2023b), crown health metrics for each target hemlock were visually estimated annually each winter from 2018 to 2021. These included percent foliage transparency (the relative amount of sunlight passing through the foliated portion of the crown) and percent crown density (the proportion of the normal, expected crown area present), which were estimated by two observers using the methodology of Schomaker et al. (2007). Both observers rated each tree simultaneously and independently but from different angles (usually 90° apart), then immediately discussed the individual estimates and jointly assigned a final rating. In addition, percent new shoot production was estimated using 12 branch tips (25 cm length) on each target hemlock (one from each of the upper and lower crown levels every 60° around the crown circumference). The outer 10 shoots of each branch tip (the terminal shoot and the nine most distal side-shoots) were examined and the number of tips that represented new growth expansion from the most recent growing season were counted and expressed as a percent (Mayfield et al. 2023b). Means of these individual crown health metrics, computed for a larger number of sites, were previously published by Mayfield et al. (2023b). In the present study, for the purposes of demonstrating hemlock health response in the specific sites monitored for pollinators, a hemlock health index was computed as a function of foliage transparency (FT), crown density (CD) and new shoot percentage (NS) using the formula

$$Health\ Index = \frac{(100 - FT) + CD + NS}{3}$$

with a potential range of 0 to 100, in which crown health improves as health index increases.

Data Analysis

Data from all pollinator traps and collection dates within each treatment plot were pooled. Three separate mixed-model analyses of variance (ANOVA) were used to evaluate whether mean bee species richness (number of species), bee abundance (number of specimens), and hemlock health index differed by treatment (gap vs. control). We analyzed observed species richness in this study, as opposed to rarefied richness, as we felt it was the more ecologically meaningful metric. However, we acknowledge that richness and abundance are not independent. In models for bee species richness and abundance, treatment was considered the main effect, with forest (2 levels: Virginia and North Carolina) and site (8 levels, nested within forest) as random effects. In the model for hemlock health index, treatment, year, and treatment x year were considered main effects, with forest and site(forest) as random effects. P-values ≤ 0.05 were considered significant and means comparison was performed using Student's t-test. The ANOVA was performed using the Standard Least Squares method and restricted maximum likelihood (REML) approach in the Fit Model procedure of JMP 14.0 (SAS Institute, Inc. 2018).

Community analysis was conducted on Hellinger-transformed abundance data. Non-metric multidimensional scaling was performed on a Bray–Curtis distance matrix using the *vegan* package (Oksanen et al. 2022) to produce a two-dimensional visualization of differences in bee community composition among plots. This was followed by PERMANOVA (Anderson 2001) using the function *adonis* to test for statistically significant differences between forests, treatments, and their interaction. Finally, we conducted Indicator Species Analysis using the *indicspecies* package (De Cáceres and Legendre 2009) to determine if any species were significantly associated with either of the two treatments or forest locations. We used the multipatt function with the default IndVal.g method, which assesses species specificity and fidelity across groups. Statistical significance was based on 999 permutations. Community analyses were conducted in R 4.2.1 (R Core Team 2022).

Results

Overall, 2977 bee specimens representing 117 species were collected in 2020 (Table 1). The most common genera included *Andrena* (miner bees, 30 species), *Lasioglossum* (sweat bees, 30 species), *Nomada* (cuckoo nomad bees, 16 species), *Osmia* (mason bees, 8 species), *Bombus* (bumble bees, 6 species), and *Sphecodes* (cuckoo sweat bees, 6 species). Nearly 60 percent of the specimens were comprised of four species: *Lasioglossum cressonii* Robertson, *Augochlora pura* (Say), *Lasioglossum versans* (Lovell) and *Lasioglossum quebecense* (Crawford) (Table 1).

Table 1 Number of bee specimens (total and by canopy treatment), and number of sites (out of 8 total) in which they were trapped, in a study evaluating effects of canopy gaps on bee abundance and diversity in western North Carolina and Virginia, April-June 2020

Species	No. of specimens by canopy treatment			No. of sites in which species was trapped
	Control	Gap	Total	
Andrena carlini Cockerell	5	18	23	3
Andrena carolina Viereck	4	4	8	2
Andrena chromotricha Cockerell	1		1	1
Andrena cornelli Viereck	2	2	4	2
Andrena crataegi Robertson	1	1	2	1
Andrena cressonii Robertson	1	1	2	2
Andrena dimorpha Mitchell		2	2	2
Andrena distans Provancher	4	5	9	3
Andrena erigeniae Robertson		1	1	1
Andrena forbesii Robertson		2	2	1
Andrena gardineri Cockerell		2	2	2
Andrena hilaris Smith	1	18	19	1
Andrena ilicis Mitchell	1		1	1
Andrena imitatrix Cresson	2	4	6	5
Andrena krigiana Robertson		1	1	1
Andrena lamelliterga Ribble		1	1	1
Andrena milwaukeensis Graenicher	2	2	4	3
Andrena nasonii Robertson	1	1	2	1
Andrena nivalis Smith	14	24	38	3
Andrena perplexa Smith		6	6	4
Andrena pruni Robertson	4	3	7	3
Andrena robertsonii Dalla Torre	1	3	4	3
Andrena rugosa Robertson	6	3	9	3
Andrena spiraeana Robertson	6	2	8	3
Andrena thaspii Graenicher	1		1	1
Andrena tridens / mandibularis Robertson	3	1	4	1
Andrena uvulariae Mitchell		1	1	1
Andrena vicina Smith	8	20	28	3
Andrena violae Robertson	10	22	32	5
Andrena wilkella (Kirby)		1	1	1
Anthophora abrupta Say		1	1	1
Apis mellifera Linnaeus		3	3	2
Augochlora pura (Say)	129	498	627	8
Augochlorella aurata (Smith)	4	7	11	3
Augochloropsis metallica (Fabricius)	17	14	31	5
Bombus bimaculatus Cresson	1	13	14	5
Bombus citrinus (Smith)		1	1	1
Bombus griseocollis (De Geer)		2	2	2
Bombus impatiens Cresson	7	19	26	5

Table 1 (continued)

Species	No. of specimens by canopy treatment			No. of sites in which species was trapped
	Control	Gap	Total	
Bombus perplexus Cresson		1	1	1
Bombus sandersoni Franklin	1	6	7	3
Calliopsis andreniformis Smith		14	14	1
Ceratina calcarata Robertson	26	59	85	8
Ceratina dupla Say		1	1	1
Ceratina strenua Smith		3	3	3
Coelioxys porterae Cockerell		4	4	2
Coelioxys rufitarsis Smith	1		1	1
Eucera atriventris (Smith)		2	2	1
Eucera rosae (Robertson)		2	2	2
Halictus ligatus Say		1	1	1
Halictus parallelus Say	1		1	1
Hoplitis producta (Cresson)		7	7	3
Hoplitis simplex Cresson/*H. nemophilae* Neff		1	1	1
Hylaeus modestus Say		8	8	3
Hylaeus sparsus (Cresson)		2	2	2
Lasioglossum abanci (Crawford)	62	101	163	7
Lasioglossum birkmanni (Crawford)	5		5	3
Lasioglossum bruneri (Crawford)	1		1	1
Lasioglossum callidum (Sandhouse)	1		1	1
Lasioglossum cattelae (Ellis)	24	8	32	6
Lasioglossum coeruleum (Robertson)	19	14	33	6
Lasioglossum coriaceum (Smith)	81	62	143	5
Lasioglossum cressonii Robertson	381	290	671	8
Lasioglossum foxii (Robertson)		2	2	1
Lasioglossum fuscipenne (Smith)	2	5	7	3
Lasioglossum gotham Gibbs		1	1	1
Lasioglossum heterognathum (Mitchell)		20	20	3
Lasioglossum hitchensi Gibbs	1	1	2	2
Lasioglossum illinoense (Robertson)		6	6	2
Lasioglossum imitatum (Walker)		11	11	2
Lasioglossum katherinae Gibbs		1	1	1
Lasioglossum laevissimum (Smith)	2	1	3	2
Lasioglossum leucozonium (Schrank)		1	1	1
Lasioglossum lineatulum (Crawford)		1	1	1
Lasioglossum nigroviride (Graenicher)	3	6	9	4
Lasioglossum oblongum (Lovell)		2	2	2
Lasioglossum quebecense (Crawford)	114	100	214	6
Lasioglossum sp.		1	1	1
Lasioglossum subviridatum (Cockerell)	21	48	69	8

Table 1 (continued)

Species	No. of specimens by canopy treatment			No. of sites in which species was trapped
	Control	Gap	Total	
Lasioglossum tegulare (Robertson)/*L. puteulanum* Gibbs	1	1	2	2
Lasioglossum timothyi Gibbs	1	4	5	3
Lasioglossum trigeminum Gibbs	1	9	10	5
Lasioglossum truncatum (Robertson)	1	3	4	2
Lasioglossum versans (Lovell)	131	100	231	5
Lasioglossum versatum (Robertson)		1	1	1
Megachile gemula Cresson		4	4	3
Nomada armatella Cockerell		2	2	1
Nomada cressonii Robertson	6	10	16	6
Nomada cuneata (Robertson)	2	9	11	3
Nomada denticulata Robertson	1		1	1
Nomada depressa Cresson	2	2	4	3
Nomada gracilis Cresson		3	3	2
Nomada imbricata Smith	6	25	31	4
Nomada lepida Cresson	3	5	8	4
Nomada luteola Olivier		2	2	2
Nomada luteoloides Robertson	1	5	6	4
Nomada maculata Cresson	3	3	6	2
Nomada obliterata Cresson		1	1	1
Nomada pygmaea Cresson	6	5	11	6
Nomada sp.1		5	5	3
Nomada sp.2	2	3	5	2
Nomada sulphurata Smith	1	3	4	1
Osmia albiventris Cresson	1	1	2	2
Osmia bucephala Cresson	2	4	6	3
Osmia collinsiae Robertson		1	1	1
Osmia cornifrons (Radoszkowski)	5	19	24	5
Osmia georgica Cresson	1	12	13	5
Osmia pumila Cresson	4	16	20	8
Osmia taurus Smith	2	11	13	7
Osmia virga Sandhouse		1	1	1
Panurginus potentillae (Crawford)	3		3	3
Sphecodes coronus Mitchell	2	4	6	3
Sphecodes cressonii (Robertson)	1	2	3	2
Sphecodes levis Lovell and Cockerell	2	1	3	2
Sphecodes ranunculi Robertson	1	1	2	1
Sphecodes smilacinae Robertson		1	1	1
Sphecodes townesi Mitchell	4	18	22	4
Total (117 species)	1178	1799	2977	

There were significant differences in predicted (least squares) mean bee species richness ($F_{1,7} = 51.0$, $p < 0.001$) and predicted mean bee abundance ($F_{1,7} = 8.0$, $p = 0.025$) between gap and control plots. On average, traps in canopy gaps captured 78% more bee species (predicted mean 32 vs. 18) and 60% more bee specimens (predicted mean 206 vs. 129) than traps in control plots (Fig. 2).

NMDS ordination (stress = 0.08) indicated a distinct separation in bee communities between forests (Virginia vs. North Carolina) and treatments (gap vs. control) (Fig. 3). Similarly, PERMANOVA revealed a significant effect of forest ($F_{1,15} = 4.0$, $p < 0.01$) and a nearly significant effect of treatment ($F_{1,15} = 1.8$, $p = 0.06$), but no interaction between forest and treatment ($F_{1,15} = 0.74$, $p = 0.74$). Indicator species analysis detected three significant indicator species, all associated with gaps: *Osmia taurus* Smith (IV (indicator value) = 0.848, p = 0.014), *Osmia pumila* Cresson (IV = 0.831, $p = 0.020$), and *Bombus bimaculatus* Cresson (IV = 0.751, $p = 0.049$). Common species accounted for much of the difference in abundance between gaps and controls. For example, of the 12 species that were represented in at least 75% of the replicate sites, six were at least 60% more abundant in gaps compared to controls: *Augochlora pura* (Say), *Ceratina calcarata* Robertson, *Lasioglossum abanci* (Crawford), *Lasioglossum subviridatum* (Cockerell), *O. pumila,* and *O. taurus* (Table 1).

The three component variables (crown density, percent new shoots, and foliage transparency) used to calculate the hemlock health index changed in similar ways during the period 2018–2021 (Fig. 4). Means for the positive measures of health (crown density and percent new shoots) increased or remained stable over time in the gap treatment but declined in the uncut control plots (Fig. 4A-B). Comparatively, foliage transparency, an indicator of poor health, displayed an inverted pattern (Fig. 4C). For the composite hemlock health index, there was a significant effect of treatment ($F_{1,49} = 28.5$, p < 0.001) and treatment x year ($F_{3,49} = 5.6$, p = 0.002). In the winter of 2018, immediately after gap treatments were implemented, there was no significant difference in the predicted (least squares) mean hemlock health index between gap and control plots (health index for both means near 70, Fig. 4D). Over the following three years, however, predicted mean hemlock health index in the control treatment declined steadily, whereas this measure remained relatively constant in the gap treatment (Fig. 4D).

Discussion

The present study indicates that using small silvicultural gaps in "mixedwood" forests (sensu Kenefic et al. 2021) to increase sunlight exposure and maintain understory eastern hemlock health (Fig. 4) has an additional ecological benefit: increasing the local diversity and abundance of bees (Fig. 2). Felled trees in our gaps were left on-site and may have provided additional nesting sites for above-ground and wood-nesting species. For example, *Osmia pumila* and *O. taurus* were significantly associated with the gaps in this study based on indicator species analysis, and this genus has been shown to be sensitive to dead wood availability in other

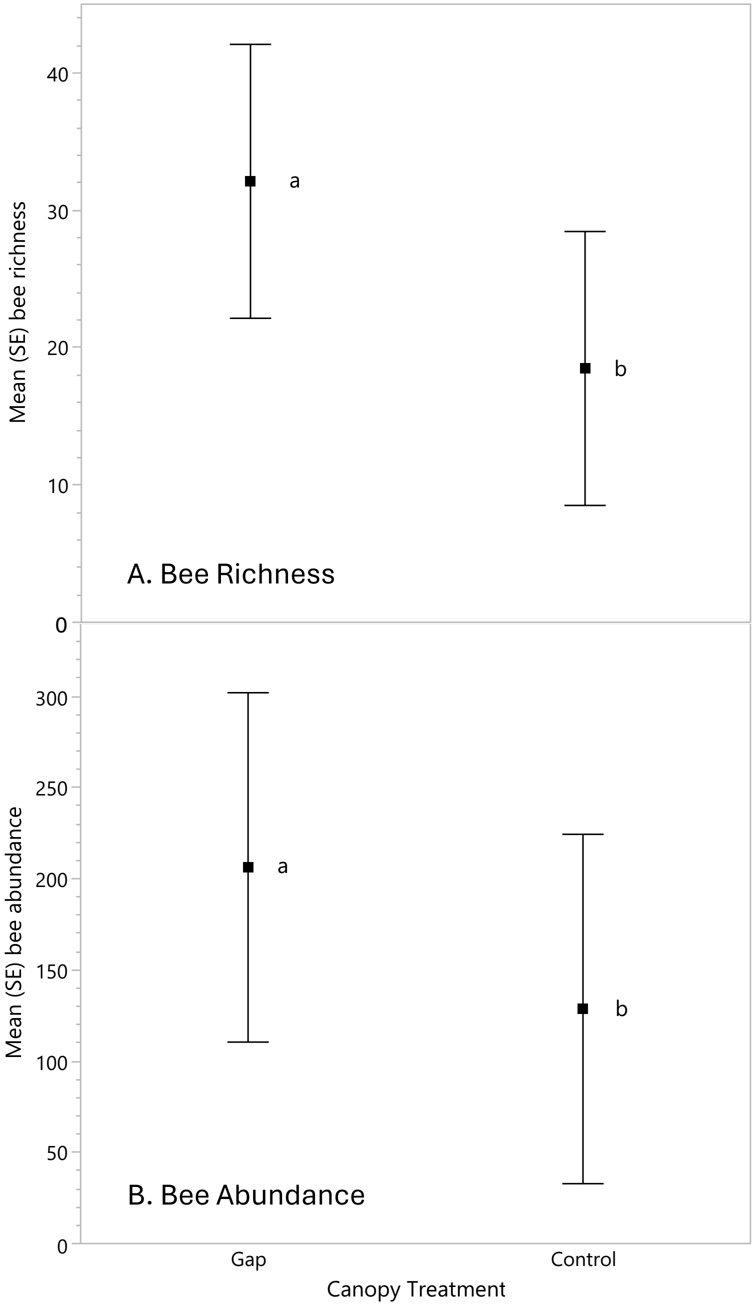

Fig. 2 Predicted (least squares) mean bee species richness (**A**) and bee abundance (**B**) in small forest canopy gaps (mean size 0.06 ha) and control plots (intact canopy) in hardwood-hemlock forests in the southern Appalachians of Virginia and North Carolina, April-June 2020. Within a panel, predicted means labeled with different letters are significantly different ($p \leq 0.05$) in a mixed linear analysis of variance model. Vertical bars indicate standard error of predicted means

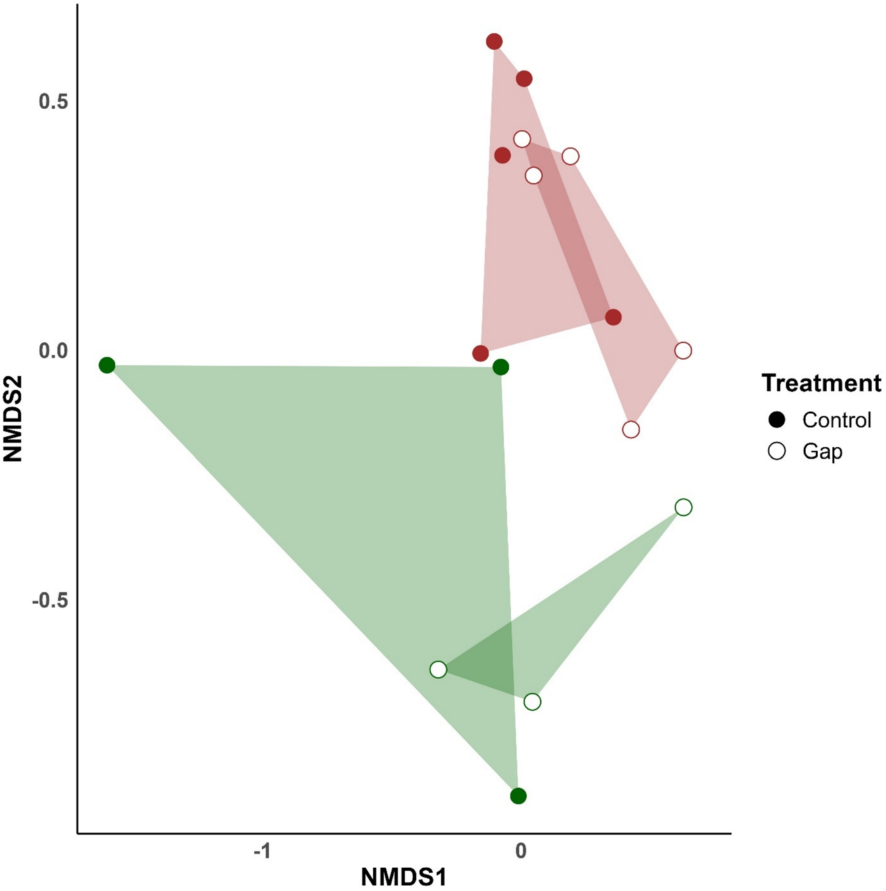

Fig. 3 NDMS ordination illustrating differences in bee communities among silvicultural treatments (gap vs. control) and forests (North Carolina in green, Virginia in red)

regions (Frank et al., In Press). Similarly, other wood-nesting bees, such as *A. pura* and *L. subviridatum*, were more than twice as abundant in gaps as compared to controls in this study (Table 1). However, this pattern was not observed for all species known to nest in dead wood, with *L. cressonii* and *L. coeruleum* being more abundant in the intact forest compared to the gaps. Light intensity from Apr-Jun was two to five times higher in gaps than in control plots (Mayfield et al. 2023b supplementary data). Although herbaceous flowering species were not characterized in this study, an increase in forest floor woody vegetation in gaps was immediately apparent in the years following gap installation (Mayfield et al. 2023b). Many previous studies have documented increases in flowering plant availability following harvests or canopy disturbances (Davies et al. 2023; Mathis et al. 2021; Zitomer et al. 2023), and it is probable that flowers were more available to bees in

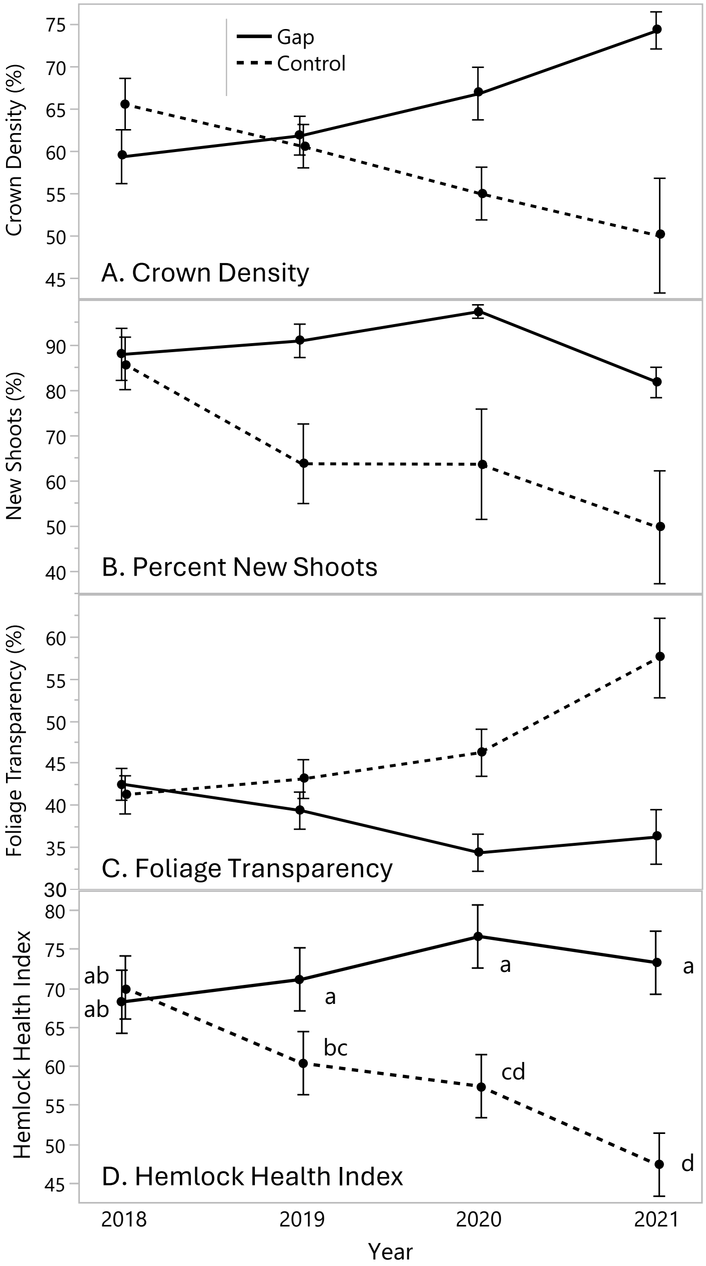

Fig. 4 Mean crown density (**A**), percent new shoots (**B**), and foliage transparency (**C**), for target hemlocks released in silvicultural gaps vs. those in undisturbed control plots in western North Carolina and Virginia, 2018–2021. Vertical bars indicate standard error. Panel **D** displays predicted (least squares) means of the hemlock health index (a composite of the other three values). A mixed linear analysis of variance model was applied only to this response variable; predicted means labeled with the same letter in panel D are not significantly different and vertical bars indicate standard error of predicted means

gaps compared to adjacent forests in the current study, and that this contributed to differences in bee numbers observed between the two treatments.

These results are consistent with other research that demonstrated an increase in bee diversity in response to silvicultural canopy gaps. Eckerter et al. (2021) found that bee richness in spruce forests in Germany was higher in plots where "structural complexity enhancement" (via girdling and uprooting trees) created small gaps. They hypothesized that this relationship was due to enhanced nesting opportunities for wood-nesting species in accumulated deadwood, the creation of newly-open ground for ground-nesters, and additional foraging resources in flowering ground-layer plants and shrubs (Eckerter et al. 2021). Roberts et al. (2017) also found higher bee abundance and diversity in forest openings (size 0.08 to 1.29 ha, created 4–8 years prior to sampling) compared to adjacent closed-canopy stands in mixed hardwood-pine-hemlock forests of western Massachusetts. Similarly, in northern hardwood forests of Ontario, Proctor et al. (2012) demonstrated that group selection silviculture increased the abundance of bees and other pollinators, particularly after leaf-out, when there was a greater contrast in light levels between gaps and intact forest. In that study, bee responses to gaps were hypothesized to be driven by increased light, warmer soil, and harvest-related soil exposure which benefit ground-nesting bees, as well as increases in floral resources for adults (Proctor et al. 2012). Most recently, Ulyshen et al. (2022) reported collecting as many species in small roadside clearings in the southern Appalachians as in the adjacent closed-canopy forest despite an 11-fold greater sampling effort in the forested locations. They suggested that the creation of small clearings with wildflowers may be a particularly effective method for improving pollinator habitat in heavily forested areas of the southern Appalachians.

Plots at our Virginia location were associated with higher bee species richness than those at our North Carolina location. Although all sampling was performed on the same dates in both states simultaneously, the combination of higher elevation and latitude of the Virginia plots (Table SI−1, supp. info.) likely resulted in a delayed phenology of insects and plants relative to the North Carolina plots. Thus, by the time pollinator trapping began on 27 Apr 2020, some of the bee species trapped in Virginia may no longer have been active in the North Carolina plots. This seems particularly likely given that bee richness in the southern Appalachian forests of North Carolina has been shown to peak in April (Ulyshen et al. 2024a), and bee richness in Virginia was highest on the first collection date of our study (data not shown). Differences in species richness between forests might also be due to differences in stand and site variables such as slope, aspect, and vegetative composition. In this study, our primary objective was to compare gaps and control plots, but it is evident that site, stand and environmental factors also contributed to the variability in bee community composition among plots.

Our results should not be considered comprehensive for bee populations in southern Appalachian forests due to methodological limitations and the short duration of the study. We chose to sample with colored pan traps because they are widely used for bee monitoring, inexpensive to deploy, help avoid observer bias associated with hand-netting, and allow for a standardized approach at multiple locations simultaneously (Krahner et al. 2024). The technique has drawbacks, however, including uncertainty about how the proximity of floral resources affect catch, and taxonomic bias toward smaller-bodied bees like *Lasioglossum* spp. and other Halictidae (Hudson et al. 2020; Portman et al. 2020). Additional research on the effect of forest gaps on bees could consider employing targeted netting or vane traps to assess effects on larger-bodied bees (e.g., genera *Apis, Bombus, Megachile, Xylocopa*) with potentially greater accuracy (Prendergast et al. 2020). The study was limited to one trapping season due to travel restrictions associated with the COVID-19 pandemic; extending the study for one or more years, and for additional months per year, may have produced captures of additional species not reported here.

Forests play a key role in supporting bee diversity globally and an estimated two thirds of bees native to the northeastern US are either dependent on or benefit from resources restricted to forests (Smith et al. 2021). However, these species can also benefit from small clearings nearby, especially later in the year when few flowers are available beneath closed canopies (Hanula et al. 2016). The gaps implemented in this study were intentionally small (~ 0.06 ha) to limit rapid growth of shade intolerant trees species that might quickly overtop understory eastern hemlocks shortly after release. Gaps of this size scattered in an otherwise mature, intact forest landscape may serve as a good balance between supplementing floral resources on the landscape while ensuring the availability of forest resources critical to a large fraction of our native bee fauna.

In conclusion, our results suggest that small silvicultural gaps implemented in mixedwood forests of the southern Appalachians have the dual benefit of improving hemlock resilience to *A. tsugae* while also increasing the abundance and diversity of bees on a local scale, at least over the short term. Long-term declines of bee populations have been recently documented in undisturbed forest stands in the southeastern US, particularly for above-ground nesting bees (Ulyshen and Horn 2023). Timber from small, scattered gaps may be difficult to harvest in the form of a commercial timber sale, but leaving the wood on-site (as was done here) likely has habitat benefits for above-ground, wood-nesting species. These group selection cuts of limited size could be a useful silvicultural tool in the effort to conserve both hemlocks and pollinators.

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Authors Contributions AEM: Study conception and design; data acquisition, analysis, and interpretation; manuscript writing, reviewing and editing. RMJ: Study conception and design; data acquisition and interpretation; manuscript reviewing and editing. MDU: Study design; data acquisition, analysis, and interpretation; manuscript writing, reviewing and editing. SH: Study design; data acquisition and interpretation; manuscript review and editing. BTM: data acquisition; manuscript reviewing and editing.

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Data Availability The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests Coauthor Michael D. Ulyshen is a Guest Editor for the special edition on forest pollinators to which this manuscript was submitted and was excluded from the peer review process.

References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Baskent, E. Z., J. G. Borges, J. Kašpar, and M. Tahri. 2020. A design for addressing multiple ecosystem services in forest management planning. *Forests* 11:1108. https://doi.org/10.3390/f11101108.

Brantley, S. T., A. E. Mayfield III., R. M. Jetton, C. F. Miniat, D. R. Zietlow, C. L. Brown, and J. R. Rhea. 2017. Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings. *Forest Ecology and Management* 385:150–160. https://doi.org/10.1016/j.foreco.2016.11.028.

D'Amato, A. W., E. J. Jokela, K. L. O'Hara, and J. N. Long. 2018. Silviculture in the United States: An amazing period of change over the past 30 years. *Journal of Forestry* 116:55–67. https://doi.org/10.5849/JOF-2016-035.

Davies, C. B., T. S. Davis, and T. Griswold. 2023. Forest restoration treatments indirectly diversify pollination networks via floral- and temperature-mediated effects. *Ecological Applications* 33 : e2927. https://doi.org/10.1002/eap.2927.

De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: Indices and statistical inference. *Ecology* 90:3566–3574. https://doi.org/10.1890/08-1823.1.

Dicks, L. V., T. D. Breeze, H. T. Ngo, D. Senapathi, J. An, M. A. Aizen, P. Basu, D. Buchori, L. Galetto, L. A. Garibaldi, and B. Gemmill-Herren. 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat Ecol Evol* 5:1453–1461. https://doi.org/10.1038/s41559-021-01534-9.

Eckerter, T., J. Buse, J. Bauhus, M. I. Förschler, and A. M. Klein. 2021. Wild bees benefit from structural complexity enhancement in a forest restoration experiment. *Forest Ecology and Management* 496:119412. https://doi.org/10.1016/j.foreco.2021.119412.

EDDMapS (2024) Hemlock woolly adelgid. Early Detection & Distribution Mapping System, University of Georgia, Center for Invasive Species and Ecosystem Health. Available online at http://www.eddmaps.org/. Accessed 31 December 2024.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, and J. Mohan. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Ellison, A. M., D. A. Orwig, M. C. Fitzpatrick, and E. L. Preisser. 2018. The past, present, and future of the hemlock woolly adelgid (*Adelges tsugae*) and its ecological interactions with eastern hemlock (*Tsuga canadensis*) forests. *Insects* 9:172. https://doi.org/10.3390/insects9040172.

Fei, S., R. S. Morin, C. M. Oswalt, and A. M. Liebhold. 2019. Biomass losses resulting from insect and disease invasions in US forests. *Proceedings of the National Academy of Sciences.* 116:17371–17376. https://doi.org/10.1073/pnas.1820601116.

Frank, G. S., J. W. Rivers., J. Verschuyl., L. R. Best., M. G. Betts., A. J. Kroll., M. E. Swanson., and M. A. Krawchuk. 2025. Comparison of early seral forest bee communities following clearcutting or wildfire depends on stand age and nesting guild. *Journal of Forestry.* https://doi.org/10.1007/s44392-025-00016-1.

Gazzea, E., A. Battisti, and L. Marini. 2024. Strategies and barriers to reconcile pest management with insect conservation in temperate and boreal forests. *Current Forestry Reports* 10:103–118. https://doi.org/10.1007/s40725-024-00215-7.

Graves, T. A., W. M. Janousek, S. M. Gaulke, A. C. Nicholas, D. A. Keinath, C. M. Bell, S. Cannings, R. G. Hatfield, J. M. Heron, J. B. Koch, and H. L. Loffland. 2020. Western bumble bee: Declines in the continental United States and range-wide information gaps. *Ecosphere* 11:e03141. https://doi.org/10.1002/ecs2.3141.

Hanula, J. L., S. Horn, and J. J. O’Brien. 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management* 348:142–152. https://doi.org/10.1016/j.foreco.2015.03.044.

Hanula, J. L., M. D. Ulyshen, and S. Horn. 2016. Conserving pollinators in North American forests: A review. *Natural Areas Journal* 36:427–439. https://doi.org/10.3375/043.036.0409.

Havill, N. P., M. E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. *Annals of the Entomological Society of America* 99:195–203. https://doi.org/10.1603/0013-8746(2006)099[0195:MDFHWA]2.0.CO;2.

Hovis, M., G. Frey, K. McGinley, F. Cubbage, X. Han, and M. Lupek. 2022. Ownership, governance, uses, and ecosystem services of community forests in the Eastern United States. *Forests* 13:1577. https://doi.org/10.3390/f13101577.

Hudson, J., S. Horn, and J. L. Hanula. 2020. Assessing the efficiency of pan traps for collecting bees (Hymenoptera: Apoidea). *Journal of Entomological Science* 55:321–328. https://doi.org/10.18474/0749-8004-55.3.321.

Kenefic, L. S., J. M. Kabrick, B. O. Knapp, P. Raymond, K. L. Clark, A. W. D’Amato, C. C. Kern, L. A. Vickers, D. C. Dey, and N. S. Rogers. 2021. Mixedwood silviculture in North America: The science and art of managing for complex, multi-species temperate forests. *Canadian Journal of Forest Research* 51:921–934. https://doi.org/10.1139/cjfr-2020-0410.

Krahner, A., A. C. Dietzsch, T. Jütte, J. Pistorius, and J. Everaars. 2024. Standardising bee sampling: A systematic review of pan trapping and associated floral surveys. *Ecology and Evolution* 14:e11157. https://doi.org/10.1002/ece3.11157.

Limbu, S., M. A. Keena, and M. C. Whitmore. 2018. Hemlock woolly adelgid (Hemiptera: Adelgidae): A non-native pest of hemlocks in eastern North America. *J Integr Pest Manage* 9:27. https://doi.org/10.1093/jipm/pmy018.

Mathis, C. L., D. J. McNeil, M. R. Lee, C. M. Grozinger, D. I. King, C. R. V. Otto, and J. L. Larkin. 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. https://doi.org/10.1016/j.foreco.2021.119373.

Mayfield, A. E., III., T. D. Bittner, N. J. Dietschler, J. S. Elkinton, N. P. Havill, M. A. Keena, D. L. Mausel, J. R. Rhea, S. M. Salom, and M. C. Whitmore. 2023a. Biological control of hemlock woolly adelgid in North America: History, status, and outlook. *Biological Control* 185:105308. https://doi.org/10.1016/j.biocontrol.2023.105308.

Mayfield, A. E., III., R. M. Jetton, B. T. Mudder, W. A. Whittier, T. L. Keyser, and J. R. Rhea. 2023b. Silvicultural canopy gaps improve health and growth of eastern hemlocks infested with Adelges tsugae in the southern Appalachian Mountains. *Forest Ecology and Management* 546:121374. https://doi.org/10.1016/j.foreco.2023.121374.

Mayfield, A., S. M. Salom,, K. Sumpter., T. McAvoy., N. F. Schneeberger., and R. Rhea. 2020. Integrating chemical and biological control of the hemlock woolly adelgid: a resource manager’s guide. FHAAST-2018–04. USDA Forest Service, Forest Health Assessment and Applied Sciences Team, Morgantown, West Virginia. 40 p. https://research.fs.usda.gov/treesearch/59529

McAvoy, T. J., R. Mays, N. G. Johnson, and S. M. Salom. 2017. The effects of shade, fertilizer, and pruning on eastern hemlock trees and hemlock woolly adelgid. *Forests* 8:156. https://doi.org/10.3390/f8050156.

McCarty, E., and K. M. Addesso. 2019. Hemlock woolly adelgid (Hemiptera: Adelgidae) management in forest, landscape, and nursery production. *Journal of Insect Science* 19:24. https://doi.org/10.1093/jisesa/iez031.

McClure, M. S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* 82:50–54. https://doi.org/10.1093/aesa/82.1.50.

Miniat, C. F., D. R. Zietlow, S. T. Brantley, C. L. Brown, A. E. Mayfield III., R. M. Jetton, J. R. Rhea, and P. Arnold. 2020. Physiological responses of eastern hemlock (Tsuga canadensis) to light, adelgid infestation, and biological control: Implications for hemlock restoration. *Forest Ecology and Management* 460:117903. https://doi.org/10.1016/j.foreco.2020.117903.

Mullally, H. L., D. S. Buckley, J. A. Fordyce, B. Collins, and C. Kwit. 2019. Bee communities across gap, edge, and closed-canopy microsites in forest stands with group selection openings. *Forestry Sciences* 65:751–757. https://doi.org/10.1093/forsci/fxz035.

Muzika, R. M. 2017. Opportunities for silviculture in management and restoration of forests affected by invasive species. *Biological Invasions* 19:3419–3435. https://doi.org/10.1007/s10530-017-1549-3.

Nagel, L. M., B. J. Palik, M. A. Battaglia, A. W. D'Amato, J. M. Guldin, C. W. Swanston, M. K. Janowiak, M. P. Powers, L. A. Joyce, C. I. Millar, and D. L. Peterson. 2017. Adaptive silviculture for climate change: A national experiment in manager-scientist partnerships to apply an adaptation framework. *Journal of Forestry* 115:167–178. https://doi.org/10.5849/jof.16-039.

Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76:521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.

Oksanen, J., G. L. Simpson., F. G. Blanchet., R. Kindt., P. Legendre., P. R. Minchin., R. B. O'Hara., P. Solymos., M. H. H. Stevens., E. Szoecs., and H. Wagner. 2022. vegan: Community ecology package (2.6–4). Comprehensive R Archive Network. https://www.researchgate.net/publication/360782912_vegan_community_ecology_package_version_26-2_April_2022.

Portman, Z. M., B. Bruninga-Socolar, and D. P. Cariveau. 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. https://doi.org/10.1093/aesa/saaa010.

Prendergast, K. S., M. H. Menz, K. W. Dixon, and P. W. Bateman. 2020. The relative performance of sampling methods for native bees: An empirical test and review of the literature. *Ecosphere* 11:e03076. https://doi.org/10.1002/ecs2.3076.

Proctor, E., E. Nol, D. Burke, and W. J. Crins. 2012. Responses of insect pollinators and understory plants to silviculture in northern hardwood forests. *Biodiversity and Conservation* 21:1703–1740. https://doi.org/10.1007/s10531-012-0272-8.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org.

Roberts, H. P., D. I. King, and J. Milam. 2017. Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management* 394:111–122. https://doi.org/10.1016/j.foreco.2017.03.027.

Romey, W. L., J. S. Ascher, D. A. Powell, and M. Yanek. 2007. Impacts of logging on midsummer diversity of native bees (Apoidea) in a northern hardwood forest. *Journal of the Kansas Entomological Society* 80:327–338. https://doi.org/10.2317/0022-8567(2007)80[327:IOLOMD]2.0.CO;2.

SAS Institute Inc. 2018. *JMP® 14 Documentation Library*. Cary, NC: SAS Institute Inc.

Schomaker, M. E., S. J. Zarnoch., W. A. Bechtold., D. J. Latelle., W. G. Burkman., and S. M. Cox. 2007. Crown-classification: A guide to data collection and analysis. USDA Forest Service General Technical Report SRS-102. USDA Forest Service, Southern Research Station, Raleigh, North Carolina.

Smith, C., T. Harrison, J. Gardner, and R. Winfree. 2021. Forest-associated bee species persist amid forest loss and regrowth in eastern North America. *Biological Conservation* 260:109202. https://doi.org/10.1016/j.biocon.2021.109202.

Stoetzel, M. B. 2002. History of the introduction of *Adelges tsugae* based on voucher specimens in the Smithsonian Institute National Collection of Insects. In *Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, 5–7 February 2002*, ed. B. Onken, R. Reardon, and J. Lashomb. East Brunswick NJ: New Jersey Agricultural Experiment.

Ulyshen, M., and S. Horn. 2023. Declines of bees and butterflies over 15 years in a forested landscape. *Current Biology* 33:1346–1350. https://doi.org/10.1016/j.cub.2023.02.030.

Ulyshen, M., K. Elliott, J. Scott, S. Horn, P. Clinton, N. Liu, C. F. Miniat, P. Caldwell, C. Oishi, J. Knoepp, and P. Bolstad. 2022. Effects of *Rhododendron* removal and prescribed fire on bees and plants in the southern Appalachians. *Ecology and Evolution* 12:e8677. https://doi.org/10.1002/ece3.8677.

Ulyshen, M., K. R. Urban-Mead, J. B. Dorey, and J. W. Rivers. 2023. Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops. *Biological Reviews* 98:1118–1141. https://doi.org/10.1111/brv.12947.

Ulyshen, M. D., C. Adams, J. Adams, S. B. Adams, M. Bland, D. C. Bragg, C. Burdine, M. Callaham, R. Chaney, G. Chapman, P. Clinton, C. Dixon, J. Floyd, P. Jordan, T. Keyser, S. Laseter, R. Mallinger, V. McDaniel, B. Mudder, C. D. Nelson, K. Odanaka, A. C. Oishi, S. Reid, S. Reynolds, K. Robertson, D. Saenz, M. A. Sayer, N. Schiff, B. Scholtens, J. Scott, M. Spetich, M. K. Taylor, J. L. Willis, and A. D. Young. 2024a. Spatiotemporal patterns of forest pollinator diversity across the southeastern United States. *Diversity and Distributions* 30:e13869. https://doi.org/10.1111/ddi.13869.

Ulyshen, M. D., K. M. Ballare, C. J. Fettig, J. W. Rivers, and J. B. Runyon. 2024b. The value of forests to pollinating insects varies with forest structure, composition, and age. *Curr for Rep* 10:322–336. https://doi.org/10.1007/s40725-024-00224-6.

United States Department of Agriculture [USDA] Forest Service, National Association of State Foresters, National Plant Board, and USDA Animal & Plant Health Inspection Service (2021) Hemlock Woolly Adelgid Coordinated Commitment to Improved Management and Restoration of Hemlock: 2021–2025 Program Direction. https://hemlock-woolly-adelgid-national-initiative-gmsts.hub.arcgis.com/pages/strategies. Accessed 7 March 2025.

United States Department of Agriculture [USDA] (2022) USDA Annual Strategic Pollinator Priorities Report. Office of the Chief Scientist, June 2022, Washington, DC. 51 p. https://www.usda.gov/sites/default/files/documents/annual-pollinator-report-2022.pdf. Accessed 2 Jan 2024.

Zattara, E. E., and M. A. Aizen. 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4:114–123. https://doi.org/10.1016/j.oneear.2020.12.005.

Zitomer, R. A., S. M. Galbraith, M. G. Betts, A. R. Moldenke, R. A. Progar, and J. W. Rivers. 2023. Bee diversity decreases rapidly with time since harvest in intensively managed conifer forests. *Ecological Applications* 33:e2855. https://doi.org/10.1002/eap.2855.