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Biological Control - Parasitoids and Predators

Tree species richness and ash density have variable effects on emerald ash borer biological control by woodpeckers and parasitoid wasps in post-invasion white ash stands

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Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) is the most destructive insect to invade North American forests. Identifying habitat features that support EAB natural enemies is necessary to enhance EAB biological control. In many forest ecosystems, tree species diversity has been linked with reduced pest abundance and increases in natural enemy abundance. We assessed the influence of tree species richness, ash density, and proportion of total ash basal area on ash canopy condition, EAB larval densities, and biocontrol by woodpeckers and parasitoids in pairs of healthy and declining overstory (DBH > 10 cm) and recruit-sized ash (DBH 2–10 cm) in 4 post-invasion forests in Michigan, USA. Tree species richness and ash density were not significantly associated with EAB larval densities, ash canopy dieback and transparency, and woodpecker predation of EAB larvae. In declining and healthy overstory ash, woodpeckers killed 38.5 ± 3.9% and 13.2 ± 3.7% of larvae, respectively, while the native parasitoid *Phasgonophora sulcata* Westwood killed 15.8 ± 3.8% and 8.3 ± 3.0% and the introduced parasitoid *Spathius galinae* Belokobylskij & Strazanac killed 10.8 ± 2.5% and 5.0 ± 2.6% of EAB larvae. Parasitism by *P. sulcata* was inversely related to ash density while parasitism by *S. galinae* was positively associated with ash density. Ash density, but not tree diversity, appears to differentially influence biological control of EAB by parasitoids, but this effect is not associated with reduced EAB densities or improved canopy condition.

Key words: emerald ash borer, tree diversity, biological control, parasitoid, woodpecker predation

Introduction

Emerald ash borer (EAB) (Coleoptera: Buprestidae) (*Agrilus planipennis* Fairmaire) is a phloem-feeding beetle native to Asia that has quickly become the most costly and destructive forest insect to invade North America (Herms and McCullough 2014, McCullough 2020). Hundreds of millions of ash (*Fraxinus* spp.) trees have been killed by EAB since it was detected in 2002 (Poland and McCullough 2006, Siegert et al. 2014, McCullough 2020), resulting in billions of dollars in economic damage (Aukema et al. 2011). Loss of ash trees resulting from EAB can alter nutrient cycles (Nisbet et al. 2015), change plant community composition (Kolka et al. 2018, Engelken et al. 2020), increase coarse woody debris (Engelken and McCullough 2020, Engelken et al. 2020), and reduce stream macroinvertebrate diversity (Larson et al. 2022), amongst other ecological consequences (Herms and McCullough 2014, Klooster et al. 2018). In some infested trees, a substantial portion of EAB larvae are killed by native woodpeckers (Lindell et al. 2008, Jennings et al. 2013, Flower et al. 2014, Duan et al. 2022) or by parasitoids, including native and introduced species (Duan et al. 2018, 2023). However, whether effects of natural enemies can reduce EAB densities enough to slow ash mortality or protect post-invasion ash regeneration in North America is unclear.

Identifying forest stand characteristics, including tree species diversity, that support biological control services provided by woodpeckers and parasitoid wasps may be an important aspect of managing forests invaded by EAB. Trees in mixed-species stands typically sustain less insect herbivory compared to their counterparts in stands dominated by one or very few species (Jactel and Brockerhoff 2007, Jactel et al. 2021). A potential mechanism to account for this pattern is based on natural enemy recruitment (Staab and Schuldt

2020, Stemmelen et al. 2022). This hypothesis, referred to as "the enemies hypothesis," suggests that where plant diversity is high, more resources are available to support natural enemies, which enhances biological control of herbivores (Root 1973). Resources to support natural enemy survival can include nectar, pollen, honeydew, alternative prey or hosts, and shelter (Root 1973, Staab and Schuldt 2020). Presumably, species-rich forests host a higher abundance and more diverse suite of natural enemies that can provide greater biological control of pests compared to species-poor forests.

Native woodpeckers typically prey on mature EAB larvae in pupal cells (i.e., J-larvae), beginning in fall and continuing through winter until adult beetles emerge from trees in spring (Cappaert et al. 2005, Lindell et al. 2008, Flower et al. 2014). Diverse forest stands may enhance woodpecker predation of EAB by providing alternative prey, particularly during summer when birds are nesting and most EAB are free-living adults or early instar larvae (Cappaert et al. 2005). Whether or not woodpecker predation of EAB is related to diversity of tree species, however, is not clear. Smith et al. (2015) found no relation between tree species diversity and density of external signs of EAB infestation on ash tree trunks, represented by the sum of D-shaped EAB adult emergence holes and larger holes from woodpecker attacks. Because EAB exit holes and woodpecker attacks were combined into a single variable, however, potential effects of tree diversity on woodpecker predation rates are unknown. Additionally, Smith et al. (2015) recorded EAB signs at breast height (1.3 m) on tree trunks but not higher in the tree. Like other *Agrilus* species, EAB typically infest trees from the top down and signs of EAB infestation on the lower 1.5–2 m of the trunk are rarely apparent until trees are heavily infested (Cappaert et al. 2005). Therefore, assessing woodpecker predation only at breast height may not accurately reflect the influence of tree diversity on woodpecker predation, especially in recently or lightly infested trees with low EAB densities.

Parasitoids that attack EAB larvae or eggs may also benefit from diverse forests due to increased availability of alternative prey and supplemental resources. At least 14 species of parasitoid wasps native to North America can develop in EAB larvae (Bauer et al. 2015a). These parasitoids all attack native phloem-borers or other subcortical insects. For example, *Phasgonophora sulcata* Westwood (Hymenoptera: Chalcidae), a native parasitoid wasp, is known to attack native *Agrilus* spp. larvae in declining, dying, or recently killed *Betula*, *Quercus*, or *Populus* spp. trees (Barter 1965, Haack and Benjamin 1981, Loerch and Cameron 1983). Diverse forests may be more likely to include trees colonized by native phloem-feeding *Agrilus* spp. larvae that serve as hosts for *P. sulcata*, along with other native parasitoids such as *Atanycolus* spp. Additionally, nectar provided by flowering hardwood trees, shrubs, or herbaceous plants can provide a supplemental resource required by many parasitoid species (Shaw 2006, Gillespie et al. 2016, Tena et al. 2016). Forests with numerous tree species may also include diverse communities of honeydew-producing Hemipterans, potentially providing supplemental nutrition for parasitoids for much of the growing season (Tena et al. 2016).

In China, multiple parasitoid wasp species can kill a high percentage of EAB larvae (Wang et al. 2010a). To manage EAB in in its invaded range, 3 specialist parasitoids of EAB were introduced from northeast China into North America in 2007, including *Tetrasticus planipennisi* (Yang), a gregarious endoparasitoid of EAB larvae, *Oobius agrili* Zhang and Huang, a solitary egg parasitoid, and *Spathius agrili* Yang, a gregarious ectoparasitoid (Bauer et al. 2015b). In 2014, another specialist gregarious ectoparasitoid of EAB larvae from the Russian Far East, *Spathius galinae* Belokobylskij & Strazanac, was introduced (Bauer et al. 2015a, Duan et al. 2019). To date, introduced parasitoids of EAB have been released in 31 states with EAB infestations and *T. planipennisi*, *O. agrili*, and *S. galinae* have become established through much of the northeastern and midwestern United States (Duan et al. 2023). Species-rich forests may support these species by providing diverse supplemental resources in the form of flowering trees and perhaps honeydew-producing Hemipterans.

Studies in southeastern Michigan forests conducted in 2006–2007 when EAB populations were at or near peak densities, found no relationship between qualitative estimates of ash canopy condition and tree diversity, ash density, DBH, basal area or other stand and site-related variables (Smith et al. 2015). This research, however, occurred before evidence of significant EAB larval parasitism by native species was first observed (Cappaert and McCullough 2009) and before introductions of introduced parasitoids began (Bauer et al. 2015a). Since then, the EAB carrying capacity, that is, the amount of live ash phloem available for larval development (McCullough and Siegert 2007), has dropped by orders of magnitude in the post-invasion stands that now characterize forests in much of Michigan (Engelken and McCullough 2020, Engelken et al. 2020, Siegert et al. 2021) compared with the period when Smith et al. (2015) collected data. In other areas, however, overstory trees of less preferred ash species along with ash regeneration, provide ample phloem to support EAB populations (Duan et al. 2017, Robinett and McCullough 2019, Robinett et al. 2021, Siegert et al. 2021, Gould et al. 2022). Establishment of 3 species of introduced EAB parasitoids in some Michigan forests over the past 15 years (Duan et al. 2022, 2023) and ample exposure of native parasitoid populations to EAB-infested ash trees, presents the opportunity to evaluate potential relationships among tree species diversity, ash density, EAB density, ash condition, and biological control.

We evaluated potential effects of tree species diversity and ash density on EAB larval densities, predation by woodpeckers, and parasitism by native and introduced species in 4 post-invasion forests in south-central Michigan, USA. Density, diameter, and basal area of live trees were recorded by species, along with canopy condition and woodpecker predation on live ash trees. A subset of overstory and recruit-sized ash trees were felled and debarked to quantify EAB larval density, egg and larval parasitism, and woodpecker predation in 2022 and 2023. We hypothesized that tree diversity would be (i) negatively related to EAB larval densities and (ii) positively associated with EAB predation and parasitism rates.

Methods

Study Sites

This study was conducted on 4 parcels of public land in south-central Michigan where live ash trees were present and relatively abundant. Sites included Rose Lake State Game Area (Clinton County), Muskrat Lake State Game Area (Clinton County), Tamarack Lake State Game Area (Eaton County), and Sleepy Hollow State Park (Clinton County) (Supplementary Fig. S1). Summary statistics for each site are provided in Table 1. In May—June 2022, we canvassed these sites to locate and delineate regions with moderate to high densities of live ash. We overlaid a 50 × 50 m grid on each site and identified grid cells within the regions where living ash trees occurred for further surveys. Number of grid cells surveyed ranged from 48 to 55 cells in 3 parcels down to 22 cells at Rose Lake, the smallest parcel (Table 1).

Tree Surveys

During the 2022 growing season, we surveyed trees in each grid cell (where live ash occurred) using a three-step protocol. First, we

Table 1. Summary data from all field sites regarding area surveyed, species diversity, ash density, basal area, and EAB densities. Each surveyed cell was 50 × 50 m and 0.03 ha of area was surveyed within each cell. Recruits ranged in DBH from 2 to 10 cm and overstory ash were >10 cm DBH

					Dissected ash trees		Overstory and recruits	**Live overstory basal area (m^2/ha)**	Overstory ash					
Site	Coordinates	Total area surveyed (ha), number of cells	Total tree species	No. ash trees dissected	**Overstory: Mean ± SE DBH (cm)**	Recruits:Mean ± SE DBH (cm)	**Live ash phloem area (m^2)** [a]	All species	**Dead basal area (m^2/ha)**	**Live basal area (m^2/ha)**	Live stems per ha	Dead ash stems per ha	**Declining: EAB larvae per m^2 ± S.E.**	**Healthy: EAB larvae per m^2 ± S.E.**
Muskrat Lake	42.90765, −84.5858	1.6 Ha, 55 cells	36	20 overstory 20 recruits	13.9 ± 0.8	5.0 ± 0.1	1042	184.7	1.5	17.6	85.4	69.6	51.5 ± 9.2	4.2 ± 2.3
Rose Lake	42.788905, −84.393406	0.6 Ha, 22 cells	19	12 overstory 12 recruits	11.3 ± 0.8	6.1 ± 1.2	500	194.6	1.4	21.7	105.3	53.4	75.5 ± 38.6	3.7 ± 2.8
Sleepy Hollow	42.93767, −84.4014	1.4 Ha, 48 cells	26	16 overstory 16 recruits	14.7 ± 0.9	4.7 ± 1.6	653	175.2	3.8	14.5	40.6	57.3	31.3 ± 11.6	0.8 ± 0.8
Tamarack Lake	42.728817, −85.053769	1.5 Ha, 53 cells	30	20 overstory 20 recruits	14.6 ± 0.9	6.3 ± 0.2	989	187.2	2.4	16.0	62.1	54.5	31.9 ± 15.3	0.8 ± 0.5

[a]Calculated using methods described in McCullough and Siegert (2007).

assessed the condition of 4 live ash trees (> 3 cm DBH) per cell. Trees were selected by walking from the center of each grid cell in a randomly selected direction to the first live ash tree we encountered. We returned to the center and repeated this process at a 90 degree angle from the first direction and then repeated the process 2 more times. If there were less than 4 live ash trees (> 3 cm DBH) in the grid cell, we dropped the cell from further surveys. For each ash tree, we recorded species, measured DBH, and visually estimated canopy dieback and transparency in 10% increments (Shoemaker et al. 2007), where higher values indicate less healthy trees. We excluded lower portions of the canopy that had died due to shading effects from the upper canopy or from neighboring trees.

After evaluating the 4 ash trees, we established a fixed radius plot (7 m radius; 154 m^2 area) at the center of each grid cell. We measured and recorded DBH of live and dead overstory trees (> 10 cm) and recruits (2–10 cm DBH) within each plot by species. Shrubs were encountered at our sites but were not included in analyses. Additionally, we recorded the number of live and dead recruits (2–10 cm DBH) by species and tallied live and dead trees by species and DBH class (5 cm classes) in four 18 × 2 m transects equally spaced along the perimeter of each fixed radius plot. The combination of the fixed radius plot and 4 transects resulted in a total of 0.03 ha surveyed per cell.

We calculated basal area by species as BA = ((DBH in cm / 2)^2) * π) /1,000 using all overstory trees and recruits recorded in our surveys. Those values were divided by the total area surveyed across all grid cells at each site yielding an estimate of basal area (m^2) by species standardized per ha per site. For trees assigned to size classes, we used the midpoint value as the DBH for the tree when calculating basal area. For example, for a tree in the size class of 15–20 cm, the mean value of 17.5 was used to calculate basal area. Finally, we calculated relative importance values (RIV) for all live overstory tree species to further characterize the study sites. RIV are calculated as the sum of the frequency, density, and dominance of each species relative to all other species, and are commonly used in forest ecology and management.

Parasitoid Releases

At least one of the 3 introduced EAB parasitoids, including *Spathius galinae* and *Tetrasticus planipennisi* which attack larvae, and *Oobius agrili,* an egg parasitoid, had previously been released in each of the 4 study sites between 2010 and 2021 (Supplementary Table S1). We released more of each species between June and September 2022. Parasitoids were released at the intersection of 4 ash-containing grid cells at each site. A one cell buffer was left around these cells before additional releases occurred at the next intersection of 4 grid cells. We repeated this process across all surveyed grid cells. Location of all parasitoid releases at each site are indicated in Supplementary Figs. S2–S5.

Prior to releasing parasitoids, we separated adults (*S. galinae* and *T. planipennisi*) or eggs (*O. agrili*) so that similar numbers of each species were released at each release point in each site. *S. galinae* and *T. planipennisi* were reared to adulthood and released as live adults while *O. agrili* was released as either adults or as pupae and pharate adults inside EAB eggs that were placed in small pill bottles and attached to trees. Because parasitoid emergence rates are variable, the number of *O. agrili* that emerged from parasitized eggs during each release period varied slightly. For *S. galinae* and *T. planipennisi*, we divided the number of adults equally across all release points. Number of individuals of each species and the date and location of each release are detailed in Supplementary Table S2. Total number of parasitoids released at each site in 2022 is listed in Supplementary Table S1.

Tree Dissections

We created blocks at each site by delineating large regions with similar areas of live ash phloem, estimated following methods of McCullough and Siegert (2007) using DBH data collected in surveys in the grid cells. For trees with DBH < 13 cm, we calculated ash phloem area as (Y = DBH * 0.3798 − 1.7587). For trees > 13 cm DBH, ash phloem area was estimated as $Y = (0.024 * DBH^2) - (0.307 * DBH) + 2.63$. In total, we delineated 14 treatment blocks across the 4 sites. Area of live ash phloem across all blocks averaged (± standard error) 227.5 ± 13.4 m^2 and ranged from 143 m^2 in block RL_R at Rose Lake to 309 m^2 in block ML_WL at Muskrat Lake (Supplementary Table S3). At individual sites, the average area of live ash phloem was 260.6 ± 16.8 m^2 at Muskrat Lake, 166.6 ± 13.6 m^2 at Rose Lake, 217.8 ± 39.8 m^2 at Sleepy Hollow and 247.3 ± 10.6 m^2 at Tamarack Lake. Total live ash phloem area in each site is listed in Table 1 and total living and dead ash phloem area in each treatment block is listed in Supplementary Table S3. Figure 1 illustrates the typically patchy nature of live ash phloem area and tree species richness across the Muskrat Lake site.

From October through December 2022, we felled and debarked pairs of overstory ash trees within each treatment block to quantify EAB larval density, predation, and parasitism. Each pair of trees consisted of one declining and one healthy ash tree identified during the 2022 summer surveys. Declining trees had > 40% canopy dieback, and multiple signs of EAB infestation such as woodpecker attack marks, EAB adult exit holes and epicormic sprouts. We felled 2 pairs of trees in treatment blocks that encompassed 4–16 surveyed grid cells (11 blocks total) and 3 pairs of trees in treatment blocks with more than 16 surveyed grid cells (3 blocks total). We dissected more trees in larger treatment blocks to account for potential spatial variation in EAB densities, ash densities, and parasitoid densities. One pair of trees at Rose Lake that were 7.0 cm and 7.6 cm in DBH, respectively, were dissected because they were the largest living ash in that cell. All other overstory ash were >10 cm. Tree pairs for felling were located within cells selected using a random number generator. We cut a total of 62 ash trees across all sites (6–9 pairs per site) (Table 1).

After felling trees, we cut the main trunk and large branches into 1 m bolts. We sampled alternate bolts, starting with the second bolt from the base of the tree and continuing with alternate bolts until we reached bolts that were <5 cm in diameter. We similarly sampled alternate bolts from branches that were >5 cm in diameter. We sampled for EAB egg parasitism by *O. agrili* by scraping a 1-m^2 area of outer bark with a draw knife from the south side of the 2-m and 6-m-high bolts from each tree. Scraped bark was collected in a paper bag and examined under a microscope in the laboratory during the 2022–2023 winter. Number of hatched EAB eggs, eggs with *O. agrili* exit holes, and unhatched EAB eggs were recorded from each bark sample.

Prior to debarking bolts, we recorded diameter at the midpoint of each bolt and then counted healed-over EAB larval galleries, D-shaped EAB adult exits, and characteristic holes left by woodpeckers preying on EAB larvae. After removing outer bark with drawknives, we tallied live and dead EAB larvae by development stage (1st—2nd instar, 3rd instar, 4th instar, or J-shaped mature larvae). We recorded whether larvae were parasitized and by which species. We removed up to 15 healthy larvae from the 2-m and 6-m-high bolts on each tree. Larvae were placed into individual well plates, transported to the laboratory, and dissected to quantify internal parasitism by *P. sulcata*.

In spring 2023, we felled and debarked pairs of healthy and declining ash recruits (2–10 cm DBH) in each treatment block to assess

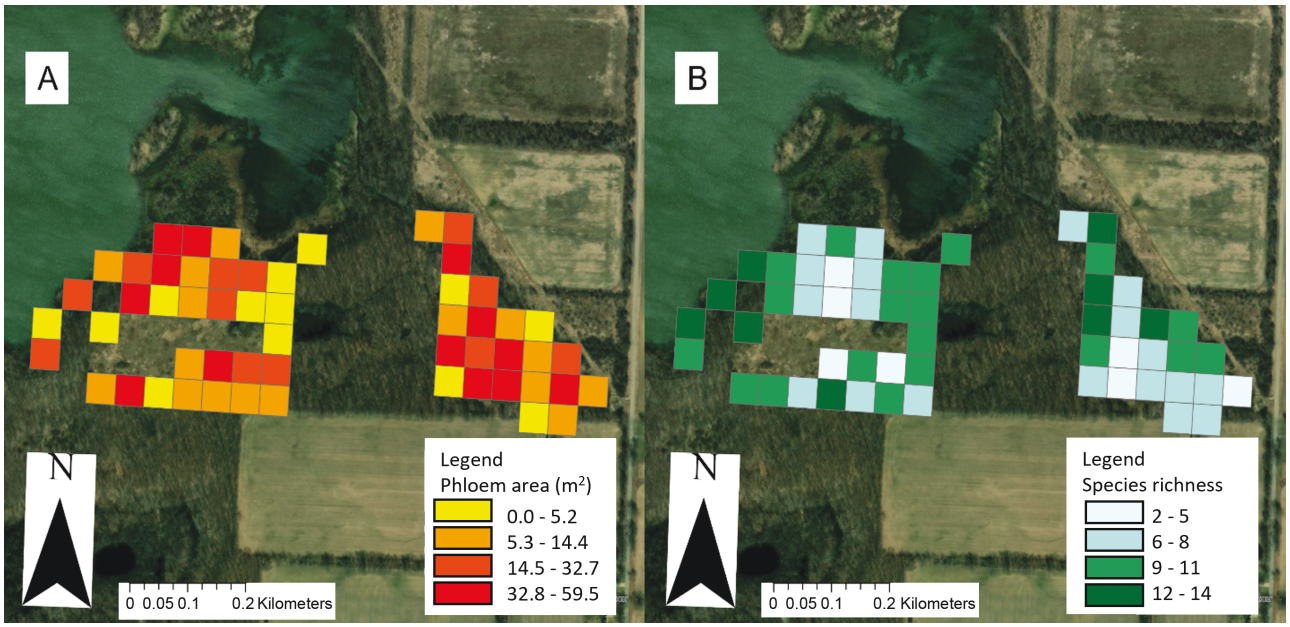

Fig. 1. Aerial image showing the distribution of A) live ash phloem area and B) Tree (DBH > 2 cm) species richness recorded in 50 × 50 m grid cells from surveys at Muskrat Lake in 2022. Ash phloem area and tree species richness varied similarly across cells at all other sites. Satellite images (using world imagery basemap from ESRI 2023) of all field sites are provided in Supplementary Figs. S2–S4.

larval densities and parasitism rates in smaller trees. *T. planipennisi* preferentially parasitizes EAB larvae in smaller trees (Duan et al. 2021), which could lead to differences in parasitism rates between ash overstory trees and recruits. Pairs of recruits for dissections were selected within a circular plot with an 18 m radius in the center of the same grid cells where overstory ash had been felled in fall 2022. Healthy recruits had no woodpecker feeding holes, healed-over larval galleries, exit holes, or other evidence of EAB infestation. Declining recruits had at least one woodpecker feeding hole or another EAB sign on the trunk. If we were unable to locate a declining recruit within the 18-m-radius plot, we moved to a randomly selected adjacent cell and repeated the search. We continued moving to other adjacent cells until suitable pairs of recruits were located. We felled and sampled a total of 62 recruits across sites (6–9 pairs of healthy and declining recruits per site) (Table 1).

Statistical Analysis

Rarefaction of Species Richness Data

We used the iNEXT package (Hsieh et al. 2020) in R v 4.2.1 (R Core Team 2022) to rarefy species richness of live overstory trees and recruits recorded within each grid cell. Rarefaction is a statistical re-sampling technique that allows tree species richness to be compared between communities with unequal sample sizes (Gotelli and Colwell 2011, Gotelli and Chao 2013). We set the number of bootstraps to 30 and the endpoint for rarefaction to 30 trees across all cells. This was the observed richness value at 3 sites and resulted in extrapolation for 79 cells and interpolation for 99 cells.

Model Fitting—Ash Canopy Condition

Prior to fitting models, we used the 'cor.test()' function in R to determine the degree to which tree species richness, ash density per Ha, and the proportion of basal area comprised of ash were correlated with each other. We found that all predictors were significantly correlated with each other (Supplementary Table S4). Therefore, we fit 3 general linear models to separately evaluate how tree species richness, ash density (stems per ha), and the proportion of basal area comprised of live ash (henceforth referred to as 'proportion basal area-ash') influenced average canopy dieback and average canopy transparency (percentages) recorded in each cell. We included site as a fixed effect term in these models because we were interested in accounting for variation in our response variables between sampling locations. We did not include site as a random effect term because we collected data at 4 sites which is below the recommended level of replication for random effect terms in mixed models (Harrison 2015, Bolker et al. 2022). Response variables in these models were logit transformed to normalize residuals (Warton and Hui 2011). We used diagnostic plots to check models for normality and heteroscedasticity. The significance of all fixed effects in each model was evaluated with type-II F-tests.

Model Fitting—Tree Dissections

We fit 3 general linear models to evaluate how tree species richness, ash density, and proportion basal area-ash influenced EAB density per m^2 (total number of recent woodpecker attacks, parasitized larvae, and live EAB larvae) using data recorded within each cell where trees were dissected. In each of these models we included tree condition (healthy or declining), tree stratum (overstory or recruit), and sample site as covariates. Each model tested a three-way interaction term between the tree diversity or ash density metric in each model with tree condition and tree stratum. We $\ln(x + 1)$ transformed EAB densities per m^2 to normalize model residuals. We chose not to fit these models as generalized linear models with a count distribution (Poisson or negative binomial) and an offset term to account for surface area, because such distributions did not fit the data well based on examination of diagnostic plots generated by the "DHARMa" package (Hartig 2022). Therefore, we chose to log-transform EAB counts per m^2 in general linear models to minimize type-I error (Ives 2015). We evaluated the significance of all fixed effects with type-II F-tests. We created diagnostic plots to assess each model for normality and heteroscedasticity.

We fit a set of generalized linear models to assess if the proportion of larvae killed by woodpeckers, *S. galinae*, and *P. sulcata* were influenced by tree species richness, ash density, and proportion basal area-ash. Each model contained tree condition, tree stratum, sampling site, as predictors and a three-way interaction of the tree diversity or ash density metric in each model with tree condition and tree stratum. These models were fit with quasibinomial distributions and logit-link functions due to the presence of overdispersion in each model that was present when models were fit with binomial distributions. We determined overdispersion was present in our models by examining diagnostic plots created via the DHARMa package. Overdispersion commonly occurs in binomial models when the variance of the data is greater than that predicted by the model (Harrison 2015). Quasibinomial models include a dispersion parameter which accounts for additional variation in the data not accounted for in a binomial model and is an effective way to account for overdispersion (Shoukri and Aleid 2022). Proportion of larvae killed by woodpeckers was calculated by dividing the total number of current-year attack marks recorded on each debarked tree by the total number of healthy, dead, and parasitized larvae plus the total number of current-year attack marks. To quantify EAB parasitism from *P. sulcata*, we only used data from bolts from which we had dissected larvae to check for internal parasitism. For all other predation and parasitism models we use data from all dissected bolts from each tree. Some trees either had no EAB larvae to dissect or EAB larvae were destroyed in the process of removing them from the tree for laboratory dissection. Therefore, *P. sulcata* models only included data from 31 declining and 21 healthy overstory trees, and 23 declining ash recruits and 6 healthy recruits. In *P. sulcata* models, we included all EAB larval stages in our calculation of EAB parasitism since *P. sulcata* parasitizes first instars (Bauer et al. 2015b) and all parasitoid larvae developing in later instars would have been detected upon dissection. To quantify parasitism by *S. galinae*, we used data from all bolts that were dissected across all trees. When calculating the proportion of larvae parasitized by *S. galinae*, we excluded first and second instars, as this species typically parasitizes third and fourth instar EAB larvae (Belokobylskij et al. 2012).

Results

We recorded tree data in a total of 178 cells (50 × 50 m) across all sites, including 55 cells at Muskrat Lake, 22 cells at Rose Lake, 48 cells at Sleepy Hollow, and 53 cells at Tamarack Lake. Across all sites, we tallied a total of 42 overstory and 37 recruit species. Tree species richness was highest at Muskrat Lake and lowest at Rose Lake (Table 1). Rarefied tree species richness recorded in each cell was inversely correlated to ash density ($r = -0.229$, $P = 0.002$, Fig. 2) and proportion basal area-ash ($r = -0.278$, $P < 0.001$) (Supplementary Table S4). Ash density per Ha and proportion basal area-ash were positively correlated with each other ($r = 0.519$, $P < 0.001$, Supplementary Table S4).

Overstory Trees

We tallied a total of 1,608 live and 465 dead overstory trees across the 4 sites. White ash (*F. americana*) was the most abundant live ($N = 245$) and dead ($N = 196$) species across all sites with an average (± SE) DBH of 16.8 ± 0.5 and 18.0 ± 0.7 cm, respectively. Other relatively abundant live species included *Ulmus americana, Acer saccharinum, A. negundo*, and *Prunus serotina* with a total of 212, 156, and 117 live trees, respectively. Common dead overstory species included *F. pennyslvanica*, *U. americana, P. serotina,* and *A. negundo* represented by 117, 71, 16, and 15 individuals, respectively.

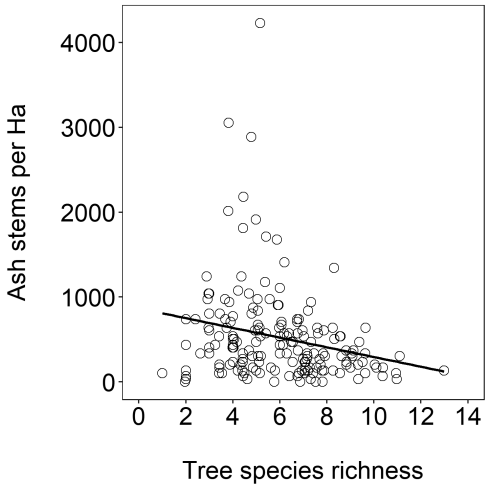

Fig. 2. Tree species richness was negatively correlated with live ash density recorded in the 50 × 50 m grid cells ($t = -3.127$, df = 176, $P = 0.002$, $r = -0.229$). See Supplementary Table S4 for all correlations between tree species richness, ash density, and proportion ash basal area.

White ash had the second highest RIV across all sites but other species including *A. saccharinum, P. serotina,* and *Quercus rubra* had higher basal areas (Table 2). White ash had the highest RIV at Muskrat Lake and was among top 5 highest RIVs at all other sites (Table 2). Green ash (*F. pennsylvanica*) had the second highest RIV at Tamarack Lake, but the lowest basal area when compared to the 4 other dominant species at this site. Although we recorded some live black ash (*F. nigra*) at Tamarack Lake and Muskrat Lake, this species was not in the top 5 highest RIV at any site (Table 2). *Acer saccharinum* had the highest RIV when all sites were analyzed together, and this species also had the highest RIV at Tamarack Lake (Table 2). Much of the *A. saccharinum* basal area occurred at Tamarack Lake, which accounted for 80% of the total 21.9 m^2 of *A. saccharinum* basal area recorded across all sites. Other species with high RIVs across sites included *U. americana, P. serotina*, and *A. negundo* (Table 2).

Recruits

We recorded a total of 4,200 live and 794 dead recruits across the 4 sites. As with overstory trees, *F. americana* was the most common live and dead recruit species; 1,442 live and 318 dead *F. americana* recruits were recorded. Other abundant recruit species included *F. pennsylvanica* (838 live, 318 dead stems), *U. americana*, (516 live, 109 dead stems) and *Crataegus sp*. (289 live, 65 dead stems), and *Carya ovata* (180 live, 3 dead stems).

Ash Dieback and Transparency

We estimated percent canopy dieback and transparency on 4 live ash trees (> 3 cm DBH) in each surveyed cell. Average canopy dieback varied significantly across sites in all models and was highest at Rose Lake (32.3 ± 2.8%), followed by Sleepy Hollow (23.6 ± 1.9%), Muskrat Lake (22.5 ± 1.6%), and Tamarack Lake (13.3% ± 1.3) (Table 3). Similarly, average canopy transparency varied significantly across all sites in all models and was highest at Rose Lake (42.3 ± 2.5%), followed by Muskrat Lake (35.1 ± 1.5%), Sleepy Hollow (32.5 ± 1.6%), and Tamarack Lake (25.0 ± 1.0%) (Table 3). Tree species richness, ash density, and proportion basal area-ash were not significantly associated with mean canopy dieback or transparency estimates recorded on monitoring trees (Table 3).

Table 2. Relative importance values[a] and basal area of live overstory trees (DBH > 10 cm) by species across 4 post-invasion forested sites in central Michigan. The 5 species with the highest relative importance values are listed for each site

Site	Species	Relative importance	Basal area ($m^2 \cdot ha^{-1}$)
All sites together	*Acer saccharinum*	41.9	4.1
	Fraxinus americana	37.2	1.2
	Ulmus americana	31.7	1.0
	Prunus serotina	25.0	2.0
	Quercus rubra	20.8	2.2
Muskrat Lake	*Fraxinus americana*	38.6	1.3
	Acer saccharum	31.6	1.9
	Ulmus americana	29.9	1.0
	Prunus serotina	26.1	1.6
	Quercus rubra	24.0	2.5
Tamarack Lake	*Acer saccharinum*	103.4	11.0
	Fraxinus pennsylvanica	34.6	0.7
	Acer negundo	31.9	1.2
	Celtis occidentalis	26.4	1.4
	Fraxinus americana	20.6	0.8
Sleepy Hollow	*Ulmus americana*	47.7	1.5
	Quercus rubra	41.2	4.9
	Carya ovata	30.9	1.8
	Fraxinus americana	24.2	1.1
	Tilia americana	21.0	1.4
Rose Lake	*Prunus serotina*	95.0	9.6
	Fraxinus americana	78.7	2.2
	Acer negundo	27.7	0.8
	Ulmus americana	26.3	1.0
	Quercus bicolor	20.2	1.7

[a]Relative importance values are calculated from the relative density, relative dominance, and relative frequency of each species.

Ash Dissections

Tree condition and tree stratum interacted to influence larval EAB densities in dissected trees across all EAB models. Densities of EAB larvae were highest in declining recruits, second highest in declining overstory trees, followed by healthy overstory ash, and healthy recruits (Tables 4 and 5). Tree diversity, ash density, and proportion basal area-ash did not affect live EAB larval densities (Table 5). While all declining overstory ash were infested with EAB larvae, only 6 healthy overstory ash had no larvae. Two uninfested, healthy overstory ash were encountered at Rose Lake, Sleepy Hollow and Tamarack Lake but none were dissected at Muskrat Lake. Only one declining ash recruit had no larvae while 19 of the 31 healthy ash recruits did not have any larvae. Number of healthy recruits with no larvae included 2 trees at Rose Lake, 5 trees at Muskrat Lake, 6 trees at Tamarack Lake, and 6 trees at Sleepy Hollow.

Woodpecker Predation

Proportion of EAB larvae killed by woodpeckers was significantly higher in declining ash (30.5 ± 2.6%) than in healthy ash (7.1 ± 1.9%) and in overstory trees (25.0 ± 3.1%) compared to recruits (12.6 ± 2.1%) in all woodpecker models. There was no significant interaction between tree condition and stratum in any woodpecker predation model (Table 5). Woodpeckers killed the highest proportion of larvae in declining overstory trees followed by declining recruits, healthy overstory trees, and healthy recruits (Table 4). The proportion of larvae killed by woodpeckers varied significantly by site in all woodpecker models and was highest at Tamarack Lake (24.9 ± 4.4%), followed by Rose Lake (20.3 ± 4.6%), Muskat Lake (15.3 ± 2.9%), and Sleepy Hollow (14.2 ± 3.1%). Tree species richness, ash density, and proportion basal area-ash did not influence the proportion of larvae killed by woodpeckers (Table 5). Only a single declining overstory ash, out of all trees dissected, did not have current-year woodpecker attack marks, while 18 healthy overstory ash had no current-year woodpecker attack marks. Four declining recruits and 28 healthy recruits had no current-year woodpecker attack marks.

Parasitism

Between 2 June and 21 September 2022, we released a total of 5,854 *S. galinae*, 5,489 *T. planipennisi*, and 3,110 *O. agrili* across all field sites (Supplementary Table S1). Total external parasitism rates were highest in in declining overstory ash, followed by declining recruits, and healthy overstory ash, while there was no external parasitism in healthy recruits (Table 4). Total average parasitism rates for overstory trees were highest at Tamarack Lake (13.9 ± 5.8%), followed by Rose Lake (11.6 ± 3.6%), Muskrat Lake (9.9 ± 4.4%), and Sleepy Hollow (7.1 ± 2.9%). Highest parasitism rates were recorded in recruits at Sleepy Hollow (13.3 ± 5.2%), followed by Rose Lake (8.4 ± 5.4%), Muskrat Lake (7.1 ± 2.3%), and Tamarack Lake (4.0 ± 2.5%). Both native and introduced external larval parasitoids killed the highest percentage of EAB larvae in declining overstory trees, followed by declining recruits and healthy overstory trees. Total EAB mortality, calculated from the total number of dead, parasitized, and predated EAB larvae, followed the same trend and was highest in declining overstory ash (56.8 ± 3.8%) and lowest in healthy recruits (36.1 ± 10.2%) (Table 4).

Spathius galinae, was the most common parasitoid recorded in debarked overstory trees (70% of all parasitized larvae), followed by *Atanycolus* spp. (14.6%), *T. planipennisi* (7.7%), and in situ *P. sulcata* pupae (1.5%). The remaining parasitoids could not be identified (6.2%). For ash recruits, *S. galinae* was the most common species (48.8% of parasitized larvae), followed by *T. planipennisi*

Table 3. Effect of tree species richness, ash density, and field site on tree dieback and transparency. The effects of tree species richness, ash density, and proportion basal area-ash on canopy dieback and transparency were evaluated in separate models due to correlations between these variables (Supplementary Table S4). Visual estimates of percent dieback and percent transparency averaged across cells in each site were logit transformed to normalize model residuals (linear models; $N = 178$ total grid cells). Significance of each model was assessed with type-II F-tests. Significant predictors are in bold-face text

Response	Predictor	Estimate ± SE	Sum sq.	df	*F*	*P*
Average percent dieback	Intercept	−1.790 ± 0.245	–	–	–	–
	Species richness	0.062 ± 0.032	2.840	1	3.667	0.057
	Site	**RL: 0.729 ± 0.234**	**22.693**	**3**	**9.767**	**< 0.001**
		SH: 0.079 ± 0.174				
		TL: −0.452 ± 0.176				
	Residuals	–	133.979	173	–	–
Average percent dieback	Intercept	−1.273 ± 0.138	–	–	–	–
	Ash density	−0.0002 ± 0.0001	1.803	1	2.311	0.130
	Site	**RL: 0.608 ± 0.223**	**22.468**	**3**	**9.596**	**< 0.001**
		SH: 0.034 ± 0.177				
		TL: −0.538 ± 0.170				
	Residuals	–	135.015	173	–	–
Average percent dieback	Intercept.	−1.281 ± 0.147	–	–	–	–
	Proportion basal area-ash	−0.235 ± 0.203	1.057	1	1.347	0.247
	Site	**RL: 0.554 ± 0.225**	**20.069**	**3**	**8.525**	**< 0.001**
		SH: 0.042 ± 0.178				
		TL: −0.535 ± 0.171				
	Residuals	–	135.762	173	–	–
Average percent transparency	Intercept	−0.841 ± 0.159	–	–	–	–
	Species richness	0.025 ± 0.021	0.470	1	1.437	0.232
	Site	**RL: 0.401 ± 0.152**	**11.894**	**3**	**12.127**	**< 0.001**
		SH: −0.115 ± 0.113				
		TL: −0.431 ± 0.115				
	Residuals	–	56.556	173	–	–
Average percent transparency	Intercept	−0.617 ± −0.089	–	–	–	–
	Ash density	−0.0001 ± 0.0001	0.514	1	1.575	0.211
	Site	**RL: 0.355 ± 0.144**	**12.059**	**3**	**12.305**	**< 0.001**
		SH: −0.139 ± 0.115				
		TL: −0.465 ± 0.110				
	Residuals	–	56.511	173	–	–
Average percent transparency	Intercept	−0.633 ± 0.095	–	–	–	–
	Proportion basal area-ash	−0.097 ± 0.131	0.180	1	0.547	0.461
	Site	**RL: 0.330 ± 0.146**	**11.292**	**3**	**11.455**	**< 0.001**
		SH: −0.130 ± 0.115				
		TL: −0.465 ± 0.110				
	Residuals	–	56.846	173	–	–

(31.7%), *Atanycolus* spp. (2.4%), and *Balcha indica* (1.2%), while 16% of parasitoids were unidentified. Of the 527 larvae checked for internal parasitism in the lab, 18.2% were parasitized by *P. sulcata*. In overstory ash, 21.2% of larvae checked for internal parasitism were parasitized by *P. sulcata* and in ash recruits, 9.6% of larvae checked for internal parasitism were parasitized by *P. sulcata*. We collected *O. agrili* from 7 declining and one healthy ash tree out of the 62 overstory ash trees we dissected. At least one egg parasitized by *O. agrili* was recorded from 4 trees at Sleepy Hollow, 2 trees at Rose Lake, and 2 trees at Muskrat Lake.

Spathius galinae and *P. sulcata* parasitism rates varied across sites, but site was only a significant predictor for *S. galinae* parasitism in the species richness model and for *P. sulcata* in the proportion basal area-ash model (Table 5). *Spathius galinae* parasitism was highest at Tamarack Lake (6.5 ± 2.5%), followed by Rose Lake (6.1 ± 2.4%), Muskrat Lake (5.6 ± 1.9%), and Sleepy Hollow (4.7 ± 1.8%). *Phasgonophora sulcata* parasitism was highest at Tamarack Lake (18.9 ± 5.6%), followed by Sleepy Hollow (13.3 ± 4.3%), Muskrat Lake (9.5 ± 4.4%), and Rose Lake (6.9 ± 5.1%). Parasitism rates by *S. galinae* and *P. sulcata* were not significantly different between declining and healthy ash and between overstory and recruit-sized ash in any model (Tables 4 and 5). *Spathius galinae* was positively associated with ash density while *P. sulcata* was negatively associated with ash density, and these effects did not depend upon tree condition or tree stratum (Fig. 3, Table 5). Proportion of EAB larvae parasitized by *S. galinae* was negatively associated with proportion basal area-ash in overstory ash while in recruits, proportion basal area-ash was positively associated with *S. galinae* parasitism (Fig. 4). Parasitism rates by either species were not significantly associated with tree species richness (Table 5).

Table 4. Mean (±SE) EAB larval densities (includes all healthy EAB larvae, current-year woodpecker marks, and parasitized larvae) along with percent EAB larval mortality[a], woodpecker mortality, and parasitism rates recorded in dissected pairs of healthy and declining overstory ash trees ($N = 31$ pairs) and recruits ($N = 31$ pairs).[b] *Phasgonophora sulcata* parasitism was recorded in 29 declining and 21 healthy overstory trees and 23 declining and 6 healthy recruits.[c]

Variable	Tree condition	Overstory mean ± SE	Recruit mean ± SE
EAB larvae per m^2	Declining	35.0 ± 4.3	45.3 ± 9.4
	Healthy	8.6 ± 13.1	2.4 ± 0.9
[a]Percent EAB mortality	Declining	56.8 ± 3.8%	43.6 ± 3.4%
	Healthy	38.1 ± 6.1%	36.1 ± 10.2%
Percent of EAB larvae killed by woodpeckers	Declining	38.5 ± 3.9%	22.4 ± 2.8%
	Healthy	13.2 ± 3.7%	5.8 ± 3.6%
[d]Percent external larval parasitism by all species	Declining	14.6 ± 3.3	12.5 ± 3.0%
	Healthy	6.1 ± 3.0%	0 ± 0%
Percent external larval parasitism by native species	Declining	3.4 ± 1.06%	2.8 ± 0.9%
	Healthy	0.6 ± 0.5%	0 ± 0%
[e]Percent parasitism by introduced species	Declining	12.9 ± 2.8%	9.7 ± 2.8%
	Healthy	6.5 ± 2.8%	0 ± 0%
Percent EAB parasitism by *S. galinae*	Declining	10.8 ± 2.5%	9.8 ± 3.02%
	Healthy	5.0 ± 2.6%	0 ± 0%
Percent EAB parasitism by *T. planipennisi*	Declining	2.1 ± 0.9%	12.5 ± 4.4%
	Healthy	1.5 ± 1.2%	0 ± 0%
Percent EAB parasitism by *Atanycolus* spp.	Declining	2.7 ± 0.9%	0.6 ± 0.5%
	Healthy	0.2 ± 0.2%	0 ± 0%
[c]Percent EAB parasitism by *P. sulcata*	Declining	15.8 ± 3.8%	15.5 ± 5.5%
	Healthy	8.3 ± 3.0%	0 ± 0%

[a]Calculated from the total number of dead, parasitized, and predated larvae.

[b]Statistical results are presented in Table 5.

[c]Calculated only from the 2 m and 6 m bolts from each tree as larvae were dissected to quantify parasitism by *P. sulcata* from these bolts.

[d]Parasitism rates from all species recorded while debarking trees, includes in-situ *P. sulcata* pupae recorded in the field but excludes larvae parasitized by *P. sulcata* found via dissections.

[e]Does not include parasitism by *O. agrili*. Does not include 1st and 2nd instar larvae as *T. planipennisi* and *S. galinae* do not parasitize these instars.

Discussion

Identifying habitat features in post-invasion forests that consistently support EAB natural enemies are necessary to support long-term reductions in EAB densities. We found that the relative prevalence of ash, but not tree species richness, had variable effects on EAB mortality attributable to parasitoid wasps. However, tree species richness and ash density did not influence woodpecker predation of EAB. Additionally, we found no association between tree diversity, ash density, or proportion basal area-ash on EAB larval densities, canopy dieback, or canopy transparency. Our results suggest that while the density of ash and proportional amount of basal area comprised of ash may influence EAB biological control by parasitoid wasps, these variables are not associated with improved ash condition nor reduced EAB densities.

Although nonhost tree species can disrupt cues that insect pests use to locate their hosts (e.g., Jactel et al. 2011), we found no evidence to suggest that such effects occur for EAB in post-invasion forest stands. Relatively high tree diversity did not prevent EAB from colonizing and damaging overstory and recruit-sized ash trees. Adult EAB beetles use a combination of visual and olfactory cues to locate and colonize ash trees in forest stands (Crook and Mastro 2010), which allow EAB adults to discriminate ash surrounded by many different species. We also found that ash density was inversely related to tree diversity. Not surprisingly, grid cells with high ash density tended to have low tree species richness while cells with high tree diversity had lower ash densities. Ash species are common early colonizers of disturbed habitats, often reaching high densities in patches or clumps following canopy gap formation (MacFarlane and Meyer 2005). Smith et al. (2015) examined relationships between tree diversity, ash density, and several other stand-level metrics of tree community composition on ash canopy decline in southeast Michigan stands during the initial phase of EAB invasion in North America. They found no effect of any stand-related variables on the rate or extent of ash decline, indicating that ash trees in diverse forest stands do not receive associational resistance to EAB. We similarly detected no effect of tree diversity, ash density, or proportion basal area-ash comprised of ash on canopy condition or EAB densities in the post-invasion sites we evaluated. Knight et al. (2013), however, reported that between 2005 and 2009, ash trees died faster from EAB in forest stands with low ash density compared to ash in high density stands. They suggested that EAB damage was concentrated on isolated trees whereas if ash density is higher, beetles are more likely to be distributed across multiple hosts, potentially slowing tree mortality rates (Knight et al. 2013). This effect—termed resource dilution—has been used to explain decreases in herbivore abundance as host plant density increases in grasslands and forests (Otway et al. 2005, Plath et al. 2012). We found no effect of ash density on estimates of canopy dieback and transparency, or EAB densities in the 4 post-invasion areas we surveyed, indicating that increased ash density did not reduce overall damage on individual trees. However, Knight et al. (2013) collected data during the initial wave of EAB invasion into Ohio when EAB densities were far higher than they are in post-invasion forests (Siegert et al. 2021), such as those we evaluated. Dilution effects may be less pronounced in post-invasion forests where the carrying capacity for EAB has dropped by orders of magnitude resulting in lower EAB population levels compared to preinvasion conditions (Siegert et al. 2021). Resource dilution effects on EAB damage may therefore be more pronounced in recently invaded forest stands in comparison to post-invasion stands.

Table 5. Model results for data recorded from dissected ash trees in 4 post-invasion sites in south-central Michigan in 2022. Living EAB per m^2 includes all current-year woodpecker attack marks, all parasitized EAB larvae, and all living EAB larvae recorded in dissected trees and is ln(x + 1) transformed to normalize model residuals. The Living EAB per m^2 model was fit as a general linear model and significance of model predictors was accessed with Type-II F-tests. All other models are fit as generalized linear models with a quasibinomial distribution and logit-link function and significance for these models was assessed with likelihood ratio tests. N = 62 trees, 6–9 pairs of healthy, and declining trees per site for all models except *P. sulcata* models. N = 52 trees, 7–17 trees per site for models with proportion *P. sulcata* parasitism as the response term. Significant predictors are in bold-face text

Response	Predictor	Estimate ± SE	Sum sq.	df	F or χ^2	P
Ln (EAB larvae per m^2 + 1)	Intercept	3.495 ± 0.585	–	–	–	–
	Species richness	0.032 ± 0.079	0.118	1	0.1191	0.731
	Tree condition	**Healthy: –0.792 ± 0.755**	**151.714**	**1**	**152.937**	**< 0.001**
	Stratum	**Recruit: –0.571 ± 0.760**	**10.177**	**2**	**10.259**	**0.002**
	Site	RL: –0.360 ± 0.284 SH: –0.543 ± 0.254 TL: –0.367 ± 0.240	5.141	3	1.727	0.165
	Richness * condition	Richness * healthy: –0.145 ± 0.107	1.701	1	1.715	0.193
	Richness * stratum	Richness * recruit: 0.069 ± 0.108	2.208	1	2.226	0.139
	Condition * stratum	**Healthy * recruit: –1.524 ± 1.078**	**6.528**	**1**	**6.581**	**0.012**
	Richness * condition * stratum	Richness * healthy * recruit: 0.091 ± 0.153	0.352	1	0.355	0.552
	Residuals	–	112.097	113	–	–
Ln(EAB larvae per m^2 + 1)	Intercept	3.853 ± 0.377	–	–	–	–
	Ash density per Ha	–0.0003 ± 0.001	1.787	1	1.785	0.184
	Tree condition	**Healthy: –1.463 ± 0.491**	**151.393**	**1**	**151.174**	**< 0.001**
	Stratum	**Recruit: –0.306 ± 0.503**	**9.907**	**1**	**9.892**	**0.002**
	Site	RL: –0.349 ± 0.266 SH: –0.603 ± 0.260 TL: –0.370 ± 0.236	5.814	3	1.935	0.128
	Ash density * condition	Ash density * healthy: –0.001 ± 0.001	1.282	1	1.280	0.260
	Ash density * stratum	Ash density * recruit: 0.0004 ± 0.001	0.198	1	0.198	0.657
	Condition * stratum	**Healthy * recruit: –0.793 ± 0.713**	**6.318**	**1**	**6.309**	**0.013**
	Ash density * condition * stratum	Ash density * healthy * recruit: –0.0002 ± 0.001	0.032	1	0.032	0.857
	Residuals	–	113.164	113	–	–
Ln(EAB larvae per m^2 + 1)	Intercept	3.801 ± 0.337	–	–	–	–
	Proportion basal area-ash	–0.251 ± 0.707	0.441	1	0.435	0.511
	Tree condition	**Healthy: –1.640 ± 0.426**	**151.464**	**1**	**149.257**	**< 0.001**
	Stratum	**Recruit: –0.356 ± 0.434**	**10.104**	**1**	**9.957**	**0.002**
	Site	RL: –0.370 ± 0.268 SH: –0.566 ± 0.264 TL: –0.368 ± 0.238	5.333	3	1.752	0.160
	Prop ash basal * condition	Prop ash basal * healthy: –0.319 ± 0.970	0.877	1	0.864	0.355
	Prop ash basal * stratum	Prop ash basal * recruit: 0.666 ± 0.984	0.236	1	0.233	0.631
	Condition * stratum	**Healthy * recruit: –0.671 ± 0.615**	**6.368**	**1**	**6.275**	**0.014**
	Prop ash basal * condition * stratum	Prop ash basal * healthy * recruit: –0.657 ± 1.382	0.229	1	0.226	0.636
	Residuals	–	114.670	113	–	–
Proportion larvae killed by woodpeckers	Intercept	–0.498 ± 0.382	–	–	–	–
	Species richness	–0.046 ± 0.047	–	1	1.456	0.228

Table 5. Continued

Response	Predictor	Estimate ± SE	Sum sq.	df	*F* or χ^2	P
	Tree condition	**Healthy: −0.473 ± 0.900**	–	**1**	**10.185**	**0.001**
	Stratum	**Recruit: −0.577 ± 0.525**	–	**1**	**11.170**	**0.001**
	Site	**RL: 0.711 ± 0.298** **SH: 0.223 ± 0.252** **TL: 0.947 ± 0.216**	–	**1**	**20.720**	**< 0.001**
	Richness * condition	Richness * healthy: −0.037 ± 0.140	–	1	0.141	0.707
	Richness * stratum	Richness * recruit: 0.0004 ± 0.075	–	1	0.002	0.961
	Condition * stratum	Healthy * recruit: 0.133 ± 3.468	–	1	0.940	0.332
	Richness * condition * stratum	Richness * healthy * recruit: −0.189 ± 0.568	–	1	0.121	0.728
Proportion larvae killed by woodpeckers	Intercept	−0.607 ± 0.238	–	–	–	–
	Ash density per Ha	−0.001 ± 0.0004	–	1	1.170	0.279
	Tree condition	**Healthy: −0.520 ± 0.603**	–	**1**	**11.260**	**0.001**
	Stratum	**Recruit: −0.956 ± 0.400**	–	**1**	**12.412**	**< 0.001**
	Site	**RL: 0.901 ± 0.256** **SH: 0.117 ± 0.252** **TL: 1.054 ± 0.204**	–	**3**	**34.397**	**< 0.001**
	Ash density * condition	Ash density * healthy: −0.001 ± 0.001	–	1	0.132	0.716
	Ash density * stratum	Ash density * recruit: 0.001 ± 0.001	–	1	1.174	0.279
	Condition * stratum	Healthy * recruit: −1.306 ± 2.174	–	1	0.859	0.354
	Ash density * condition * stratum	Ash density * healthy * recruit: 0.001 ± 0.004	–	1	0.036	0.850
Proportion larvae killed by woodpeckers	Intercept	−0.626 ± 0.205	–	–	–	–
	Proportion basal area-ash	−0.788 ± 0.470	–	1	1.449	0.229
	Tree condition	**−0.651 ± 0.408**	–	**1**	**10.982**	**0.001**
	Stratum	**Recruit: −1.224 ± 0.393**	–	**1**	**12.626**	**< 0.001**
	Site	**RL: 0.966 ± 0.246** **SH: 0.151 ± 0.248** **TL: 1.119 ± 0.211**	–	**3**	**35.637**	**< 0.001**
	Prop ash basal * condition	Prop ash basal * healthy: −0.231 ± 1.050	–	1	0.079	0.779
	Prop ash basal * stratum	Prop ash basal * recruit: 1.590 ± 0.850	–	1	3.511	0.061
	Condition * stratum	Healthy * recruit: −0.576 ± 1.911	–	1	0.878	0.349
	Prop ash basal * condition * stratum	Prop ash basal * healthy * recruit: −1.178 ± 4.994	–	1	0.058	0.809
Proportion *S. galinae* parasitism	Intercept	−3.975 ± 0.692	–	–	–	–
	Species richness	0.177 ± 0.080	–	1	2.876	0.090
	Tree condition	Healthy: −0.219 ± 2.294	–	1	2.690	0.101
	Stratum	Recruit: 1.665 ± 0.987	–	1	0.372	0.542
	Site	**RL: 1.044 ± 0.537** **SH: 0.646 ± 0.441** **TL: 0.980 ± 0.407**	–	**3**	**7.217**	**0.065**
	Richness * condition	Richness * healthy: −0.078 ± 0.342		1	0.051	0.821
	Richness * stratum	Richness * recruit: −0.196 ± 0.130		1	2.359	0.125
	Condition * stratum	Healthy * recruit: −16.301 ± 7324.148	–	1	0.861	0.353

Table 5. Continued

Response	Predictor	Estimate ± SE	Sum sq.	df	*F* or χ^2	P
	Richness * condition * stratum	Richness * healthy * recruit: 0.100 ± 990.417	–	1	0	1.0
Proportion *S. galinae* parasitism	Intercept	−3.216 ± 0.461	–	–	–	–
	Ash density	**0.001 ± 0.001**	–	**1**	**7.977**	**0.005**
	Tree condition	Healthy: −0.753 ± 1.278	–	1	2.507	0.113
	Stratum	Recruit: −0.310 ± 0.686	–	1	0.414	0.520
	Site	RL: 0.678 ± 0.453 SH: 1.118 ± 0.423 TL: 0.651 ± 0.387	–	3	7.699	0.053
	Ash density * condition	Ash density * healthy: 0.0001 ± 0.002	–	1	0.001	0.978
	Ash density * stratum	Ash density * recruit: 0.001 ± 0.001	–	1	0.900	0.343
	Condition * stratum	Healthy * recruit: −14.100 ± 460.0	–	1	0.633	0.426
	Ash density * condition * stratum	Ash density * healthy * recruit: −0.003 ± 10.510	–	1	0	1.0
Proportion *S. galinae* parasitism	Intercept	−2.282 ± 0.383	–	–	–	–
	Proportion basal area-ash	−1.159 ± 0.879	–	**1**	0.105	0.746
	Tree condition	Healthy: −0.707 ± 0.878	–	1	3.453	0.063
	Stratum	Recruit: −1.543 ± 0.837	–	1	0.562	0.454
	Site	RL: 0.581 ± 0.529 SH: 0.821 ± 0.430 TL: 0.887 ± 0.425	–	3	5.934	0.115
	Proportion basal area-ash * condition	Prop. basal area-ash * healthy: −0.834 ± 2.913	–	1	0.086	0.769
	Proportion basal area-ash * stratum	**Prop. basal area-ash * recruit: 4.747 ± 1.779**	–	**1**	**8.000**	**0.005**
	Condition * stratum	Healthy * recruit: −14.480 ± 3755.313	–	1	0.448	0.503
	Prop basal area-ash * condition * stratum	Prop. basal area-ash * healthy * recruit: −1.498 ± 8575.403	–	1	0	1.0
Proportion *P. sulcata* parasitism	Intercept	−2.552 ± 0.732	–	–	–	–
	Species richness	0.114 ± 0.088	–	**1**	1.862	0.172
	Tree condition	Healthy: 2.230 ± 1.839	–	1	0.196	0.658
	Stratum	Recruit: −1.264 ± 1.670	–	1	2.752	0.098
	Site	RL: −0.401 ± 0.867 SH:0.289 ± 0.497 TL: 0.980 ± 0.438	–	3	6.491	0.090
	Richness * condition	Richness * healthy: −0.288 ± 0.271	–	1	1.142	0.285
	Richness * stratum	Richness * recruit: 0.079 ± 0.204	–	**1**	0.152	0.697
	Condition * stratum	Healthy * recruit: −16.286 ± 5886.193	–	1	0.917	0.338
	Richness * condition * stratum	Richness * healthy * recruit: 0.083 ± 732.971		1	0	1.0
Proportion *P. sulcata* parasitism	Intercept	−0.716 ± 0.411	–	–	–	–
	Ash density	**−0.002 ± 0.001**	–	**1**	**9.565**	**0.002**
	Tree condition	Healthy: −0.345 ± 0.945	–	1	0.069	0.792
	Stratum	Recruit: −0.883 ± 0.821	–	1	3.121	0.077
	Site	RL: −0.340 ± 0.820 SH: 0.146 ± 0.457 TL: 0.980 ± 0.421	–	3	6.781	0.079

Table 5. Continued

Response	Predictor	Estimate ± SE	Sum sq.	df	*F* or χ^2	P
	Ash density * condition	Ash density * healthy: 0.002 ± 0.002	–	1	0.478	0.489
	Ash density * stratum	Ash density * recruit: 0.001 ± 0.002	–	**1**	0.119	0.730
	Condition * stratum	Healthy * recruit: −16.600 ± 4080.0	–	1	1.225	0.268
	Ash density * condition * stratum	Ash density * healthy * recruit: 205.0 ± 10.150	–	1	0	1.0
Proportion *P. sulcata* parasitism	Intercept	−1.280 ± 0.329	–	–	–	–
	Proportion basal area-ash	−1.704 ± 0.869	–	**1**	1.883	0.170
	Tree condition	Healthy: −0.833 ± 0.775	–	1	0.181	0.670
	Stratum	Recruit: −0.739 ± 0.794	–	1	2.992	0.084
	Site	**RL: −0.448 ± 0.812 SH: 0.375 ± 0.449 TL: 1.128 ± 0.433**	**–**	**3**	**9.032**	**0.029**
	Proportion basal area-ash * condition	Prop. basal area-ash * healthy: 3.195 ± 1.711	–	1	3.557	0.059
	Proportion basal area-ash * stratum	Prop. basal area-ash * recruit: 0.294 ± 2.291	–	**1**	0.016	0.898
	Condition * stratum	Healthy * recruit: −15.276 ± 2829.601	–	1	0.962	0.327
	Prop basal area-ash * condition * stratum	−1.173 ± 8168.069	–	1	0	1.0

Woodpeckers consumed a higher proportion of EAB larvae from overstory trees compared to recruits and from declining trees compared to healthy trees. Our findings indicate that in post-invasion stands, woodpeckers are more likely to remove a higher proportion of larvae from large trees with high EAB densities, as was documented by other researchers in the early stages of EAB invasion (Lindell et al. 2008, Flower et al. 2014, Murphy et al. 2018, Gaudon and Smith 2020). Flower et al. (2014) found that woodpeckers were more likely to forage on ash exhibiting canopy decline, leading the authors to suggest that woodpeckers may recognize canopy dieback as a sign of prey availability. Large heavily infested trees are likely easier for woodpeckers to locate relative to small infested trees and woodpeckers may spend less time locating prey to remove from large infested trees in comparison to large healthy trees with low EAB densities. However, the average diameter of overstory ash that we dissected ranged from 11 to 15 cm while dissected ash recruits ranged from 5 to 6 cm across our sites. Large ash trees are uncommon in post-invasion forests such as those we sampled (Robinett and McCullough 2019, Siegert et al. 2021), but the trends we detected indicate that even small differences in ash diameter may influence woodpecker predation rates. We also found no effect of tree species richness, ash density, or proportion basal area-ash on EAB predation by woodpeckers. It is unclear if post-invasion stands with high tree diversity or ash density increase the duration of woodpecker foraging bouts within a stand, increase the likelihood that woodpeckers will forage within a stand, or both. However, if such effects occur, they do not appear to increase the proportion of EAB larvae killed by woodpeckers. Manipulative experiments may be needed to better understand variables that influence woodpecker foraging behavior, especially in post-invasion stands.

Ash density was positively associated with parasitism by *S. galinae* for both tree strata; however, proportion basal area-ash was positively associated with *S. galinae* parasitism in recruits but negatively associated with parasitism in overstory trees. Since *S. galinae* is a specialist on EAB, availability of EAB hosts may be higher in cells with high ash density. Although ash density did not affect EAB densities in dissected trees, higher ash density indicates that more trees could host EAB larvae within a forest stand. This effect could increase the probability that introduced parasitoids encounter and parasitize hosts, facilitating establishment. Additionally, introduced parasitoids may be attracted to ash-produced volatiles rather than specific cues emitted by EAB larvae. For example, ash volatiles play an important role in host location by *S. agrili*, an introduced EAB parasitoid closely related to *S. galinae* (Wang et al. 2010b, Johnson et al. 2014). However, Chen et al. (2016) reported that *T. planipennisi* was not attracted to volatiles from white ash phloem and it is unclear if ash volatiles are important for other introduced EAB parasitoids. Nonetheless, our results suggest that *S. galinae* parasitizes a higher proportion of EAB larvae in stands where ash is relatively dominant and abundant. However, it is unclear what mechanism drives the differential association of proportion basal area-ash and with *S. galinae* parasitism in overstory trees compared to recruits. *S. galinae* tends to parasitize a higher proportion of EAB larvae in pole-sized trees (DBH = 9–19 cm) compared to small recruits (2.8–5.8 cm) (Duan et al. 2022). In our sites, ash recruits were more plentiful than pole-sized trees and therefore comprised a substantial proportion of total ash basal area. Total ash basal area within cells with high proportion basal area-ash may be represented primarily by smaller trees, which are typically more prevalent than large ash in post-invasion forests (Robinett and McCullough 2019, Siegert et al. 2021, Morris et al. 2023). Greater parasitism in recruits where there

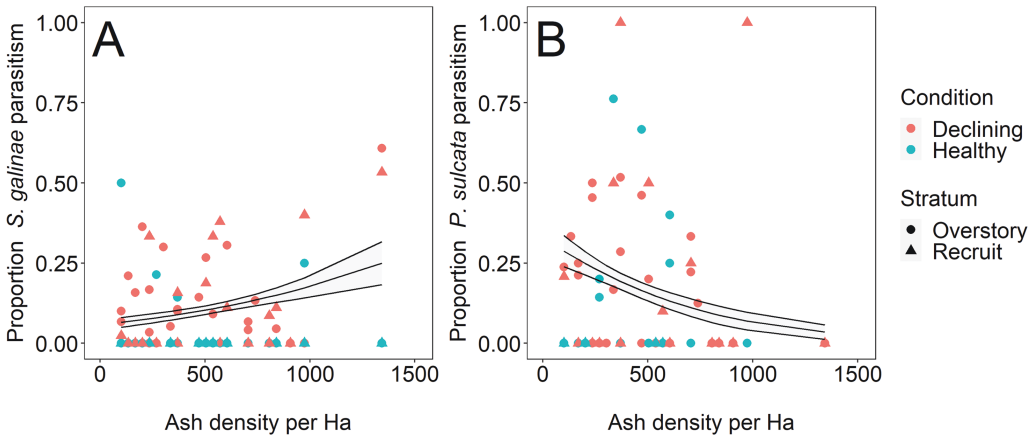

Fig. 3. Relationship between ash stem density per Ha and A) the proportion of larvae parasitized by *S. galinae* and B) the proportion of larvae parasitized by *P. sulcata*. For. *S. galinae* parasitism, $N = 62$ overstory trees, and 62 recruits. For *P. sulcata* parasitism ($N = 52$ overstory trees and 29 recruits). Model fits are plotted as lines and shaded regions represent the standard error of the best fit line. Statistical results are presented in Table 5.

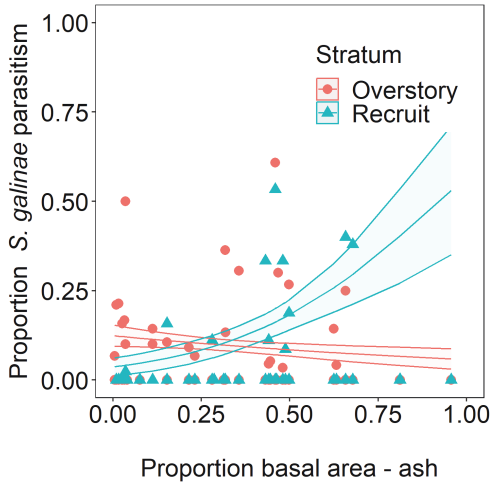

Fig. 4. Proportion basal area-ash was positively associated with *S. galinae* parasitism in recruits and negatively associated with *S. galinae* parasitism in overstory trees. Model fits are plotted as lines and shaded regions represent the standard error of the best fit line. Statistical results are presented in Table 5 ($N = 62$ overstory trees and 62 recruits).

is greater proportion basal area-ash may indicate that *S. galinae* are parasitizing more larvae across all trees and that most ash in such locations are small trees. Therefore, our results may reflect greater availability of hosts for *S. galinae* in stands with high proportion basal area-ash rather than ovipositional preferences of *S. galinae*.

Reduced *P. sulcata* parasitism, and increased *S. galinae* parasitism associated with ash density may be indicative of competition between *P. sulcata* and *S. galinae*. Duan et al. (2015) documented a rise and then fall in both EAB densities and parasitism by native species between 2008 and 2014 in forested parks within south-central Michigan. In these areas, *T. planipennisi*, *O. agrili*, and *S. agrili* were released annually from 2007 to 2010 and increasing *T. planipennisi* parasitism was observed from 2008 to 2014. The authors speculated that the decline in native parasitism that occurred concurrent with the rise in parasitism by *T. planipennisi* was a result of lower EAB densities, but they could not discount *T. planipennisi* out-competing native parasitoids. Duan et al. (2015) suggested that generalist parasitoids are opportunistic and preferentially utilized locally abundant hosts, rather than EAB larvae, but it remains unclear as to why parasitism by native species dropped. In addition to EAB, *P. sulcata* will parasitize native *Agrilus* spp. larvae developing in *Betula*, *Quercus*, or *Populus* trees (Barter 1965, Haack and Benjamin 1981, Loerch and Cameron 1983). Of these genera, oaks were common at our field sites, however it is highly unlikely that native *Agrilus* species outnumbered EAB larvae at our sites because white or green ash had higher RIVs than any oak species at 3 of the 4 sites, and average EAB larval densities ranged from 8 to 30 larvae per m^2 in healthy and declining ash, respectively. The high relative importance of ash and the high densities of EAB in ash at our sites indicate that EAB is likely far more common as a host than native *Agrilus*. Additional research is needed to assess whether introduced parasitoids such as *S. galinae* are capable of out-competing native species including *P. sulcata*.

The proportion of EAB larvae that were parasitized was low in both overstory trees and recruits. This is despite releases of introduced parasitoid species at or near study sites 2 or more years prior to our study, and additional releases made the year we conducted our study. Low parasitism rates may be because we dissected trees in the same year that we released parasitoids and additional time is needed to observe substantial increases in parasitism rates. All dissected ash were within 50–100 m of the nearest locations where we released parasitoids the year of this study. Although the dispersal rate of *O. agrili* is relatively low due to its small size, both *S. galinae* and *T. planipennisi* adults can disperse several km per year (Jones et al. 2019, Rutledge et al. 2021, Quinn et al. 2022). However, it may still require multiple years for parasitoid densities to build to levels that can have a significant impact on EAB populations (Duan et al 2017, Quinn et al. 2022, Duan et al. 2023). Another possibility is that parasitoid releases in previous years resulted in low levels of establishment. Mean parasitism rates for *T. planipennisi* and *S. galinae* were less than 15% even in declining, and presumably attractive, overstory and recruit-sized ash, and EAB eggs parasitized by *O. agrili* wasps were only recovered 13% of all sampled trees. In contrast, woodpeckers killed an average of 39% of larvae in declining overstory ash and 22% of larvae in declining recruits. While introduced EAB parasitoids are becoming established in North America (Duan et al. 2022, 2023), parasitism rates by these species are below densities necessary to prevent decline of overstory ash trees (Kashian et al. 2018). Parasitism rates may increase over time as populations of introduced wasps build and spread throughout invaded areas. For example, Gould et al. (2022) infested ash saplings

(DBH = 1.9–7.1 cm) each with 10 EAB eggs in early summer in New York and reported parasitism rates of fourth instar EAB larvae that ranged from 50 to 60% in the fall of the same year. At this point, however, woodpeckers remain the most effective biological control agent of EAB, especially in locations where introduced parasitoids are not established (Herms and McCullough 2014, McCullough 2020).

Current best management practices for managing EAB include regular scouting and integrated tactics including selective girdling and felling of ash trees, release of introduced parasitoids, and systemic insecticide application (McCullough 2020). Our results indicate that biological control services provided by parasitoid wasps are differentially affected by ash density, but that neither parasitoids nor woodpeckers are supported by tree diversity. Further research into silvicultural practices that could enhance EAB biological control are warranted to support a long-term reduction in EAB populations across North America.

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Data Availability

All data reported in this manuscript will be provided upon reasonable request to the corresponding author.

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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