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Positive association between emerald ash borer residence time and accumulation of invasive plants

Andrew V. Gougherty[1] | **Jessica M. Elliott**[1] | **Elizabeth A. LaRue**[1] | **Joey Gallion**[2] | **Songlin Fei**[1]

[1]Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana, USA

[2]Indiana Department of Natural Resources, Indianapolis, Indiana, USA

Correspondence
Songlin Fei
Email: sfei@purdue.edu

Present addresses
Andrew V. Gougherty, USDA Forest Service, Northern Research Station, 359 Main Road, Delaware, OH, USA; and Elizabeth A. LaRue, Department of Biological Sciences, The University of Texas at El Paso, El Paso, TX, USA.

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Abstract

Invasive forest pests can affect the composition and physical structure of forest canopies that may facilitate invasion by non-native plants. However, it remains unclear whether this process is generalizable across invasive plant species at broad spatial scales, and how other landscape characteristics may simultaneously facilitate non-native plant invasion. Here, we assembled a dataset of over 3000 repeatedly measured forest plots and quantified the impact of emerald ash borer (EAB, *Agrilus planipennis*) residence time, land cover, and forest structure on the accumulation and coverage of invasive plants. We show plots in counties with longer EAB residences tended to accumulate more invasive plants than plots with shorter EAB residences. On average, nearly half of the plots with ash (*Fraxinus* spp.) in counties with EAB accumulated an additional 0.48 invasive plant species over the 5- to 6-year resample interval compared to plots with ash in counties without EAB at the time of sampling. Increases in invasive species coverage were also evident in counties with EAB—although residence time did not have a strong effect, while forest gap fraction and vertical complexity were each negatively associated with increased coverage. This work has implications for understanding how invasive forest pests can facilitate the spread of non-native plants.

KEYWORDS
emerald ash borer, forest pests, forest structure, invasive species

INTRODUCTION

Non-native forest pests pose a major threat to native forests globally. Not only can insect pests and diseases cause excessive tree mortality and disrupt ecosystem services (Fei et al., 2019) but they may also have indirect effects on forest systems, including shifting forest's successional trajectories, affecting nutrient cycling, and impacting the availability and quality of water (Boyd et al., 2013; Lovett et al., 2006). Mortality and damage caused by non-native pests can also facilitate the spread of non-native plants by opening forest canopy gaps and promoting environmental conditions conducive to non-native plant establishment (Gandhi & Herms, 2010). While pest-induced "invasion meltdowns" (whereby the occurrence of an

Andrew V. Gougherty and Jessica M. Elliott contributed equally to the work reported here.

invasive species accelerates the accumulation and impact of other invasive species) are poorly documented (Simberloff, 2006), growing evidence suggests pest-induced tree mortality can increase the growth, abundance, and number of non-native plants (e.g., Baron & Rubin, 2021). However, it remains uncertain whether these effects are strong enough to be evident at broad spatial scales given the constraints of other landscape features affecting non-native plant accumulation.

The increase in abundance and/or richness of non-native plants in the presence of forest pests is thought to result from the opening of niche space from pest-induced tree damage. As trees are damaged by pests (via defoliation, flagging, or mortality), environmental conditions on the forest floor can shift in ways that facilitate non-native plant establishment and spread—in particular due to increased light availability, and shifts in moisture and temperature. Native plants can also benefit from pest-induced canopy gaps (Eschtruth et al., 2011), but the ability of many non-native plants to outcompete native flora may allow non-native plants to disproportionately flourish in newly open, disturbed areas. The increased spread and abundance of non-native plants can shift forest composition, affect ecosystem services (Castro-Díez et al., 2019), contribute to biotic homogenization both locally and globally (Olden, 2006), and sometimes lead to landscape metamorphosis (Fei et al., 2014).

Despite theoretical expectations regarding a link between pest-induced mortality and invasive plants, support in the literature is mixed. Hoven et al. (2017), for instance, found basal area of bush honeysuckle (*Lonicera maackii*) tended to be higher in areas with ash decline due to emerald ash borer (EAB, *Agrilus planipennis*), and Eschtruth et al. (2011) found the occurrence of non-native plants increased following invasion by hemlock woolly adelgid (*Adelges tsugae*). Likewise, Hausman et al. (2010) showed efforts to control the spread of EAB (by preemptively removing ash trees ahead of the invasion front) likely facilitated the introduction of non-native plants. In contrast, Engelken et al. (2020) found no difference in the cover or richness of non-native plants in either canopy gaps or forests infested with EAB. Many of these studies have been conducted at relatively few sites in a narrow geographic region often during a single period of time and focused on one or a few invasive plants. Thus, it remains unclear under what circumstances tree pests may facilitate the regional occurrence or expansion of non-native plants or the influence of pest residence time on non-native plant accumulation.

Here, we sought to test whether non-native plant accumulation is greater in the presence of EAB, an invasive forest pest, across a range of landscapes. Since its discovery in the early 2000s, EAB has resulted in extensive mortality of its main host, ash (*Fraxinus* spp.) in the Midwest United States and nearby regions. Although EAB has slight host preferences among its ash hosts in the region, mortality near the introduction site has been in excess of 95% (Klooster et al., 2018), leading it to be considered among the most ecologically and economically damaging non-native insect species yet introduced into the United States. EAB's impact is predicted to eventually be similar to that of chestnut blight (caused by the fungal pathogen *Cryphonectria parasitica*), which was responsible for the effective extirpation of chestnut as a canopy tree, in the Appalachian region in the Eastern United States (Herms & McCullough, 2014). EAB is spreading rapidly on the landscape, occurring in nearly every US state and Canadian province in eastern North America and has recently been found for the first time in the Western United States, where it may threaten Oregon ash (*Fraxinus latifolia*) (Oregon Department of Forestry, 2022). The IUCN Red List classifies eight North American ash species as near threatened, or worse, due to mortality caused by EAB, with six species being considered endangered or critically endangered (*F. americana*, *F. caroliniana*, *F. nigra*, *F. pennsylvanica*, *F. profunda*, and *F. quadrangulata*), bringing them close to functional extinction (Ward et al., 2021).

Because of its high and quick impacts on host trees, EAB offers a unique system to understand how non-native forest pests may facilitate the expansion of invasive plants in disturbed forests. In this work, we sought to (1) address whether EAB residence time (i.e., the approximate length of time EAB has been present in a region) was associated with a greater accumulation of non-native plant richness and coverage, and (2) quantify the role of forest structural diversity on non-native plant accumulation in the presence of EAB. We hypothesize that the presence of EAB will be associated with relatively gap-rich forests, and that as EAB residence time increases, and its hosts decline, non-native plant accumulation will be greater.

METHODS

Non-native plant accumulation and coverage

We used Indiana Continuous Forest Inventory (CFI) data to assess the drivers of non-native plant accumulation on the landscape. The CFI covers much of the forested areas in Indiana, which are largely classified as oak-hickory and maple-beech-birch forests. The CFI largely follows the protocols of the US Forest Service Forest Inventory & Analysis (FIA) program, with a few notable differences.

The Indiana CFI samples a single 7.3-m (24-ft) radius plot (0.02 ha, 1/24 acre) in forested areas, where all trees with >12.7 cm (5 in.) dbh are measured. A 2.07-m (6.8-ft) radius microplot is also sampled, where all trees >2.54 cm (1 in.) dbh trees are measured. Within plots, numerous characteristics are measured in addition to tree identity and dbh, including forest type, any visible recent disturbances, and the presence and coverage (in percentage) of invasive plants. The CFI seeks to have one plot for every ~16.2 ha (40 acres) of forested lands in Indiana (Gallion, 2016), and plots are revisited every 5–6 years. In our analyses, we assessed 3802 plots which had an average sampling interval of 5.1 years (first sample year range: 2008–2012, second year sample: 2013–2017).

For each plot with available data, we determined the number of non-native plants present within plots during the two most recent sampling dates and calculated the difference in the number of non-native plant species between the two samples, as a metric of the accumulation of non-native plants. Non-native plants included 34 potential taxa, including many of the most widespread and damaging non-native plants in the Eastern United States, including multiple honeysuckle species (e.g., *Lonicera japonica*, *L. maackii*), Japanese knotweed (*Polygonum cuspidatum*), multiflora rose (*Rosa multiflora*), and tree of heaven (*Ailanthus altissima*), among others (see Appendix S1: Table S1 for detailed species list). Species suspected of being invasive, but not identified to species level were removed from the analyses, including undifferentiated shrubs, woody vines, and herbaceous vines (i.e., those coded as 2SHRUB, 2VW, and 2VH, respectively, by CFI). As many *Lonicera* species can only be readily distinguished by flowers, following FIA protocols, all bush honeysuckle were grouped as *Lonicera* spp. Because all other non-native plants were identified to species, we tested three approaches for addressing this slight taxonomic inconsistency, including (1) removing undifferentiated *Lonicera*, (2) aggregating all *Lonicera* to the genus, and (3) treating undifferentiated *Lonicera* as its own grouping. We found metrics of non-native plant accumulation were very similar regardless of how *Lonicera* were treated (all $r > 0.95$, $p < 0.01$); thus, we decided to treat undifferentiated *Lonicera* as its own grouping, as we feel both species-defined and undifferentiated bush *Lonicera* provide useful information on invasive plant accumulation. In addition to the difference in the number of invasive species, we also calculated the difference in invasive plant coverage within each plot. Coverage is estimated in plots as a percentage for each invasive species. Total invasive coverage was calculated by summing the total cover of each invasive species within plots during each sampling period and calculating the difference. These two metrics (i.e., difference in non-native plant richness and difference in non-native plant coverage) were used as response variables in the models described below.

Predictors and analyses

We assessed the effect of 11 variables on the change in the number and coverage of invasive plants. These variables included two representing the potential impact of EAB on invasive plant accumulation (i.e., residence time of EAB within counties, the presence/absence of ash tree as the EAB hosts in plots), five forest canopy metrics (mean max canopy height, height variability, gap fraction, vegetative area index, and vegetation condition index), land cover (relative cover of forests and developed land in counties), tree richness, and ecoregion.

The residence time of EAB in each county was calculated as the number of years EAB had been present within the county at the time of the second sampling. The year of first EAB documentation within counties was accessed from Ward et al. (2020). While plot-level data on EAB occurrence or population levels would be useful in these analyses, such systematic temporal data are unavailable for most areas. County-level data may be coarser than plot-level data, and thus introduce some uncertainty in our analyses (as EAB may be present within a county before it is present within each plot), but county-level data should provide a reasonable approximation for when EAB appeared near plots and started impacting ash trees. The presence or absence of ash within counties was determined using tree-level data from the Indiana CFI. Ash (including undifferentiated *Fraxinus* spp.) was considered present if any species were recorded during the first or second sampling. Tree richness, at the time of the second sampling, was calculated as the sum of individual tree species.

Forest structural metrics were calculated from 2016 to 2020 3DEP aerial LiDAR collected by U.S. Geological Survey. LAS tiles contained a minimum of two laser pulse returns per square meter (although the average density was ~6 points/m^2; Oh et al., 2022) and were projected into one of two state plane coordinate systems: Indiana east (EPSG 2967) or west (EPSG 2968), to prevent overlapping tiles. In ArcGIS Pro (ESRI, Redlands, California, USA), we created a shapefile of CFI plot locations for each of the two projections to ensure that their locations would overlay with point cloud data. We read the catalog of LAS tiles into R (R Core Team, 2019) using the lidR package (version 3.1.4) (Roussel et al., 2020), along with the two east/west shapefiles of plots. Using each shapefile as a template, we clipped a 23-m radius point cloud around each CFI plot center with the clip_roi function. We included a 5-m buffer to avoid edge effects

while processing the data. We accounted for elevation using the las normalize function, which automatically generates a digital terrain model (DTM) for each plot and ensures that ground points have a value of 0. We then filtered for outliers by removing Z values that fell more than 6 SD from the mean Z value. Using the filter_poi function, we then removed the remaining points that fell outside of the 99.5th percentile and those that fell below 0 m after normalizing. Next, we clipped each plot to its final extents of 12.19 m and 17.08 radius using clip_roi and the previously described methodology, removing the extraneous buffer area, and created a canopy height model (CHM) at a pixel resolution of 1 × 1 m. Finally, we calculated the following metrics using both the CHM and the raw normalized point cloud to use in our models: vertical variability, gap fraction, vegetation area index (VAI), vertical complexity index (VCI), and the 25% height quantile. Vertical variability was calculated as the average SD of average Z values across a plot. We calculated gap fraction as the average proportion of sky points versus leaf returns in each 1 × 1 m tile. VAI was the sum of leaf area point density values for each 3 × 3 m horizontal tile. VCI was calculated as a function of the proportion of LiDAR returns in each height bin, and the 25% height quantile represents the 25th Z value percentile. See Appendix S1: Table S2 for a description of these metrics.

County-level land cover data were calculated from the NLCD 2016 (Yang et al., 2018). Land cover was extracted within each county, and the relative proportion of forested lands (codes: 21, 22, 23, and 24) and developed lands (codes: 41, 42, and 43) was calculated. We considered including the proportion of agricultural land within counties, but found it to be strongly correlated with the proportion of forested land across counties ($n = 92$ counties, $r = -0.86$, $p < 0.01$). The maximum correlation between any pair of remaining variables was between vertical variability and gap fraction ($r = 0.65$). We also included ecoregions as a factor in the model (Omernik & Griffith, 2014; accessed at https://www.epa.gov/eco-research/ecoregions), to represent unmeasured physical and biological differences in the regions where plots occur. Level 3 ecoregions in Indiana included "Eastern Corn Belt Plains," "Huron/Erie Lake Plains," "Interior Plateau," "Southern Michigan/Northern Indiana Drift Plains," "Interior River Valleys and Hills," and "Central Corn Belt Plains." All continuous variables were scaled and centered (to mean of 0 and SD of 1.0) before inclusion in the model.

Analyses

We used linear models to test the effect of EAB, tree richness, land cover, and forest structure on the change in the number and coverage of invasive plants over time. Because LiDAR data were collected at different times of the year throughout the states, which could affect forest canopy metrics, we included only plots in areas sampled during the growing season (i.e., defined as between day-of-year 120 and 275) in the regression. Furthermore, we tested for spatial autocorrelation in the change in the number and coverage of invasive plants over time and modeled residuals, as spatial autocorrelation can bias parameter estimates and obscure patterns in the data (Dormann, 2007). We used Moran's I as a metric of autocorrelation, calculated in 50-km bins. Significance was assessed using 1000 permutations. Correlograms were calculated using the correlog function in the ncf package (Bjornstad, 2018) in R.

We also conducted four randomization schemes to isolate the individual and combined effects of EAB and its main host genus, ash, on the accumulation and coverage of non-native plants. Randomizations were structured as comparisons between plots with and without ash, in counties with and without EAB. The four comparisons we considered were (1) EAB/ash versus non-EAB/non-ash, (2) EAB/ash versus non-EAB/ash, (3) EAB/ash versus EAB/non-ash, and (4) non-EAB/ash versus non-EAB/non-ash. The first comparison is meant to capture the combined effect of EAB and ash, the second and third comparisons are meant to isolate the respective effects of EAB and ash, when the other is held constant, and the last comparison is meant to capture the base-level accumulation of invasive plants in plots with ash when EAB is absent (which is expected to be near 0). For each comparison, we randomly paired plots that matched the respective criteria and calculated the mean difference between pairs of plots. We conducted each randomization 1000 times and tested for significance using the t test.

RESULTS

EAB was first detected in northeast Indiana in 2004, two years following the first detection in Michigan, and by 2017 had arrived in all 92 counties (Indiana Department of Natural Resources, 2022). Of the plots that we assessed, approximately 8.8% had been sampled before EAB had been recorded in the county, while the estimated mean (±SD) EAB residence time across all plots was 4.4 years (±2.6). Few plots (<1%) were sampled after EAB had been present for 10 years or more. Many plots (55.3%, $n = 2101$) had no invasive plant species during either sampling period, and most plots (87.0%, $n = 3308$) had no ash during the first or second sampling, but it is worth noting that the effects of EAB may still be felt in plots without ash, if ash are present nearby, but outside the sampled plot area (see Figure 1a).

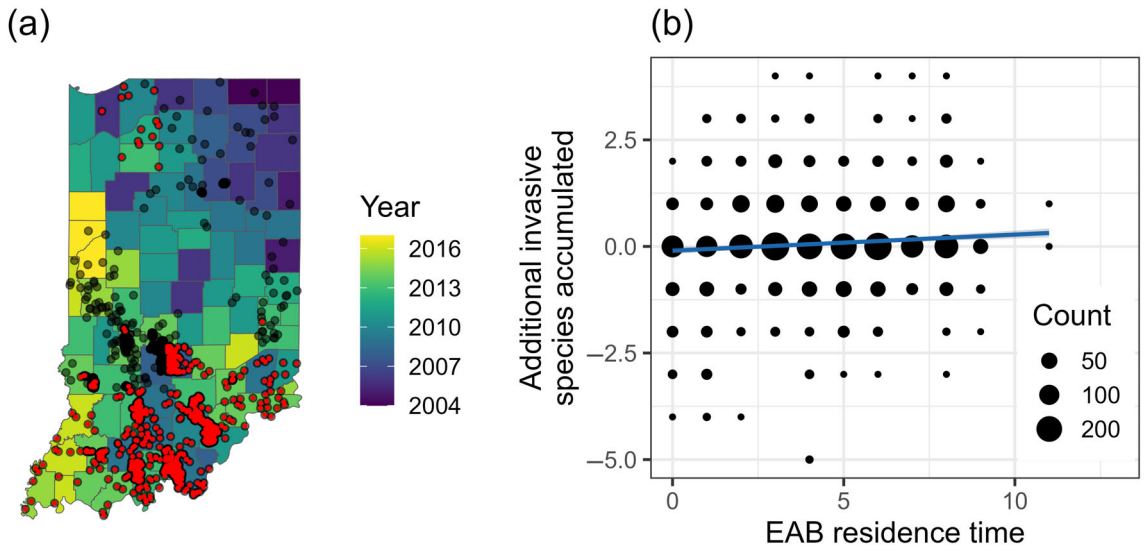

FIGURE 1 (a) Spatial distribution of plots used to calculate invasive plant accumulation, and the year emerald ash borer (EAB) was first detected in counties in Indiana. Black and red points are plots used in the randomization analyses, and red points are used in the regression model (see *Methods*). Plots used in the regression are a subset of all plots due to the timing of LiDAR acquisition. (b) Relationship between EAB residence time and invasive plant accumulation during the 5- to 6-year resampling interval. Blue line is the marginal effect of EAB residence time on invasive plant accumulation, derived from a regression model (see Figure 2). The regression line was back-transformed to years (which was centered and scaled in the model), to improve interpretability, and was estimated as $y = -0.1 + 0.04x$.

Across all plots, regardless of the presence of EAB or ash, there was little change in the number of invasive plants between the two sample periods ($n = 3802$ plots, mean $= 0.1$, median $= 0$, SD $= 0.87$). At the extremes, approximately 5.6% of plots ($n = 213$) had an increase of two or more invasive species, while 3.4% ($n = 130$) had a decrease of two or more invasive species. Plots in counties with EAB had a significantly greater increase in the number of invasive plants compared to plots without EAB (Welch two-sample t test, $t = -7.7076$, df $= 394.65$, $p < 0.01$), but there was a large imbalance in the two samples (n plots in counties with EAB: 3469, n plots in counties without EAB: 333). See randomization results below in the *Permutations* section for a thorough comparison between plots in counties with and without EAB.

Changes in invasive coverage followed a similar trend—many plots showed minimal or no change in the percentage of coverage ($n = 3802$, mean $= 0.7$, median $= 0$, SD $= 11.3$). Few plots had greater than 10% increase (6.0% plots, $n = 230$) or decrease (4.2%) in invasive coverage. There was no significant difference in change in invasive plant coverage between plots in counties with EAB and those without ($t = -1.6876$, df $= 365.43$, $p = 0.09$).

Regression models

Regression models showed that plots in counties with longer EAB residence times, in the presence of ash, and in counties with larger portion of developed areas tended to have a larger accumulation of invasive plants during the resampling interval (Figure 2). Canopy structure metrics, however, tended not to be significant in the accumulation of invasive plant richness. In modeling the change in invasive plant cover, vertical complexity and gap fraction were both significantly associated with change in cover, while EAB residence time and the presence of ash were not. Curiously, both vertical complexity and gap fraction were negatively associated with change in invasive plant coverage, indicating that plots with more uniform vertical structure and with fewer gaps tended to have the greatest expansion of invasive plant coverage (Figure 2). Furthermore, EAB residence time was only weakly associated with forest canopy metrics (all $r < 0.11$). We detected only very weak spatial trends in either the raw metrics or model residuals (Appendix S1: Figure S1). Although spatial autocorrelation was sporadically significant ($p < 0.025$, $p > 0.975$), across the 300-km gradient we assessed, autocorrelation was consistently weak for both raw metrics and residuals of the models (for residuals, all $|I| < 0.005$).

Permutations

We used four randomization schemes to further test the effect of the occurrence of EAB and its main host, ash, on invasive plant species accumulation and change in

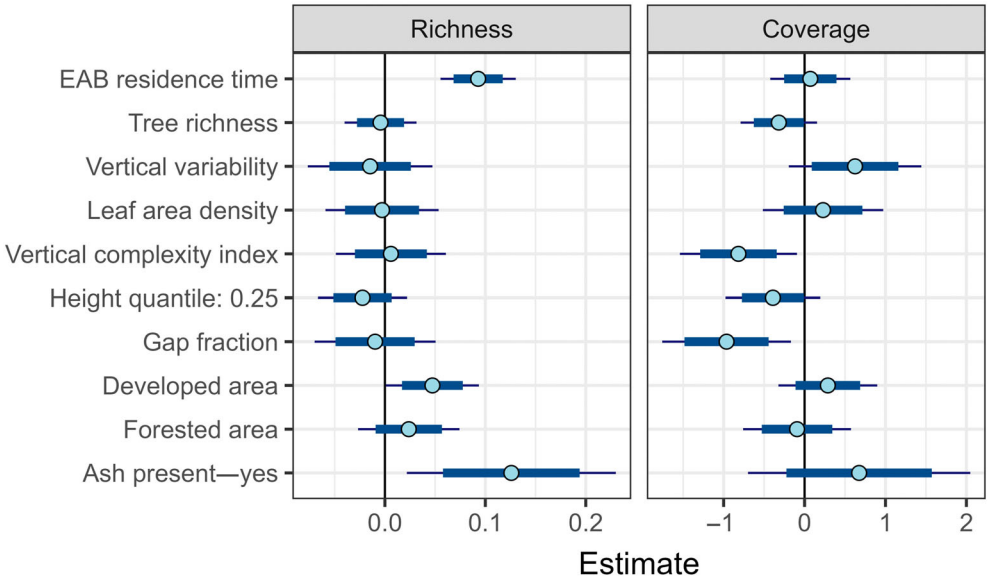

FIGURE 2 Parameter estimates from regression models predicting the change in invasive species richness and coverage between sample periods. Wider segments are 80% CIs, and thinner lines are 95% CIs. All variables were centered and scaled before model fitting. Presence of ash is categorical. EAB, emerald ash borer.

coverage. We found that when ash was present, EAB was associated with an average increase of 0.44 invasive plant species per plot, and 1.5% expansion in coverage of invasive plants (both $n = 1000$, $p < 0.01$) when compared to plots where EAB was not present (Figure 3). Alternatively, we found that the presence of ash, when EAB was present, was associated with an average increase of 0.11 additional invasive plants per plot, and 0.06% expansion in coverage versus plots where ash was not present. Not surprisingly, the combined effect of EAB and ash had the greatest effect on invasive plant accumulations (compared to plots without EAB or ash), which was associated with an additional 0.48 invasive plant accumulation and 1.5% expansion in coverage. Finally, when EAB was not present, plots with ash tended to have 0.05 additional invasive plants and 0.01% larger increase in invasive coverage—consistent with EAB being an important driver of invasive plant richness accumulation (Figure 3).

DISCUSSION

Overview

The impact and the accumulation of invasive plants on the landscape have important implications for the trajectory of future forests, especially in the context of climate change and land use change. Our work shows that invasive forest pests can play an important role in invasive plant accumulation, which tends to amplify as residence time lengthens. These findings have the potential to help identify regions that may be vulnerable to future invasive plant accumulation and where management efforts may be most effective. This is especially important as high-impact non-native pests, capable of killing mature forest tree species and disrupting native forests, continue to be introduced from abroad (Aukema et al., 2010).

Influence of EAB residence time and forest structure

The increase in invasive plant richness (and coverage) due to invasive pests is expected to be due to an increase in canopy gaps that allow additional light and moisture to reach the forest floor, encouraging the growth of understory species. While the loss of canopy trees and increased forest gaps due to non-native pests is a frequent, and often rapid, consequence of non-native pest invasions, impacts on other, nonhost, plants are likely to be more gradual and cumulative over time. The progressive and cumulative nature of pest impacts on forests is an important component to understanding pest impacts, as lagged effects can be felt on host trees and forests for years (e.g., Day & McClean, 1991; James et al., 2017; Magnussen & Alfaro, 2012; Muzika & Liebhold, 1999), or even decades afterward, as in the cases of host extirpation. Our findings and those in the literature suggest that the contemporary patterns of local forest composition and invasive plant occurrences are partially shaped by present and past occurrences of tree pests, and that

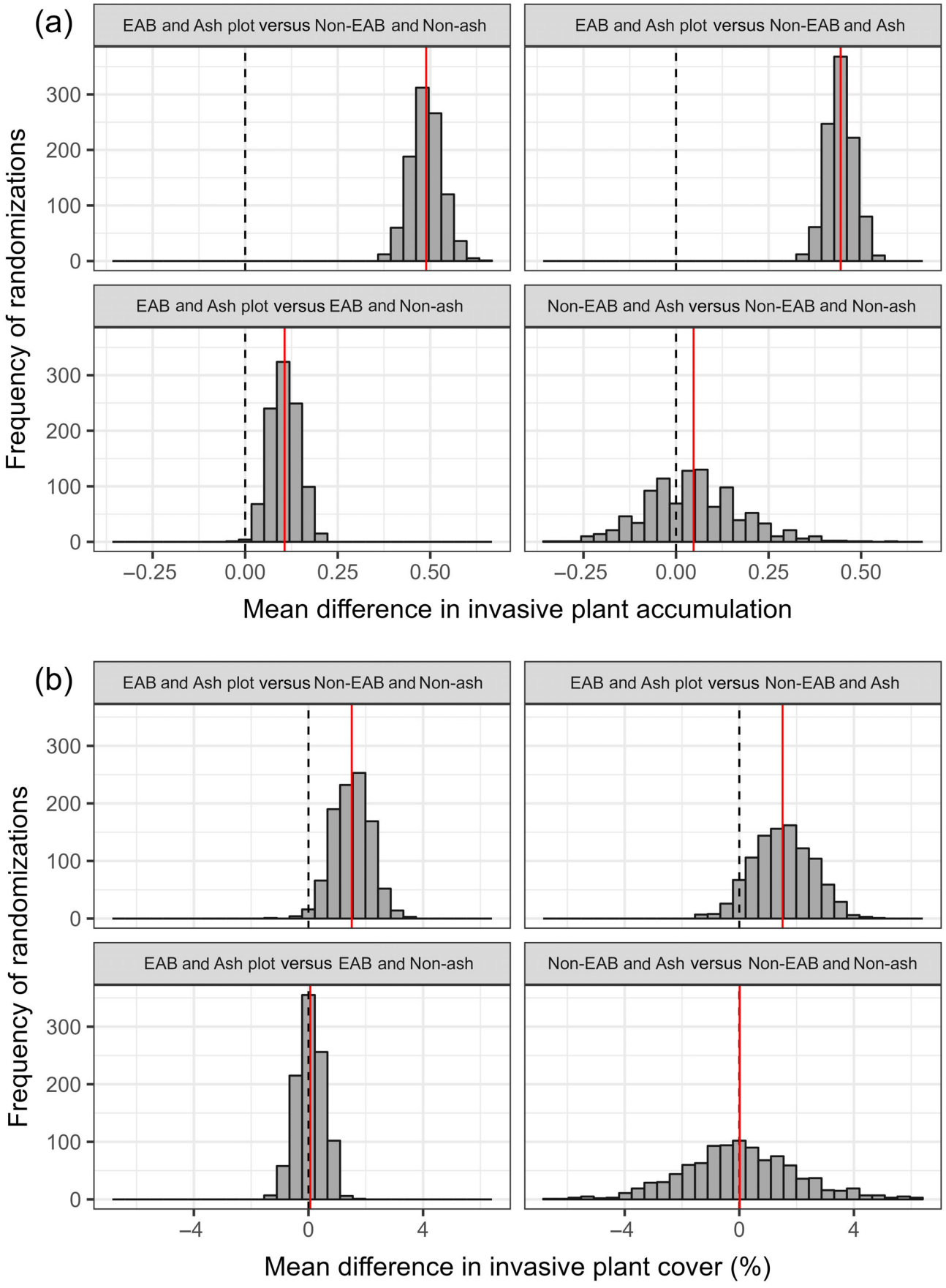

FIGURE 3 Legend on next page.

although the effect may be weak, it has the potential to improve our understanding of invasive species distributions.

Our work shows that EAB residence time has a significant effect on the accumulation of invasive plants but not the change in invasive plant coverage. Despite this, we found only a weak relationship between EAB residence time and gap fraction ($n = 2576$, $r = -0.08$, $p < 0.01$), and similar weak associations with other forest canopy metrics. The lack of a strong link between residence time and forest canopy metrics could be due to multiple factors, including how EAB interacts with its hosts, lag times, and LiDAR data collection. First, EAB can damage trees in ways that might not be readily apparent from LiDAR data. The first readily apparent external symptoms of EAB damage are likely to be bark loss, crown flagging, and branch death (Persad & Tobin, 2015), but these types of symptoms are not unique to EAB, and can be caused by a variety of biotic or abiotic agents on any tree species. Dramatic changes in forest structure are unlikely to be apparent until the dead ash trees fall, but even then, although ash is common in Indiana, it is not a major canopy species, so effects on forest structure may still be muted. Furthermore, there is likely to be a lag between when EAB first appears and the onset of substantial ash mortality and forest structural change (Choi et al., 2023). Typically ash tree mortality begins to increase 6–7 years after EAB is first detected in a county (Morin et al., 2017), which could be several years after EAB originally arrives (Herms & McCullough, 2014), and dramatic canopy effects may not be evident for several additional years until beetle-killed trees begin to fall. Although these temporal lags add some uncertainty to our analyses, our metric of EAB residence time should nevertheless provide a reasonable approximation of when EAB could begin to affect ash in a region. Finally, because we had LiDAR data for one time period, we were unable to distinguish between forests with high gap fraction due to EAB-induced tree mortality and gaps due to other, natural or human-caused, processes (e.g., tree species characteristics, successional stage, soil characteristics, and abiotic damage) (Muscolo et al., 2014). Future work focused on changes in forest structure, ideally before and after pest invasion, could help isolate the effects of non-native pests and distinguish them from intrinsically gappy forests.

Despite the lack of a clear signal between EAB residence time and forest canopy metrics, we nonetheless detected an effect of EAB and its primary host, ash, on the accumulation and spread of invasive plants—evidenced by both our regression model and randomized plot comparisons. This finding is largely consistent with other work at smaller scales that has shown EAB and other invasive pests, can enhance the spread, coverage, and growth of invasive plants (Baron & Rubin, 2021; Eschtruth et al., 2011; Hoven et al., 2017). The lack of association between EAB and forest structure metrics, discussed above, complicates the interpretation somewhat, but could indicate that EAB can facilitate the spread of invasive plants even without large systematic shifts in overall forest structure, perhaps due to the low ash abundance. Flagging or death of large branches of host trees could open the canopy enough to allow light and moisture to reach the forest floor that could facilitate the spread of non-native plants, even before tree death. Relatively few studies have attempted to link LiDAR to the impacts of forest pests (Senf et al., 2017), and many of those have often focused on defoliating insects, where hosts are in large abundance, or on identifying individual pest-attacked trees (Lin et al., 2019; Oblinger et al., 2022). More work may yet be needed to link LiDAR with other types of pests (e.g., wood borers like EAB) especially when hosts are not the dominant tree species (e.g., Choi et al., 2023).

The occurrence (but not residence time) of EAB residence time had a minor effect on the expansion of invasive plant coverage (Figure 3), but we also found multiple forest canopy metrics affected the change in coverage—in particular vertical complexity and gap fraction. The negative association between vertical complexity and change in coverage could be due to low-complexity forests being particularly vulnerable to the expansion of invasive plants. If, for instance, forests lack a well-developed understory, greater space and resources may be available for invasive plants to expand coverage. The negative association between gap fraction and invasive species coverage is more challenging to explain as, in general, we expect greater expansion of invasive plants in forests with a greater number of gaps. The lag period between when plots were sampled and when LiDAR was collected may partially explain this relationship.

The presence of non-native forest pests represents just one dimension that may affect the accumulation of invasive plants. Previous work, for instance, has shown forest

FIGURE 3 Mean differences in (a) invasive plant accumulation and (b) invasive plant cover among random pairs of plots in counties with and without emerald ash borer (EAB), in the presence and absence of ash. Randomizations were conducted 1000 times. Red lines are means of the distribution. In general, positive values indicate plots with EAB and/or ash tend to accumulate more invasive plants and have a greater expansion in invasive plant coverage.

biomass, species richness, phylogenetic diversity, propagule pressure, distance from roads, stand age and density, climate, and various socioeconomic factors can each affect invasive plant richness and cover at a variety of spatial scales (Essl et al., 2019; Flory & Clay, 2006; Iannone et al., 2015). Silvicultural practices and landscape history may also affect the establishment and spread of non-native plants. In a synthesis of the effects of silvicultural treatments on invasive plant richness and coverage, Sutherland and Nelson (2010) showed treatments (typically tree harvesting, sometimes associated with burning) were frequently, although not always, associated with increased occurrence of invasive plants. The effect of disturbance is also evident in our dataset as illustrated by the effect of developed areas on the accumulation of invasive plants—consistent with disturbed areas being a source for additional invasive species in forests. Although it is not clear whether invasive pests impact the accumulation of invasive plants at the broadest spatial scales (especially as the relationship may be reversed—non-native plants can also facilitate the spread of invasive pests; Bonnamour et al., 2023; Gougherty & Davies, 2022), accounting for the impacts of invasive pests may improve our understanding of the spread of invasive plant species.

Long-term impacts and future directions

Although the measured impacts of EAB on the accumulation and spread of invasive plants were low (in an absolute sense), it is important to point out that our study was conducted only a short time after EAB was introduced to the region. The longest estimated EAB residence time for an individual plot was 13 years, and the resampling interval of plots was also relatively short (5–6 years). Given the short residence times and resample intervals, it is not surprising that many plots do not accumulate any additional invasive plant species, and there was no detectable trend between EAB residence time and invasive plant coverage. Regardless, if the small effects we detected (over a relatively short time period) continue into the future, the small effects could accumulate over time and play a significant effect on the distribution and abundance of invasive plants on the landscape. For instance, if invasive plants continue to accumulate in the way we detected, by the next sampling, nearly all plots with ash would be expected to have accumulated an additional invasive plant species due to EAB invasion. Similarly, although the increase in invasive plant cover due to the presence of EAB was relatively low in plots (on average, counties with EAB had 1.5% greater expansion by invasive plants compared to counties without EAB, when ash was present), when aggregated across the entire state, this could translate into hundreds of additional acres of land invaded by invasive plants over the coming decades.

Although our model detected a significant association between LiDAR-derived forest canopy metrics and an expansion of invasive plant species coverage, more work is yet needed to understand how pest-induced tree mortality can affect forest canopy structure. Understanding these effects when hosts are rare and do not make up a large component of forest diversity is especially important as, historically, many of the most impactful forest pests in eastern North America have been host specialists (e.g., EAB, hemlock woolly adelgid, chestnut blight, butternut canker, and Dutch elm disease each primarily attacks one host genus). Being able to parse the effects of invasive pests from natural canopy change (e.g., mortality) will require a time series of forest canopy structure, ideally before and after pest invasion, lasting at least until affected hosts begin to experience excessive mortality. Addressing these issues will likely improve our ability to link invasive pests to changes in forest structure and ultimately to invasive plant accumulation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data used for modeling and randomization analyses (Gougherty et al., 2023) are available from Figshare: https://doi.org/10.6084/m9.figshare.21504828.

ORCID

Andrew V. Gougherty https://orcid.org/0000-0002-3905-8539

Elizabeth A. LaRue https://orcid.org/0000-0002-9535-0630

Songlin Fei https://orcid.org/0000-0003-2772-0166

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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