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Population dynamics of ash across the eastern USA following invasion by emerald ash borer

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ABSTRACT

Non-native insects and pathogens can alter the composition and successional trajectories of forests and, in exceptional cases, drive their host trees functionally extinct. Emerald ash borer has killed millions of ash trees in its invaded range across eastern North America. Predicting the future ecological role of ash requires information on the extent of ash regeneration and recruitment in the wake of invasion. Variable levels of ash regeneration have been observed in stands invaded by emerald ash borer, although recruitment rates of young ash trees into the overstory remain unclear. Here, we used forest inventory data to quantify ash recruitment and regeneration across the eastern United States, and we linked these observed patterns to emerald ash borer invasion history. Inventory data from 2013-2018 indicate there has been extensive ash regeneration in invaded regions, totaling > 1,200 seedlings per ha in counties invaded in 2002–2006. Plots in counties with the longest invasion histories contained the highest densities of ash seedlings and saplings, likely due to the high densities of overstory ash in these areas prior to invasion by emerald ash borer. Seedling densities also remained generally unchanged between inventory periods ending in 2007 and 2018 irrespective of invasion history. Despite this widespread regeneration, ash trees in the smallest overstory class died at faster rates than they were recruited from seedlings or saplings, resulting in negative population trajectories on plots that have been invaded for more than ~ 10 years. This trend suggests that ash will continue to decline in abundance and may become functionally extinct across the invaded range of emerald ash borer. However, the future ecological role of ash will ultimately be determined by the iterative production and survival of ash seeds to reproductive ages in the presence of emerald ash borer populations, along with effective management practices.

1. Introduction

Invasions by insects and diseases can have catastrophic economic and ecological impacts on the structure and function of forest ecosystems (Aukema et al., 2011; Boyd et al., 2013; Liebhold et al., 2017; Fei et al., 2019). For example, the fungus *Cryphonectria parasitica*, the causative agent of chestnut blight, has reduced American chestnut, *Castanea dentata* (Marsh.) Borkh., a once dominant component of deciduous forests in the eastern USA, to a rare species that is only occasionally found as a suppressed understory tree (Anagnostakis, 1987). Similarly, hemlock woolly adelgid and beech bark disease have altered the current and future composition of late successional forests in eastern North America (Morin and Liebhold, 2015).

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire; Coleoptera: Buprestidae) is an invasive phloem and wood boring beetle native to eastern Asia that was first detected near Detroit, MI, USA in 2002 (Poland and McCullough, 2006). The beetle has killed millions of *Fraxinus* spp. in the eastern USA and could cause the functional extinction of ash in North America (Herms and McCullough, 2014). The invasion will likely alter successional patterns and composition of large areas of naturally regenerating forests (Burr and McCullough, 2014; Iverson et al., 2016), causing a cascade of ecological impacts in ash-containing ecosystems (Gandhi and Herms, 2010; Herms and McCullough, 2014).

There has been substantial spatial heterogeneity in the impacts of EAB and responses of invaded forests. Interspecific and intraspecific

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differences in susceptibility of *Fraxinus* spp. can explain some of that variation (Rebek et al., 2008; Herms and McCullough, 2014; Koch et al., 2015; Steiner et al., 2019; Robinett and McCullough, 2019), but percent mortality of ash has not been associated with ash density or other metrics of forest composition (Smith et al., 2015; Klooster et al., 2018). Across sites where green ash is present near the invasion epicenter, for example, mortality in overstory ash averaged 58% (Kashian, 2016) up to > 99% (Klooster et al., 2018). Similar to mortality, regeneration of ash following invasion exhibits marked variability (Klooster et al., 2018). Ash regeneration can be non-existent and, when mortality approaches 95%, seed banks may be depleted within a few years (Klooster et al., 2018). In other stands, however, post-invasion regeneration can be extensive, driven by seed production from surviving overstory trees and/or by sprouts from top-killed trees that are able to produce seeds at less than seven years of age (Kashian and Witter, 2011; Kashian, 2016).

Investigations of ash demographics to date have largely consisted of stand-level analyses, primarily near the invasion epicenter in southeastern Michigan. Region-wide patterns in ash mortality following invasion (Pugh et al., 2011; Morin et al., 2017) and the abundance of ash seedlings and saplings in different forest types have been quantified across the eastern USA (Granger et al., 2017), but these studies did not investigate ash recruitment in the wake of invasion. More importantly, the risk of mortality for young ashes as they develop from seedlings to saplings, and, eventually, to overstory trees, remains unknown.

Here, using repeated measurements on plots surveyed by the US Department of Agriculture Forest Service (USDA-FS) Forest Inventory and Analysis (FIA) program, we quantified region-wide patterns in ash demographics in response to invasion by EAB across the eastern USA. Our specific aims were to (i) quantify changes in the density and mortality of overstory ash species (ii) estimate densities of ash seedlings and saplings, and (iii) compare rates of annual recruitment vs. mortality for overstory ash following invasion. We intend that these analyses of regional demographic trends will provide insight into the potential for ash to persist across the eastern USA following invasion by EAB.

2. Materials and methods

Historical county-level records documenting annual invasion status for EAB were obtained from the USDA Animal and Plant Health Inspection Service (USDA APHIS) (Fig. 1a). Invaded counties were categorized into one of three invasion cohorts based on the year that EAB was first detected: 2002–2006 (101 counties), 2007–2012 (261 counties), and 2013–2018 (598 counties) (Fig. 1b) to reflect different phases of invasion. There are no widely used classifications for EAB invasion phases, but at the county level measurable impacts generally begin to appear ~ 5 years after establishment and are widespread at 10 years (Morin et al., 2017). Thus, we used 5–6 year intervals, but caution that trends and estimates are likely to shift with number and width of intervals even though general trends, at least for tree mortality, are well established for impacts from EAB (Pugh et al., 2011; Morin et al., 2017; Fei et al., 2019).

We then obtained forest inventory data from the USDA-FS FIA program, which tracks attributes of forest ecosystems nationwide. Only data from counties invaded by EAB in the eastern US were extracted. The FIA sampling design divides the USA into hexagons of ~ 2,448 ha, each containing at least one permanent plot (Bechtold and Patterson, 2005). Plots are hierarchical, comprised of four, 18 m fixed-radius macroplots each containing a 7.3 m fixed-radius subplot that contains a 2.1 m fixed-radius microplot. In the eastern USA, plots are sampled at ~ 5- to 7-year intervals such that a subset of 14–20 percent of plots is sampled each year in each state. Data on trees ≥ 12.7 cm DBH, referred to here as overstory trees, are measured on subplots, whereas data on seedlings (individuals < 2.54 cm in diameter at the root collar (DRC) but > 30.48 cm in height) and saplings (trees ≥ 2.54 cm in DRC but < 12.7 cm in diameter at breast height (DBH) measured ~ 1.37 m above the ground) are collected on microplots.

We used the rFIA package (Stanke and Finley, 2020; Stanke et al., 2020) in R (R Core Team, 2020) to extract plot and county-level data across the eastern USA. Data were summarized for two inventory periods (2002–2007 and 2013–2018). For simplicity, we refer to the intervals of time during which data were collected, ~2002–2007 and ~ 2013–2018, as inventory periods INV-2007 and INV-2018, respectively. Analyzing these inventory periods enabled us to quantify ash demographics before and after widespread impacts from EAB. The INV-2007 inventory period was chosen to balance data availability (e.g., more plots were available in later years) with temporal proximity to 2002, the year EAB was first detected in North America. Note that inventory periods and invasion cohort intervals were not meant to coincide perfectly, given that the former reflect sampling dates and the latter were used to assign counties to bins by year of invasion (i.e., a proxy for invasion history length as of 2018). Thus, invasion cohort intervals were constructed independent of inventory years and to create a spectrum of invasion history lengths and impacts.

For both inventory periods, we extracted numbers of live overstory ash trees, numbers of ash seedlings, numbers of ash saplings, and percent annual mortality of overstory ash trees (estimate of mean percent of individuals subject to mortality annually). Diameter classes for overstory tree data were categorized into ~ 5 cm intervals and assigned to each tree using the center of each diameter interval for analysis (e.g., ash trees 12.7–17.5 cm in DBH were assigned values of ~ 15.2 cm). Additionally, for INV-2018, we extracted annual recruitment and annual mortality for trees in the smallest diameter class (12.7–17.5 cm) to

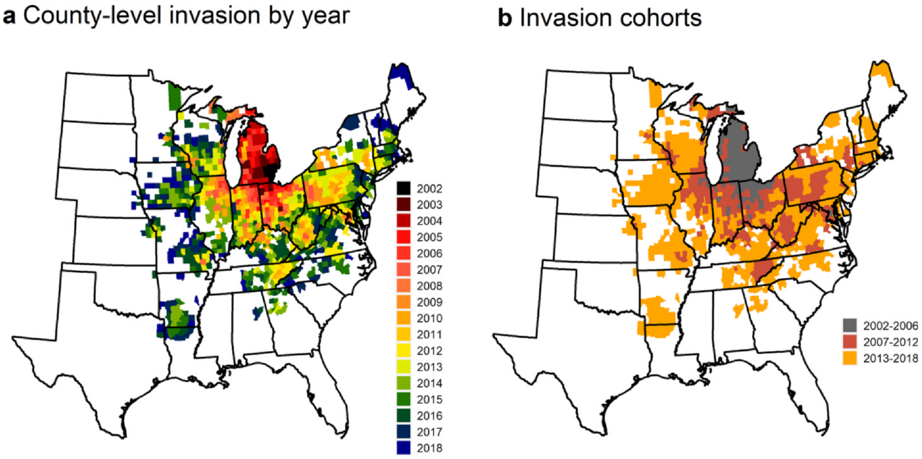

Fig. 1. County-level maps of the eastern USA depicting (a) year of initial discovery of emerald ash borer and (b) categorization of counties into one of three invasion cohorts.

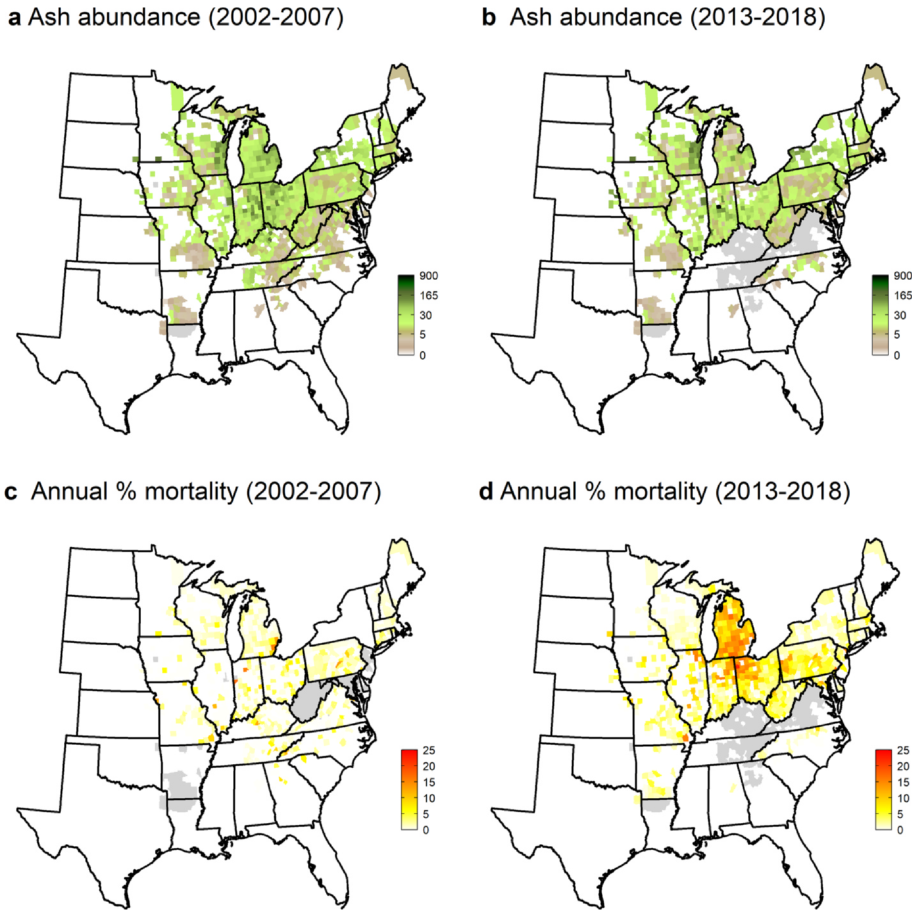

Fig. 2. County-level maps of the eastern USA depicting number of live overstory ash trees per ha of forested land in (a) 2002-2007 (INV-2007 in main text) and (b) 2013-2018 (INV-2018 in main text) along with annual percent mortality of ash in (c) 2002-2007 and (d) 2013-2018. Gray areas indicate invaded counties not reported in the FIA database for the corresponding inventory period on the date of extraction.

gain insight into whether trees were recruited into the overstory at comparable rates to which they were lost via mortality (Zhang et al., 2011). Note that trees are tracked individually between inventories as part of the FIA sampling protocol, which enables accurate plot-level counts of trees that grew beyond the 12.7 cm threshold (recruitment or ingrowth) and trees that died since the previous inventory. Comparing these metrics can provide insight on population trajectories of ash representation in forests, and, ultimately, the potential for ash trees to reach reproductive ages/sizes. Harvested trees ("removals" in the FIA database) are also tracked but were inconsequential (< 0.006 removal trees per ha across each inventory year × invasion cohort) and were not analyzed further. All tree count data were extracted as trees per acre and converted to trees per hectare.

We caution that the initial occurrence of EAB in a county may precede its spread onto an FIA plot by several years and thus not all plots located within invaded counties have been invaded. Moreover, because FIA plots in the eastern USA are sampled every ~ 5 years, some plots could have been measured up to 5–7 years prior to the specified inventory year (i.e., effectively outside the cohort) or up to 5–7 years after being invaded. These irregularities may introduce some uncertainties in the quantification of the relationship between EAB invasion and changes in forest conditions, though their impact may be minimal since measurements are highly replicated. Nevertheless, our regional analysis provides a macroscale assessment of ash demographics that complements, rather than replaces, focused stand-level evaluations of ash population dynamics.

All metrics were mapped at the county-level to visualize spatial patterns of ash demographics. We then graphed the number of live ash trees and annual mortality in INV-2007 and INV-2018 by tree diameter class × invasion cohort. In addition, we graphed numbers of seedlings, numbers of saplings, annual recruitment, and annual mortality of tress 12.7–17.5 cm in DBH and compared estimates by invasion cohort × inventory year. Groupings with non-overlapping confidence intervals were deemed significantly different. However, we did not carry out all pairwise comparisons between inventory periods, invasion cohorts, and/or diameter classes; our focus was not to conduct formal comparisons between all of these different possible classifications, but rather to describe broader trends in ash demographics.

We also regressed county-level seedling and sapling densities on (i) overstory ash densities in INV-2007 (ii) invasion cohort and (iii) their interaction. We repeated each analysis using overstory ash densities in INV-2018, resulting in four models (two each for seedlings and saplings in INV-2007 and INV-2018). We conducted these analyses to investigate whether current regeneration patterns were in part driven by the density of seed sources prior to and/or after invasion. All predictors and response variables were $\log(x + 1)$-transformed for this analysis.

Regeneration analyzed here included seedlings persisting from prior to EAB invasion, seedlings originating from surviving overstory trees, basal sprouts from killed overstory trees, and/or seedlings resulting from reproduction by those sprouts; these different origins are not differentiated in the FIA data. Moreover, we elected to summarize demographic properties at the genus (*Fraxinus*) level because, despite known interspecific variation in ash susceptibility to EAB (Rebek et al., 2008; Herms and McCullough, 2014; Koch et al., 2015; Steiner et al., 2019; Robinett and McCullough, 2019), ash seedlings and saplings are not always identified to species in the FIA database and we sought comparable analyses across age classes (e.g., between overstory trees and seedlings). Our landscape-level analyses are not necessarily reflective of dynamics in specific stands and stand-level investigations might provide additional mechanistic understandings of seedling growth, competition, and survival. All statistical analyses were conducted using R statistical software (R Core Team, 2020).

3. Results

3.1. Overstory trees

The region initially invaded by EAB had a uniquely high density of overstory ash compared to most of the rest of the eastern USA (Fig. 2a), but overstory ash densities near the epicenter have declined substantially. In INV-2018, overstory ash in some counties in southeastern Michigan had been nearly eliminated (0 stems/ha) (Fig. 2b). Impacts near the epicenter in southeastern Michigan were apparent in INV-2007 (> 10% annual mortality of overstory), but mortality was generally much lower (< 3% annual mortality) across the rest of the study area (Fig. 2c). In INV-2018, impacts across invaded areas were striking, with > 10% annual mortality of overstory trees in several counties in Michigan, Indiana, and Ohio (Fig. 2d). Estimated annual mortality rates were near zero in the 2–3 epicenter counties in southeastern Michigan, owing to the absence of overstory ash in that area (Fig. 2d).

Densities of small diameter overstory ash trees in the earliest invasion cohort differed significantly from densities in the later invasion cohorts. Analysis of numbers of trees per ha by diameter class in INV-2007 indicated that there were over five more ash stems per ha in the smallest diameter class for the 2002–2006 invasion cohort compared to the 2007–2012 and 2013–2018 invasion cohorts (Fig. 3a). For each diameter class up to 40 cm in DBH, there were significantly more trees per ha in the 2002–2006 invasion cohort in INV-2007; for trees > 40 cm, however, densities were approximately equivalent across invasion cohorts (Fig. 3a). In INV-2018, trees per ha were either statistically equivalent or lower when comparing 2002–2006 to the other invasion cohorts across all diameter classes, meaning that this cohort exhibited substantial losses in tree densities between the inventory periods, and particularly in smaller diameter classes (Fig. 3b). Between the INV-2007 and INV-2018 inventory periods, ash densities decreased in the 2007–2012 cohort for the smallest diameter class, but densities were otherwise comparable; the most recently invaded cohort (2013–2018) exhibited very little change in densities between INV-2007 and INV-2018 and there was, for example, a slight increase in tree densities within the smallest diameter class (Fig. 3b).

Mortality was uniformly low in INV-2007 (< 2.1%), irrespective of diameter class (Fig. 3c), but in INV-2018, mortality had reached 8–11% and 3–5% across diameter classes in the 2002–2006 and 2007–2012 invasion cohorts, respectively (Fig. 3d). Annual mortality rates in INV-2018 were only slightly elevated for the 2013–2018 invasion cohort (~1–2%) compared to levels in INV-2007 (~0.1–1.4%). Annual mortality rates in INV-2018 were still highest for the 2002–2006 invasion cohort across all diameter classes except the largest class of trees > 76.2 cm in DBH (Fig. 3c). Regardless of inventory year (INV-2007 vs. INV-2018) and/or invasion cohort, there were no apparent trends in mortality rates across diameter classes (Fig. 3c,d).

3.2. Seedlings and saplings

Ash seedlings were generally abundant in both INV-2007 (Fig. 4a) and INV-2018 (Fig. 4b) across the eastern USA. Seedling density was approximately constant between INV-2007 and INV-2018 within each invasion cohort (Fig. 4c), However, during both inventory periods, density in the 2002–2006 invasion cohort was higher than in the two later invasion cohorts by > 500 seedlings per ha. Ash saplings were also generally abundant in INV-2007 and INV-2018 across the region (Fig. 5a,b), but sapling densities were greater in INV-2007 than in INV-2018 by > 50 additional saplings per ha within the 2002–2006 invasion cohort (Fig. 5c). For the other two invasion cohorts, sapling counts were approximately equal.

Ash seedlings increased significantly with densities of overstory ash trees in INV-2007 (Fig. 6a; $F_{1,806} = 244.63$, $P < 0.0001$) but there was no significant interaction between invasion cohort and overstory ash densities in INV-2007 ($F_{2,806} = 0.58$, $P = 0.56$). During INV-2018, there was a significant interaction between overstory ash density and invasion cohort (Fig. 6b; $F_{2,809} = 8.96$, $P = 0.0001$), in part driven by

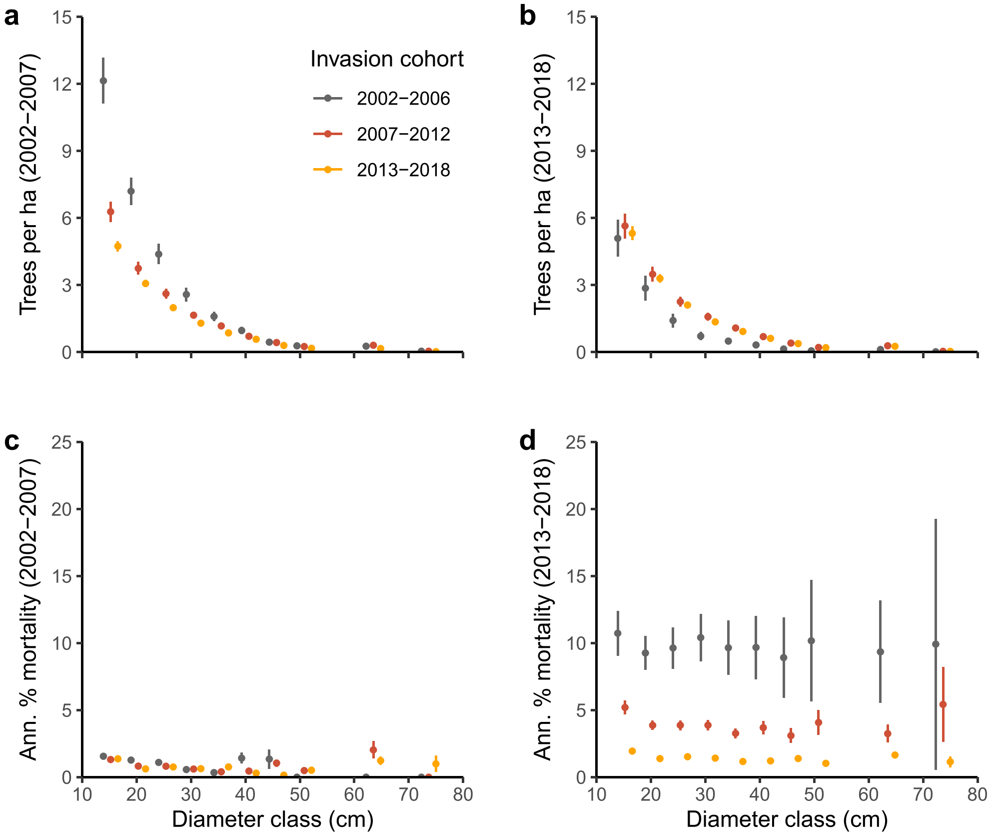

Fig. 3. Changes in overstory ash demographics. Mean (± 95% CIs) number of live ash trees per ha forested land in (a) 2002-2007 (INV-2007 in main text) and (b) 2013-2018 (INV-2018 in main text) and annual percent mortality of ash in (c) 2002-2007 and (d) 2013-2018 by diameter class across the eastern USA. Each panel has groups for diameter class (*x*-axis) × year of invasion at the county-level (invasion cohort). Points and confidence intervals for each invasion cohort × size class combination are shifted to the right to prevent overlap. Estimates and error bars were obtained using plot-level data.

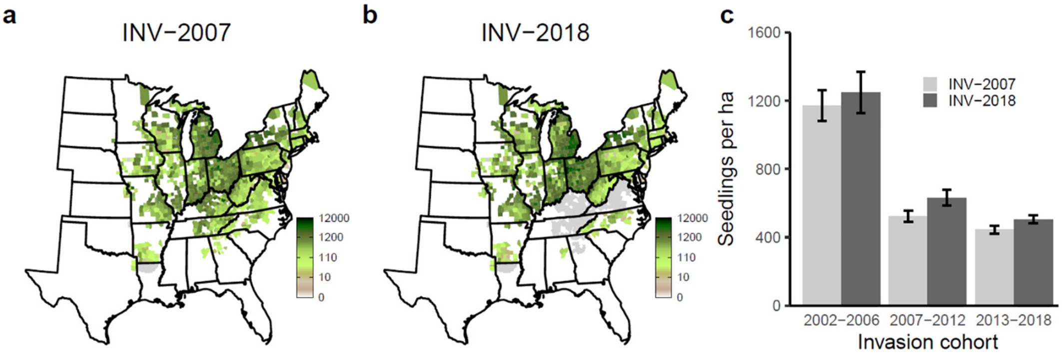

Fig. 4. Spatial patterns in density of ash seedlings. (a-b) Maps of the eastern USA depicting number of ash seedlings per ha of forested land at the county-level in (a) 2002-2007 (INV-2007 in main text) and (b) 2013-2018 (INV-2018 in main text). Gray areas indicate invaded counties not reported in FIA database for the corresponding inventory period on the date of extraction. (c) Mean counts (± 95% CIs) of seedlings by inventory period × invasion cohort using plot-level data.

the fact that seedling density was not strongly correlated with overstory ash density for the 2002–2006 cohort (slope = 0.11 ± 0.14, $t_{809} = 0.78$, $P = 0.43$). Otherwise, seedling and overstory densities were significantly, positively correlated (Fig. 6b). Trends in seedling densities by invasion cohort in both models, which analyzed county-level data, unsurprisingly reflected analyses of plot-level data presented in Fig. 4c. Similarly, ash saplings increased significantly with densities of overstory ash trees in INV-2007 (Fig. 6c; $F_{1,800} = 120.90$, $P < 0.0001$) and INV-2018 (Fig. 6d; $F_{1,802} = 187.35$, $P < 0.0001$). For models of sapling densities, no statistically significant interactions were detected between invasion cohort and overstory ash density in INV-2007 ($F_{2,800} = 0.35$, $P = 0.71$) or INV-2018 ($F_{2,802} = 1.50$, $P = 0.22$). Trends in sapling densities by invasion cohort in both models again reflected analyses of plot-level data (Fig. 5c). Summary statistics for regression models of seedling and sapling counts as a function of overstory trees are provided in Appendix S1.

3.3. *Recruitment vs. mortality*

There was a striking difference between the two inventory periods when comparing annual recruitment and mortality of trees in the smallest overstory diameter class. Recruitment was generally widespread in both INV-2007 (Fig. 7a) and INV-2018 (Fig. 7d), with averages of 0.5 and 0.4 trees recruited per ha, respectively. Annual mortality in the smallest trees increased substantially across the region, averaging 0.08 trees per ha in INV-2007 (Fig. 7b) but reaching 0.37 trees per ha in INV-2018 (Fig. 7e). When comparing trends by invasion cohort within inventory years, recruitment was significantly higher than mortality across all invasion cohorts in INV-2007 (Fig. 7c). By INV-2018, recruitment in the 2002–2006 invasion cohort had significantly decreased from levels in INV-2007 and was ~ 50% less than tree mortality levels (Fig. 7c, f). In INV-2018, recruitment and mortality were approximately equivalent for the 2007–2012 cohort and recruitment was significantly higher than mortality in the 2013–2018 invasion cohort (Fig. 7f).

4. Discussion

The invasion by EAB has resulted in millions of dead ash trees across the eastern USA, threatening the ecological role of ash. The emerald ash borer invasion began in regions with the highest densities of ash (Fig. 2a) and annual mortality rates of ash are still ~ 10% across diameter classes in counties invaded between 2002 and 2006 (Fig. 3d). Overstory ash has been nearly extirpated from southeastern Michigan (Fig. 2), although thousands of ash seedlings and tens of ash saplings per ha are established there and in other areas with the longest invasion histories. Prior to widespread invasion by EAB, recruitment of young ash trees to the overstory appeared to be substantially higher than ash tree mortality in the smallest diameter class (Fig. 7c, f). However, as the invasion continues, many of these young ash trees appear to be succumbing to EAB populations before reaching reproductive age. Most eastern North American ash species begin producing seeds when they are around 20 years old (Bonner and Karrfalt, 2008), which for urban white ash would translate to an average DBH of ~ 20 cm (Peper et al., 2014), or ~ 3 cm larger than the smallest overstory class analyzed here. If this age-diameter relationship reflects those of North America ashes in rural settings, then rates of overstory ash mortality are currently exceeding recruitment, a pattern that would eventually result in the extirpation of ash.

Across the eastern USA, annual percent mortality of ash in INV-2007 was approximately equal across all diameter classes irrespective of invasion history (Fig. 3c); although rates were substantially higher in

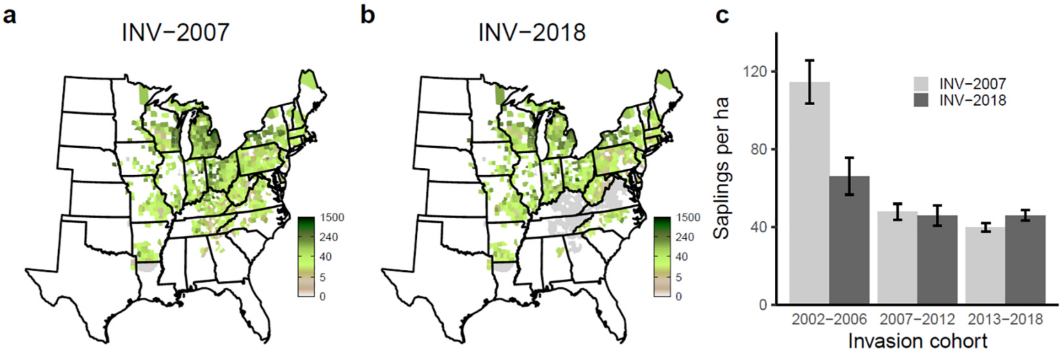

Fig. 5. Spatial patterns in density of ash saplings. (a-b) Maps of the eastern USA depicting number of ash saplings per ha of forested land at the county-level in (a) 2002-2007 (INV-2007 in main text) and (b) 2013-2018 (INV-2018 in main text). Gray areas indicate invaded counties not reported in FIA database for the corresponding inventory period on the date of extraction. (c) Mean counts (± 95% CIs) of saplings by inventory period × invasion cohort using plot-level data.

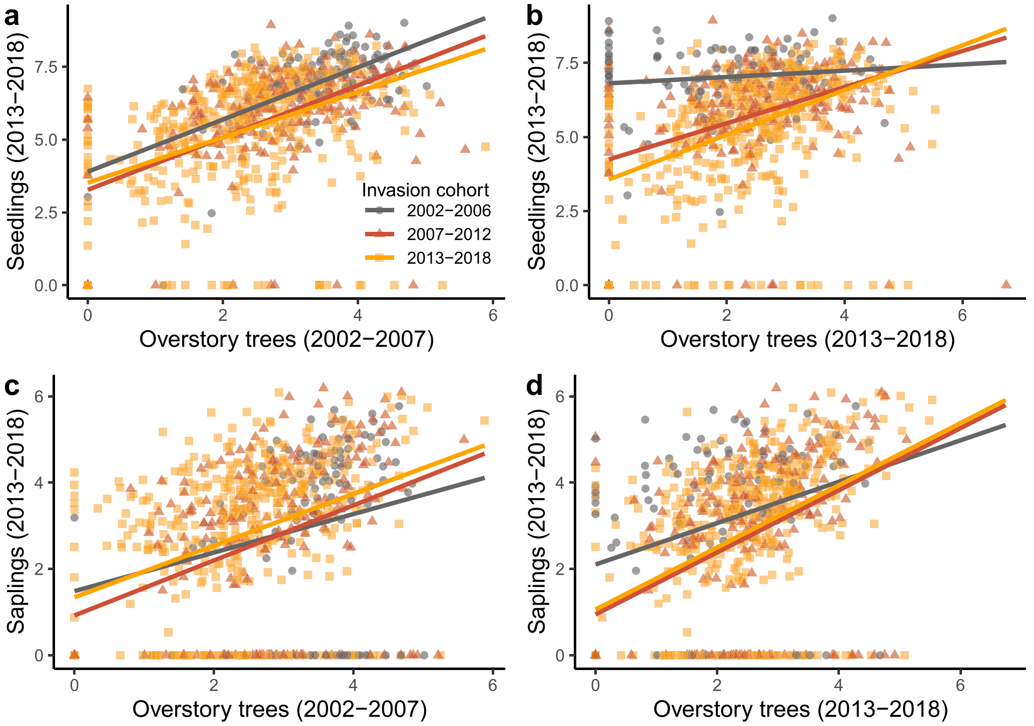

Fig. 6. Spatial patterns in ash seedlings per ha of forested land by county. (a-b) Numbers of seedlings in 2013-2018 (INV-2018 in main text) as a function of overstory ash trees in (a) 2002-2007 (INV-2007 in main text; overstory: $F_{1,806} = 244.63$, $P < 0.0001$; no invasion cohort × overstory interaction) and (b) 2013-2018 (invasion cohort × overstory: $F_{2,809} = 8.96$, $P = 0.0001$) by invasion cohort. (c-d) Numbers of saplings in 2013-2018 as a function of overstory ash trees in (c) 2002-2007 (overstory: $F_{1,800} = 120.90$, $P < 0.0001$) and (d) 2013-2018 (overstory: $F_{1,802} = 187.35$, $P < 0.0001$) by invasion cohort. For models in (a), (c), and (d), no interactions between overstory × invasion cohort were detected (summary statistics for all models are provided in Appendix S1). Values were log(x + 1)-transformed for analysis and display.

INV-2018, mortality was still relatively uniform across diameter classes (Fig. 3d). If EAB did not exhibit a host preference based on size and beetle populations were dispersed homogenously in a stand, elevated mortality rates presumably would be observed in smaller diameter trees for which fewer larvae can cause mortality. In previous studies, larger diameter ash trees that are dominant or co-dominant have exhibited lower mortality rates than smaller trees, potentially because larger trees (i) require more insects to be killed (ii) are not preferred for oviposition during the early stages of stand invasion by EAB and (iii) may be more capable of defending against EAB owing to increased access to nutrients

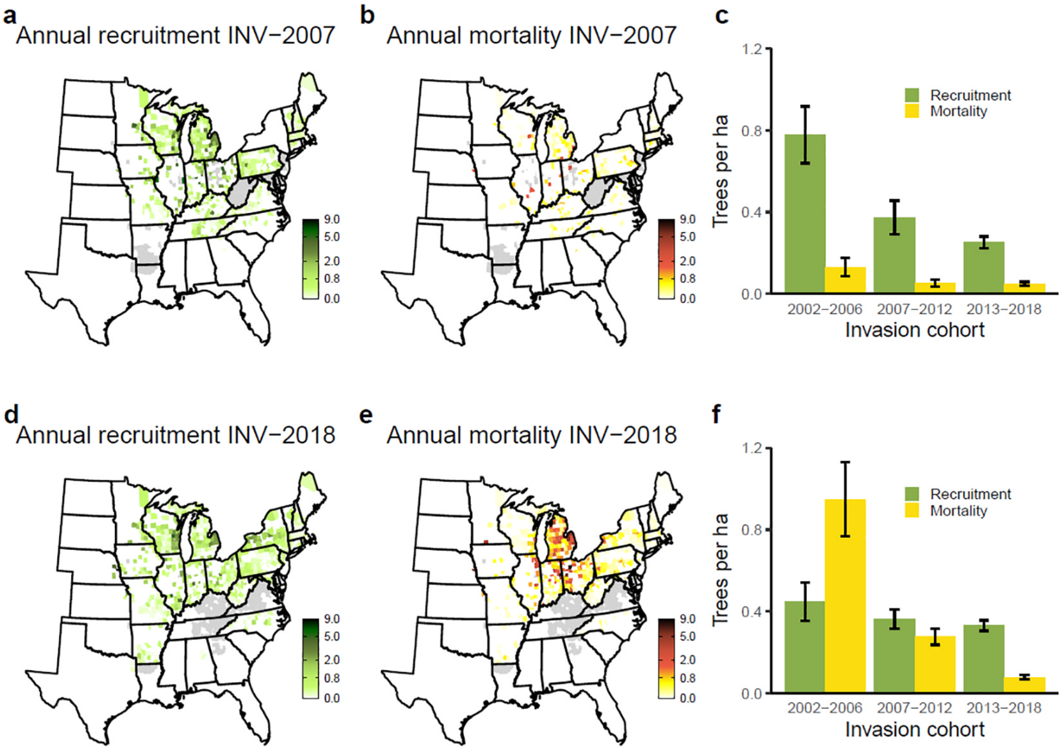

Fig. 7. Spatial patterns in annual recruitment and mortality of ash per ha of forested land in the 12.7–17.5 cm diameter class. County-level maps of the eastern USA depicting (a,d) recruitment, defined as the annual number of ash trees growing into the 12.7–17.5 cm diameter class, (b,e) annual number of trees dying in the 12.7–17.5 cm diameter class, and (c,f) comparisons between recruitment and mortality by invasion cohort for trees 12.7–17.5 cm in diameter in 2002-2007 (INV-2007 in main text) (a-c) and 2013-2018 (INV-2018 in main text) (d-f) Gray areas in maps indicate invaded counties not reported in FIA database for the corresponding inventory period on the date of extraction.

and/or sunlight (Knight et al., 2012; Steiner et al., 2019). Thus, equal mortality rates across diameter classes could reflect the coarse assignment of plots using county-level invasion status; that is, inclusion of non-invaded plots into analyses could have artificially reduced mortality rates in small stems when averaged across larger areas. Conversely, especially in long-invaded areas, mortality rates of smaller diameter trees could be slowing due to decreases in EAB population densities as hosts are depleted, which would potentially homogenize annual (vs. cumulative) mortality rates.

For the most recent invasion cohort (2013–2018), tree mortality rates in INV-2018 were only slightly elevated compared to INV-2007 (Fig. 3), but increases in mortality associated with longer invasion histories suggest that rates in the 2013–2018 cohort are likely to accelerate through the next 5–10 years (Fig. 3c,d). Indeed, accelerating mortality rates following a post-detection lag period are common (Herms and McCullough, 2014; Morin et al., 2017). More recently invaded areas do have lower densities of ash (Fig. 3a,b), but differences in host density may not influence mortality rates (Smith et al., 2015). Although annual mortality rates are still significantly higher in the longest invaded areas (2002–2006 cohort), some counties in southeastern Michigan had low or 0% mortality rates (Fig. 2c), owing to the extremely low densities of overstory ash trees in such counties (Fig. 2a). Thus, some areas might be reaching a plateau in annual mortality rates (Morin et al., 2017) as suitable hosts are depleted. Nonetheless, some larger diameter trees have survived in the longest invaded cohort (Fig. 3b), and survival of some overstory trees has been reported even in the most heavily impacted stands (Herms and McCullough, 2014; Kashian, 2016; Robinett and McCullough, 2019).

Ash regeneration (measured by seedling and sapling densities) occurred at higher levels in areas where EAB has been the longest (Figs. 4c, 5c). This is likely in part due to the high overstory ash densities in this region prior to invasion (Figs. 2a, 3a), but it also may reflect greater survival and growth of seedlings and saplings following overstory ash mortality, which likely increases gaps and the amount of light reaching the forest floor (Granger et al., 2017). Ash regeneration is widespread at some sites near the invasion epicenter, with patterns influenced by site hydrology and potentially interspecific competition (reviewed in Klooster et al., 2018). Klooster et al. (2014) found ~ 9,000 to > 270,000 ash seedlings (< 1.37 m in height) per ha in the Upper Huron River Watershed in southeastern Michigan and ~ 3,000–20,000 seedlings per ha on sites throughout Ohio. However, Klooster et al. (2014) also found zero first year seedlings at several sites in Michigan, meaning that seed banks and potential seed sources, except for the "orphaned" cohort, are nonexistent at some sites. Kashian and Witter (2011) found similar widespread regeneration (e.g., > 10,000 ash seedlings > 0.5 m in height per ha) across sites in Michigan and found > 400 new seedlings per ha, but reported temporal declines in new seedlings (reviewed in Klooster et al., 2018). Other investigations have found densities of 500 to > 1,200 seedlings per ha that established post-invasion and > 1000 basal sprouts from top-killed ash per ha (Kashian, 2016). Such sprouts from top-killed trees are able to produce seeds at less than seven years of age (Kashian and Witter, 2011; Kashian, 2016), but, potentially due to interspecific competition from non-ash species, might only occur in stands with high, almost pure ash components (Klooster et al., 2018). Regeneration reported here was comparable, totaling > 1,200 seedlings per ha in the 2002–2006 invasion cohort, which included most invaded counties in Michigan and several in Ohio (Fig. 2b). We note, however, that (i) regeneration types (sprouts vs. first year seedlings) were not differentiated in our analysis and (ii) FIA employs stratified random sampling, which likely resulted in some differences in site selection between this and previous studies.

Within each invasion cohort, seedling densities remained generally unchanged between INV-2007 and INV-2018 (Fig. 4c), but seedlings in INV-2018 appear less likely to reach the overstory, especially in areas with longer invasion histories. In regions where EAB has been present the longest (the 2002–2006 invasion cohort), sapling counts were significantly reduced in INV-2018 compared to INV-2007 (Fig. 5c). Moreover, in INV-2018, ash populations exhibited negative population trajectories – higher annual mortality than annual recruitment in the smallest DBH class – on plots in the 2002–2006 invasion cohort but exhibited positive trajectories in the two more recent invasion cohorts (Fig. 7f). Thus, seedling and sapling densities do not appear to offset increased tree mortality in the lowest diameter class (Fig. 7f). Regenerating ash stems as small as 2 cm in basal diameter have been attacked by EAB (Aubin et al., 2015), and thus, in terms of size definitions used by FIA, all ash saplings are susceptible to EAB colonization. As the invasion progresses and hosts are depleted, mortality rates could slow (Morin et al., 2017), but, for ash to persist, it is critical that sufficient numbers of trees reach reproductive age before succumbing to residual EAB populations (Klooster et al., 2014).

Ash typically exists in mixed stands and coexists with other tree species in eastern North America. Long term demographics of the ash component in these stands will be determined not only by ash recruitment, but also by the responses of non-*Fraxinus* species (Smith et al., 2015) and interspecific competition for light and nutrients that likely affects ash regeneration (Granger et al., 2017; Klooster et al., 2018). The competitive balance between ash and other species may change as EAB epidemics subside following initial invasion. Indeed, the demographic stochasticity of both ash and beetle populations will be important (Kappler et al., 2019) and, in young ash forests with residual beetle populations, imported natural enemies may suppress beetle populations and increase the likelihood of ash persistence (Duan et al., 2015, 2017; Kashian et al., 2018). Furthermore, *Fraxinus* spp. exhibit masting (Boerner and Brinkman, 1996), and so seed production in post-invasion ash forests, along with seedling survival as mature trees succumb to EAB and other causes, will need to be frequent and widespread enough to offset expected mortality. Changes in forest composition could be mediated by climate (Iverson et al., 2016; Fei et al., 2017; Knott et al., 2020) and by inter- and intra-specific variation in ash susceptibility (Robinett and McCullough, 2019). Initial impacts from EAB and stand responses could also exhibit novel patterns as beetle populations spread into warmer areas of the southeastern USA and/or colder regions in Canada, and could also be mediated by climate change (Liang and Fei, 2014).

5. Conclusions

Invasion by emerald ash borer causes high rates of overstory ash mortality, but regeneration can also be abundant. It appears that few young ash trees reach the overstory in invaded areas, however, and given that size of *Fraxinus* spp. is typically correlated with age, even fewer might reach reproductive ages. Predicting ash persistence is complicated by several important unknowns, such as uncertainty about future EAB population levels in areas with reduced ash densities, impacts of imported natural enemies on EAB epidemics, and spatiotemporal variation in climatic regimes. Nonetheless, our results provide regional context for several important, stand-level studies by indicating that, in addition to substantial impacts on overstory ashes, high densities of seedlings in long-invaded areas are, at present, not recruited into the overstory at sufficient rates to offset mortality.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118574.

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