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Change in Forest Tree Composition on the Lake Erie Islands due to the Invasion of the Emerald Ash Borer (*Agrilus planipennis*) and Invasive Plants

Emma Land^{1,*}, Lisa Kutschbach-Brohl², and Douglas D. Kane³

Abstract - Since its initial invasion in 2002, *Agrilus planipennis* (Emerald Ash Borer [EAB]) has devastated *Fraxinus* (ash) species in forest communities of the Midwestern United States. The forests of the Lake Erie Islands have a unique composition that is typically divided into 2 categories: upland forests, which have rockier soil and bedrock above lake level, and lowland forests, which have deeper soil and bedrock below lake level. We used plot-sampling methods in selected wooded preserves of both upland and lowland forests on South Bass and North Bass islands, OH. We compared our findings with data collected on those 2 islands as well as Middle Bass and Kelleys islands in previous studies from before infestation, during initial infestation in the 2000s, and approximately one decade later to monitor ash loss and to determine which species were regenerating in these new canopy gaps. We calculated importance values and subsequent Boerner values through determination of relative frequency, relative coverage, and relative density of individual tree species within study plots. *Fraxinus pennsylvanica* (Green Ash) was most negatively impacted by the EAB while *Fraxinus quadrangulata* (Blue Ash) was still important in upland forests due to regeneration seen in small saplings. *Lonicera maackii* (Amur Honeysuckle) began filling in canopy gaps in upland forests and lowland forests, while invasive species like *Morus alba* (White Mulberry), *Rhamnus cathartica* (Common Buckthorn), and *Elaeagnus umbellata* (Autumn Olive) filled in the canopy gaps of lowland woods. The decline in ash populations due to the EAB has allowed for further growth of numerous invasive plant species and transformed the composition of Lake Erie Island forests.

Introduction

The Lake Erie Island archipelago is unique with regard to the region's climate, topography, surface geology, and soil composition. The combination of these edaphic features on the islands in Lake Erie contributes to increased niche diversity amongst plants and wildlife (Boerner 1984). The islands typically experience considerably less precipitation and a longer frost-free period than the mainland, which further contributes to the region's distinct natural environment (Boerner 1984).

The maturation and composition of these wooded preserves on the islands is also influenced by previous land use. Many of the woods on these islands are abandoned vineyards and orchards which contribute to variance in successional patterns of the forests, so different tree species are present due to this sequence

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(Boerner 1985). The composition of these lowland forests has undergone considerable change due to the introduction of the *Agrilus planipennis* Fairmaire (Emerald Ash Borer [EAB]) to the Great Lakes region. Invasive pests like EAB can cause drastic changes to the forest composition by causing rapid decline in an important hardwood that transforms the forest understory through an increase in canopy gaps. The increase in canopy gaps leads to an increase in sunlight exposure on the forest floor that many existing native floras are not accustomed to. Many invasive plant species thrive in environments with increased sunlight and can rapidly grow and multiply in such conditions (Luken and Thieret 1996). These accelerated environmental changes can be cause for concern to the native forest composition of the Lake Erie Islands.

EAB is an invasive beetle from East Asia that was initially introduced to the Great Lakes region of the United States in 2002. EAB larvae inhabit ash trees by burrowing within the tree bark to keep sheltered from the elements and to feed on the bark (Herms and McCullough 2014). This incubation of the boring beetle deprives the ash tree of access to vital nutrients and water, which ultimately kills the tree (Herms and McCullough 2014). The signs of an infested ash tree can include increased woodpecker activity, dying sections of tree, sprout growth from the base of the tree, D-shaped exit holes, and a serpentine pattern underneath the tree's bark (Haack et al. 2002). EAB can begin invasion of ash trees when the trees have a measurable diameter at breast height (dbh) of 1.00 cm (Poland and McCullough 2006). Although EAB prefers stressed ash trees, all ash tree species in a variety of different health conditions are susceptible to infestation (McCullough et al. 2009).

The devastation of ash trees in the upland and lowland forests of the Great Lakes region has led to extensive changes to surrounding ecosystems. Ash trees were once a substantial contribution to the tree assemblages of the forests of Ohio at the time of settlement of Euro-Americans (Deines et al. 2016). Ash trees composed ~12% of the forest composition of Ohio as of 2005 (Syndor et al. 2005). Like many trees and herbaceous plants in an ecosystem, ash trees provide numerous ecological benefits to the surrounding area. Ash is vital to forest ecosystems due to the various tree species' ability to rapidly colonize a recently disturbed wooded area (Herms and McCullough 2014). Ash is also tolerant of various soil conditions, which makes these trees desirable in forest environments with alkaline soil, such as in the Lake Erie Island archipelago (Herms and McCullough 2014). The ash tree species (e.g., *Fraxinus quadrangulata* Michx. [Blue Ash], *Fraxinus pennsylvanica* Marshall [Green Ash], and *Fraxinus americana* L. [White Ash]) observed in the research studies conducted on the islands of Lake Erie are of some of the most prominent ash species within the forests of North America (MacFarlane and Meyer 2005). Ash trees provide food and habitat for wildlife in the woods and have high economic value in the lumber industry (Waldron 2003). Ash trees support the surrounding wildlife such as birds and squirrels with food and shelter and provide for important pollinator species like butterflies, moths, and various insects (Waldron 2003). The loss of such important tree species has had cascading effects on the surrounding forest ecosystems. The disappearance of ash trees can also impact the soil conditions

of the area, as ash trees absorb calcium from the soil, and loss of ash trees can have negative effects on microorganisms (Poland and McCullough 2006).

Our goal of this longitudinal study was to determine whether the invasion of the EAB has affected forest composition in upland and lowland forests of the Lake Erie Islands. Due to the infestation of EAB, along with the spread of various invasive plants and animals to the islands, we hypothesized that an increase in the importance of invasive plants on the forest understory would occur in both upland and lowland forests as the importance of ash trees declined. An increase in invasive plant species can have detrimental effects to the forest ecosystem including but not limited to changes in soil chemistry, food and habitat for wildlife, and the overall abundance and health of existing native flora and fauna (Iacarella et al. 2015).

Methods

We used 3 different wooded preserves on South Bass Island, OH, as well as 1 on North Bass Island, OH, for site location and data collection of forest composition.

Description of upland and lowland forests

The plant community of the Lake Erie Islands can be categorized into either upland or lowland forests. The Lake Erie lowland typically consists of flatlands or occasional rolling hills (Waldron 2003). The most significant determining factor in forest composition within the Lake Erie islands is the relationship between the level of bedrock and the lake; the lowland forests occur when the bedrock level is lower than lake level (Duncan et al. 2010). Upland forests are similar in composition to forests commonly found on morainal ridges further north of the Laurentian Great Lakes (Boerner 1984). Tree species that commonly inhabit upland mainland forests include *Liriodendron tulipifera* L. (Tulip Poplar), *Quercus prinus* L. (Chestnut Oak), *Quercus rubra* L. (Northern Red Oak), *Quercus alba* L. (White Oak), *Acer rubrum* L. (Red Maple), *Carya tomentosa* (Lam.) Nutt. (Mockernut Hickory), *Carya glabra* (Mill.) Sweet (Pignut Hickory), and White Ash (Waldron 2003). The islands of Lake Erie are mostly comprised of Carolinian upland forests composed of *Acer saccharum* Marshall (Sugar Maple), *Celtis occidentalis* L. (Common Hackberry) and *Tilia americana* L. (American Basswood) (Waldron 2003). The reason for this difference in forest composition of the upland forest and the neighboring mainland can be attributed to low levels of precipitation, shallow rocky soil, and the lack of small mammal species to disperse seeds (Boerner 1984). Much of the vegetation that comprises the lowland forests of Lake Erie frequently consists of Green Ash, *Populus deltoides* W. Bartram ex Marshall (Eastern Cottonwood), *Cornus drummondii* C.A. Mey. (Roughleaf Dogwood), and *Acer saccharinum* L. (Silver Maple) (Boerner 1984). This lowland environment and the vegetation present influence the soil moisture, evapotranspiration processes, as well as precipitation patterns. (Boerner 1984).

The Put-in-Bay Township Park District preserves where we conducted research in 2022 include Ladd Carr Woods, Cooper's/Heineman's Woods, and Duff Woods. In addition to these 3 studied preserve sites on South Bass Island, we also conducted

research at a preserve on North Bass Island to allow for more inclusive comparisons of data. Table 1 provides exact GPS coordinates of these listed 2022 field sites on South Bass and North Bass Islands. Previous research was conducted at these 3 sites on South Bass Island by Eckardt and Kane (2008), Kane et al. (2009), and Boerner (1984), so we chose these same preserved sections to perform a comparative data analysis of changing forest composition over time. The approximate site locations for our own sampling and that of other studies referred to in this paper on the Lake Erie Islands can be seen in Figure 1. We based our preserve site selection on the presence of well-developed woody canopies and understories.

In 2022, before beginning field research, we conducted an initial visual scan of each nature preserve to determine locality prioritization and assess optimal

Table 1. 2022 study site GPS coordinates.

Site	Latitude	Longitude
Ladd Carr Site 1	41°38.148'N	82°50.128'W
Ladd Carr Site 2	41°38.125'N	82°50.145'W
Cooper's	41°38.862'N	82°49.387'W
Heineman's	41°38.167'N	82°49.399'W
Duff's Site 1	41°39.213'N	82°49.926'W
Duff's Site 2	41°39.261'N	82°49.932'W
North Bass Site 1	41°43.082'N	82°49.860'W
North Bass Site 2	41°43.082'N	82°49.592'W

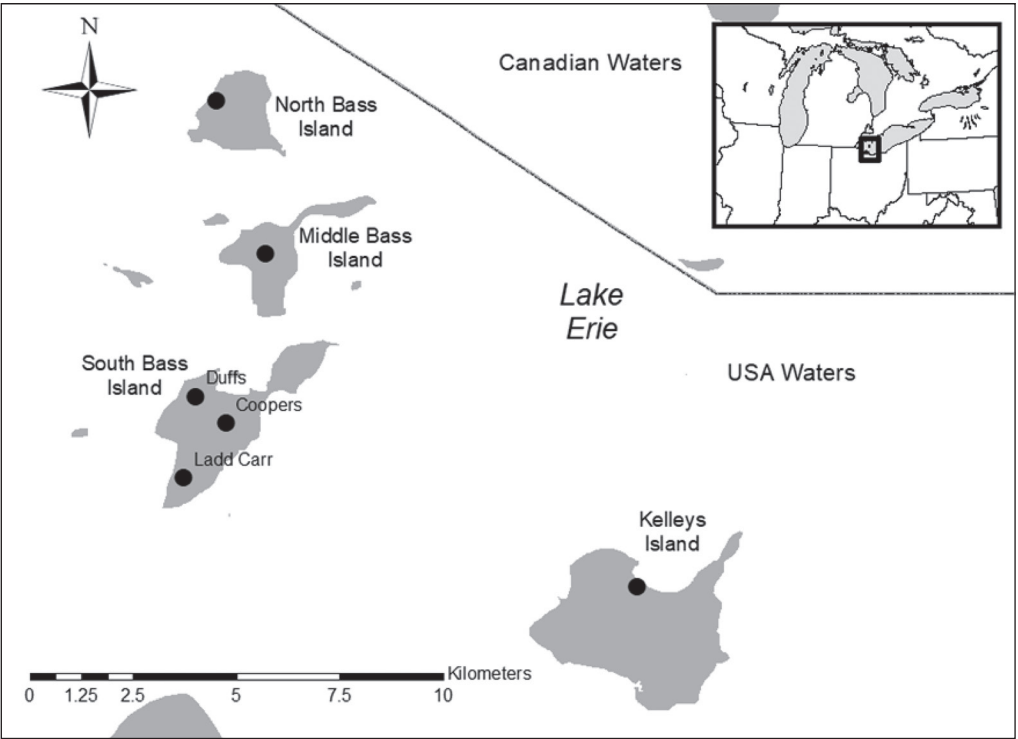


Figure 1. Map of the Lake Erie Islands study sites

locations for consistency with previous research studies. We then compared potential locations to previous studies to ensure the research would be conducted in similar areas under similar topographical conditions with low disturbance. In applicable locations, the same wooded preserves were used; however, as residential development on the Lake Erie Islands has continued to increase, some forests that were previously used by Dr. Boerner were no longer available for study. On South Bass Island, Boerner used Victory Woods East and West in 1982 as 2 transect study sites within upland forests. We used Ladd Carr Woods on South Bass Island for comparative studies as this wooded area was similar in upland forest composition to Victory Woods.

In each nature preserve, we established 2 transects using the same field methods as Boerner in 1981 and 1982 (Boerner 1984). We created transects in alternating quadrants, with 5 10 m x 10 m quadrats laid. Within each 10 m x 10 m quadrat, there was nested a 5 m x 5 m quadrat in the northeast corner, and a 2.0 m x 0.5 m quadrat nested within in the northeast corner of that quadrat (Boerner 1984). Nested quadrants allowed for organized data collection of diameters at breast height (dbh). Within the 10 m x 10 m quadrats, we properly identified and recorded the dbh of each tree over 2.5 cm. In each 5 m x 5 m quadrat, we identified and measured the dbh of each tree with a diameter between 1.0 cm and 2.5 cm. In the 2.0 m x 0.5 m quadrat, we counted and identified the woody saplings. For multiple trunked trees, we measured the dbh of each trunk and then calculated the square root of the summation of the dbh for each trunk to determine a single integer value for the tree's diameter at breast height (Powell 2005).

After data collection, we calculated the importance values (IV) using the plot-sampling and calculation methods detailed in *Field and Laboratory Methods for General Ecology* (Brower et al. 1998). We used the following calculation for density (D_i): $D_i = n_i / A$, where n_i is the number of trees of species i and a is the total area. We then calculated the relative species density (RD_i) through the equation, $RD_i = n_i / \sum n$, where $\sum n$ is the total number of all trees. We calculated the relative frequency (Rf_i) using the equation, $Rf_i = f_i / \sum f$, where f_i is the frequency of species i and $\sum f$ is the total frequency of all species. We calculated cover (C_i) as $C_i = a_i / A$, where a_i is the area covered by species i and a is the total area. The calculations for relative density, relative frequency, and cover for each species observed are necessary to determine the relative cover (RC_i) for species i , which we calculated using the equation $RC_i = C_i / TC = C_i / \sum C$, where tc and $\sum c$ are the total cover. We used the sum of the relative measures detailed above for each individual species to determine the IV for a given species through the equation $IV_i = RD_i + Rf_i + RC_i$. Dividing the IV_i by 3 then gives the importance percentage, which provides an overall estimate of a plant species' influence within the community. The IV is a numerical indication of how imperative an individual species of tree is to the surrounding forest.

We calculated the IV and then converted this number into a Boerner value (Boerner 1984) by dividing the IV by 3 to get an integer between 0 and 1. We then multiplied that integer value by 100 to get a percentage value for each tree species. Boerner values (BV) are assigned based on the percentage values as follows: 1 =

1.0–4.9%, 2 = 5.0–9.9%, 3 = 10.0–24.9%, 4 = 25.0–49.9%, and 5 = >50% (Boerner 1984). We calculated BV and compared them to those reported in previous studies within each study site. The higher the BV on a scale of 1–5, the more significant an individual tree species is to a forest at the time of study.

We performed the above calculations for each tree species found within each transect at each preserve site studied. We then collected the IV and used them for comparison of previous data before the introduction of EAB, during the initial infestation period of the 2000s, and then once again approximately one decade later. We compared the IV of data collected from Ladd Carr (Victory) Woods, Duff Woods, and Cooper’s/Heineman’s Woods to previous field data on South Bass Island. In addition, we compiled and compared forest composition data from other previous studies from North Bass Island, Middle Bass Island, and Kelleys Island (Boerner 1984, Eckardt and Kane 2008, Hamilton and Forsyth 1972, Manoukian et al. 2018, Primer and Kane 2010, Southard and Kutschbach-Brohl 2020). The compilation and comparison of this data and subsequent calculations from the various Lake Erie Islands throughout 3 different, distinct time periods allowed for us to thoroughly examine this forest composition transformation over time.

Results

Blue Ash

As previously stated, Blue Ash trees are more prevalent in upland forest environments on the islands. In 1967, the BV of Blue Ash in Cooper’s/Heineman’s Woods was 1 (Hamilton and Forsyth 1972) but then increased to 3 in 1982 (Boerner 1984) (Table 2, Fig. 2). This change represents a substantial increase in the level of importance within that area, which suggests fast growth and escalated expansion rates of Blue Ash. However, when these sites were revisited in 2022, Blue Ash did not have a BV because there were very few Blue Ash still present in the area. Although the importance of Blue Ash in these upland woods virtually disappeared, the BV

Table 2. Species importance values for Cooper’s/Heineman’s Woods on South Bass Island. Importance values calculated after Boerner (1984). Data from Boerner (1984), Hamilton and Forsyth (1972), and this study.

Species	Forsyth and Hamilton 1967	Boerner 1982	Land 2022
<i>Acer platanoides</i> L. (Norway Maple)	-	3	-
Sugar Maple	4	4	3
Common Hackberry	4	2	4
White Ash	-	-	1
Blue Ash	1	3	-
<i>Juglans nigra</i> L. (Black Walnut)	1	-	2
Eastern Red Cedar	1	-	2
Amur Honeysuckle	2	1	3
<i>Prunus serotina</i> Ehrh. (Black Cherry)	1	-	-
<i>Prunus virginiana</i> L. (Choke Cherry)	-	1	1
Common Buckthorn	-	1	-
American Basswood	3	3	1

of White Ash increased to a 1, in comparison to previous studies where White Ash had never had a significant presence in this area. Unlike results from Cooper’s/Heineman’s Woods, Duff’s Woods saw an increase in the BV of Blue Ash to 2 in 2022 (Table 3, Fig. 2). This higher value suggests an increased growth of Blue Ash in the area, but unfortunately, these saplings are likely candidates to house EAB larvae when they reach optimal height and diameter of 1.00 cm. Similar trends of increased importance of Blue Ash from Ladd Carr Woods and Victory Woods were

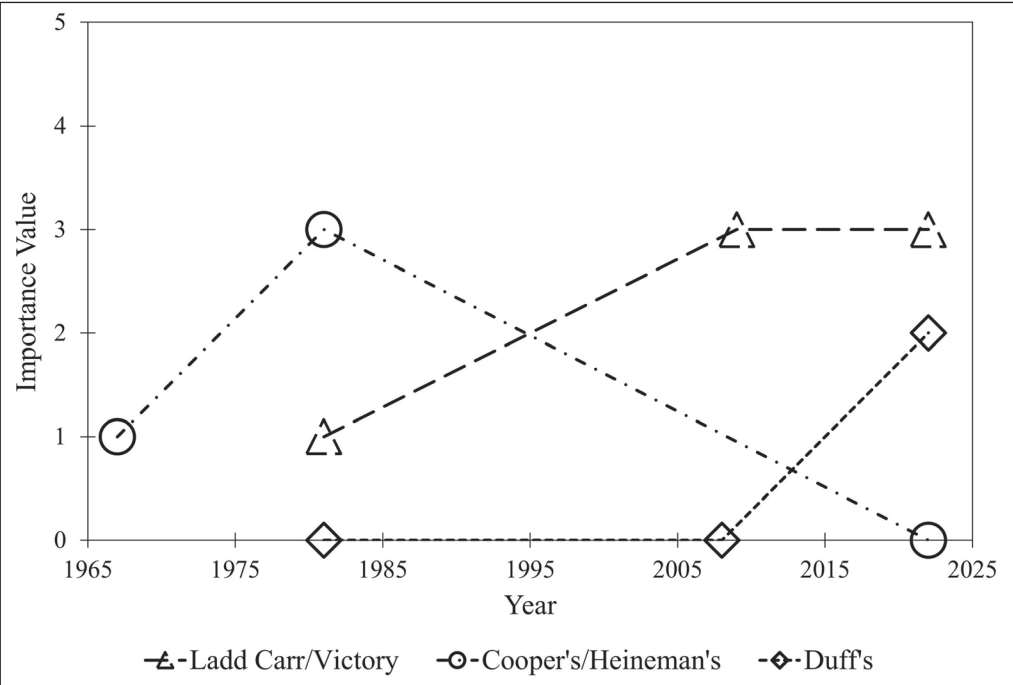


Figure 2. Importance values of *Fraxinus quadrangulata* (Blue Ash) on South Bass Island (Ladd Carr Woods, Cooper’s/Heineman’s Woods, and Duff’s Woods) between 1967 and 2022. Importance values were calculated after Boerner (1984).

Table 3. Species importance values for Duff’s Woods on South Bass Island. Importance values calculated after Boerner (1984). Data from Boerner (1984), Eckardt and Kane (2008), and this study.

Species	Boerner 1982	Eckardt 2008	Land 2022
Norway Maple	-	-	1
Sugar Maple	4	5	4
<i>Carya glabra</i> Miller (Pignut Hickory)	-	1	-
Common Hackberry	2	1	4
Blue Ash	-	-	2
Amur Honeysuckle	-	-	3
<i>Ostrya virginiana</i> (Mill.) K. Koch (American Hophornbeam)	2	-	-
White Oak	-	2	1
<i>Quercus muehlenbergii</i> Engelm. (Chinquapin Oak)	-	-	1
American Basswood	-	-	1
<i>Ulmus rubra</i> Muhl. (Slippery Elm)	-	-	1

observed (Table 4, Fig. 2). In 1982, Boerner surveyed Victory Woods on South Bass Island (Boerner 1984), but due to development, we deemed the remainder of that forest too small for our field studies. Ladd Carr Woods had a similar forest composition, so we used it as a comparable location to Victory Woods in both 2008 and 2022. In 1982, Blue Ash had a BV of 1 in Victory Woods, and increased to a value of 3 in both 2008 and 2022 in Ladd Carr Woods. Once again, this significant Blue Ash regrowth largely consists of saplings that may well succumb to EAB once they grow to optimal size for EAB larvae habitat. The increase in BV of Blue Ash (Tables 3, 4; Fig. 2) can be attributed to large amounts of saplings noted in these study plots, as very few healthy, mature Blue Ash trees were present.

Green Ash

Blue Ash prefers drier, upland forest environments, whereas Green Ash trees prefer lowland forest and wetland environments (McFarlane and Meyer 2015). South Bass Island has upland forest environments, whereas North Bass and Middle Bass Islands have more wet, lowland Maple-Ash Swamp Forests (Arbour and Gardner 2008). Due to this difference in the environment, Green Ash has not been present in the areas studied on South Bass. On North Bass Island, Green Ash had a BV of 5 in 1982, a value of 4 in 2009, and a value of 1 in 2022 (Table 5, Fig. 3). This substantial decrease from 1982 and 2009 to 2022 depicts the importance that ash trees had on the forest and shows the rapid devastation of the EAB on the lowland island forests. The site at Kelleys Island has a similar wetland forest composition to the sites at both North Bass and Middle Bass Islands (Boerner 1984). Data from Boerner (1984) and Eckardt and Kane (2008) from Kelleys Island both show a BV of 4 for Green Ash, whereas in 2019 the value had decreased to 3 (Table 6, Fig. 3; Southard and Kutschbach-Brohl 2020). Similar results were seen at the Middle Bass Island preserve sites with the decline of Green Ash over time (Table 7, Fig. 3).

Table 4. Species importance values for Victory Woods and Ladd Carr Woods on South Bass Island. Importance values calculated after Boerner (1984). The Victory Woods site used by Dr. Ralph Boerner in 1982 was no longer feasible for site analysis due to deforestation and the growth of residential development, which lead to significant forest disturbance near the original study site. Ladd Carr Woods was comparable for field research due to similar forest composition to Victory Woods. Data from Boerner (1984), Kane et al. (2009). and this study.

Species	Victory East Boerner 1982	Victory West Boerner 1982	Ladd Carr Miller 2008	Ladd Carr Rose 2008	Ladd Carr Land 2022
Sugar Maple	5	4	5	3	4
Common Hackberry	3	4	-	4	4
Blue Ash	1	1	3	3	3
Amur Honeysuckle	1	-	-	3	3
Red Mulberry	-	1	-	-	-
American Hophornbeam	1	-	-	-	-
Black Cherry	1	-	-	-	-
Northern Red Oak	2	2	-	-	-
American Basswood	1	1	-	2	-
Slippery Elm	1	-	-	-	-

Table 5. Species importance values for North Bass Island. Importance values calculated after Boerner (1984). Data from Boerner (1984), Primer and Kane (2009), and this study.

Species	Boerner 1982	Primer 2009	Land 2022
Sugar Maple	-	-	3
Common Hackberry	3	3	4
Roughleaf Dogwood	-	-	2
Green Ash	5	4	1
Amur Honeysuckle	-	3	3
Red Mulberry	1	1	-
American Hophornbeam	-	2	-
Choke Cherry	1	2	1
Common Elderberry	-	1	2

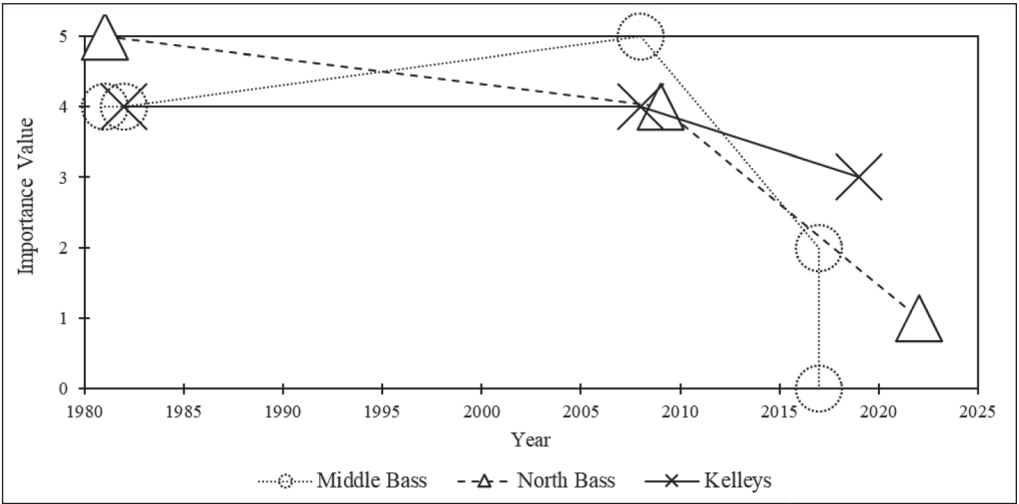


Figure 3. Importance values of *Fraxinus pennsylvanica* (Green Ash) between 1981 and 2022. Importance values were calculated after Boerner (1984).

Table 6. Species importance values for Kelleys Island. Importance values calculated after Boerner (1984). Data from Boerner (1984), Eckardt and Kane (2008), and Southard and Kutschbach-Brohl (2020).

Species	Boerner 1982	Eckardt 2008	Southard 2019
<i>Acer negundo</i> L. (Boxelder Maple)	1	-	-
Silver Maple	1	3	-
Sugar Maple	-	1	-
Common Hackberry	2	-	-
Roughleaf Dogwood	3	4	5
Autumn Olive	-	-	3
Green Ash	4	4	3
White Mulberry	2	-	-
Red Mulberry	1	-	-
Eastern Cottonwood	-	-	2
Choke Cherry	1	-	-
<i>Ulmus americana</i> L. (American Elm)	-	-	3
<i>Ulmus rubra</i> Muhl. (Slippery Elm)	-	1	-

In 1984, Green Ash had a BV of 4 at 2 different sites surveyed on Middle Bass (Table 7, Fig. 3; Boerner 1984). One Middle Bass site was surveyed again in 2008 and showed BV of 5 for Green Ash (Table 7, Fig. 3; Eckardt and Kane 2008). The 2 sites Boerner surveyed in the early 1980s were once again analyzed in 2017, in which one preserve displayed a BV of 2, whereas the other collection site did not have enough Green Ash to have a BV for the tree species anymore (Table 7, Fig. 3; Manoukian et al. 2018).

Invasive species

The decrease of importance in ash trees due to the EAB has drastically changed the composition of the Lake Erie Island forests. This decline of ash trees allowed the importance of established invasive species to increase. The invasive species observed throughout these sites included *Lonicera maackii* (Rupr.) Herder (Amur Honeysuckle), *Elaeagnus umbellata* Thunb. (Autumn Olive), *Rhamnus cathartica* L. (Common Buckthorn), and *Morus alba* L. (White Mulberry). Amur Honeysuckle is more frequently found growing in upland forests, whereas invasives like Autumn Olive and Common Buckthorn may be more commonly seen in lowland forests and wetter environments (Hutchinson and Vankat 1997). In Victory Woods in 1982, Amur Honeysuckle had a BV of 1 in one transect and was not present within the second (Table 4; Boerner 1984). In Ladd Carr Woods in 2008, this invasive was undetected in 1 transect and had a BV of 3 in the other sampling plot (Table 2). In 2022, the BV had increased to 3 in both transects, which thus signaled a large increase in the overall importance of Amur Honeysuckle to this forest. In Cooper’s/Heineman’s Woods, data from 1967 showed a BV of 2 (Hamilton and Forsyth 1972), whereas that value then decreased to 1 in 1982 (Table 4). Although these results show an initial decline in the importance of Amur Honeysuckle, the BV had increased to 3 in 2022. In Duff’s Woods, Amur Honeysuckle was not present in data collection in 1982 (Boerner 1984) but had a BV of 3 in 2022 (Table 3). Research on North Bass Island showed no presence of Amur Honeysuckle in 1982 (Boerner 1984) but had a BV of 3 in both 2009 (Primer and Kane 2010) and 2022 (Table 4). Although Amur Honeysuckle is much more prevalent in upland forests, this invasive can inhabit some lowland forest environments of the islands as well.

Table 7. Species importance values for Middle Bass Island. Importance values calculated after Boerner (1984). Data from Boerner (1984), Eckardt and Kane (2008), and Manoukian et al. 2018).

Species	Field site 1 Boerner 1981–1982	Field site 2 Boerner 1981–1982	Middle Bass Eckardt 2008	Field site 1 Manoukian 2017	Field site 2 Manoukian 2017
Silver Maple	4	2	-	-	4
Roughleaf Dogwood	1	4	3	5	3
Green Ash	4	4	5	2	-
Amur Honeysuckle	-	-	-	3	3
White Mulberry	-	-	2	3	3
Common Buckthorn	-	-	-	-	2
Elderberry sp.	-	-	-	-	1

On Kelleys Island, Amur Honeysuckle was not present throughout plot sampling, but the invasive Autumn Olive was prevalent within these lowland forests. Results of the research conducted at Kelleys Island in both 1982 (Boerner 1984) and 2008 (Eckardt and Kane 2008) showed that there was no presence and/or significance of Autumn Olive within the study sites. On Middle Bass Island, no invasives were present in research done in the early 1980s (Boerner 1984) or 2008 (Primer and Kane 2010). In 2017, both transect sites at Middle Bass showed data results of Amur Honeysuckle with an increased Boerner Value of 3 (Table 7; Manoukian et al. 2018). The sampling plots at Middle Bass Island also showed an increase in the invasive Common Buckthorn tree species. Common Buckthorn had a calculated BV of 2 in both transect sites in 2017 (Table 7; Manoukian et al. 2018). The invasive White Mulberry has become more important to the forest composition of Middle Bass Island (Table 7). There was no BV recorded for White Mulberry in 1981–1982 (Boerner 1984) but grew in significance to a value of 2 in 2008 (Eckardt and Kane 2008) and a value of 3 in 2017 (Manoukian et al. 2018) (Table 7).

The decline in ash trees may also have affected the presence and importance of other native trees. The more notable native tree species found most consistently within the research plots of the various islands were Common Hackberry and Sugar Maple.

Sugar Maple

In the upland forests of Ladd Carr Woods and Victory Woods on South Bass Island, Sugar Maple maintained importance from 1982 (Boerner 1984) to 2022, with the lowest recorded BV of 3 occurring in 2008 (Table 4; Kane et al. 2009). In Duff's Woods, Sugar Maple had a BV of 4 in 1982 (Boerner 1984), 5 in 2008 (Eckardt and Kane 2008), and to 4 in 2022 (Table 3). Sugar Maple has remained highly important within upland forests of the Lake Erie Islands. In studies conducted on North Bass Island in 1982 (Boerner 1984) and 2009 (Primer and Kane 2010), there was no substantial presence of Sugar Maple (Table 5). By 2022, the BV of Sugar Maple in this area increased to 3. Throughout the various research studies done at Middle Bass Island, Sugar Maple did not hold substantial value within the lowland forests present. On Kelleys Island in 1982, there was no presence of Sugar Maple in the island's lowland forests (Boerner 1984) but rose to a BV of 1 by 2008 (Table 6; Eckardt and Kane 2008). This value diminished as of 2019, with no calculated BV of Sugar Maple on Kelleys Island (Table 6; Southard and Kutschbach-Brohl 2020). Although fluctuations of Sugar Maple importance occurred in both upland and lowland forests, Sugar Maple remained a relatively important tree species to the upland forests of the Lake Erie Islands.

Common Hackberry

Differing from the patterns for Sugar Maple, Common Hackberry had an overall trend of increased importance within upland forests. Common Hackberry on South Bass Island had a BV of 3 and 4 in the respective Boerner transects within Victory Woods in 1982, with mixed results reported for Ladd Carr Woods in 2008 (a BV of 4 in one site and no substantial measurements in another), and then a BV of 4 in 2022

(Table 4). In Duff's Woods, the importance of Common Hackberry diminished from 2 in 1984 to 1 in 2008, and then increased to 4 by 2022. North Bass lowland forests showed a BV of 3 in both 1982 (Boerner 1984) and 2009 (Primer and Kane 2010) (Table 5). The BV of Common Hackberry on North Bass Island had increased to 4 as of 2022. In 1982, Kelleys Island displayed a BV of 2 (Boerner 1984) for Common Hackberry, but when revisited in both 2008 (Eckardt and Kane 2008) and 2019 (Southard and Kutschbach-Brohl 2020), there was no longer a substantial presence of Common Hackberry in these lowland forests (Table 6).

Discussion

This research details how the Lake Erie Islands Forest composition has changed due to the spread of multiple invasive flora and fauna and how events like the EAB infestation can contribute to the degradation and destruction of native landscapes. The data collected by Boerner (1984, 1985) before the invasion of the EAB in North America allowed for a comprehensive comparison of the ongoing destructive impact that this boring beetle has had on the forests of the Lake Erie Islands archipelago. Further, this research has allowed for a more detailed timeline of the response of ash tree species within a Great Lakes Island Forest community to the EAB. The importance of invasive understory plants has increased within the upland and lowland forests of the Lake Erie Islands. From this study, it cannot be concluded the direct causal relationship between the infestation of the EAB and invasive flora, but our timeline of study suggests that as ash importance declined, these new canopy gaps allowed more habitable environment for invasive flora to grow and spread rapidly in the forest understory. Our key findings show the decline of ash and a corresponding change in composition of the understory, including an increase in invasive species.

The patterns of ecological succession within a forest community allow for predictable reactions to natural ecosystem change. Certain tree species and herbaceous vegetation are quite sensitive to environmental change, and are typical of early succession through their presence, growth, and/or health (King and Schlossberg 2014). The presence of early successional species was prevalent within this research. The Roughleaf Dogwood is an early successional tree that was present in the lowland forests of North Bass, Middle Bass, and Kelleys Island. Roughleaf Dogwood forms shrub thickets that exemplify early successional habitats and can eventually grow into a young forest if left undisturbed. These early successional habitats can be crucial to dependent wildlife in the area (King and Schlossberg 2014). *Juniperus virginiana* L. (Eastern Red Cedar) is also an early successional tree species. Eastern Red Cedar is typically found in dry, upland conditions with relatively low species diversity (Lawson 1990). Eastern Red Cedar was prevalent in the Heineman's Woods on South Bass Island in 1982 (Boerner 1984). In 1982, Boerner conducted research in both Cooper's and Heineman's Woods on the island but divided the 2 sections into terms of "old forest" and "young forest" based on the distinct vegetation and tree growth. The "young forest" in Boerner's work refers to the locality of Heineman's Woods because there was a high density of Eastern Red Cedar trees

within that area but not in Cooper's Woods. In the 2022 field collection, a transect of five 10 m x 10 m plots was laid within Heineman's "young forest" and an identical transect was laid in Cooper's "old forest". The presence of Eastern Red Cedar is indicative of the early stage of succession of these upland woods. The condition of the Eastern Red Cedar in 2022 was very poor, with many of the trees being downed, dead, or in worsening tree health. The poor condition of the successional Eastern Red Cedar could be due to a maturing forest, and the species becoming shaded out by other tree species (Waldron 2003). However, it is to be noted that the Eastern Red Cedar is vulnerable to annosus root rot caused by the fungus *Heterobasidion annosum* (Fr.) Bref., with this disease potentially being the main contribution to the diminished health of the species (Burns and Honkala 1990).

Although the importance of Sugar Maples remained relatively high throughout the upland forests present in the Lake Erie Islands archipelago, deteriorating health was noticed during our field research in 2022. Sugar Maples are susceptible to numerous insects, borers, fungus, rot, and various diseases (Godman et al. 1990). Around the Great Lakes region, a decline in health and abundance in Sugar Maple and other hardwood species have been observed within the last half-century (Bal et al. 2017). In research conducted by Bal et al. (2017), a probable cause for this significant decline was attributed to the soil conditions and the microorganisms of the area. The Lake Erie Islands underwent significant glacial activity dating back to the Quaternary Period (Lewis et al. 2023). During this glacial period, native earthworm populations drastically declined (Bohlen et al. 2004). Due to this lack of native earthworms, and the subsequent increase in global trade and transportation, non-native earthworms invaded this region (Seamans et al. 2015). Invasive earthworms, largely from Europe have changed the soil chemistry of the Great Lakes region and have significantly altered the growing environment for Sugar Maples (Bal et al. 2017). This environmental change along with the many fungal diseases that affect Sugar Maple are likely contributions to the declining appearance of the tree species that was observed during our 2022 field research.

Amur Honeysuckle was prevalent throughout the upland forests on South Bass Island in 2022. It is important to note that in the previous year, Cooper's Woods was treated with herbicide to prevent additional growth and spread of this invasive species (L. Kutschbach-Brohl, pers. observ.). Amur Honeysuckle is a highly invasive shrub that was first discovered within the Lake Erie Islands in 1973 (Stuckey and Duncan 2010). Amur Honeysuckle has displaced various native shrubs in Ohio due to the invasive shrub's high tolerance to herbivory and shade, rapid growth rate, and prolific seeding (McNeish and McEwan 2016). Previous research about Amur Honeysuckle states that the invasive shrub does considerably well and has higher density and spread in forested areas with low canopy cover and forest connectivity (Henkin et al. 2013). Although Amur Honeysuckle is a very resilient species, various dead Amur Honeysuckle shrubs were noted in field research conducted at North Bass Island in 2022. This expiration and diminished health in Amur Honeysuckle in the lowland forests could be possibly attributed to a recent rise in the water levels of Lake Erie, as Amur Honeysuckle thrives more in upland, dry woods (L. Kutschbach-Brohl, pers. observ.).

White Mulberry and *Morus rubra* L. (Red Mulberry) were both present in these studies. White Mulberry is an invasive species in the Great Lakes region that has a relatively high tolerance to climatic and precipitation changes (Waldron 2003). In initial research studies conducted by Boerner in 1981–1982, this invasive did not have a recorded significance in the forests on Middle Bass Island (Boerner 1984). When Middle Bass was revisited for research in 2008 (Eckardt and Kane 2008), White Mulberry had a BV of 2, which had increased to a value of 3 as of 2017 (Manoukian et al. 2018). The data collected in the lowland forests of Middle Bass Island suggest an increase in the growth of invasive species in the canopy gaps created due to the infestation of the EAB. Red Mulberry, however, is not an invasive shrub. Red Mulberry had a BV of 1 at 1 site in Victory Woods on South Bass Island in 1982 but had little to no presence in the upland forests in subsequent studies (Table 4). Red Mulberry had a BV of 1 on both Kelleys Island and North Bass Island in 1982 (Boerner 1984). In 2009, Red Mulberry was still present on North Bass Island with a BV of 1 (Primer and Kane 2010), but in studies afterward, Red Mulberry no longer had any notable presence in either the upland or lowland forests within the Lake Erie Island archipelago (Tables 4, 5, 6). This decline in a native understory tree like Red Mulberry concurrent with the increase in an invasive species like White Mulberry is an example of the relationship invasives have with native plant species. Based on our observations, White Mulberry appears to be more resilient than Red Mulberry to environmental change and can rapidly grow in newly formed canopy gaps.

The increase in importance of invasive plant species cannot be attributed solely to pest infestations like the EAB. These invasive plants, like Amur Honeysuckle, have invaded much of the eastern United States and lower regions of Canada due to global plant trades that largely began in the 19th century (Luken and Thieret 1996). The time between first introduction in the late 19th century and the recognition of the plant's uncontrolled spread occurred around half a century later—a common timeline for many non-native plants (Luken and Thieret 1996). Autumn Olive is a prolific spreader and has successfully invaded many freshly disturbed ecosystems throughout the eastern United States (Oliphant et al. 2016). Autumn Olive fruit is desirable for many bird species, who contribute to further growth and spread of the invasive (Oliphant et al. 2016). This invasive plant can rapidly take advantage of newly formed canopy gaps in forests because Autumn Olive leafs out much earlier in the spring than typical native understory plants and does not go through abscission until late autumn (Riffe 2018). These characteristics likely give it a competitive advantage against native understory flora of the Lake Erie forests. The introduction of EAB into the region in 2002 did not cause these plants to become invasive to the islands, as they were identified as problematic decades prior (L. Kutschbach-Brohl, pers. observ.). However, the large increase in canopy gaps of the forests due to the decimation of ash species likely further allows for this invasive understory to continue to dominate and out-compete native flora. These invasive plants have dramatically affected forest ecosystems as they continue to outcompete native tree species for vital resources like water, light, and nutrients (Deering and Vankat 1999).

Every species of ash tree is susceptible to the invasion of the EAB; however, some species of ash trees are more vulnerable to the predation of the boring beetle than others. Research reports have detailed the projected total loss of Green Ash and *Fraxinus nigra* Marshall (Black Ash) trees but have calculated that ~60–70 percent of Blue Ash will be lost (Herms and McCullough 2014). The results of the research conducted on the Lake Erie Islands archipelago align with these predictions because although there has been a near complete loss of all Green Ash and White Ash on the islands, there appears to be substantial Blue Ash regrowth and distribution within the upland forests of South Bass Island (E. Land, pers. observ.). It was initially believed that Blue Ash was resistant to the EAB because it is genetically distinct from other ash tree species native to North America (MacFarlane and Meyer 2005), but the EAB subsequently began to infest and devastate the Blue Ash population as well (Spei and Kashian 2017). Blue Ash had a higher BV than any other ash species found in the research transects after the invasion of the EAB on the studies conducted on the Lake Erie Islands.

The loss of trees due to an invasive species is unfortunately not a new phenomenon, as North American forests have faced this challenge of alien pathogens and pests numerous times in the past. As reliant as the world has become on global trade, it is expected for future pest infestations to occur, as a new invasive insect like EAB establishes in the United States approximately every 2 years (Morin et al. 2016). Due to this continued pattern of infestation, it is critical to examine past events and how forests react and adapt to such drastic, rapid change.

This change in the forest community due to infestation of the EAB has been well documented in North American forests. Marshall (2020) surveyed forest locations in Indiana, Michigan, and Ohio. His results showed a substantial change to these forest ecosystems that illustrated a much larger impact than solely the devastation of ash. Engelken et al. (2020) conducted longitudinal studies that found variation in the recovering forest composition between field sites, but several tree species remained of high relative importance throughout the various watershed sites. In their studies (Engelken et al. 2020), hardwoods such as American Basswood and American Elm had high relative IV. Our studies also noted that while the presence and abundance of various invasive plants could not be linked to the EAB infestation, in every plot where there was an EAB-caused canopy gap in the forest, invasive understory was increasing. Additionally, subsequent studies conducted by Morin et al. (2016) found that the degree of mortality of target tree species by the EAB is substantially higher than when compared to other recent pest infestations including *Adelges tsugae* Annand (Hemlock Woolly Adelgid) and *Lymantria dispar* (L.) (Spongy Moth or Gypsy Moth) (Morin et al. 2016). This rapid decline of an important hardwood initiates not only a change in the surrounding abundance of native and invasive plant and tree species, but also a shift in ecological pathways like the carbon cycle and net primary production. Research examining this relationship found that the consequences of the EAB infestation depict a substantial change in both these crucial natural cycles that are already being affected by climate change; therefore, this infestation can have a much larger impact on the forest communities than just the physical loss of ash trees (Flower et al. 2012).

Conclusion

This longitudinal study of the forest composition of upland and lowland forests within the Lake Erie Island archipelago over the last half century depicts the change a forest ecosystem undergoes during a pest infestation. The decline and almost total loss of adult ash trees due to the infestation of the EAB has likely allowed for the continued population growth and spread of various established invasive plant species (Amur Honeysuckle, Common Buckthorn, Autumn Olive, and White Mulberry) within the forests. Sugar Maple also has continued to have a significant presence within the upland forests on South Bass Island, with an increased importance in the lowland forests of North Bass Island as well. Trend analyses of the importance of various members of the forest tree community indicate a highly changed forest composition that coincides with the invasion of EAB and the above-mentioned population growth and spread of invasive plant species to the Lake Erie Islands. The introduction of the EAB to North America in 2002 has significantly altered forest composition in infested areas where ash trees were once a dominant hardwood species.

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