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Review

Ecological Impacts of Emerald Ash Borer in Forests at the Epicenter of the Invasion in North America

Wendy S. Klooster [1,*], Kamal J. K. Gandhi [2], Lawrence C. Long [3], Kayla I. Perry [4], Kevin B. Rice [5] and Daniel A. Herms [6]

1 Department of Entomology, The Ohio State University, Columbus, OH 43210, USA
2 Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA; kgandhi@warnell.uga.edu
3 Department of Entomology and Plant Pathology, North Carolina State University, Raleigh, NC 27695, USA; lclong2@ncsu.edu
4 Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development Center, Wooster, OH 44691, USA; perry.1864@osu.edu
5 Division of Plant Sciences, University of Missouri, Columbia, MO 65211, USA; ricekev@missouri.edu
6 The Davey Tree Expert Company, Kent, OH 44240, USA; dan.herms@davey.com
* Correspondence: klooster.2@osu.edu; Tel.: +1-614-292-2764

Received: 31 March 2018; Accepted: 3 May 2018; Published: 5 May 2018

Abstract: We review research on ecological impacts of emerald ash borer (EAB)-induced ash mortality in the Upper Huron River watershed in southeast Michigan near the epicenter of the invasion of North America, where forests have been impacted longer than any others in North America. By 2009, mortality of green, white, and black ash exceeded 99%, and ash seed production and regeneration had ceased. This left an orphaned cohort of saplings too small to be infested, the fate of which may depend on the ability of natural enemies to regulate EAB populations at low densities. There was no relationship between patterns of ash mortality and ash density, ash importance, or community composition. Most trees died over a five-year period, resulting in relatively simultaneous, widespread gap formation. Disturbance resulting from gap formation and accumulation of coarse woody debris caused by ash mortality had cascading impacts on forest communities, including successional trajectories, growth of non-native invasive plants, soil dwelling and herbivorous arthropod communities, and bird foraging behavior, abundance, and community composition. These and other impacts on forest ecosystems are likely to be experienced elsewhere as EAB continues to spread.

Keywords: Invasive species; *Fraxinus* spp.; *Agrilus planipennis* Fairmaire; disturbance; gap ecology; coarse woody debris; non-target impacts; forest succession; soil arthropods; tri-trophic interactions

1. Introduction

Alien phytophagous insects, including emerald ash borer (EAB, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)), have altered forest composition, structure, and function throughout much of North America [1–3]. EAB was first detected in North America in 2002 in southeast Michigan and neighboring Ontario [4–6]. Subsequent analyses of dendrochronological data indicated that the beetle was established and killing trees by the 1990s [7]. Since its introduction to North America, EAB has caused extensive mortality of ash (*Fraxinus* spp.) [8–15], and to a lesser degree white fringetree (*Chionanthus virginicus* L.) [16,17]. Since its initial detection, numerous studies have examined the biology, ecology, and management of EAB [5,18–20].

The objective of this paper is to review research on the direct and indirect ecological impacts of the EAB invasion on the flora and fauna of forests in the Upper Huron River watershed, which extends across western Oakland County, southeastern Livingston County, and north central Washtenaw County in southeast Michigan. These forests are near the presumed epicenter of the EAB invasion in Canton Township, Michigan [7], and thus have been impacted by EAB longer than others in North America. Prior to the EAB invasion, black (*F. nigra* Marshall), green (*F. pennsylvanica* Marshall), and white (*F. americana* L.) ash were the most common ash species on hydric swamps, mesic lowlands and flood plains, and xeric upland sites, respectively [14,21]. As EAB continues to expand its distribution in North America, the results of these studies provide insights into the ways EAB may impact other ecosystems, which are predicted to be substantial at multiple scales [22,23]. Furthermore, EAB is also causing extensive mortality of European ash (*F. excelsior* L.) in eastern Europe [24,25] where it may have ecological impacts comparable to those in North America.

2. Timing and Patterns of Ash Mortality

EAB has caused extensive ash mortality in the Upper Huron River watershed [8,11–14]. Dendrochronological analyses revealed that EAB-induced ash mortality occurred in this watershed as early as 1994 (L. Becker, D.A. Herms, and G.C. Wiles, unpublished data), and overall mortality of ash with stem diameters >2.5 cm had reached 40% by 2005 [14,21]. Initially, decline of black ash slightly exceeded that of green and white ash [14]. By 2008, however, mortality of all three species was greater than 95%, and peaked at 99.7% in 2009 [13]. Hence, following a long lag period since the onset of mortality, nearly 60% of trees died over a five-year period from 2005–2009, resulting in nearly simultaneous, widespread gap formation (Figure 1). The extremely high mortality of these North American ash species has been attributed to their low resistance to EAB relative to coevolved Asian ash hosts [26]. As EAB continues to spread in "defense free space" [3], white, green, and black ash may experience functional extirpation (sensu [27]) in which their populations decline to the point that they no longer provide significant ecosystem function and services [22].

Figure 1. Widespread formation of canopy gaps occurred throughout forests of the Upper Huron River watershed in southeast Michigan as mortality of ash increased from 40% to >99% between 2005 and 2009.

The relationships between host density or tree species diversity and population and impact of alien phytophagous insects have been documented [28–30]. However, Smith et al. [14] found no relationship between EAB-induced ash mortality and ash density, nor any other measure of community composition including ash basal area, ash importance, total stand density, total stand basal area, or any indices of tree diversity. Similarly, Knight et al. [10] observed no relationship between ash density and percentage ash mortality in Ohio, although ash mortality proceeded faster in stands with lower density of ash. These studies, conducted across an ash density gradient from low to very high and across a broad spatial area, suggest the potential to prevent ash mortality via silvicultural management is extremely limited [10,14].

From 2004–2006, there was a negative relationship between percentage ash mortality in the Upper Huron River watershed and distance from the presumed epicenter of the invasion in Canton Township, Michigan [7], with mortality decreasing 2% per km from the epicenter [14]. By 2007, however, this relationship plateaued as ash mortality exceeded 90% across the entire watershed [14]. Decreasing ash decline and mortality with increasing distance from the invasion epicenter was also documented by other studies conducted at various spatial scales [8,31].

3. Ash Recruitment and Regeneration

3.1. Ash Seed Bank, Seedling Regeneration and Basal Sprouting

Where mature ash trees are present, their regeneration is generally substantial [32]. This was the case in the Upper Huron River watershed, where ash recruitment and regeneration have been assessed in several studies in response to the near complete mortality of reproductively mature trees [8,13,33]. Klooster et al. [13] conducted extensive soil sampling from 2005–2008 to characterize changes in the ash seed bank. The soil seed bank depleted quickly as ash mortality approached 95%, and the number of viable ash seeds declined until none were detected in 2007 or 2008. Rapid depletion of the seed bank was confirmed by the lack of newly germinated ash seedlings (with cotyledons), which were not detected after 2008 despite extensive sampling of the seedling layer [13]. These data from both soil samples and forest floor surveys suggest that new ash regeneration ceased completely as mortality of ash trees exceeded 95%. Kashian and Witter [8] also observed steep declines in the density of ash seedlings in the Upper Huron River watershed.

Epicormic basal sprouting can contribute to ash regeneration [34] and is a common response of ash trees that have had their canopies killed by EAB [33,35], especially for open-grown trees (Figure 2). However, no such regeneration was observed by Klooster et al. [13] in the closed-canopy mixed deciduous forests of the Upper Huron River watershed, where basal sprouts exhibited low vigor and died with the canopy or soon thereafter, perhaps due to strong interspecific competition for light and other resources in the understory of these diverse forests [14]. Conversely, Kashian [33] observed significant regeneration from basal sprouts (with some producing seed) in small, nearly pure stands of green ash where interspecific competition would not have been a factor. In addition, the 58% ash mortality documented by Kashian [33] would have generated larger canopy gaps than observed by Klooster et al. [13], where ash was a significantly lower component of more diverse forest stands [14]. In southeastern Ontario, Aubin et al. [35] also observed substantial ash regeneration from basal sprouting. However, inter- and intraspecific competition experienced by regenerating ash would have been limited there as well, because the amount of pre-EAB ash basal area in the sampled stands was greater than twice that of all other species combined, and more than 99% ash basal area died following EAB establishment [35].

Figure 2. Vigorous epicormic basal sprouting often occurs in response to canopy decline in open-grown ash infested with emerald ash borer (EAB) but was not observed by Klooster et al. [13] in closed canopy, mixed deciduous forests of the Upper Huron River watershed in southeast Michigan.

3.2. The Orphaned Cohort: Demography of Regenerating Ash

Prior to the EAB invasion, ash recruitment and regeneration were substantial in the Upper Huron River watershed, as *Fraxinus* was the most common genus in the understory and seedling layers of the stands sampled by Smith et al. [14] (Figure 3). As ash mortality exceeded 99%, the ash seed bank became depleted and ash seedling recruitment ceased, leaving only an orphaned cohort of previously established ash seedlings and saplings too small to be colonized by EAB, where they may persist for many years (Figure 4). The EAB population also continued to persist in the region at low levels despite the precipitous decline in its carrying capacity [36]. Each year, a proportion of ash saplings grows large enough to be colonized by EAB, and in aftermath forests in southeastern Ontario, EAB was found to be colonizing 19% of regenerating stems as small as 2.0 cm in diameter [35]. The fate of ash in the Upper Huron River watershed will depend on the degree that the orphaned cohort of regenerating saplings can survive and reproduce in the presence of low-density EAB populations [13].

Figure 3. Regenerating ash seedlings and saplings too small to be infested by EAB were the most common woody species in the forest understory in the Upper Huron River watershed in southeast Michigan.

Figure 4. Ash seedlings and small saplings can persist in the understory for long periods with little growth, as evidenced by this plant that grew less that one cm between 2009 when it was tagged and 2016 when it was remeasured.

3.3. Biological Control and the Fate of the Orphaned Cohort

The degree to which ash survive to reproduce may be dependent in large part on whether natural enemies can regulate EAB populations at low levels [32,37]. Woodpeckers are the most important predators of EAB and are capable of causing high mortality on individual trees [38–42]. Predation rates by woodpeckers, however, were highly variable across sites and from tree-to-tree [38,40,42]. Woodpeckers caused limited mortality of EAB in saplings [43] and have been observed to decrease parasitoid populations by preying on parasitized EAB larvae, which may interfere with biological control [41]. In another study, however, woodpeckers did not affect rates of EAB parasitism [44].

Native and introduced parasitoids can also be important sources of EAB mortality [39,40]. Braconid wasps (*Atanycolus* spp.) native to North America parasitize EAB in Michigan, but with variable effects on EAB populations [43,45]. In a classical biological control program, several EAB parasitoids native to Asia have been introduced to North America [46]. Although *Spathius agrili* Yang (Hymenoptera: Braconidae) has had little success becoming established in the northern United States, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae) has contributed to EAB mortality, and *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae) has become the dominant biotic factor causing EAB mortality in southeastern Michigan [37,43,47]. Based on life table analyses, Duan et al. [43] concluded that *T. planipennisi* decreased the growth rate of EAB populations in saplings by more than 50%, and Margulies et al. [48] found more live ash saplings where higher numbers of parasitoids had been released. However, given the long residence time of ash seedlings and saplings in the understory, this may reflect their density when parasitoids were initially released, which was not reported.

If biological control agents and other natural enemies can regulate EAB at low levels, perhaps ash can regenerate at densities sufficient to restore significant ecosystem services lost during the EAB invasion [13,33,37]. However, it remains to be demonstrated that parasitoids and other mortality agents can exert temporal density dependent effects powerful enough to regulate EAB at low densities. Parasitism rates by *T. planipennisi* declined substantially in trees with stem diameters >12 cm due to the inability of their short ovipositors to penetrate thicker bark [37,40,43]. Furthermore, North American ash species planted in Asia have experienced high mortality from EAB [49,50], even in the presence of coevolved natural enemies.

4. Impacts on Other Flora and Fauna

Widespread and relatively simultaneous mortality of ash has been predicted to have substantial direct and indirect ecological impacts on forest structure, function, and community composition via gap formation as trees die, as well as accumulation of coarse woody debris as dead trees fall [3,51]. This disturbance can alter soil microbial communities [52], hydrology [53,54], and carbon and nutrient cycling [22,52,54], ultimately leading to community-level effects on successional trajectories [55], facilitation of the establishment and spread of exotic plants [56], and impacts on native fauna [57,58]. Some effects of ash mortality will dissipate relatively quickly as canopy gaps close via regeneration in the understory and growth of dominant and subdominant trees [59,60]. For example, the effects of increased light availability on soil moisture and the foliar chemistry of understory plants will be more ephemeral than the ecological impacts of the accumulation and decomposition of coarse woody debris, and the persistent legacy of altered succession.

4.1. Successional Trajectories Following Ash Mortality

EAB-induced ash mortality is likely to alter successional trajectories, as other overstory and understory species respond to widespread, relatively simultaneous gap formation [14,22,61]. As ash mortality in the Upper Huron River watershed reached a peak, the most common genera in the overstory were oak (*Quercus*) and maple (*Acer*), which thus appear likely to benefit from released competition, at least in the short term [14]. Conversely, oaks were underrepresented in the understory [14], perhaps due to limited recruitment and/or deer browsing (e.g., [62,63]), while maple and basswood (*Tilia*) species were the most common taxa in the understory (other than ash), suggesting that their dominance could increase over time [14]. Elm (*Ulmus*) was underrepresented in the overstory relative to the understory [14], probably due to the impact of Dutch elm disease [64].

The effects of ash mortality and gap formation on radial trunk growth varied by species [65]. Of 11 taxa sampled, all of which are native to the study site, the majority of species that exhibited positive correlations between ash importance value (prior to EAB-induced mortality) and diameter growth (increased ring width) were shade-tolerant (sugar maple, *A. saccharum* Marshall; red maple, *A. rubrum* L.) or intermediate (hickory, *Carya*; white oak, *Q. alba* L.; red oak, *Q. rubra* L.) tree species. Diameter growth of most shade-intolerant species (black cherry, *Prunus serotina* Ehrh.; poplar, *Populus*; larch, *Larix*; tulip tree, *Liriodendron tulipifera* L.) was not correlated with ash importance value, with the exception of walnut (*Juglans*). At sites in Ohio, the radial growth of maples and elm increased following EAB-induced ash mortality [22,61].

4.2. Facilitation of Invasive Plants

Some invasive plants are more vigorous and reproductive in forest gaps than under closed canopies where light is limited (e.g., [56,66,67]). EAB may trigger an "invasional meltdown" [68] if widespread gap formation caused by ash mortality facilitates the establishment and spread of invasive plants by increasing light availability and/or relaxing interspecific competition for other resources [3]. Consistent with this hypothesis, Klooster [69] found that in the Upper Huron River watershed the growth rate of alien woody shrubs—specifically multiflora rose (*Rosa multiflora* Thunb.), Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder), and autumn olive (*Elaeagnus umbellata* Thunb.)—increased to a much greater degree in canopy gaps created by ash mortality than did the growth rate of native understory plants, such as ash seedlings, spicebush (*Lindera benzoin* (L.) Blume), American hornbeam (*Carpinus caroliniana* Walter), and American hophornbeam (*Ostrya virginiana* (Mill.) K. Koch). Hoven et al. [56] observed a similar pattern in Ohio forests where radial growth of Amur honeysuckle was directly related to the degree of ash mortality. These patterns are consistent with the species' adaptions to light availability. The dominant species of alien flora are adapted to respond to increased light availability, while the native shrubs consisted largely of shade-adapted, understory species, which typically exhibit lower phenotypic plasticity in response to variation in light availability [70,71]. However, Klooster [69] found no effect of EAB-induced gap formation on the density of alien plants, perhaps because not enough time had lapsed since the onset of ash mortality to impact their population dynamics.

4.3. Arthropod Herbivores of Ash

The decline and mortality of ash trees are expected to directly impact phytophagous arthropods that use ash as a host for at least part of their life cycle [72,73]. In a review of published literature, Gandhi and Herms [72] found host records for 281 arthropod herbivores of ash in six taxa (Arachnida: Acari; Hexapoda: Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera), including folivores, sap feeders, phloem/xylem feeders, gall formers, and seed predators. Most species (208) were polyphagous and thus were considered to face a low risk of population decline in response to ash mortality due to the prevalence of alternative host plants. However, 43 native and one alien species were reported to be specialist herbivores of ash, and thus were considered to face a high risk of local extirpation [72]. Wagner and Todd [73] conducted an appraisal of published and unpublished host records for specialist invertebrate herbivores of ash based on expert assessment by taxonomic authorities and concluded that 98 species may be imperiled by the EAB invasion.

In the short term, populations of some wood-borers and bark beetles that colonize declining and dead ash trees may increase in parallel with availability of suitable hosts [72]. However, their populations are predicted to eventually decline as snags fall and subsequently decay (e.g., [74]). For example, in a study conducted in the Upper Huron River watershed, Ulyshen et al. [75] reared 18 species of saproxylic beetles from ash limbs that had been suspended in the canopy or placed on the ground. The highly polyphagous cerambycid, *Neoclytus acuminatus* Fabricius, was the most common species collected. The buprestid *Agrilus subcinctus* Gory and the curculionid *Hylesinus aculeatus* Say, were also collected and face greater threat of local extirpation because they are largely or entirely restricted to ash [75]. Population declines of arthropod species that utilize ash as a host will likely have cascading impacts on biota with which they interact (e.g., symbionts and natural enemies), and the impacts may reverberate across the food web [72,73].

4.4. Ground-Dwelling Invertebrates

Widespread tree mortality caused by alien insects may also have indirect effects on invertebrate populations and communities [3]. Perry and Herms [76] proposed a model of dynamic temporal effects of disturbance caused by tree-killing invasive insects, including gap formation and accumulation of coarse woody debris (CWD) (Figure 5), on ground-dwelling invertebrate populations and communities. The model predicts the magnitude of effects of gap formation and accumulation of CWD will transition over time in opposing ways as ash mortality in the stand progresses from early to late stages. The formation of canopy gaps is predicted to have the greatest impact on ground-dwelling invertebrate diversity and abundance during early stages of ash mortality when gaps are presumably at their maximum size after tree death, with impacts diminishing over time as gaps close. Impacts of CWD, in contrast, are predicted to increase over time [76] as ash trees die, standing snags fall, and CWD accumulates and decomposes on the forest floor. For example, Higham et al. [74] observed rapid accumulation of CWD across a chronosequence of ash mortality in Ohio, and in the Upper Huron River watershed, the number of fallen ash trees increased by 76% from 2008–2012, and volume of ash CWD increased by 53% [77].

Experimental tests have been broadly consistent with these predictions. In a study conducted in stands experiencing early stages of ash mortality in northern Ohio, gap formation decreased the abundance of ground beetles (Carabidae) and other ground-dwelling arthropod taxa, as well as species richness and diversity, while the effects of CWD were less substantial [78,79]. Similarly, during early stages of ash mortality in the Upper Huron River watershed in southeast Michigan, ground beetle abundance and diversity decreased as ash mortality and gap size increased [80]. At the same sites during late stages of ash mortality, the effects of gaps—which by then were smaller—on ground-dwelling invertebrate communities were minimal, while the abundance, evenness, and diversity of soil arthropods and exotic earthworms were highest adjacent to decomposing ash CWD [81,82].

Figure 5. Coarse woody debris (CWD) accumulates steadily on the forest floor as dead ash trees fall.

4.5. Tri-Trophic Impacts on Swallowtail Butterflies

As ash mortality generates canopy gaps, insect herbivores of understory plants may be impacted indirectly by the effects of increased light availability on the quality of their host plants. For example, foliar concentrations of secondary metabolites are often higher in plants in the sun than in the same species growing in shade [83,84]. Common prickly ash (*Zanthoxylum americanum* Mill.), a native understory shrub in southeast Michigan, is the only host in the Upper Huron River watershed for giant swallowtail butterfly (*Papilio cresphontes* Cramer) larvae (Figure 6). The foliage of prickly ash contains furanocoumarins [85], which are photoactivated secondary metabolites that become more bioactive and toxic to herbivores when exposed to ultraviolet light [86]. Rice [87] found that prickly ash growing in canopy gaps created by ash mortality contained higher foliar concentrations of furanocoumarins than conspecifics in the shaded understory. Although giant swallowtail butterfly larvae are capable of detoxifying furanocoumarins [88], larvae still grew more slowly on plants in canopy gaps [87].

Figure 6. Prickly ash is the only host for giant swallowtail larvae in the Upper Huron River watershed.

The slow growth–high mortality hypothesis predicts that slower growing larvae will experience greater mortality because of their longer exposure to natural enemies [89,90]. Average daily probability of mortality from natural enemies (15%) was equivalent for larvae feeding on plants in gaps and shade [87]. Hence, if the lower growth rate of larvae feeding on plants in canopy gaps delays completion of the larval stage, mortality from natural enemies should increase as indirect effects of EAB-induced ash mortality and gap formation cascade across trophic levels [87].

4.6. Effects on Bird Behavior and Communities

EAB-induced ash mortality may also affect bird behavior and communities indirectly by altering the availability of food resources and nesting habitat. Woodpeckers and other insectivorous birds that forage primarily on bark or dead wood may be ecologically primed to benefit from the EAB invasion, at least temporarily, as a dramatic pulse of food from the EAB outbreak leads to increased reproduction and population growth, followed by a sharp population decline caused by resource depletion as ash trees die and the EAB population crashes (e.g., [5,91]). For example, data from the citizen science program Project FeederWatch revealed a signature of the EAB invasion near the epicenter in southeast Michigan that was not detected elsewhere, as Red-bellied Woodpecker (*Melanerpes carolinus* L.) and White-breasted Nuthatch (*Sitta canadensis* L.) numbers initially increased, while those of Downy Woodpecker (*Picoides pubescens* L.) and Hairy Woodpecker (*Picoides villosus* L.) initially declined and then increased several years later [92].

Long [93] monitored bird communities and foraging behavior during the winter across a gradient of EAB impact ranging from near complete ash mortality in southeast Michigan to early stages of EAB invasion in southwestern Ohio. He found that Downy, Hairy, Red-bellied, and Pileated (*Dryocopus pileatus* L.) Woodpecker all spent more time foraging on ash trees in stands with active EAB infestations, and that these stands had higher numbers of Downy Woodpecker. Red-bellied Woodpecker was significantly less abundant in stands in which the EAB outbreak had run its course.

Forest stands with high ash mortality had more diverse bird assemblages than did stands experiencing low ash mortality. Stands with high ash mortality had greater herbaceous groundcover, shrubby regeneration, and canopy fragmentation relative to stands with low ash mortality, which created nesting habitat and resulted in a shift in the breeding bird community to species more typical of open habitats [93].

5. Summary and Conclusions

It is clear from this review that EAB already has substantially impacted forests near the epicenter of the invasion of North America. In the Upper Huron River watershed in southeast Michigan, mortality of black, green, and white ash exceeded 99% by 2009, with nearly 60% occurring over a five-year period. As would be expected when mortality is so comprehensive, there were no relationships between ash mortality and ash density, species diversity, or any other measure of stand composition. New ash recruitment ceased as the ash seedbank was depleted and no new seedlings were detected, leaving only an orphaned cohort of previously established ash seedlings and saplings too small to be infested by EAB. The degree to which ecosystem services provided by ash can be restored may depend in large part on whether introduced biological control agents and other natural enemies can regulate EAB populations at densities low enough to facilitate significant ash regeneration.

The relatively simultaneous, widespread canopy gap formation followed by a steady accumulation of downed coarse woody debris has triggered a cascade of direct and indirect effects on plant and animal communities. Forest successional trajectories have been altered, growth rates of exotic plants have increased, specialist herbivores of ash are threatened with local extirpation, and the abundance and diversity of ground-dwelling invertebrates have been impacted, as have behavior and abundance of overwintering and breeding birds.

While these studies have increased our understanding of the ecological impacts of EAB, future research may focus on elucidating rates and patterns of gap closure and successional trajectories in different forest types; whether ash mortality and accumulation of CWD alter nutrient cycling and hydrological processes; long-term impacts of gap formation on alien and native understory flora; and impacts of ash mortality on ash herbivores and biodiversity at the landscape-level. Such studies will inform efforts focused on increasing resilience and restoration of ash ecosystems as the EAB invasion of North America proceeds.

Author Contributions: W.S.K. and D.A.H. conceived of the review, wrote many of the sections, and organized all contributions into the final version. All other co-authors contributed equally and substantially and are listed in alphabetical order.

Acknowledgments: Annemarie Smith and Diane Hartzler conducted the field-work to establish the long-term monitoring plots within the Upper Huron River watershed where much of the research reviewed in this paper was conducted from 2004–2014 with cooperation and approval from Paul Muelle of the Huron-Clinton MetroParks and Glenn Palmgren of the Michigan Department of Natural Resources. This research was funded by grants from the United States Department of Agriculture (USDA) Forest Service Northeastern Research Station's Research on Biological Invasions of Northeastern Forests program; USDA National Research Initiative Biology of Weedy and Invasive Species in Agroecosystems competitive grants program; the National Institute of Food and Agriculture; Cooperative Agreements with the USDA Forest Service Northern Research Station, Delaware, OH; and state and federal funds appropriated to the Ohio Agricultural Research and Development Center and The Ohio State University. We thank Catherine Herms and John Cardina for reviews of earlier drafts, which greatly improved this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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