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ORIGINAL PAPER

North American arthropods at risk due to widespread *Fraxinus* mortality caused by the Alien Emerald ash borer

Kamal J. K. Gandhi · Daniel A. Herms

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Abstract Emerald ash borer (*Agrilus planipennis* Fairmaire) (EAB), an alien invasive wood-boring buprestid beetle, is causing large-scale decline and mortality of the most widely distributed species of ash (*Fraxinus* spp.) trees endemic to eastern North America. We determined which arthropod species that are associated with ash may become threatened, endangered, and co-extinct with the demise of ash as a dominant tree species. A literature survey revealed that 43 native arthropod species in six taxonomic groups (Arachnida: Acari; Hexapoda: Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera) are known to be associated only with ash trees for either feeding or breeding purposes, and thus face high risk of endangerment. Most of these species are gall-formers followed by folivores, subcortical phloem/xylem feeders, sap feeders, and seed predators. Another 30 arthropod species are associated with 1–2 host plants in addition to ash, and herbivory on these hosts may increase as these arthropods shift from declining ash trees. Extirpation of arthropods dependent upon ash may unleash multiple extinctions of affiliated species with which they may be inextricably linked. The demise of North American ash species due to EAB is expected to lead to biotic loss with cascading ecological impacts and altered processes within forested ecosystems.

Keywords *Agrilus planipennis* · Arthropods · Ash · Biodiversity · Emerald ash borer · Extirpation · Extinction · *Fraxinus* · Invasive species · North America

Introduction

During the last two centuries, anthropogenic disturbances have resulted in large-scale alterations to North American forests, leading to widespread decline in forest biodiversity (Lovett et al. 2006). Species extinction rates have increased 1,000 fold since pre-settlement times, with up to 20% of native species becoming extinct in many taxonomic groups (Chapin et al. 2000). Major disturbances include loss and changes in habitat, fragmentation, climatic changes, and establishment of alien species (Gandhi and Herms 2009). In particular, invasion by exotic species is

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K. J. K. Gandhi (✉)
Daniel B. Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602, USA
e-mail: kgandhi@warnell.uga.edu

D. A. Herms
Department of Entomology, Ohio Agricultural and Research Development Center, The Ohio State University, 1680 Madison Avenue, Wooster, OH 44691, USA

among the most insidious cause of decline and extirpation of native species diversity within forested landscapes (Vitousek et al. 1997; Lovett et al. 2006). The number of exotic insects and other species that are introduced and established in North America is predicted to continue climbing concurrently with international trade (Liebhold et al. 1995; McCullough et al. 2006).

Emerald ash borer (*Agrilus planipennis* Fairmaire) (EAB) is a phloem-feeding wood-boring beetle (Coleoptera: Buprestidae) indigenous to eastern Asia (Cappaert et al. 2005). It was first detected in North America in 2002 in Michigan near Detroit (Haack et al. 2002; Cappaert et al. 2005). This invasive insect aggressively colonizes and kills all major North American species of ash (*Fraxinus* spp.) that it has encountered (Cappaert et al. 2005; Poland and McCullough 2006). Millions of ash trees have died within urban and forested areas in Michigan, and billions of ash trees throughout the continent are threatened as EAB continues to spread (Herms et al. 2004; Cappaert et al. 2005). In southeastern Michigan, ash mortality due to EAB increased to more than 50% within 3 years from 2004 to 2006 (Smith 2006; Gandhi et al. 2007), and now approaches nearly 100% in all forest stands near the epicenter of the invasion (Gandhi et al. 2008). We anticipate similar trends in other forested landscapes as EAB continues to spread. As of September 2009, EAB has been detected in 13 US states including Illinois, Indiana, Kentucky, Maryland, Michigan, Minnesota, Missouri, New York, Ohio, Pennsylvania, Virginia, West Virginia, and Wisconsin, as well as Ontario and Quebec in Canada (http://www.emeraldashborer.info), and may well exist elsewhere.

Unlike most other wood-borers, EAB colonizes healthy as well as stressed trees in North America, thus creating a wood-borer epidemic of unprecedented intensity (Cappaert et al. 2005). Asian ashes appear to be much more resistant, perhaps by virtue of their coevolutionary history with EAB (Rebek et al. 2008). Because of the current lack of effective containment and eradication tactics (United States Government Accountability Office 2006), EAB is expected to continue to spread creating the possibility that the entire genus *Fraxinus* will be functionally extirpated from North America within the next few decades.

The wide-scale decimation of an important overstory tree species within a short-time could unleash a staggering cascade of direct and indirect effects on forest ecosystems (Mattson 1997; Gandhi and Herms 2009). *Fraxinus* ranks among the most abundant tree genera in forests of northeastern US. Ash species rank among the most widely distributed tree species in eastern North America, and are a component of more than 26 forest cover types (Burns and Honkala 1990; Cappaert et al. 2005). In communities in which they occur, ash can also rank among the most abundant tree species. For example, a survey estimated 3.8 billion white ash (*F. americana* L.) trees in Ohio, ranking it among the five most common tree species in the state (Griffith et al. 1993). Ash species contribute significantly to nutrient cycling within hardwood forests (Reiners and Reiners 1970), and are important sources of food and habitat for numerous bird and mammal species (Martin et al. 1951; Faanes 1984). Thus, the ecological impacts of widespread ash mortality may rival or even exceed resulting from decline of American elm (*Ulmus americana* L.) and chestnut [*Castanea dentata* (Marshall) Borkh.] caused by Dutch elm disease [fungal agents: *Ophiostoma novo-ulmi* Brasier and *O. ulmi* (Buisman)] and chestnut blight [fungal agent: *Cryphonectria parasitica* (Murrill) Barr], respectively (Dunn 1986; Smock and MacGregor 1988). Ironically, large-scale mortality of American elm led to an increase in the abundance and dominance of white ash trees in eastern forests (Barnes 1976).

While the loss of biodiversity due to habitat alteration and destruction are well documented (e.g., Brook et al. 2003), there is relatively little information about the impacts on native biodiversity of wide-scale mortality and extinction of an entire tree genus caused by an alien species. Widespread ash mortality will have direct effects on the fauna dependent upon ash for food, shelter, and reproduction during some part of their life-cycle. Indirect effects of ash mortality will occur at other trophic levels, impacting, for example, parasites and predators that are dependent upon the faunal communities associated with ash trees (Koh et al. 2004). The objective of this paper is to catalog the native arthropod fauna of ash, and assess their relative risk of endangerment and perhaps extirpation, should EAB decimate ash throughout North America.

Methodology

To identify arthropods associated with ash, exhaustive information searches were conducted on 16 North American (north of Mexico) ash species including *F. americana* L. (white ash), *F. anomala* Torr. ex S. Wats. (singleleaf ash), *F. berlandieriana* DC (Mexican ash), *F. caroliniana* P. Mill. (Carolina ash), *F. cuspidata* Torr. (fragrant ash), *F. dipetala* Hook. and Arn. (two-petal ash), *F. gooddingii* Little (Goodding's ash), *F. greggii* A. Gray (Gregg's ash), *F. latifolia* Benth. (Oregon ash), *F. nigra* Marsh. (black ash), *F. papillosa* Lingelsh. (Chihuahuan ash), *F. pennsylvanica* Marsh. (green ash), *F. profunda* Bush (Bush) (pumpkin ash), *F. quadrangulata* Michx. (blue ash), *F. texensis* (Gray) Sarg. (Texas ash), and *F. velutina* Torr. (velvet ash) (Wallander 2008). Sources included journal articles, book chapters, conference proceedings, extension publications, and reliable internet sources and databases such as JSTOR, AGRICOLA, and Web of Science (Electronic supplementary material). We focused on arthropods that feed and/or breed on any part of ash trees including twigs, flowers, leaves, seeds, stems, and roots. Some species known to utilize ash as ephemeral habitats were also included. To generate host specificity information, all known plant hosts for each arthropod species were recorded. We are aware of no extensive survey and rearing studies of arthropods on ash trees. Hence, this host specificity list is likely an underestimation of the numbers of arthropod species associated with ash and other plant species, and we anticipate more discoveries will be made in the future.

We assigned an endangerment risk rating to each arthropod species as follows with greater host specificity reflecting greater risk of endangerment: (1) high risk—monophagous arthropods associated only with ash trees; (2) high-moderate risk—biphagous arthropods associated with one host species other than ash; (3) moderate risk—triphagous arthropods associated with two host species other than ash; and (4) low risk—polyphagous arthropods associated with ≥ three host species other than ash. To better understand how each trophic level may respond to ash decline, high risk arthropods were further categorized on their feeding and breeding habits as foliage feeders, gall formers, phloem/xylem feeders, sap feeders, and seed predators.

Results

Our survey revealed 282 native and exotic arthropod species in eight orders associated with North American ash species with 44 (43 native and one exotic), 17, 13, and 208 species, respectively, categorized in the high (monophagous species), high-moderate (biphagous), moderate (triphagous), and low (polyphagous) endangerment risk rankings (Fig. 1, Electronic supplementary material). The most commonly represented taxa was Lepidoptera (137 species), followed by Coleoptera (76), Hemiptera (38), Diptera (12), Hymenoptera (9), Acari (7), Orthoptera (2), and Thysanoptera (1) (Table 1). Orders with the highest numbers of monophagous species (classified as high risk) were Diptera (11 species), Coleoptera (9), Lepidoptera (9), and Hemiptera (8) (Table 1). Among those ranked as high risk of endangerment, species richness is the greatest for gall formers (12 species), followed by foliage feeders (9), phloem/xylem feeders (9), sap feeders (8), and seed predators (5) (Fig. 2).

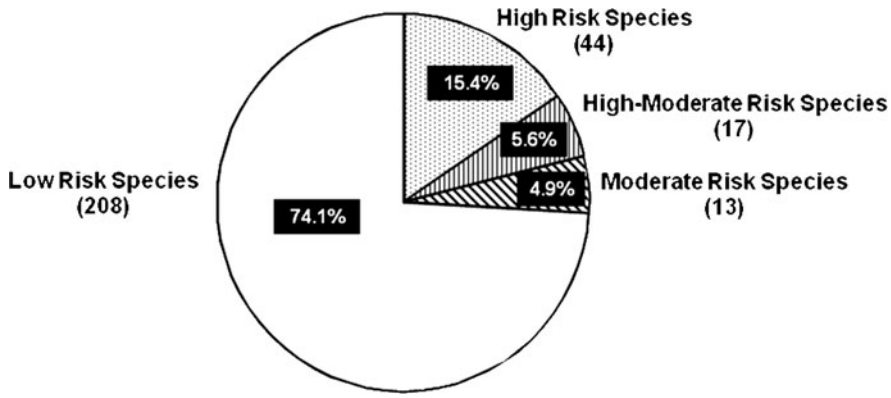

Fig. 1 Percentage of arthropod species in high (associated only with ash), high-moderate (ash and one other plant species), moderate (ash and two other plant species), and low (ash and ≥ three other plant species) risk endangerment categories

Table 1 Taxonomic distribution of arthropod species associated with ash in different endangerment risk categories resulting from mortality of ash caused by emerald ash borer

Arthropod taxa	Endangerment risk category				Total number of species
	High	High-moderate	Moderate	Low	
Arachnida	3	1	0	3	7
Coleoptera	9	6	3	58	76
Diptera	11	0	0	1	12
Hemiptera	8	5	4	21	38
Hymenoptera	4	1	0	4	9
Lepidoptera	9	4	6	118	137
Orthoptera	0	0	0	2	2
Thysanoptera	0	0	0	1	1
Total number of species	44	17	13	208	282

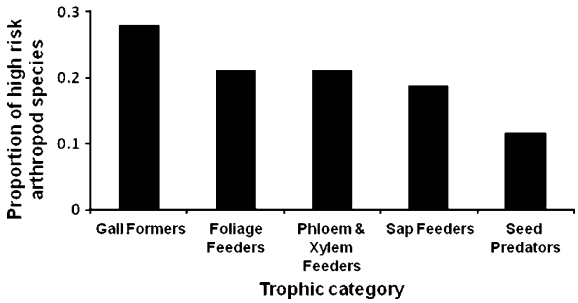

Fig. 2 Feeding guilds of monophagous arthropods in the high risk endangerment category

Discussion

Ash has a diverse associated faunal community comprising of 282 arthropod species. The 43 monophagous native species in the high risk category (*ca.* 15% of the total ash fauna) are clearly threatened by widespread ash mortality, as was predicted for seven moth species that fed exclusively on chestnut trees (Opler 1978). A current listing in the IUCN (International Union of Conservation of Nature) Red List database indicates that two of these chestnut moth species, *Ectodemia castaneae* (American chestnut moth) and *E. phleophaga* (Phleophagan chestnut moth), are considered regionally extinct in the USA (IUCN 2009a, b). High risk arthropods of ash include ash flower gall mite [*Aceria fraxiniflora* (Felt)], black-headed ash sawfly [*Tethida barda* (Say)], eastern ash bark beetle [*Hylesinus aculeatus* (Say)], and banded ash clearwing moth (*Podosesia aureocincta* Purrington and Nielsen) (Fig. 3). We also anticipate cascading effects on other affiliated species including fungal, bacterial, and invertebrate associates and parasites, as well as vertebrate and invertebrate predators and mutalists (Purrington and Nielsen 1987; Langor and Hergert 1993; Koh et al. 2004).

The responses of monophagous arthropods to elimination of their host may differ depending upon their feeding guild (Fig. 4). Because the North American wood-borers and bark beetles that utilize ash colonize declining and dead ash trees, their populations will initially increase as EAB increases availability of suitable hosts. Furthermore, once these species reach a critical population threshold, some may be able to overwhelm host defenses through mass attacks. For example, in the mid-1980s in Alberta, a severe drought resulted in large-scale mortality of green ash trees; triggering outbreaks of the western ash bark beetle, *Hylesinus californicus* (Swaine), which were then able to mass-attack and successfully colonize live trees (Langor and Hergert 1993; Langor 1994). Such responses by members of the subcortical phloem/xylem feeding guild may accelerate the demise of ash trees in EAB-infested stands. Once ash trees are in an advanced stage of decay, the populations of wood-borers and bark beetles will decline. In contrast, we expect species in other feeding guilds to experience a more linear population decline as ash mortality increases, including seed-predators, folivores, sap-feeders, and gall-makers. Populations of seed-predators may be among the first to decline rapidly (Fig. 4), as seed production declines quickly in EAB-infested trees (*personal observation*).

As density of ash diminishes, polyphagous arthropods associated with ash may increase herbivory on their alternative hosts. For example, *Prociphilus americanus* (Walker), a sap-sucking aphid, uses ash

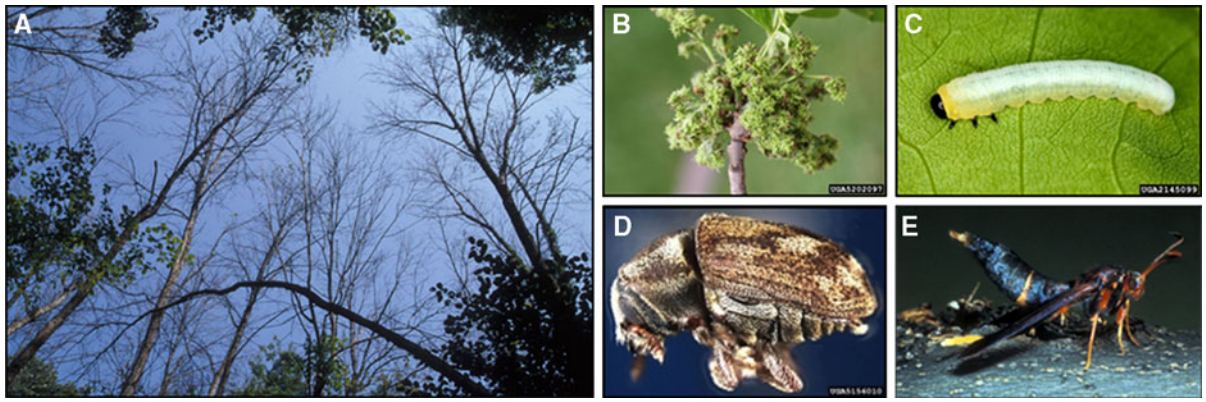

Fig. 3 Examples of arthropods at risk of extinction with the demise of North American ash (*Fraxinus* spp.) trees. **a** Dead ash trees in a central hardwood forest of southeastern Michigan. **b** Ash flower gall mite [*Aceria fraxiniflora* (Felt)]. Photo Credit: Steven Katovich, USDA Forest Service, Bugwood.org. **c** Blackheaded ash sawfly [*Tethida barda* (Say)]. Photo Credit: David Cappaert, Michigan State University, Bugwood.org. **d** Eastern ash bark beetle [*Hylesinus aculeatus* (Say)]. Photo Credit: J. R. Baker and S. B. Bambara, North Carolina State University, Bugwood.org. **e** Banded ash clearwing moth Purrington and Nielsen (*Podosesia aureocincta*). Photo Credit: D. G. Nielsen, The Ohio State University

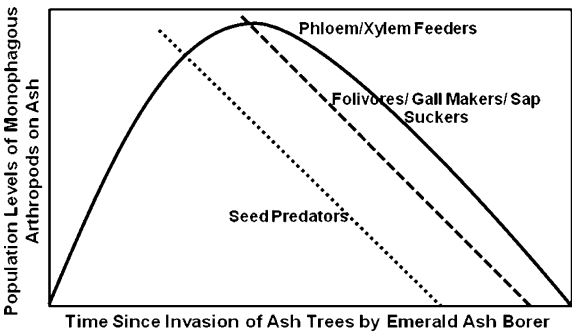

Fig. 4 Hypothetical responses by populations of monophagous arthropod species to widespread mortality of ash (*Fraxinus* spp.) due to emerald ash borer

and fir (*Abies* spp.) as primary and secondary hosts, respectively (DeAngelis 1998). On ash, it forms sexual colonies on the terminals, suckers, and base in early spring, and on fir, it forms asexual colonies on the roots in the summer (DeAngelis 1998). If ash is eliminated, then the asexual form on fir will likely continue to develop indefinitely and the loss of sexual form may decrease genetic variability within the species (DeAngelis 1998).

More than half of ash arthropod species in the high-moderate (biphagous species) and moderate (triphagous species) risk categories utilize exotic plants as alternate hosts, especially in the family Oleaceae. For example, the ash seed weevil (*Ligny-odes* spp.) feeds also on the seeds of lilac (*Syringa* spp.) (Solomon et al. 1993). Seed predation rates by these weevils on ash are high, exceeding 95% in some areas. As ash is decimated, their populations will decline precipitously, as they may be relegated to ornamental plantings of lilac (Wagner 2007), which no doubt is less common than ash.

Emerald ash borer (EAB) currently continues to spread unchecked (United States Government Accountability Office 2006), threatening endemic ash with extinction throughout North America and consequently, its associated native fauna. Much remains to be known about the natural history and ecology of arthropods and their affiliates and interactions associated with ash. This rich evolutionary diversity will be irreplaceably lost with the demise of North American ash species. Future studies should focus on quantifying effects of ash decline on natural history, population dynamics, ecological genetics, and community level interactions of arthropods associated with ash. Host shifts by ash arthropods to other tree species should also be monitored and documented. Research on the effects of gap formation due to ash mortality on non-target taxa, such as ground beetles, and the spread of invasive plants is already underway (e.g., Herms et al. 2008; KJK, Gandhi et al., unpublished data). Stronger quarantine measures, early detection, and prompt eradication will be necessary to prevent future threats to biodiversity posed by invasive species.

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