

Biology and Control of Emerald Ash Borer



Edited by Roy G. Van Driesche and Richard C. Reardon



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On the cover: Cover design by Sheryl Romero and Denise Binion, Forest Health Technology Enterprise Team. Background image: Understory green ash seedlings (*Fraxinus pennsylvanica*, Oleaceae) released after large ash trees were killed by emerald ash borer in Okemos, Michigan in 2014, photo by Leah S. Bauer; (bottom row, left to right) Fully mature *Tetrastrichus planipennis* larvae break free of emerald ash borer larval skin and pupate in the larval gallery under the tree bark. (Photo credit: Clifford Sadof); EAB adult and typical leaf feeding damage. (Photo credit: Deborah Miller, USDA Forest Service, Bugwood.org); Emerging *Tetrastrichus plannipennis* adults. (Photo credit Leah S. Bauer).

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CHAPTER 2: ECOLOGICAL IMPACTS OF EMERALD ASH BORER

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INTRODUCTION

The genus *Fraxinus* includes 16 North American species. Flowers et al. (2013) estimate that there are more than 8.7 billion ash trees and saplings in the continental United States, and these are all potentially susceptible to emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) infestation. Since its invasion, this beetle has established in more than 20 states, from Minnesota to Maine, south to Georgia and Missouri, as well as in southern Ontario and Quebec,

and is expanding its range on all edges of its current distribution. Because timber and firewood from infested areas can be transported long distances, the beetle has the potential to establish virtually anywhere where ash species grow. It is considered to be among the most destructive forest insect pests to have been introduced into North America (Herms and McCullough, 2014; McCullough and Usborne, 2014). More than 200,000 million ash trees have been killed – especially in the Great Lakes region where the insect first established in the early 1990s (Cappaert et al., 2005a; Poland and McCullough, 2006, Siegert et



Figures 1-4. Affected communities in Ohio; dead trees are green ash (*F. pennsylvanica*) killed by the emerald ash borer: (1) Saint Mary's River west of Decatur, June 2014. (Photo courtesy Jim McCormac); (2) Willow Point Wildlife Area in Vickery, August 2011. (Photo courtesy Jim McCormac); (3, 4) Ottawa National Wildlife Refuge in Oak Harbor, August 2014. (Photos courtesy Judy Semroc)

al., 2007) (Figs. 1-4).

Fraxinus americana L. (white ash) and especially *Fraxinus pennsylvanica* Marshall (green ash) – strong, stately, rapidly growing trees – are widely planted in yards, parks, and along city streets, in part because both species are known to be hardy and relatively insect- and disease-free (Burns and Honkala, 1990). Ash is also preferred for firewood because its sap is flammable and, as such, the potential for EAB to be spread throughout North America by human transport of infested wood is greatly heightened. A lower bound economic estimate for treating, removing, and replacing EAB-infested ash trees in urban landscapes for 2010 to 2020 is \$12.5 billion (Kovacs et al., 2011). White ash and, to a lesser extent, green ash are commercially important trees whose strong but flexible wood is used for flooring, paneling, furniture, tool handles, and baseball bats (Elias, 1987; Burns and Honkala, 1990). White ash has long been the preferred wood for the Louisville Slugger – a bat popular with professional baseball players.

Ash typically grows as a component in hardwood forests (Figs. 5-11); furthermore, *Fraxinus* species are classified as either the dominant or co-dominant species in 150 forest and shrubland communities (NatureServe Explorer, 2014, see below). In some wetlands, species such as *Fraxinus nigra* Marshall (black ash) (Figs. 8, 10) and *Fraxinus profunda* (Bush) Bush (pumpkin ash) (Figs. 7, 9) form almost pure monocultures that are highly susceptible to EAB (Tardif and Bergeron, 1992; Rebek et al., 2008; Klooster et al., 2014; NatureServe Explorer, 2014; Jim McCormac and Jim Bissell pers. comms). Laboratory trials suggest that all 16 species of North American *Fraxinus* may be suitable hosts for larval development of EAB and thus are susceptible to attack (Anulewicz et al., 2008; Leah Bauer pers. comm, Deb McCullough pers. comm). Even small-stemmed western species have the potential to support the beetle given that saplings of white and green ash as narrow as 1 cm in diameter are exploited by the beetle and its immature stages in the eastern United States. Once infested, tree death typically follows within 2 to 6 years (Knight et al., 2013). In addition, the related (olive family) fringetree (*Chionanthus virginicus* L.) is also susceptible to attack, but the beetle's impact on that host is as yet unstudied

(Entomology Today, 2014).

Climate models for the beetle and projections for its spread are still in development and burdened with considerable uncertainty (Sobek-Swant et al., 2012; Liang and Fei, 2014), thus it is impossible to know how far north, south, and west the beetle might spread in North America and which *Fraxinus* populations are most at risk. Consequently, for the purposes of this assessment, we consider the entirety of the North American ash flora to be vulnerable. We first examine the forest community types where ash is a dominant or co-dominant and then provide a brief assessment for each of the sixteen *Fraxinus* that grow north of Mexico. Each treatment includes a synopsis of a species' habitat, range, conservation status, known susceptibility to EAB, and a summary of its specialist herbivores. We then include a brief discussion of the importance of ash to vertebrate wildlife before addressing the core of our contribution – a comprehensive evaluation of the invertebrate herbivore fauna of North American *Fraxinus* likely to be threatened by the spread of EAB. Our evaluation is constructed from reviews of literature, correspondence with taxonomic authorities, and DLW's 30-year rearing program. We ignore generalist herbivores known to feed on ash, although a few oligophagous species are discussed.

Our assessment is novel in that we considered feeding records in older and derivative literature as unconfirmed, given the large number of misattributed records plaguing recent compendia and risk-assessment literature. Instead, we adopted an authority-driven approach whereby we contacted one or more active systematists or experts for taxa known to have specialist herbivores on woody plant taxa. We received information from more than 80 taxonomic authorities with first-hand knowledge of appropriate literature, species-level taxonomy, life history data, and ecological associations. Compared to previous assessments, our approach yielded a dramatically different list of potentially imperiled herbivores, essentially half of which are newly reported here. Our work includes a revised set of risk rankings for 98 species that we believe to be threatened by the emerald ash borer.



Figures 5-11. Ash trees and ash-dominated communities: (5) Google Earth view of black ash swamp west of Lincoln, Wisconsin; *Fraxinus nigra* is dominant over thousands of hectares of this boreal wetland; (6) Majestic blue ash (*F. quadrangulata*) tree near Lexington, Kentucky. (Photo courtesy Daniel Boone); (7) Vernal pool with canopy of pumpkin ash (*F. profunda*), Momence Wetlands Land and Water Reserve, Illinois; note buttress roots or knees which help the trees uptake oxygen when the pool is inundated. (Photo courtesy Judy Semroc); (8) Black ash dominated swamp near Black Lake, Michigan. (Photo courtesy Anton Reznicek); (9) Vernal pool near Astabula, Ohio with pumpkin ash as the dominant canopy tree; the dry vernal pool shown here is a breeding area for mole salamanders. (Photo courtesy Judy Semroc)—see *Effects to Vertebrates*; (10) Northern hardwood swamp dominated by black ash near Wallon Lake, Michigan. (Photo courtesy Anton Reznicek); (11) Upland hickory-white ash glade (*F. americana*) in Litchfield County, Connecticut. (Photo courtesy Ken Metzler)

METHODS AND RATIONALE

To determine ecological impacts of EAB infestations on communities, we contacted 20 people with first-hand experience (botanists, reserve managers, Department of Natural Resources (DNR) ecologists, State Nature Conservancy chapters, forest managers, land managers, seasoned naturalists, wildlife biologists, and especially those with extensive field experience) in the forests and woodlands where EAB has been resident for four or more years (Appendix 1). We focused our surveys and correspondence on three states and one province with conspicuous EAB impacts: Michigan, northern Ohio, northeastern Indiana, and southwestern Ontario. For each state or province we initially contacted a lead biologist in the DNR (or its functional equivalent) and a state or provincial office for The Nature Conservancy and then made efforts to approach additional state or provincial authorities that had been endorsed for their knowledge of the impacts of EAB. Vertebrate biologists that we contacted for information on the ecological (especially dietary) importance of *Fraxinus* are listed in Appendix 1. Conversations with Anton Reznicek (University of Michigan), renowned Great Lakes Region botanist, Jim Bissell (Cleveland Museum of Natural Science), and Jim McCormac (Ohio Division of Wildlife) carried special force.

To identify and assess imperilment of plant communities containing ash, we used the U.S. National Vegetation Classification (USNVC) revised in 2008 and subsequently developed by NatureServe Explorer and state Heritage Programs (NatureServe Explorer, 2014). The classification system for the North America's plant community types – a jurisdictional subset of the International Vegetation Classification – is a spatially extensive, range-wide, on-going collaboration of federal, international, academic, and state partners, housed and managed by NatureServe. Our treatment focuses on ecological communities recognized at the Group level in the International Vegetation Classification system and tallies the biological communities in which any one of North America's 16 *Fraxinus* species is named as a dominant or co-dominant plant species. We capitalize Group when the word is meant to convey rank in the

USNVC classification.

Ash specialists were defined as those species for which *Fraxinus* was deemed a principal larval or adult host. Stated differently, specialists are those taxa that would be expected to be severely compromised were *Fraxinus* eliminated from the taxon's range. We excluded more than 180 ash-feeding herbivores that are known to feed on hosts outside the family Oleaceae (Gandhi and Herms, 2010; Robinson et al., 2014). Host records were verified by contacting principal taxonomic experts (listed with affiliations in Appendix 2). Frequently, multiple experts, with differing regional data or taxonomic knowledge, were consulted for the same taxon. We were not able to make contact with an active North American thrips (Thysanoptera) systematist and caution that much remains to be learned about North America's mite fauna. Documentation for all taxa and the listed hosts is given in the References column and, as appropriate, in the Comments column of Table 4. Conversations are referenced as “pers. comm.” and letters and emails are referenced as “in litt.”

We use the term *polyphagous* to refer to cases where herbivores feed on members of more than two families, *oligophagous* to refer to cases where the herbivores feed on more than one genus in the Oleaceae, and *specialist* to refer to cases where *Fraxinus* is the sole or principal host in nature¹. We restrict use of *monophagous* to those instances where only a single species is (known to be) consumed, and *ecological monophagy* to instances where a species' diet is restricted to a single member of the Oleaceae because only one host species grows in a given geographic location; presumably the herbivore would use other congeners (*Fraxinus*) or perhaps confamilials (Oleaceae) were these available. Throughout this paper, our diet-breadth assessment of invertebrates applies to the most specialized life stage; thus, if a leaf beetle eats just *Fraxinus* as a larva but browses on a spectrum of plants as an adult, our discussion and risk assessment is based on the larval stage.

¹This is more restrictive than most insect-plant literature, where oligophagous refers to herbivores that consume plants from just 2-3 families and polyphagous is used to refer to herbivores consuming four or more families.

We follow Hinsinger et al. (2013) in recognizing four Sections of *Fraxinus* in North America. Section is capitalized when the word is meant to convey nomenclatural rank (and phylogenetic membership), i.e., roughly equivalent to a subgenus. Authors for scientific names of imperiled arthropods are given in Table 4; author names for arthropod species not treated in Table 4 are given in the text the first time that taxon is discussed. Arthropod family names are given in the text and Table 4 except where family membership has been made obvious by accompanying text. Authors for *Fraxinus* species appear in the section entitled *North America's Sixteen Fraxinus*.

Species-level taxa ($n = 98$) were assigned an imperilment or risk category after we had verified host records for each. Four categories of risk were adopted: *Very High*, *High*, *Moderate*, and *Low*, with all examples of the latter excluded from this work. If only *Fraxinus* and native *Chionanthus* L. (fringetree) species were among the reliably reported hosts, individuals were given a *High* risk rating. If additional Oleaceae hosts were recorded, we assigned risk ratings in the following manner: herbivores known to include *Forestiera* Poir. (swamp privet or desert olive) species were regarded as *Moderate* risk species because native *Forestiera* are abundant enough to serve as an alternative host to *Fraxinus*; ash-feeding and fringetree-feeding

herbivores also reported from non-native Oleaceae hosts, e.g., *Olea* L. (olive), *Ligustrum* L. (privet), and *Syringa* L. (lilac) were given a *High to Moderate* risk rating as these hosts are either considered not abundant enough in wildlands or too infrequently used to serve as viable (sole) hosts for these taxa over extended time periods were ash to be functionally eliminated. If a species was believed to have a strong preference for *Fraxinus* over other Oleaceae, its risk rating was increased; conversely, those with a preference for *Forestiera* resulted in a reduced rating. One species, *Prociphilus americanus* (Aphididae), was determined as *High* risk despite feeding on *Abies* Miller (fir) because both *Fraxinus* and fir are primary hosts in different stages of this aphid's alternating life cycle.

In a few cases where we suspected an apparent specialist may prove to be a polyphage, e.g., *Banasa rolstonii* (Pentatomidae), *Diaspidiotus fraxini*, and *Diaspis fraxini* (both Diaspididae), we invoked the precautionary principle and assigned these species a *High* risk rating. Likewise, species in need of taxonomic study were still included and generally ranked as *High*; e.g., *Sphinx* near *chersis*, *Sympistis fortis*, *Hyrdelia* near *inornata*, and *Zelleria* near *hepariella*. In these cases and others, our thinking is conveyed in the Comments section of Table 4.

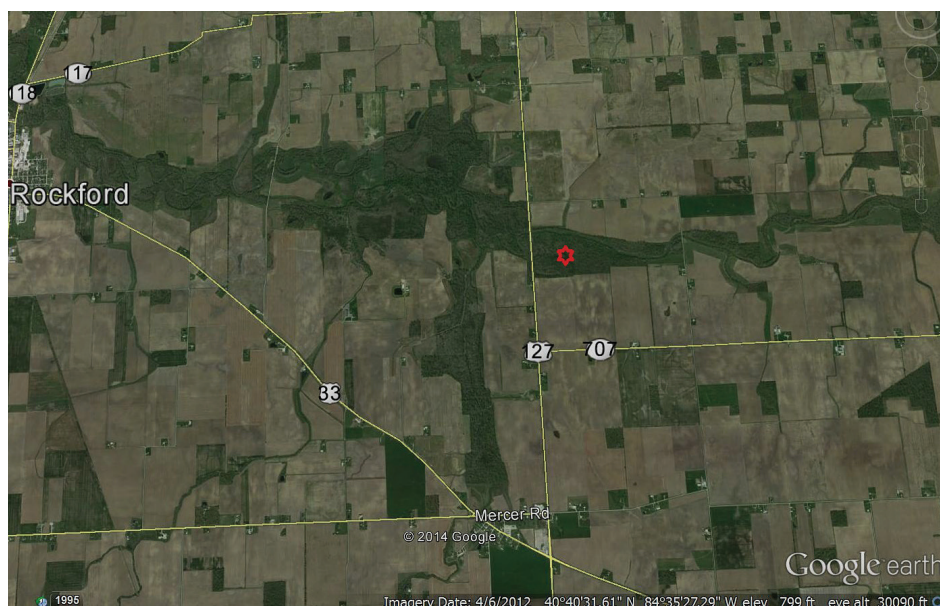


Figure 12. Google Earth image of Saint Mary's River west of Decatur, Ohio. The dead trees in this image about the periphery in the riparian corridor east of Rockford are essentially all green ash. The red star indicates the approximate location of the stand shown in Figure 1.

ECOLOGICAL IMPACTS TO NORTH AMERICAN ASH

Flowers et al. (2013) estimate that there are 8.7 billion ash trees and saplings in the lower 48 states – making up roughly 2.5% of the aboveground forest carbon mass in this region. Over most of North America, ash trees tend to grow in mixed hardwood woodlands and forests and are infrequently an ecologically dominant tree at landscape levels. Even in regions of the Midwestern United States, where a significant portion of all *Fraxinus* have been killed, we were unable to easily detect affected communities using Google Earth satellite imagery; although one such example – a severely damaged area along the Saint Mary’s River, east of Decatur, Ohio – is shown in Fig. 12. Another important exception are black ash forests, which can be ecologically dominant at larger spatial scales; in many northern woodlands, *F. nigra* grows in virtual monocultures over hundreds of hectares (see below and Figs. 5, 8, 10). Furthermore, over smaller spatial scales, ash species have great ecological importance and, by definition, are essential elements in the woodlands and forests where they are dominant or co-dominant species. The U.S. National Vegetation Classification and NatureServe Explorer (2014) identify 150 U.S. and Canadian forest and shrubland community types where a *Fraxinus* species is named as a dominant or co-dominant element. Just four *Fraxinus* species account for 82% of the 150 community Groups where ash is regarded to be a key community element: green ash (n = 55), white ash (n = 43), black ash (n = 14), and Oregon ash, *Fraxinus latifolia* Benth. (n = 12). Likewise, only eight species of *Fraxinus* grow as the (lead) dominant tree species in 51 community types: green ash (n = 18 community Groups), Oregon ash (n = 10), white ash (n = 8), black ash (n = 6), Carolina ash, *F. caroliniana* Miller (n = 3), blue ash, *F. quadrangulata* Michx. (n = 3), singleleaf ash *F. anomala* (n=2) and pumpkin ash (n = 1). Ecological contributions of each of North America’s 16 native *Fraxinus*, as identified in the U.S. National Vegetation Classification and NatureServe Explorer (2014), are summarized in Table 1.

In Table 2 we list 16 North American forest community types where a *Fraxinus* is the dominant

tree and the assemblage is regarded as either critically imperiled (G1) or imperiled (G2) in NatureServe Explorer (2014). Most of these imperiled forest types occur south of Pennsylvania; three are restricted to Oregon and Washington. Fortunately, none occur in the most severely affected areas of the Midwestern United States.

A few community types warrant special mention because of their spatial extent or because of their vulnerability. In Wisconsin and elsewhere, swamps with black ash as the sole dominant canopy species may encompass >1000 ha (Fig. 5). Palik et al. (2012) speculated that many such black ash swamps, should ash disappear, may change permanently to shrublands as no other tree species exists in large enough concentrations to form a new canopy. Similarly, along the Atlantic Coastal Plain, Carolina ash sometimes accounts for much of the above-ground biomass in bottomlands and wetlands.

The most significant ecological impacts of EAB to woodlands and forests will be determined by what plant associations establish post-invasion (Flowers et al., 2013; Knight et al., 2013; Burr and McCullough, 2014). Future projections for communities formerly dominated by ash are still a matter of conjecture because no EAB infestations, with their concomitant ecological consequences, have run full course. Undoubtedly, there will be taxonomic variation in which species replace ash due to differences in soil type, hydrology, light, seed banks, and the local pools of potential colonists. In the vicinity of Ann Arbor, Michigan – where EAB was first documented – the ecological vacuum created by the loss of green ash has been filled by spicebush (*Lindera benzoin* L.), pawpaw (*Asimina triloba* Dunal), and prickly ash (*Zanthoxylum americanum* Mill.). In the same area, one wetland formerly dominated by black ash has changed into a monoculture of sedge (*Carex* L.). While both ash habitats changed structurally, neither gave way to invasive species (Anton Reznicek, pers. comm). In Indiana and Ohio, silky (*Cornus amomum* Mill.) and gray dogwoods (*C. racemosa* Lam.) have flourished in communities where ashes (mostly green and black) have been lost (Jim Bissell, Mike Homoya, and Jim McCormac, all pers. comm). Invasive shrubs that have increased

in post-EAB woodlands and bottomlands in Indiana and Ohio include multiflora rose (*Rosa multiflora* Thunb.), honeysuckle (*Lonicera morrowii* A. Gray and three other honeysuckles), and glossy buckthorn (*Rhamnus alnifolia* L'Hér), but not to the extent that many feared. As noted above, even in southeastern Michigan where EAB was first documented, it is still too early to know what the ecological consequences of ash decline will be. Over time, sedge meadows, reed canary grass (*Phalaris arundinacea* L.) bottomlands, and various shrublands that arise following ash die-off will give way to forest communities, but the composition of these replacement forests remains to be seen. It is also too soon to disregard *Fraxinus* as an eventual component of replacement forests as virtually all EAB-affected communities in the Midwestern United States have seedling and sapling ash recruiting presently (Anton Reznicek pers. comm). If native and introduced natural enemies (e.g., Duan et al., 2013; also see Chapters 8 and 9) are able to reduce emerald ash borer density, *Fraxinus* could regain some of its former ecological importance.

Where significant physiognomic changes occur, e.g., where a woodland is initially replaced by a graminoid wetland or shrubland, the biota, species interactions, hydrology (Slesak et al., 2014), light regimen, nutrient cycling, vertebrate food value, and other core ecosystem characteristics will be altered. Beyond the obvious loss of ash-specialized herbivores, structural changes in affected woodlands may change a forest's suitability as breeding habitat and cover for resident vertebrates and invertebrates (e.g., see discussion of mole salamanders [*Ambystoma* species] in pumpkin ash swamps later in this chapter). On a smaller spatial scale, all of the above applies to the forest gaps that form when stands or glades of ash are killed by EAB. Such canopy gaps are noted to cause microclimate effects altering, among other biota, ground beetle populations (Gandhi et al., 2014). These gaps also open up forests for invasions by plant species normally limited by light availability (Herms and McCullough, 2014).

When native plants are replaced by exotic species, such as glossy buckthorn and exotic honeysuckles in Indiana and Ohio (see above), there can be cascading consequences to higher trophic levels. Exotic plants

often carry lower herbivore loads (Tallamy and Shropshire, 2009) and as a consequence would not support as many insectivorous birds, mammals, or other wildlife. However, we are compelled to interject here that we generally find ash to be relatively herbivore free. Low insect/pest loading is one reason that ashes are often chosen for city plantings (see species treatments in Elias [1987]). In Tallamy and Shropshire (2009)'s compilation of the Lepidoptera feeding on 1385 plant genera grown in the Mid-Atlantic States, *Fraxinus* ranks sixteenth in richness. Green and white ash trees planted in cities, towns, and parks in the western United States show little evidence of herbivory (DLW pers. observation). Likewise, in European woodlands, ash trees have been documented to have low herbivore loads relative to many other genera of forest trees (Fischbacher et al., 1998). Among four tree genera surveyed near Basel, Switzerland (*Carpinus* L. [hornbeams], *Fagus* L. [beech], *Fraxinus* L. [ash], and *Quercus* L. [oak]), ash yielded only about half the caterpillar frass observed on other surveyed genera. Moreover, while invasive plants generally have depauperate herbivore loads, at least *Lonicera* and *Rhamnus* produce abundant fruits that are exploited by a range of birds and other vertebrates. As with all ecological change, some species will benefit, and others will suffer.

A final note, brought to our attention by Anton Reznicek, is that considerable demographic differences exist among North American *Fraxinus* as to their age and size of first reproduction. Green ash begins flowering and fruiting as a young tree – at diameters frequently ignored by EAB, and thus the species has the potential to persist as young trees, e.g., in open riparian and floodplain communities. By contrast, white and pumpkin ash fruit later, and typically young trees will succumb to EAB infestation before they can bear seed. Hence these species' fate and those of their dependent herbivore faunas are likely to differ substantially from those of green ash.

NORTH AMERICA'S SIXTEEN *FRAXINUS*

Below we provide a synopsis addressing the range, preferred habitat, ecological importance, known susceptibility to EAB, and herbivore specialists of

Table1 . Native ash species found North of Mexico with their USNVC/NatureServe importance and tally of specialist herbivore fauna.

Clade	Species	Common Name	Forest Community Group			Approx. Region	Specialist Herbivores						Total Species
			Dominant	Co-dominate	Total		Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera		
Dipteralae	<i>Fraxinus dipetala</i>	California Ash	1	1	1	West	1	1	1	2	4		
	<i>Fraxinus anomala</i>	Singleleaf Ash	2	1	3	Southwest							
	<i>Fraxinus quadrangulata</i>	Blue Ash	3	3	6	East				1	1		
Melioides	<i>Fraxinus cuspidata</i>	Fragrant Ash				Southwest							
	<i>Fraxinus latifolia</i>	Oregon Ash	10	2	12	West	2	4	4	2	5		
	<i>Fraxinus papillosa</i>	Chihuahuan ash				South							
	<i>Fraxinus americana</i>	White Ash	8	35	43	Midwest/East	2	11	6	9	3	15	
	<i>Fraxinus profunda</i>	Pumpkin Ash	1	4	5	East	1					1	
	<i>Fraxinus pennsylvanica</i>	Green Ash	18	37	55	Midwest/East	1	6	4	6	1	11	
	<i>Fraxinus velutina</i>	Velvet Ash		5	5	Southwest	2	5	8	8	5	20	
	<i>Fraxinus berlandieriana</i>	Mexican Ash	2	2	2	Texas		3				3	
	<i>Fraxinus caroliniana</i>	Carolina Ash	3	6	9	Southeast					1	1	
	<i>Fraxinus albicans</i>	Texas Ash	2	2	2	Texas	1	1				2	
Pauciflorae	<i>Fraxinus greggii</i>	Gregg's Ash				Texas						2	
	<i>Fraxinus gooddingii</i>	Goodding's Ash				Arizona						1	
Fraxinus	<i>Fraxinus nigra</i>	Black Ash	6	8	14	Midwest/Northeast		1	1	1	1	7	
NA	<i>Fraxinus</i> spp.	various ashes	1	1	1	East	1	1	1	5	2	10	

Footnote: In-the-wild host ranges are poorly known for most of the arthropod species in this table. We suspect that virtually all of the taxa that appear to be specialized in this table, in fact, have broader host ranges than indicated above due to undersampling—see *Feeding Guilds and Specificity of Arthropod Herbivores* discussion. Diets of southern and western taxa are especially poorly known.

Table 2. Sixteen globally imperiled forest communities dominated by *Fraxinus*. See NatureServe Explorer (2014) for details on distribution, ranking, and additional plant associations.

Ecological Community dominated by <i>Fraxinus</i> sp.	NatureServe Status	Distribution*	Division
<i>Fraxinus americana</i> / <i>Andropogon gerardii</i> - <i>Sorghastrum nutans</i> - <i>Schizachyrium scoparium</i> - <i>Pycnanthemum tenuifolium</i> Herbaceous Vegetation	Critically imperiled	MD, VA	Eastern North American Dune & Coastal Grassland & Shrubland
<i>Fraxinus americana</i> - <i>Juniperus virginiana</i> / <i>Talinum teretifolium</i> - <i>Polygonum tenue</i> - <i>Opuntia humifusa</i> Wooded Herbaceous Vegetation	Critically imperiled	VA	Eastern North American Grassland, Meadow & Shrubland
<i>Fraxinus americana</i> / <i>Physocarpus opulifolius</i> / <i>Carex pensylvanica</i> - <i>Allium cernuum</i> - (<i>Phacelia dubia</i>) Wooded Herbaceous Vegetation	Imperiled	VA	Eastern North American Grassland, Meadow & Shrubland
<i>Fraxinus americana</i> - <i>Carya glabra</i> / <i>Symphoricarpos orbiculatus</i> - <i>Rhus aromatica</i> / <i>Piptochaetium avenaceum</i> Woodland	Imperiled	GA, NC	Eastern North American Cool Temperate Forest
<i>Fraxinus americana</i> - <i>Carya ovata</i> / <i>Frangula caroliniana</i> / <i>Helianthus hirsutus</i> Woodland	Critically imperiled?	VA	Eastern North American Cool Temperate Forest
<i>Fraxinus americana</i> - <i>Carya glabra</i> / <i>Muhlenbergia sobolifera</i> - <i>Helianthus divaricatus</i> - <i>Solidago ulmifolia</i> Woodland	Imperiled	MD, VA, WV	Eastern North American Cool Temperate Forest
<i>Fraxinus americana</i> - <i>Juglans nigra</i> - <i>Ulmus rubra</i> / <i>Acer barbatum</i> - <i>Ostrya virginiana</i> / <i>Ptelea trifoliata</i> Forest	Imperiled	AL?, FL, GA?	Southeastern North American Warm Temperate Forest
<i>Fraxinus latifolia</i> / <i>Carex deweyana</i> - <i>Urtica dioica</i> Forest	Critically imperiled	OR, WA	Vancouverian Flooded & Swamp Forest
<i>Fraxinus latifolia</i> / <i>Juncus patens</i> Forest	Imperiled	OR	Vancouverian Flooded & Swamp Forest
<i>Fraxinus latifolia</i> - <i>Populus balsamifera</i> ssp. <i>trichocarpa</i> / <i>Rubus spectabilis</i> Forest	Imperiled	OR, WA?	Vancouverian Flooded & Swamp Forest
<i>Fraxinus nigra</i> - <i>Abies balsamea</i> / <i>Rhamnus alnifolia</i> Forest	Critically imperiled	PA?, WV	Eastern North American Flooded & Swamp Forest
<i>Fraxinus pennsylvanica</i> - (<i>Ulmus americana</i>) - <i>Pinus taeda</i> / <i>Morella cerifera</i> - <i>Juniperus virginiana</i> var. <i>silicicola</i> Tidal Forest	Critically imperiled - Imperiled	NC	Eastern North American Flooded & Swamp Forest
<i>Fraxinus pennsylvanica</i> - (<i>Carya aquatica</i>) / <i>Forsiera acuminata</i> / <i>Phanopyrum gymnocarpon</i> Depression Forest	Imperiled?	TX	Southeastern North American Flooded & Swamp Forest
<i>Fraxinus pennsylvanica</i> - <i>Populus heterophylla</i> - <i>Ulmus americana</i> - (<i>Quercus texana</i>) Forest	Imperiled?	AR?, LA	Southeastern North American Flooded & Swamp Forest
<i>Fraxinus quadrangulata</i> - <i>Juniperus virginiana</i> var. <i>virginiana</i> / <i>Schizachyrium scoparium</i> - <i>Lithospermum canescens</i> Woodland	Imperiled	KY	Eastern North American Cool Temperate Forest
<i>Fraxinus quadrangulata</i> - <i>Quercus macrocarpa</i> - <i>Quercus muhlenbergii</i> / <i>Arundinaria gigantea</i> ssp. <i>gigantea</i> / <i>Elymus</i> spp. Woodland	Critically imperiled?	KY	Eastern North American Cool Temperate Forest

* AL - Alabama; AR - Arkansas; FL - Florida; GA - Georgia; KY - Kentucky; LA - Louisiana; MD - Maryland; NC - North Carolina; OR - Oregon; PA - Pennsylvania; TX - Texas; VA - Virginia; WA - Washington; WV - West Virginia

each North American *Fraxinus*. We group ash species by four phylogenetic sections based on Hinsinger et al. (2013), beginning with the nominate Section *Fraxinus*, which is monotypic in the Americas and represented only by black ash (*F. nigra*). Of these four phylogenetic groupings, Section Melioides (in its broad sense) contains the most ecologically important, widespread species of ash; it is also the most speciose section, with 10 North American species. For the purposes of our evaluation, we make the assumption that all 16 North American species are vulnerable to the emerald ash borer, given initial host preference studies and the uncertainty in climate niche models for the insect (Sobek-Swant et al., 2012; Liang and Fei, 2014). However, it seems unlikely to us that the beetle will pose a major threat to the nine species of western arid land ash (*F. albicans* Buckley, *F. anomala* Torr. ex S. Watson, *F. berlandieriana* DC., *F. cuspidata* Torr., *F. dipetala* Hook. & Arn., *F. gooddingii* Little, *F. greggii*, *F. papillosa* Lingelsh, and *F. velutina* Torr.), given that EAB does not inhabit xeric and desert areas in its native range.

Section *Fraxinus*

Black ash. *Fraxinus nigra*, a small tree that is the most northern member of its genus, is distributed across southern Canada from eastern Manitoba to Newfoundland, south in mountains through West Virginia, in the Ohio River Valley to southern Indiana and Illinois, and in much of Iowa (Elias, 1987). Black ash is a major component of 14 forest community Groups (NatureServe Explorer, 2014): six as a dominant tree species and eight as a co-dominant. It is the dominant tree in one critically imperiled (G1) forest community type, the *Fraxinus nigra* - *Abies balsamea* / *Rhamnus alnifolia* forests of West Virginia and Pennsylvania – two states with established EAB populations.

Black ash grows in damp woods, bottomlands, swamps, and other wetlands; it tolerates considerable inundation (Fig. 8). Common associates include black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.), white cedar (*Thuja occidentalis* L.), tamarack (*Larix laricina* [Du Roi] K. Koch), birch (*Betula* L.), and especially red maple (*Acer rubrum* L.). It sometimes grows in nearly pure stands over

hundreds of hectares, principally in the North American Great Lakes region (Fig. 5). Red maple-black ash swamps cover thousands of hectares in southern Canada and the northern United States. Where *Fraxinus nigra* grows in monocultures or as a dominant in either the canopy or subcanopy, the emerald ash borer represents a special threat. Black ash is considered to be the most vulnerable North American ash species as its range lies within the presumed climate niche for the beetle (Klooster et al., 2014; Liang and Fei, 2014; Leah Bauer pers. comm.). Of additional concern is how plant community composition will change in black ash stands post-EAB invasion. Where the canopies are lost there is added risk that the local biota, forest structure, hydrology, and other core ecological attributes will be harmed.

We recorded ten ash specialist herbivores from black ash: one aphid, one seed weevil, one sawfly, one gracillariid leafminer, two noctuids, one pyralid, and three sphingids (Table 4). All but one of these arthropods are also known from Section Melioides sensu stricto *Fraxinus*, and especially *F. americana*, *F. pennsylvanica*, or both. The rarely encountered Canadian sphinx (*Sphinx canadensis*) (Sphingidae) warrants special consideration. Tuttle (2007) wrote: “In northeastern Indiana, [*Sphinx canadensis*] is closely associated with the understory of dense hardwood stands along the perimeter of wetlands. Over several seasons larvae were found exclusively on black ash (*Fraxinus nigra*: Oleaceae), although two additional ash species [*F. americana*, *F. pennsylvanica*] were present. Just as significant, larvae were never found on black ashes growing in open areas, although those same trees supported the larvae of two other sphingid species.” The northern range of the Canadian sphinx closely follows that of black ash. Southward the moth’s range extends beyond that of *F. nigra*, south of the Ohio River, where the species is rare and its *Fraxinus* hosts are unknown.

Section Pauciflorae

Goodding’s ash. *Fraxinus gooddingii* is a narrowly distributed shrubby ash limited to southeastern Arizona and northern Sonora. It grows on rocky slopes (often on limestone), in desert scrub, oak woodlands, and riparian associations, scattered

among other woody shrubs on lower canyon slopes; most records are from arroyos and canyon bottoms from 1100 to 1500 meters (SEINet, 2014).

No previous literature has identified specialist herbivores on this host. Jim Verrier and DLW found *Philtraea elegantaria* (Geometridae) feeding on Goodding's ash in Rock Corral Canyon in the Tumacácori Range. *Sphinx libocedrus* (Sphingidae) feeds on this ash in Arizona (Tuttle, 2007), but species of *Forestiera* are presumed to be its principal hosts.

Gregg's ash. *Fraxinus greggii* is found in the Trans-Pecos region of southwestern Texas south at least to Hidalgo, Mexico. Gregg's ash is often limited to riparian corridors in arroyos, canyon bottoms, and along water courses from 400 to 1800 meters (Powell, 1998; SEINet, 2014). It grows on cliffs, rocky slopes, and canyon bottoms, frequently on limestone. Throughout its range, it grows as a subdominant: typically as scattered plants, in desert canyons and foothills, usually upslope from water.

Noel McFarland (pers. comm.) found caterpillars of *Philtraea paucimacula* (Geometridae) in high densities on Gregg's ash near Laredo, Texas. *Sphinx libocedrus* (Sphingidae) is known from this ash, as well as *Forestiera* (Table 4).

Section Melioides

White ash. *Fraxinus americana* is the second most abundant and widespread native North American ash. It is a common component in many forest types, including bottomlands, open upslope woodlands (Fig. 11), and mixed hardwood forests. Typically, white ash occurs in sites with enriched, but well drained, moist soils, where it grows in association with sugar maple (*Acer saccharum* Marshall), tulip tree (*Liriodendron tulipifera* L.), cherry (*Prunus* L.), beech, sweet gum (*Liquidambar styraciflua* L.), red maple, and willow (*Salix* L.). NatureServe Explorer (2014) identifies eight ecosystems with white ash as a dominant tree and 35 where it is a co-dominant. Of the eight forest community Groups where white ash is dominant, three are critically imperiled (G1) and four are imperiled (G2) (NatureServe Explorer, 2014) (Table 2). White ash seeds are eaten by many birds and squirrels (Burns and Honkala, 1990) and it is

commonly planted as shade trees in yards, parks, and along streets (Elias, 1987; Burns and Honkala, 1990). EAB is thought to prefer other *Fraxinus* species over white ash (Anulewicz et al., 2008), but *F. americana* is still attacked and generally suffers very high mortality. However, apparent resistance of white ash to EAB has recently been seen in Ohio, with some white ash trees surviving in forests where green ash have succumbed to the beetle (Jim Bissell pers. comm.).

White ash has the richest fauna of ash-specialized herbivores in North America – three times as many as any western ash. We list 46 species in Table 4, but suspect that virtually all of the eastern specialists listed only from *Fraxinus* (without an associated species epithet) probably use white ash. Specialist arthropods feeding on *F. americana* include 2 mites, 1 leaf beetle, 5 bark beetles, 4 seed weevils, 1 scarabaeid, 1 agromyzid, 5 gall midges, 2 aphids, 6 mirids, 1 lace bug, 3 sawflies, 2 inchworms, 2 gracillariid miners, 3 owlets (Noctuidae), 1 pyralid, 1 clearwing borer, and 5 sphingids (Table 4). Sixteen herbivores are recorded only from white ash: 2 *Hylesinus* (Curculionidae), 2 *Lignyodes* (Curculionidae), 1 *Xyloryctes* (Scarabaeidae), 4 *Dasineura* (Cecidomyiidae), 1 *Prociophilus* (Aphididae), 3 *Tropidosteptes* (Miridae), 1 *Tethida* (Tenthredinidae), 1 *Hydrelia* (Geometridae), and 1 *Copivaleria* (Noctuidae), although none of these are known to be strictly monophagous.

Green ash. *Fraxinus pennsylvanica* is a small-to-medium-sized, fast growing tree that is the most widely distributed ash species in North America, extending from southwestern Saskatchewan to Cape Breton Island, south to northern Florida and eastern Texas. It is an abundant, ecologically important species throughout much of this range and thrives in floodplains and other bottomlands. Elias (1987) notes that *F. pennsylvanica* is especially abundant through the Mississippi Valley. Green ash is the most common *Fraxinus* to grow as a dominant tree in the U.S. National Vegetation Classification (USNVC) system. Fifty-five ecological community Groups contain *F. pennsylvanica* as a dominant (n = 18) or co-dominant tree (n = 37) (NatureServe Explorer, 2014). Green ash is the dominant tree in three forest Groups considered to be Critically Imperiled to Imperiled; all three of which are flooded swamp forests in the

southeastern United States (Table 2). In forests where green ash is dominant, Burr and McCullough (2014) note that green ash is “unlikely to persist as a dominant species” after EAB invasion. Its seeds are an important forage for a variety of birds, small mammals, and other wildlife; deer and moose (*Alces alces L.*) feed on new growth (Elias, 1987). Its strong wood is sold commercially for bats, oars, and tool handles but is not as desirable for wood working as white ash (Burns and Honkala, 1990).

We record 29 *Fraxinus*-Oleaceae specialists from green ash; thus, it ranks only behind white ash in its importance to *Fraxinus*-specialist herbivores: 1 mite, 1 buprestid, 3 bark beetles (*Hylesinus*), 2 seed weevils (*Lignyodes*), 1 agromyzid, 3 gall midges (Cecidomyiidae), 1 aphid, 5 mirids, 1 sawfly, 4 gracillariid miners, 2 owlets (Noctuidae), 1 pyralid, 1 clearwing borer (Sesiidae), and 3 sphingids. Seven species are recorded only from green ash: one undescribed *Dasineura* (Cecidomyiidae), two *Tropidosteptes* (Miridae), and the two gracillariids *Marmara basidendroca* and *Marmara corticola*. The last two of these, so far as known, are monophages, at least at the type locality and surrounding areas of upstate New York (Fitzgerald, 1973; Terry Fitzgerald pers. comm.). See also *Imperilment Risk Rating* discussion.

Mexican ash. *Fraxinus berlandieriana* is a small tree that occurs from the vicinity of Austin, Texas southward and westward into Mexico. The core of its range is in the Mexican states of Coahuila, Nuevo Leon, and Tamaulipas. It grows in moist canyons and along streams and rivers of the Rio Grande Plains and southern prairies (Vines, 1984) and is frequently planted as a shade tree in parks and cities. Two community types in Texas include Mexican ash as a co-dominant (n = 2), one of which is considered critically imperiled/imperiled (G1G2) (NatureServe Explorer, 2014).

Ash specialists reported from the United States include the buprestid *Trigonogya reticulaticollis*, the chrysomelid *Capraita sexmaculata*, and the seed weevil *Lignyodes helvolus*. While Mexican ash is the only reported host for *T. reticulaticollis*, based on the biology of related metallic wood boring beetles, it is probable that its host range will be found to include other Oleaceae.

Carolina ash. *Fraxinus caroliniana* is a small tree of the Atlantic Coast Plain from Virginia, south through much of Florida, west to east Texas and southern Arkansas. It grows in swamps, wetlands, bottomlands, and other mesic to wet forest types. Like many other members of the genus, it does especially well in marl soils (SEINet, 2014). Carolina ash commonly grows with gums (*Nyssa L.*), hollies (*Ilex L.*), sweet gum, sugarberry (*Celtis laevigata Willdenow*), and others (Elias, 1987); it can be locally abundant as an understory member of bald cypress-tupelo swamps (SEINet, 2014). *Fraxinus caroliniana* is a dominant in nine forest community Groups: three as a dominant and six as a co-dominant tree (NatureServe Explorer, 2014). It occurs in dense monospecific stands in coastal plain areas of Louisiana and Texas (in “*Fraxinus caroliniana* Seasonally Flooded Forests”), which are deemed G2G3 imperiled-vulnerable communities. Only one herbivore, the sphingid moth *Ceratonia undulosa*, an oligophage on Oleaceae, is recorded from this *Fraxinus*. The lack of feeding records for this ash is almost certainly an artifact of limited sampling, presumably because its preferred habitat is in swamps and wetlands and it is not a commercially important ash.

Fragrant ash. *Fraxinus cuspidata* is a shrub (or sometimes small tree) that is found in scattered populations across the southwestern United States from northwestern Arizona to western Texas and south into Mexico, mostly in the foothills of desert ranges (SEINet, 2014). It prefers well-drained, rocky soils in canyons, and north facing cliffs of limestone, sandstone, or igneous soils (Elias, 1987; Powell, 1998; SEINet, 2014). It tends to occur in low densities intermixed among oaks, leguminous trees, and other woody plants.

Two specialist herbivores have been recorded from this small ash: DLW collected caterpillars of a *Sympistis heterogena* (Noctuidae) feeding on new spring leaves in May 2014 and a second unidentified noctuid² species in July of 2014.

Oregon ash. *Fraxinus latifolia* is a Pacific Coast tree that grows from the Olympia area in

² The caterpillar, seen in late July, was banded with smoky red in the early instars and is a new foliage specialist.

western Washington south to the San Francisco Bay Area (California) and southern Sierra Nevada, as well as in disjunct populations in southern California's mountains. The tree grows in "moist rich soils along streams and rivers, and in canyons" to 500 meters (Elias, 1987). It is an abundant and ecologically important tree along riparian corridors throughout much of its range, and is the only commercially important *Fraxinus* in western North America. Oregon ash is a dominant tree in ten forest community Groups and a co-dominant in two others. While it will grow in monocultures, at least along streams and in floodplains, it more typically grows in mixed hardwood stands with maple, alder (*Alnus* Mill.), poplar (*Populus* L.), and willow; Elias (1987) also adds California laurel (*Umbellularia californica* [Hook. & Arn.] Nutt.) and grand fir (*Abies grandis* [Douglas ex D. Don] Lindley) as associates of *F. latifolia*. Three forest communities in the Pacific Northwest dominated by Oregon ash are regarded as critically imperiled/imperiled in NatureServe Explorer (2014) (See Table 2).

We record 17 species of ash specialists from Oregon ash, many for the first time: 2 mites, 2 bark beetles, 2 seed weevils, 1 aphid, 2 mirids, 1 tingid, 2 sawflies, and 1 inchworm (Geometridae), 1 gracillariid leafminer, 1 owlet moth, and 1 ermine moth (Yponomeutidae). Five of these are only known from Oregon ash: *Hylesinus oregonus* (Curculionidae: Scolytinae); *Lignyodes auratus* (Curculionidae: Curculioninae); *Philtraea latifoliae* (Geometridae), *Caloptilia* n. sp. (Gracillariidae), and *Sympistis fortis* (Noctuidae). We suspect that their strict monophagy is either an artifact of undersampling or because *Fraxinus* specialists whose ranges are restricted to the Sierra and areas north of San Francisco are monophagous simply because *F. latifolia* is the only ash that grows where they occur.

Chihuahua ash. *Fraxinus papillosa* is a geographically restricted ash that grows to become a small tree. It is found in small populations through desert ranges of southeast Arizona, southwestern New Mexico, the Chinati Mountains of west Texas, and southward into the Sierra Madre Occidental Mountains of Mexico (Elias, 1987; Powell, 1998). Typically *F. papillosa* grows in canyon bottoms and

on north-facing cliffs (SEINet, 2014). Like other desert ashes, it occurs as scattered plants in woody associations near water or in microhabitats with reduced moisture stress. No ash specialists are currently recorded on *F. papillosa*. In Hinsinger et al.'s (2013) study, Chihuahuan ash grouped with Oregon ash (*F. latifolia*), in a clade outside of all other members of the *Melioides sensu stricto* section of the genus. Because of this phylogenetic difference and its taxonomic and geographic isolation, Chihuahuan ash strikes us as a likely candidate for hosting unique herbivores.

Pumpkin ash. *Fraxinus profunda* grows in scattered locations across eastern North America, with most occurrences along the Atlantic Coastal Plain and through the Ohio and Mississippi River Valleys. It is restricted to very wet soils that include bottomlands, floodplains, swamps (especially bald cypress and tupelo swamps), and coastal marshes (Elias, 1987; Burns and Honkala, 1990; Nesom, 2010) (Figs. 7, 9). *Fraxinus profunda* is a dominant (n = 1) and co-dominant (n = 4) in five eastern forest community types, one of which is imperiled (NatureServe Explorer, 2014). This ash species is quite susceptible to EAB; devastated would not be an overstated descriptor for some local Ohio preserves where pumpkin ash once grew as a dominant species (Jim Bissell pers. comm.)

Only one arthropod species is recorded from *F. profunda*: a mite that is not a specialist on pumpkin ash (Table 1). No doubt pumpkin ash's poorly sampled herbivore fauna is a reflection of the difficulty involved with sampling the inundated wetlands where this tree thrives. Certainly it is a candidate for more study, especially given its susceptibility and because its range falls entirely within the predicted climatic niche of EAB.

Velvet ash. *Fraxinus velutina* is a small ash of the southwestern United States and northwestern Mexico. Its U. S. range is concentrated in Arizona and extends westward through arid portions of southern California, Nevada, Utah, and eastward into the Trans-Pecos region of Texas. It grows near streams, rivers, washes, and other areas of reduced moisture stress. Common associates include hackberry (*Celtis occidentalis* L.), oak, poplar, sycamore (*Platanus* L.), and willow. It reaches greatest importance in mesic stretches of

canyons between 1200 and 1600 meters where it “can form almost pure stands” (Elias, 1987). Velvet ash is listed as a co-dominant tree in five forest community Groups in NatureServe Explorer (2014).

We record 20 ash specialist herbivores from velvet ash, the third most of any *Fraxinus* species and the greatest number for any western species: 2 mites, 1 bark beetle, 2 seed weevils, 2 scarab beetles, 2 aphids, 2 scale insects, 2 plant bugs, 1 stink bug, 1 lace bug, 2 owl moths (Noctuidae), and 3 sphingids. Most of these are known only from *F. velutina*: the mite *Brevipalpus cardinalis* (Tenuipalpidae), the weevil *Lignyodes arizonicus* (Curculionidae), the beetles *Dynastes granti* and *Xyloryctes thestalus* (both Scarabaeidae), the armored scales *Diaspidiotus fraxini* and *Diaspis fraxini* (both Diaspididae), the plant bug *Tropidosteptes illitus* (Miridae), the stink bug *B. rolstoni* (Pentatomidae), and the moths *Chloronycta tybo* and *Sympistis punctilinea* (both Noctuidae) and *Ceratonia sonorensis* and *Sphinx near chersis* (both Sphingidae). In the Sonoran and Chihuahuan deserts of the western United States, velvet ash is the only *Fraxinus* considered to be an ecologically dominant or, more commonly, co-dominant species. Consequently, the loss of velvet ash would have an impact on all southwestern *Fraxinus* herbivores, given that it accounts for most of the ash biomass in the southwestern United States.

Section Dipetalae

Singleleaf ash. *Fraxinus anomala* is a shrub or small spreading tree that grows in canyons, desert drainages, washes, and along water bodies of the North American Great Basin region. It exists as scattered stands in western Colorado, Utah (where it is widespread), southern Nevada, and southeastern California, central and northern Arizona, and extreme northwestern New Mexico (SEINet, 2014). *Fraxinus anomala* is a common riparian element between 600-1,900 meters. NatureServe Explorer (2014) recognizes singleleaf ash as a dominant (n = 2) or co-dominant (n = 1) in three southwestern plant community associations (all three are currently unranked or unrankable due to lack of data). We do not know of any specialist ash herbivores from *F. anomala*, although we suspect that it is the primary

host for *Philatraea utahensis* Buckett.

California or two-petal ash. *Fraxinus dipetala* is a shrubby ash that grows in scattered populations in central and southern California’s coastal ranges and the foothills of the Sierra Nevada Mountains. It thrives either on slightly acidic granite slopes, often near watercourses, or on slightly alkaline clays in chaparral associations. Below 500 meters, it is usually restricted to the upslope vicinities of washes and watercourses. Above this, California ash occurs in chaparral and other foothill communities, typically as a scattered element growing with *Pinus* L. (pine), oak, *Arctostaphylos* Adans. (manzanita), and others (Elias, 1987; SEINet, 2014). *Fraxinus dipetala* is listed as a co-dominant (along with *Prunus ilicifolia* [Nutt. ex Hook. & Arn.] Walp.) in one U.S. forest community Group by NatureServe Explorer (2014).

The herbivore fauna of California ash is not well known – the plant is easily overlooked, and rarely common. Four ash-specialist herbivores are recorded from California ash: 1 mite, 1 aphid, 1 inchworm (Geometridae), and 1 ermine moth (Yponomeutidae). Two moths are known exclusively from this ash: *Philtraea surcaliforniae* (Geometridae) and *Zelleria near semitincta* (Yponomeutidae) (Buckett, 1970) (Table 4).

Blue ash. *Fraxinus quadrangulata* is a small to large tree (Fig. 6) whose core distribution is in the Midwestern United States from eastern Kansas to extreme southern Ontario, south into Arkansas and northern Alabama. Blue ash grows in upland woods and on slopes usually over limestone, but also in moist woodlands and evidently even bottomland forests (Elias, 1987). Typically it occurs as a subdominant species (n = 3) intermixed in stands dominated by oak, mockernut hickory (*Carya tomentosa* Sarg.), sweet gum, and others. It is listed as the dominant tree species in three Kentucky forest community types (NatureServe Explorer, 2014): critically imperiled (G1) blue ash-oak savannah woodlands (Bryant et al., 1980; NatureServe Explorer, 2014); imperiled (G2) blue ash - eastern red-cedar / little bluestem - hoary puccoon woodlands; and possibly no longer extant (GH) *Fraxinus quadrangulata* - *Quercus macrocarpa* / *Arundinaria gigantea* ssp. *gigantea* wooded shrublands. *Fraxinus*

quadrangulata is believed to be the most EAB-resistant *Fraxinus* in eastern North America and, consequently, its relative abundance may increase in woodlands and forests where other ash succumb to the beetle (Anulewicz et al., 2007; Tanis and McCullough, 2012).

Blue ash has a surprisingly modest herbivore fauna. Only one ash specialist is recorded from this ash, the moth *Plagodis kuetzingi* (Geometridae), which also occurs on *F. americana* and presumably other ashes. Robinson et al. (2014) lists only two generalist Lepidoptera for blue ash. Its diminished herbivore fauna no doubt is a reflection of its taxonomic isolation: it is the only member of the Dipetalae Section in eastern North America (Hinsinger et al., 2013). Given the above, perhaps it is not surprising that blue ash is more resistant to EAB than other eastern members of the genus. Given that it represents a unique taxonomic entity in eastern North America, blue ash is a candidate for a focused herbivore survey, especially for cecidomyiids, leaf or bast miners, and other herbivores known to show extreme monophagy.

Texas ash. *Fraxinus albicans* (= *F. texensis*) is a small drought-tolerant relative of white ash that grows on limestone from the Arbuckle Mountains of southern Oklahoma southward across the Edwards Plateau into south central Texas (Vines, 1984; Elias, 1987). It is a co-dominant (with oak) in two forest community types (NatureServe Explorer, 2014). We know of only two reports of specialist herbivores from Texas ash: 1 mite and 1 weevil, neither of which is monophagous on *F. albicans*. Robinson et al. (2014) does not list any lepidopterans from Texas ash. The dearth of feeding records for this ash is surely a reflection of its limited geographic distribution and thus a sampling artifact. Presumably because of its close relation to *F. americana* (Vines, 1984), *F. caroliniana*, and other members of the *Melioides sensu stricto* section of the genus (Hinsinger et al., 2013), *F. albicans* will be found to share many herbivores with other *Fraxinus*.

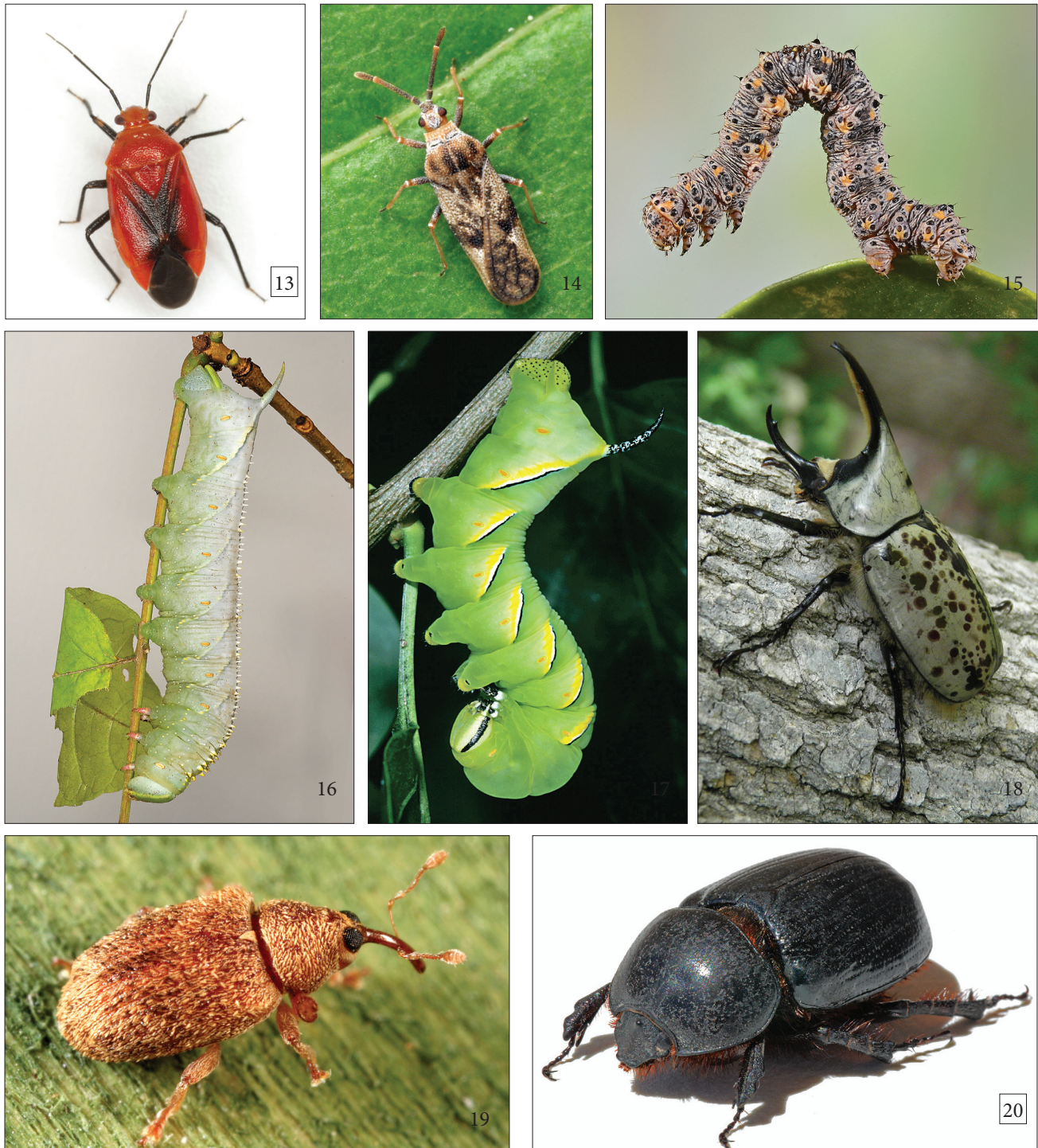
EFFECTS ON VERTEBRATES

Martin et al. (1951) regarded North American ashes to be “only of moderate importance to wildlife.” No vertebrates are monophagous or otherwise exclusively dependent on ash or ash-dominated communities, although some local populations might be energetically or ecologically dependent on ash simply due to the fact that *Fraxinus* are the dominant or co-dominant trees in the woodland or forest types where they live (northern black ash swamps provide compelling examples of such) (Fig. 5). A summary of vertebrates using ash as a food source is given in Table 3, with the proviso that the published literature is greatly biased towards game species. We also note that the literature for vertebrates is largely qualitative, with little data on the importance of ash relative to other food resources; we suspect that the paucity of studies addressing the ecological importance of ash may be a reflection of the fact that, by itself, ash trees rarely serve as a core food or sheltering resource.

We know most about the six species of *Fraxinus* where ash has been identified as being a community dominant tree species: black, blue, green, Oregon, pumpkin, and white. Among mammals, ungulates and lagomorphs (rabbits) are often mentioned as feeding on non-woody tissues of ash. Northward, green and especially black ash are browse sources for moose (Elias, 1987) and the white-tailed deer (*Odocoileus virginianus* Zimmermann). A wide range of rodents, but especially chipmunks, mice, and squirrels, consume the winged seeds. And, while we found little mention of such in the literature, undoubtedly North American beavers (*Castor canadensis* Kuhl) consume ash across their range. Ash seeds are regarded to be of moderate importance to seed-eating, woodland or forest dwelling birds such as cardinals, chickadees, finches, and grosbeaks. Grouse, quail, and turkey are ground feeders known to consume ash seeds (Martin et al., 1951). Given the propensity of the genus for wetlands, the importance of ash seeds to waterfowl has likely been underestimated – we only found specific mention of wood ducks (*Aix sponsa* [L.]) feeding on ash samaras (Martin et al., 1951). In forests where *Fraxinus* are dominants, ashes also provide cover (e.g., for

Table 3. Vertebrates that feed on *Fraxinus*.

Ash Tree	Mammals	Birds	Literature	Comments
<i>Fraxinus albicans</i>				
<i>Fraxinus americana</i>	white tail deer, fox squirrels	wood ducks, quail, turkey grouse, bobwhite, finches (esp. purple finch), grosbeaks (esp. pine grosbeak), cardinals, other songbirds	Elias, 1987; Burns and Honkala, 1990	
<i>Fraxinus anomala</i>				
<i>Fraxinus berlandieriana</i>				
<i>Fraxinus caroliniana</i>				
<i>Fraxinus cuspidata</i>	deer			
<i>Fraxinus dipetala</i>				
<i>Fraxinus gooddingii</i>				
<i>Fraxinus greggii</i>	deer, rabbits, ground squirrels, other rodents	many birds		
<i>Fraxinus nigra</i>	white tail deer, moose, small mammals	wood ducks, grouse, turkey, song birds	Elias, 1987; Burns and Honkala, 1990	
<i>Fraxinus papillosa</i>				
<i>Fraxinus profunda</i>	white tail deer	wood ducks, many other birds	Elias, 1987; Burns and Honkala, 1990	
<i>Fraxinus pennsylvanica</i>	white tail deer, mule deer, moose, rabbits, squirrels, and other rodents	wood ducks, quail, turkey, cardinals, finches	Elias, 1987; Burns and Honkala, 1990	large seed crops
<i>Fraxinus quadrangulata</i>	white tail deer	wood ducks, quail, turkey, songbirds	Elias, 1987	
<i>Fraxinus nigra</i>	white tail deer, moose, small mammals	wood ducks, grouse, turkey, song birds	Elias, 1987; Burns and Honkala, 1990	
<i>Fraxinus velutina</i>			Elias, 1987	*little value to wildlife ²
<i>Fraxinus</i> spp.	chipmunks		Martin et al., 1951; Rhoads and Block, 2005	



Figures 13 - 20. Ash-specialist insects that represent some of the larger taxa threatened by EAB. (13) *Tropidosteptes cardinalis*, Family Miridae (Photo courtesy Mike Quinn); (14) *Leptoypa mutica*, Family Tingidae. (Photo courtesy Tom Murray); (15) *Philtraea elegantaria*, Family Geometridae (Photo DLW); (16) *Sphinx franckii*, Family Sphingidae (Photo DLW); (17) *Sphinx kalmiae*, Family Sphingidae (Photo DLW); (18) *Dynastes granti*, Family Scarabaeidae (Photo courtesy Margarethe Brummerman); (19) *Lignyodes helvolus*, Family Curculionidae (Photo courtesy Bill Johnson); (20) *Xylorctes thestalus*, Family Scarabaeidae. (Photo courtesy Richard Hayes)

moose [Gould and Bauer, 2009]) and above-ground structure important to vertebrate wildlife for roosting and nesting. Ash trees with broken tops or otherwise damaged stems sometimes form cavities which are used by a variety of birds, bats, and other animals.

One ash community type warrants special mention, i.e., woodland pools dominated by pumpkin ash (*F. profunda*) (Figs. 7, 9). In southeastern Michigan, portions of Ohio, and presumably elsewhere, pumpkin ash is sometimes the sole or dominant tree that grows in the standing water of vernal and permanent (fishless) forest pools and as such provides all or much of the canopy closure. Ash-dominated woodland and forest pools are an important breeding habitat for five species of mole salamanders in the Midwestern United States (spotted [*Ambystoma maculatum* Shaw], Jefferson [*A. jeffersonianum* (Green)], blue-spotted [*A. laterale* Hallowell], small-mouthed [*A. texanum* Matthes], and marbled [*A. opacum* Gravenhorst]), and an occasional breeding habitat for the eastern tiger salamander (*A. tigrinum* Green). Many of these salamanders are important conservation targets that receive legal protection. Of these, the marbled salamander may be the most vulnerable because females lay their eggs in mud during the fall, in anticipation of autumn and winter rains (Degraaf and Rudis, 1986; Pfungsten et al., 2013; Kenney, 1995). Greater sun exposure due to canopy loss could affect the hydrology of wetlands, especially in the fall, before rains and snow melt have had a chance to fill them. Most worrisome is that, in Ohio, pumpkin ash is sometimes the only tree found growing in these saturated to flooded soils where mole salamanders and other wildlife breed (Jim McCormac, pers. comm.).

While much wildlife will experience detrimental effects from ash elimination, no doubt some vertebrates will benefit. Where EAB has invaded in the Midwestern United States, woodpecker numbers have spiked in the vicinity of infestations because EAB larvae serve as an abundant, easily harvested food resource and dying ash provide nesting trees for the birds (Cappaert et al., 2005b; Koenig et al., 2013). Similarly, standing dead ash trees are preferred roosting and nesting sites for many other vertebrates and will, for a limited time, benefit wildlife posthumously. Canopy gaps left by these dying ash

species may also allow fruit-producing shrubs such as *Cornus*, *Lonicera*, and *Rhamnus* (two of which are, unfortunately, non-native invasives) to colonize and thrive, the fruits of which will benefit a variety of fruit-eating birds and mammals.

EFFECTS ON ASH-FEEDING INVERTEBRATES

We identify 98 *Fraxinus*-dependent invertebrate herbivores (or inquilines) as potentially threatened by the spread of EAB, 45 of which are reported here for the first time (Figs. 13-20). Because our compilation of *Fraxinus* feeders was a bottom-up tabulation for all insects and mites, built upon the collective knowledge of more than 80 taxonomic experts, we feel the data in Table 4 offer a unique look at the taxonomic distribution of ash-specialist herbivores from the estimated 70,000 species of North American insects (Arnett, 2000) and Acari (mites). Specialist herbivores that would be imperiled or extirpated in the United States and Canada by the loss of *Fraxinus* include mites (n = 6) and members of five insect orders: Lepidoptera (n = 32), Hemiptera (n = 25), Coleoptera (n = 24), Diptera (n = 9), and Hymenoptera (n = 3) (Fig. 21). The most speciose lineage of metazoans on the planet, beetles, had fewer specialists than Lepidoptera and essentially equivalent richness to that of Hemiptera. While the focal taxon of our study was *Fraxinus* and related Oleaceae, we suspect that the proportions represented here are likely to apply across most temperate woody, broadleaf plant taxa, and may well apply to other continental biogeographic provinces as well.

Four genera contain six or more species that will be threatened by the spread of EAB; in decreasing diversity these include *Tropidosteptes* plant bugs (Miridae) (n = 14) (Fig. 13), *Hylesinus* bark beetles (Curculionidae) (n = 7), *Lignyodes* seed weevils (Curculionidae) (n = 7) (Fig. 19), and *Sphinx* hawkmoths (n = 6) (Sphingidae) (Figs. 16, 17). Four other genera contain noteworthy radiations on *Fraxinus*: *Dasineura* gall midges (Cecidomyiidae), *Prociphilus* aphids (Aphididae), *Philtraea* inchworms (Geometridae) (Fig. 15), and *Sympistis* sawflies (Noctuidae).

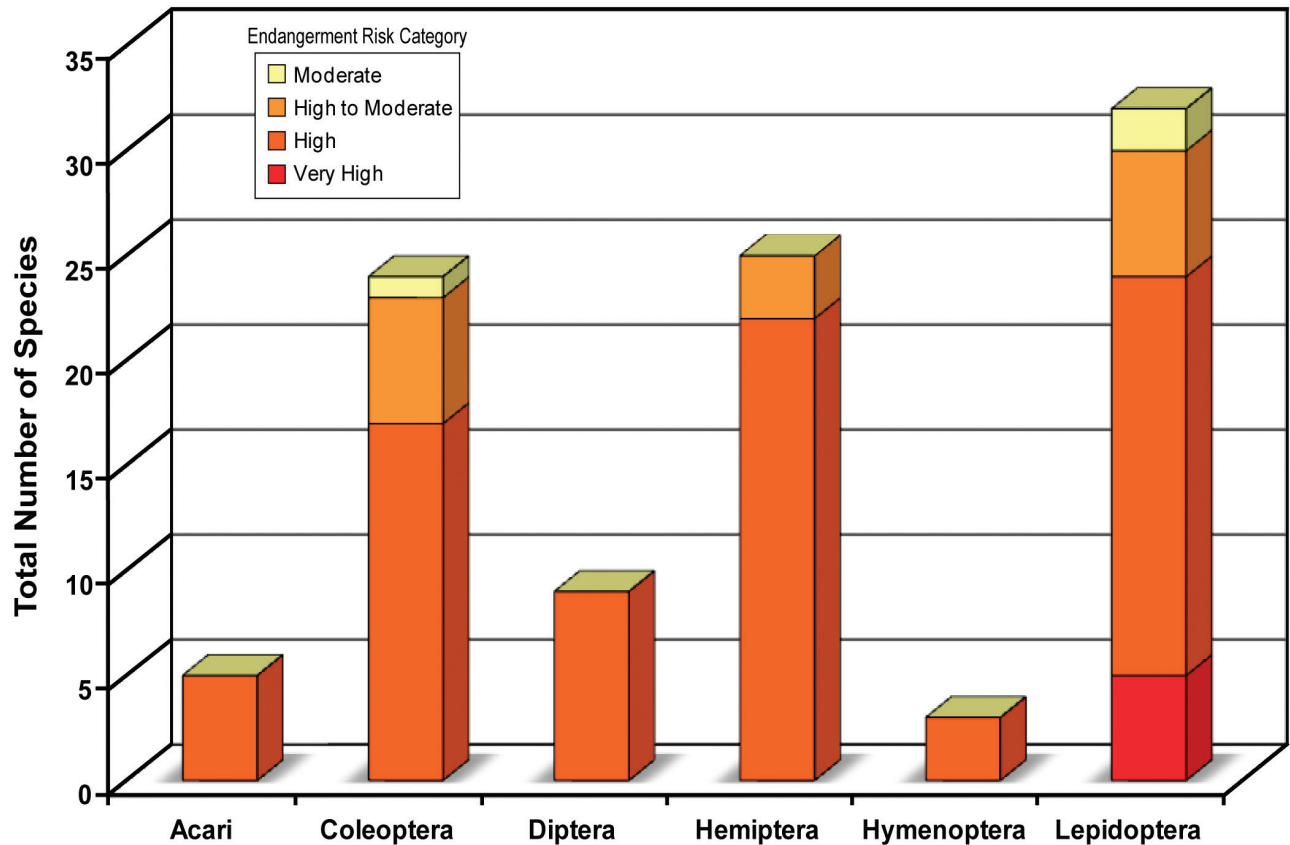


Figure 21. At risk arthropod herbivores by taxon and imperilment score.

Charismatic Arthropod Herbivores

The sphingids or hawkmoths deserve special mention because of their beauty, size, and popularity (with moth watchers, photographers, and collectors), as well as their vulnerability and importance in vertebrate diets. Furthermore, the degree of sphingid imperilment has heretofore been underestimated. Gandhi and Herms (2010) listed eight native and one exotic species of sphingids as potentially affected by EAB invasion; the only sphingid that they ranked as highly to moderately imperiled by EAB was *Manduca brontes*, a Caribbean and South Florida species that feeds on *Tecoma stans* (L.) Juss. ex Kunth in the Bignoniaceae. *Fraxinus* host records for the moth were determined to be erroneous by Robinson et al. (2002); we exclude this species from our assessment. Six sphingids that were regarded as generalists³ of

³ *Sphinx canadensis*, *S. chersis*, *S. kalmiae*, and *S. franckii*, *Manduca jasminearum*, and *Ceratomia undulosa* could be classified

low or moderate endangerment risk in their compilation are treated here as imperiled ash specialists: *Ceratomia undulosa*, *Manduca jasminearum*, *Sphinx canadensis*, *S. chersis*, *S. franckii* (Fig. 16), and *S. kalmiae* (Fig. 17). We add three resident hawkmoths not mentioned in previous ecological assessments of the North American sphingid fauna: *Ceratomia sonorensis*, *Sphinx libocedrus*, and *S. near chersis*. We assign endangerment risks to these nine ash-dependent

as polyphagous taxa if one consults treatments such as Covell (2005), Wagner (2005), Tuttle (2007), Robinson et al. (2014), etc. But if records >50-years old or exceptional reports are excluded, all are better regarded as imperiled *Fraxinus* or *Oleaceae* specialists. Older literature is fraught with misidentifications and erroneous host records: For example, the host records of *Ulmus* for *S. franckii* and *M. jasminearum* are almost certainly based on misidentifications of larval *Ceratomia amyntor* (Geyer, 1835), an elm feeder. To the best of our knowledge (and that of Jim Tuttle in litt.) none of these six species has been collected on host plants outside of the *Oleaceae* in our lifetimes, and all but *S. kalmiae* (which can be found on other *Oleaceae*) are best considered *Fraxinus* specialists.

Table 4. Specialist herbivores on *Fraxinus* and related Oleaceae.

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Acari	Eriophyiidae	<i>Aceria fraxiniflora</i> (Felt)	<i>Fraxinus americana</i> , <i>F. latifolia</i>	High	flower gall	Felt, 1918; Baker et al., 1996; Ron Ochu pers. comm.	
Acari	Eriophyiidae	<i>Aceria fraxini</i> (Garman)	<i>Fraxinus americana</i> , <i>F. latifolia</i> , <i>F. pennsylvanica</i>	High	leaf gall	Felt, 1918; Baker et al., 1996	
Acari	Eriophyiidae	<i>Tegolophus califraxini</i> (Keifer)	<i>Fraxinus dipetala</i> , <i>F. velutina</i>	High	leaves	Jeppson et al., 1975; Baker et al., 1996	
Acari	Tenuipalpidae	<i>Brevipalpus fraxini</i> DeLeon	<i>Fraxinus</i> , <i>F. profunda</i>	High	leaves	DeLeon, 1961; Baker and Suigong, 1988; Ron Ochu pers. comm.	
Acari	Tenuipalpidae	<i>Brevipalpus cardinalis</i> (Banks)	<i>Fraxinus velutina</i> , <i>F. albicans</i>	High	unknown	Banks, 1915; Baker and Suigong, 1988; Johnson, 2007	
Coleoptera	Buprestidae	<i>Agrilus subcinctus</i> Gory	<i>Fraxinus pennsylvanica</i> , <i>Ligustrum</i>	High to Moderate	cambium	Bright, 1987; Ted MacRae unpubl. data; Richard Westcott in litt.	
Coleoptera	Buprestidae	<i>Trigonogya reticulatipennis</i> (Schaeffer)	<i>Fraxinus berlandieriana</i>	High?	recently dead wood	MacRae, 2006; Ted MacRae unpubl. data; Richard Westcott in litt.	Confirmed larval host; Knull (1937) recorded adults collected on <i>F. caroliniana</i> , but that is a misidentification of <i>F. berlandieriana</i> (Richard Westcott in litt.). Host range needs more study.
Coleoptera	Chrysomelidae	<i>Capraita sexmaculata</i> (Illiger)	<i>Chionanthus virginicus</i> , <i>Fraxinus americana</i> , <i>F. berlandieriana</i> , <i>Forestiera ligustrina</i>	High to Moderate	leaves	Clark et al., 2004; Shawn Clark in litt.; Ed Riley in litt.	Probably obligatory on ash; adult diet includes other Oleaceae hosts.
Coleoptera	Chrysomelidae	<i>Trichaltica tibialis</i> (Jacoby)	<i>Fraxinus</i>	High	root	Clark et al., 2004; Shawn Clark in litt.; Ed Riley in litt.	Larvae root feeders; almost certainly specialists.
Coleoptera	Chrysomelidae	<i>Trichaltica scabricula</i> (Crotch)	<i>Fraxinus</i>	High	root	Clark et al., 2004; Shawn Clark in litt.	Larvae root feeders; almost certainly specialists.
Coleoptera	Curculionidae	<i>Hylesinus aculeatus</i> (Say)	<i>Fraxinus americana</i> , <i>F. pennsylvanica</i>	High	cambium	Blatchley and Leng, 1916; Wood, 1982; Atkinson, 2014, Anthony Cognato in litt.	

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Coleoptera	Curculionidae	<i>Hylesinus californicus</i> (Swaine)	<i>Fraxinus americana</i> , <i>F. latifolia</i> , <i>F. pennsylvanica</i> , <i>F. velutina</i> , <i>Olea europaea</i>	High to Moderate	cambium	Wood, 1982; Langor and Hergert, 1993; Atkinson, 2014; Anthony Cognato in litt.	
Coleoptera	Curculionidae	<i>Hylesinus criddlei</i> (Swaine)	<i>Fraxinus americana</i> , <i>F. pennsylvanica</i>	High	cambium	Atkinson, 2014; Anthony Cognato in litt.	
Coleoptera	Curculionidae	<i>Hylesinus fasciatus</i> LeConte	<i>Fraxinus americana</i>	High	cambium	Blatchley and Leng, 1916; Wood, 1982; Atkinson, 2014; Anthony Cognato in litt.	
Coleoptera	Curculionidae	<i>Hylesinus mexicanus</i> (Wood)	<i>Fraxinus albicans</i> , <i>Forestiera</i> , <i>Ligustrum</i> , <i>Olea</i>	Moderate	cambium	Atkinson, 2014; Anthony Cognato in litt.	
Coleoptera	Curculionidae	<i>Hylesinus oregonus</i> (Blackman)	<i>Fraxinus latifolia</i>	High	cambium	Wood, 1982; Burns and Honkala, 1990; Atkinson, 2014; Anthony Cognato in litt.	
Coleoptera	Curculionidae	<i>Hylesinus pruinosis</i> Eichhoff	<i>Fraxinus americana</i>	High	cambium	Wood, 1982; Atkinson, 2014; Anthony Cognato in litt.	
Coleoptera	Curculionidae	<i>Lignyodes arizonicus</i> (Sleeper)	<i>Fraxinus velutina</i>	High	seed	Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Lignyodes auratus</i> Clark	<i>Fraxinus latifolia</i>	High	seed	Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Lignyodes bischoffi</i> (Blatchley)	<i>Fraxinus americana</i> , <i>F. nigra</i> , <i>F. pennsylvanica</i> , <i>Syringa</i>	High to Moderate	seed	Knoll, 1932; Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Lignyodes fraxini</i> (LeConte)	<i>Fraxinus americana</i>	High	seed	Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Lignyodes helvolus</i> (LeConte)	<i>Fraxinus americana</i> , <i>F. berlandieriana</i> , <i>F. nigra</i> , <i>Syringa</i>	High to Moderate	seed	Clark, 1980; Robert Anderson pers. comm.	

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Coleoptera	Curculionidae	<i>Lignyodes helvulus</i> (LeConte)	<i>Fraxinus americana</i> , <i>F. berlandieriana</i> , <i>F. nigra</i> , <i>Syringa</i>	High to Moderate	seed	Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Lignyodes horridulus</i> (Casey)	<i>Fraxinus latifolia</i> , <i>F. pennsylvanica</i> , <i>F. velutina</i> , <i>Syringa</i>	High to Moderate	seed	Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Lignyodes ocularis</i> (Casey)	<i>Fraxinus</i>	High	seed	Clark, 1980; Robert Anderson pers. comm.	
Coleoptera	Curculionidae	<i>Psomus armatus</i> (Dietz) (including <i>politus</i>)	<i>Fraxinus americana</i>	High	seed	Blatchley and Leng, 1916; Arnett et al., 2002; Charles O'Brien in litt.; Richard Westcott in litt.	
Coleoptera	Scarabaeidae	<i>Dynastes granti</i> Horn	<i>Fraxinus velutina</i>	High-see comments	new shoot feeder	Bill Warner in litt.; Pat Sullivan pers. comm.; Margarethe Brummerman pers. comm.	Larvae may be generalists but adults feed on ash; beetle rare or absent away from <i>Fraxinus</i> (Bill Warner in litt.).
Coleoptera	Scarabaeidae	<i>Dynastes tityus</i> L.	<i>Fraxinus</i>	High-see comments	new shoot feeder	Glaser, 1976	Adults feed (and mate?) at wounds gnawed into ash shoots.
Coleoptera	Scarabaeidae	<i>Xyloryctes jamaicensis</i> (Drury)	<i>Fraxinus americana</i>	High	root	Ratcliffe, 2009	See discussion in Ratcliffe 2009.
Coleoptera	Scarabaeidae	<i>Xyloryctes thestalus</i> Bates	<i>Fraxinus velutina</i> and likely other <i>Fraxinus</i> species, esp. in Mexico	High	root	Ratcliffe, 2009	See discussion in Ratcliffe 2009.
Diptera	Agromyzidae	<i>Phytobia</i> sp.	<i>Fraxinus americana</i> , <i>F. pennsylvanica</i>	High	cambium	Solomon, 1995; Sonja Sheffer in litt.	
Diptera	Cecidomyiidae	<i>Contarinia thalactri</i> (Felt) (including <i>fraxini</i>)	<i>Fraxinus</i> , <i>F. americana</i>	High	leaf gall (inquiline)	Gagné, 1989	Phytophagous inquiline in galls of <i>Dastineura tumidosae</i> .
Diptera	Cecidomyiidae	<i>Contarinia</i> n. sp.	<i>Fraxinus pennsylvanica</i>	High	samara gall	Gagné, 1989	Samara exocarp gall; gregarious; undescribed evidently; near European species <i>C. marchali</i> .

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Diptera	Cecidomyiidae	<i>Contarinia</i> n. sp.	<i>Fraxinus pennsylvanica</i>	High	seed or samara gall	Raymond Gagné in prep.	Seed or samara gall; undescribed; not near European species <i>C. marchali</i> .
Diptera	Cecidomyiidae	<i>Dasineura apicata</i> (Felt)	<i>Fraxinus americana</i>	High	leaflet gall	Felt, 1918; Gagné, 1989	
Diptera	Cecidomyiidae	<i>Dasineura fraxinifolia</i> (Felt)	<i>Fraxinus americana</i>	High	leaflet gall	Felt, 1918; Gagné, 1989	
Diptera	Cecidomyiidae	<i>Dasineura pellex</i> (Osten Sacken)	<i>Fraxinus americana</i>	High	leaflet gall	Felt, 1918; Gagné, 1989; Raymond Gagné in litt.	
Diptera	Cecidomyiidae	<i>Dasineura tumidosae</i> (Felt)	<i>Fraxinus americana</i>	High	leaflet gall	Gagné, 1989	
Diptera	Cecidomyiidae	<i>Dasineura</i> n. sp.	<i>Fraxinus pennsylvanica</i>	High	seed gall	Raymond Gagné in prep.	Reared from seed collection from Ontario (Raymond Gagné in prep.).
Hemiptera	Aphididae	<i>Prociphilus americanus</i> (Walker)	<i>Abies, Fraxinus dipetala, F. latifolia, F. velutina</i>	High	phloem	DeAngelis, 1998; TTD, 2014; Carol von Dohlen in litt.	<i>Abies</i> is alternate host.
Hemiptera	Aphididae	<i>Prociphilus fraxinifolii</i> (Riley)	<i>Fraxinus americana, F. nigra, F. velutina</i>	High	phloem	TTD, 2014; Carol von Dohlen in litt.	
Hemiptera	Aphididae	<i>Prociphilus pergandei</i> Smith	<i>Fraxinus americana</i>	High	phloem	Blackman and Eastop, 1994; Carol von Dohlen in litt.	
Hemiptera	Aphididae	<i>Prociphilus probosceus</i> (Sanborn)	<i>Fraxinus</i>	High	phloem	Blackman and Eastop, 1994; Carol von Dohlen in litt.	
Hemiptera	Diaspididae	<i>Diaspidiotus fraxini</i> (McKenzie)	<i>Fraxinus velutina</i>	High	phloem	Miller et al., 2014a; Douglass Miller in litt.	Few Diaspididae are specialists; confirmation of monophagy is needed.
Hemiptera	Diaspididae	<i>Diaspis fraxini</i> Ferris	<i>Fraxinus velutina</i> var. <i>tourneyi</i>	High	phloem	Miller et al., 2014b; Douglass Miller in litt.	Type locality about 42 miles from Arizona border. Uncertain if species has been reported from US; few Diaspididae are specialists (Ben Normark pers. comm.); confirmation of monophagy is needed.

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Hemiptera	Miridae	<i>Bisulcopsallus texanus</i> (Knight)	<i>Fraxinus</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes adustus</i> (Knight)	<i>Fraxinus americana</i>	High	phloem	Henry, 1980; TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes amoenus</i> (Reuter)	<i>Fraxinus americana</i> , <i>F. latifolia</i> , <i>F. pennsylvanica</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes brooksi</i> Kelton	<i>Fraxinus</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes canadensis</i> Van Duzee	<i>Fraxinus</i> , <i>F. pennsylvanica</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes cardinalis</i> Uhler	<i>Fraxinus americana</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes glaber</i> (Knight)	<i>Fraxinus americana</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes illitus</i> (Van Duzee)	<i>Fraxinus velutina</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes neglectus</i> (Knight)	<i>Fraxinus pennsylvanica</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes pacificus</i> (Van Duzee)	<i>Fraxinus latifolia</i> , <i>F. velutina</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes pettiti</i> Reuter	<i>Fraxinus</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes populi</i> (Knight)	<i>Fraxinus americana</i> , <i>F. pennsylvanica</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes rufivenosus</i> (Knight)	<i>Fraxinus</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes tricolor</i> Van Duzee	<i>Fraxinus pennsylvanica</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Miridae	<i>Tropidosteptes vittiscutis</i> (Knight)	<i>Fraxinus americana</i>	High	phloem	TTD, 2014; Michael Schwartz in litt.	
Hemiptera	Pentatomidae	<i>Banasa rolstoni</i> Thomas & Yonke	<i>Fraxinus velutina</i>	High	phloem	Donald Thomas pers. comm.	More study needed; other <i>Banasa</i> sp. are known to be generalists.

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Hemiptera	Tingidae	<i>Leptopypha costata</i> Parshley	<i>Chionanthus</i> , <i>Fraxinus</i>	High to Moderate	phloem	Usinger, 1945; Drake and Ruhoff, 1965; Tom Henry in litt; <i>Chionanthus</i> record from Laura Miller in litt.	<i>Carya ovata</i> , <i>Corylus</i> , and <i>Hamamelis</i> records for this species likely in error (Tom Henry in litt.).
Hemiptera	Tingidae	<i>Leptopypha minor</i> McAtee (including <i>nubilis</i>)	<i>Fraxinus latifolia</i> , <i>F. velutina</i> , and other Oleaceae	High to Moderate	phloem	Usinger, 1945; Drake and Ruhoff, 1965; Tom Henry in litt.	<i>Ceanothus</i> , <i>Populus</i> and other non-Oleaceae hosts in error (Tom Henry in litt.).
Hemiptera	Tingidae	<i>Leptopypha mutica</i> (Say)	<i>Chionanthus</i> , <i>Fraxinus americana</i>	High to Moderate	phloem	Froeschner, 1944; Usinger, 1945; Drake and Ruhoff, 1965; Tom Henry in litt.; Laura Miller in litt	<i>Forestiera</i> records likely refer to another species (Tom Henry in litt.).
Hymenoptera	Tenthredinidae	<i>Eupareophora parca</i> (Cresson)	<i>Fraxinus americana</i> , <i>F. nigra</i> , <i>F. latifolia</i> , <i>F. pennsylvanica</i>	High	new leaves	Williams, 2007; David Smith in litt.	Pecan record is doubtful (David Smith in litt.).
Hymenoptera	Tenthredinidae	<i>Tethida barda</i> (Say)	<i>Fraxinus americana</i>	High	new leaves	David Smith in litt.	
Hymenoptera	Tenthredinidae	<i>Tomostethus multictinctus</i> (Rohwer)	<i>Fraxinus americana</i> , <i>F. latifolia</i>	High	new leaves	Langford and McConnell, 1935; David Smith in litt.	
Lepidoptera	Apatelodidae	<i>Olecclostera angelica</i> (Grote)	<i>Fraxinus</i> , <i>Syringa</i>	High to Moderate	mature leaves	Wagner, 2005, 2007; Robinson et al., 2014	
Lepidoptera	Geometridae	<i>Hydrelia</i> near <i>inornata</i>	<i>Fraxinus americana</i>	High	mature leaves	Wagner et al., 2002	Validity of this taxon in need of (molecular) verification.
Lepidoptera	Geometridae	<i>Philtraea elegantaria</i> (Hy. Edwards)	<i>Fraxinus gooddingii</i>	High	leaves	DLW unpubl. data	
Lepidoptera	Geometridae	<i>Philtraea latifoliae</i> Buckett	<i>Fraxinus latifolia</i>	Very High	leaves	Buckett, 1970; Wagner, 2007	Only known from a few counties in Central California and evidently declining.

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Lepidoptera	Geometridae	<i>Phyltraea paucimacula</i> Barnes and McDunnough	<i>Fraxinus greggii</i> and <i>Lycium</i>	Moderate but see comments	leaves	Noel McFarland pers. comm.; Wag- ner unpubl. data	<i>F. greggii</i> record from Laredo, TX (Noel Mc- Farland pers. comm.) and Big Bend by DLW; <i>Lycium</i> in Big Bend NP from Wagner unpubl. data but possibly two taxa involved in which case the ash feeder is imperiled.
Lepidoptera	Geometridae	<i>Phyltraea surcaliforniae</i> Buckett	<i>Fraxinus dipetala</i>	High	leaves	Buckett, 1970; Wag- ner, 2007	
Lepidoptera	Geometridae	<i>Plagodis kuetzingi</i> (Grote)	<i>Fraxinus americana</i> , <i>F.</i> <i>quadrangulata</i>	High	leaves	Wagner, 2007	
Lepidoptera	Gracillariidae	<i>Caloptilia fraxinella</i> (Ely)	<i>Fraxinus americana</i> , <i>F.</i> <i>nigra</i> , <i>F. pennsylvanica</i>	High	new leaves	Johnson and Lyon, 1988; Pohl et al., 2004; Wagner, 2007	<i>Ligustrum</i> as a host is listed in error in previous tabulations; that record traces to <i>C.</i> <i>cucullipennella</i> (Charley Eiseman in litt.).
Lepidoptera	Gracillariidae	<i>Caloptilia</i> n. sp.	<i>Fraxinus latifolia</i>	High	new leaves	Wagner, 2007, unpubl. data	Found along creeks in central and northern California.
Lepidoptera	Gracillariidae	<i>Marmara basidendroca</i> Fitzgerald	<i>Fraxinus pennsylvanica</i>	Very High	bark miner that tunnels into root crown	Fitzgerald, 1973; Wagner, 2007	Currently known only from Upstate New York. Feeds on single cell layer in cork cambium.
Lepidoptera	Gracillariidae	<i>Marmara corticola</i> Fitz- gerald	<i>Fraxinus pennsylvanica</i>	Very High	green bark miners	Fitzgerald, 1973; Wagner, 2007	Currently known only from Upstate New York. Feeds on single cell layer in cork cambium initial- ly and then tunnels into deeper cork layers.
Lepidoptera	Gracillariidae	<i>Marmara fraxinicola</i> Braun	<i>Fraxinus americana</i> , <i>F.</i> <i>pennsylvanica</i>	High	green bark miners	Fitzgerald and Simeone, 1971; Fitzgerald, 1973; Wagner, 2007	Feeds on single cell layer in cork cambium.
Lepidoptera	Noctuidae	<i>Chloronycta tybo</i> (Barnes)	<i>Fraxinus velutina</i>	High	mature leaves	Schmidt et al., 2014	

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Lepidoptera	Noctuidae	<i>Copivaleria grotei</i> Morrison	<i>Fraxinus americana</i>	High	new leaves	Wagner, 2007; Robinson et al., 2014	Non- <i>Fraxinus</i> hosts are insignificant, incidental, or erroneous (Eric Quinter in litt.). Larvae feed only in vigorous growing shoots usually of saplings.
Lepidoptera	Noctuidae	<i>Papaipema furcata</i> (J. B. Smith)	<i>Fraxinus americana</i> , <i>F. nigra</i> , <i>F. pennsylvanica</i>	High	new shoot feeder (borer)	Wagner, 2007; Robinson et al., 2014	<i>Triosteum</i> records likely in error and refer to <i>S. forbesi</i> (Zacharczenko et al. 2014).
Lepidoptera	Noctuidae	<i>Sympistis chionanthi</i> (J. E. Smith)	<i>Chionanthus virginicus</i> , <i>Fraxinus americana</i> , <i>F. nigra</i> , <i>F. pennsylvanica</i>	High to Moderate	new leaves	Wagner, 2007; Wagner et al., 2011; Robinson et al., 2014	CDEA record for <i>Keckia antirrhinoides</i> as a host likely derives from a misidentification of <i>S. picina</i>
Lepidoptera	Noctuidae	<i>Sympistis fortis</i> (Grote)	<i>Fraxinus</i> , <i>F. latifolia</i>	High	new leaves	Robinson et al., 2014; CDEA card file pest database	
Lepidoptera	Noctuidae	<i>Sympistis punctilinea</i> (Hampson)	<i>Fraxinus</i> , <i>F. velutina</i>	High	new leaves	Crumb, 1956; CDEA card file pest database	
Lepidoptera	Noctuidae	<i>Sympistis heterogena</i> (A. Blanchard)	<i>Fraxinus cuspidata</i>	High	new leaves	DLW unpubl. data	New leaves of <i>F. greggii</i> growing in Chisos Basin, Big Bend NP. Spring active.
Lepidoptera	Pyralidae	<i>Palpita magniferalis</i> (Walker)	<i>Fraxinus americana</i> , <i>F. nigra</i> , <i>F. pennsylvanica</i>	High	leaves	Robinson et al., 2014	
Lepidoptera	Sesiidae	<i>Podosesia aureocincta</i> Purrington & Nielson	<i>Fraxinus</i> , <i>F. americana</i> , <i>F. pennsylvanica</i> , <i>Olea</i>	High to Moderate	xylem	Eichlin and Duckworth, 1988; Wagner, 2007; Robinson et al., 2014	Sister to <i>syringae</i> : slight flight period and genitalic differences; COI barcode shared with <i>syringae</i> ; reports from <i>Olea</i> should be verified.
Lepidoptera	Sphingidae	<i>Ceratomia sonorensis</i> Hodges	<i>Fraxinus velutina</i>	High	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	
Lepidoptera	Sphingidae	<i>Ceratomia undulosa</i> (Walker)	<i>Chionanthus virginicus</i> , <i>Fraxinus americana</i> , <i>F. caroliniana</i> , <i>F. nigra</i> , <i>F. pennsylvanica</i> , <i>Ligustrum</i> , and <i>Syringa</i>	High to Moderate	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	DLW discounts all records other than those on Oleaceae: <i>Fraxinus</i> preferred host.

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Lepidoptera	Sphingidae	<i>Manduca jasminearum</i> (Guérin)	<i>Fraxinus</i> , <i>Syringa</i>	High	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	DLW discounts all records other than those on Oleaceae.
Lepidoptera	Sphingidae	<i>Sphinx canadensis</i> Boisduval	<i>Fraxinus americana</i> (origin of this host requires verification) <i>F. nigra</i> (preferred host)	Very High	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	DLW discounts all records other than those on Oleaceae. another <i>Fraxinus</i> species likely to be principal host species south of Ohio River.
Lepidoptera	Sphingidae	<i>Sphinx chersis</i> (Hübner)	<i>Fraxinus americana</i> , <i>F. pennsylvanica</i> , <i>F. velutina</i> , <i>Ligustrum</i> , <i>Syringa</i> , other Oleaceae	High to Moderate	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	DLW discounts all records other than those on Oleaceae.
Lepidoptera	Sphingidae	<i>Sphinx</i> near <i>chersis</i>	<i>Fraxinus velutina</i>	High	mature leaves	Chris Schmidt in litt.	DNA barcodes suggestive that Arizona populations of <i>S. chersis</i> represent n. sp. sister to <i>S. mexicana</i> (Chris Schmidt in litt.)
Lepidoptera	Sphingidae	<i>Sphinx franckii</i> Neumoegen	<i>Fraxinus americana</i> , <i>Ligustrum</i>	Very High	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	DLW discounts all records other than those on Oleaceae; already uncommon and declining; <i>Fraxinus</i> preferred host.
Lepidoptera	Sphingidae	<i>Sphinx kalmiae</i> J. E.	<i>Chionanthus virginicus</i> , <i>Fraxinus americana</i> , <i>F. nigra</i> , <i>F. pennsylvanica</i> , <i>Ligustrum</i> , <i>Syringa</i>	High to Moderate	mature leaves	Tuttle, 2007; Wagner, 2005, 2007	DLW discounts all records other than those on Oleaceae.
Lepidoptera	Sphingidae	<i>Sphinx libocedrus</i>	<i>Forestiera</i> spp., <i>Fraxinus gooddingii</i> , <i>F. greggii</i>	Moderate	mature leaves	Tuttle, 2007	<i>Forestiera</i> likely the principal host.
Lepidoptera	Yponomeutidae	<i>Zelleria</i> near <i>hepariella</i>	<i>Fraxinus latifolia</i>	High	leaves	Wagner, 2007	Report by Wagner (2007) as <i>Z. hepariella</i> in error; the use of <i>hepariella</i> traces to preliminary determination by Tom Eichen (in litt.); taxonomy still under study.

Table 4. (continued)

Taxon	Family	Scientific Name	Confirmed Hosts	Risk Rating	Guild	Reference(s)	Comments
Lepidoptera	Yponomeutidae	<i>Zelleria</i> near <i>semitincta</i>	<i>Fraxinus dipetala</i>	High?	leaves	John DeBenedictis unpubl. data	A similar appearing moth occurs in southern California on <i>Forestiera</i> .



Figure 22. Mating pair of North America's largest beetle, *Dynastes granti* (Photo courtesy Margarethe Brummerman). So far as known, actively growing ash shoots are the principal feeding site for this behemoth, which sometimes exceeds 80 mm in length. Males chew a lesion into new growth and females are paired as they arrive at the wound. Curiously, its more widespread cousin, the Eastern Hercules beetle; *Dynastes tityus*, is virtually unstudied as an adult. The only adult feeding record of which we are aware, again is for a *Fraxinus* (Glaser 1976). Grant's rhinoceros beetle is quite sought-after by photographers and collectors; persons (even families) with interests in Coleoptera, sometimes travel from as far away as Japan and Korea to see the beetle. See also caption for Figure 23.

species as Very High (n = 2), High (n = 3), High to Moderate (n = 3), and Moderate (n = 1). Three of the nine have restricted global distributions and are ranked as G4 species in NatureServe Explorer (2014): *Manduca jasminearum*, *Sphinx canadensis*, and *S. franckii* (Fig. 16). The first of these is already in decline along the northern portion of its range (NatureServe Explorer, 2014), and sphingids (and especially members of the nominate genus *Sphinx*) have been identified as a group in decline across much of the northeastern United States, perhaps due to the exotic tachinid *Compsilura concinnata* (Meigen) (Wagner, 2012) or an as yet unidentified egg parasitoid (Sam Jaffe, unpublished data).

One of the most surprising findings from our study is that one of North America's largest, and

attention-worthy insects may be threatened by EAB: the western rhinoceros beetle (*Dynastes granti*), whose adults occasionally exceed 80 mm in length (Figs. 18, 22). While this large scarab is a generalist as a larva, feeding in dead wood of various tree species, its adult may prove to be a specialist that feeds primarily on the new growth of velvet ash in Arizona. Courting males chew into the cambial layers of an ash tree and then await the arrival of females (which presumably feed and mate at the wound site). The best known and most reliable locations for the beetle occur in the vicinity of velvet ash, where the adults have access to vigorously growing green shoots (Margarethe Brummerman, Patrick Sullivan, and Bill Warner, all in litt.). Beetle collectors visit the southwestern United States with

the Grant's rhinoceros beetle as a common focus of their itineraries. Rhinoceros beetles are also popular pets in some Asian countries; we know of instances of Asian families traveling to Arizona primarily to acquire living *Dynastes* adults to keep as pets and captive breeding (Fig. 23). *Dynastes granti* is even occasionally sold in Japanese pet shops and has appeared in staged beetle fights.

Less is known about the habits and dietary proclivities of the eastern rhinoceros beetle (*Dynastes tityus*), but it too is known to chew into shoots of ash and feed at the wounds (Glaser, 1976); no other adult food plants are known to us. Ratcliffe (2009) called attention to the threat of EAB to two other rhinoceros beetles in the genus *Xyloryctes*, which reach lengths close to 30 mm (Fig. 20). Both North American species are specialists on ash roots as larvae. If even a few of the species mentioned above were to disappear, the losses to North American arthropod fauna would be great (in both senses of the word).



Figure 23. Entomophily. The insect zoo at the United States Museum of Natural History, ranks only behind dinosaurs as a public draw. Insects also enjoy considerable favorable attention in many Asian countries. This photo is from an insect exhibition held in the Tokyo Tower over a six-week span in 2013 (<http://www.japantrends.com/tokyo-tower-insect-exhibition/>) (Photo courtesy of Tokyo Tower, Nippon Television City Corporation). More than 16,000 insects were on display, many of which were alive in the featured insect jungle. The scene above shows a beetle enclosure with many horned scarabs, kindred to and perhaps even including the North American *Dynastes* and *Xyloryctes* that are listed in Table 4 and shown in Figures 18, 20, and 22. Asian families are also known to travel annually to the Southwest United States to look for live *D. granti* adults to be kept as family pets and bred.

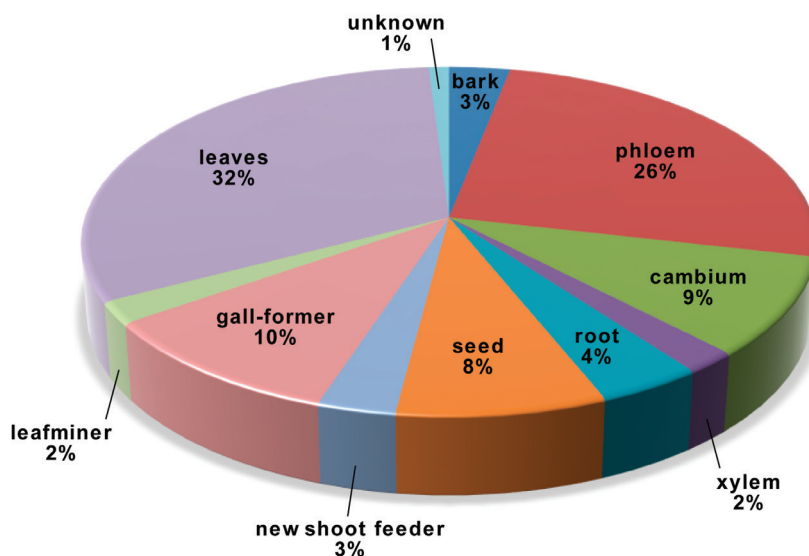


Figure 24. Feeding guilds of specialist herbivores on ash. Chart shows 98 species of ash specialists divided by feeding guild: bark (3), phloem (26), cambium (9), xylem (2), root (4), seed (8), new shoot feeder (3), gall-former (10), leaf miner (2), leaves (32), and unknown (1). Some species could be included into two feeding guilds, e.g., gall formers may form galls on seeds or leaves, etc. In these cases, we grouped individuals into the most applicable guild. See Table 4 for additional notes on feeding guilds.

Feeding Guilds and Specificity of Arthropod Herbivores

We group the 98 phytophagous arthropods identified in Table 4 into ten feeding guilds (Fig. 24). The degree of host specificity for the majority of the species listed in Table 1 is not known in detail. We are unaware of any taxonomically comprehensive study of ash herbivores where researchers thoroughly sampled across the spectrum of available *Fraxinus* (and other Oleaceae). It is our belief that most *Fraxinus* specialists (as defined in this work) consume a spectrum of available ash species growing in a given locale. Stated differently, we see little indication that the phylogenetic, physiological, and morphological differences across the genus *Fraxinus* are so great that ash-specialized herbivores are routinely restricted to a single species or even Section of the genus (contrary to what one might be led to believe from published host records). In the western United States many of the herbivores listed in Table 4 are associated with a single ash species simply because only one *Fraxinus* (or member of the Oleaceae) occurs at a given locale. In eastern North America, in cases where only *Fraxinus* (without a species indicated) is listed in Table 4, the host is likely assignable to *F. americana* and/or *F. pennsylvanica*. Based on our literature review, communications with >80 taxonomists, and DLW's 30-year rearing program of North American Lepidoptera (that has encompassed more than 2,000 species representing more than 50 families, including miners, gall-formers, wood feeders, and others), the following generalities emerged.

Wood feeders. As reflected in our results, wood feeders (restricted here to taxa consuming mostly subcambial tissues including dead and live wood feeders) are seldom specialized in diet, e.g., not one of North America's 1000 cerambycids is known to be a *Fraxinus* specialist as a larva. We list only two wood feeders: the buprestid, *Trigonogya reticulaticollis*, whose host range is not well investigated and the clearwing borer *Podosesia aureocincta*, which is likely oligophagous on Oleaceae.

Phloem feeders. We identify 25 *Fraxinus* specialist, phloem-feeding hemipterans. While several of these appear to be monophagous, we believe that this is a sampling artifact and that the species in Table



Figure 25. *Marmara fraxinella*, Family Gracillariidae (Photo courtesy Charley Eiseman). Leafminers of the genus *Marmara* are specialized herbivores. Three North American *Marmara* are known only to feed on *Fraxinus*, and two of these mine only in the bark of young, actively growing ash trees.



Figure 26. Four males of the two-tailed swallowtail (*Papilio multicaudata*), Arizona's state butterfly, puddling in Oak Creek canyon, outside of Sedona, Arizona. Larvae feed on members of three plant families, but only ashes are present in some of the western canyons where this large swallowtail butterfly occurs. (Photo courtesy Tyger Gilbert, www.TygerGilbert.com)

4 will be found to feed on multiple species of ash. The aphids ($n = 3$), diaspidid scales ($n = 2$), and mirids ($n = 15$) appear to be obligate *Fraxinus* feeders. Tom Henry (in litt.) believes that the three tingids listed in Table 4 are oligophagous on Oleaceae and that contrary host records are unreliable. The diet breadth of the pentatomid *B. rolstoni* requires further study as very few stink bugs are known to be host plant specialists.

Cambium feeders. We record seven bark beetles and a cambium-mining agromyzid (*Phytobia* sp.) as ash specialists. The only buprestid identified as an ash specialist – from a family with more than 760 North American species – was *Agrilus subcinctus*, a cambium miner (of course, we exclude *A. planipennis*).

As a subcategory to cambium feeders, we include the three gracillariids that mine in green bark. *Marmara basidendroca* tunnels into cambial layers at least for part of its life cycle (Fitzgerald, 1973). This gracillariid and two of its congeners, *M. corticola* and *M. fraxinicola* are all highly specialized insects regarded to be at high risk (Fig. 25).

New shoot feeders. We include the borer *Papaipema furcata* (Noctuidae), which so far as is known, tunnels only in new growth of *Melioides fraxinus*. Both western and eastern rhinoceros beetles (*D. granti* and *D. tityus*) can be provisionally placed here because adults are only known to feed at vigorously growing shoots of ash.

Root borers. We report four coleopterans whose larvae are ash root specialists – two leaf beetles: *Trichaltica tibialis* and *T. scabricula* and two scarab beetles: *Xyloryctes jamaicensis* and *X. thestalus* (Fig. 20). The extent to which the larvae of these beetles accept different species of ash has not been studied, although their ranges are broad enough to suggest that none is monophagous.

Seed feeders. Members of this guild, or at least the weevils of the genus *Lignyodes* (Fig. 19), appear to be oligophagous. *Psomus armatus*, so far known only from white ash, is expected to feed on other ashes based on what is known of the diet breadth of related weevils.

Gall formers. Gall insects are widely recognized to be among the most specialized insect herbivores (Felt, 1918, Gagné, 1989). The two gall-forming eriophyid mites that we list have been reported from more than one species of Section *Melioides* ashes. Gagné (in litt.) believes that all the cecidomyiid gall formers in Table 1 will be found to occur on more than one species within a *Fraxinus* Section, but that significant differences are likely to exist among Sections.

Leafminers. There are only two leafminers in our study, both members of the genus *Caloptilia* (Gracillariidae). One leafminer, *Caloptilia* n. sp., is an ecological specialist on *F. latifolia*; its eastern sister taxon, *C. fraxinella*, feeds on at least three species from two *Fraxinus* sections.

External (chewing) leaf feeders. Only one externally feeding lepidopteran is recorded as monophagous: *Philtraea latifoliae* (Geometridae), and

its dependency on Oregon ash is likely a geographical artifact because its host is the only member of the Oleaceae that grows where the moth occurs. One surprising outcome of our compilation is how proportionately few specialist external leaf feeders were detected (<32% of the 98 *Fraxinus*-dependent herbivores), though this guild comprises most of the insect biomass using ash and the most conspicuous herbivores on *Fraxinus*. Clearly, the insects that live and feed inside seeds, stems, or leaves dominate our list of species threatened by EAB.

Oligophages, Polyphages, and Other Trophic Levels

Our ecological assessment focused on specialists; it ignored oligophages and polyphages that might be affected by ash decline. However, over the course of preparing this manuscript, we discovered a few instances where an oligophage not treated in our list might be affected by EAB. For example, the two-tailed swallowtail (*Papilio multicaudatus*) (Fig. 26) uses *Fraxinus*, *Prunus*, and *Ptelea* as hosts in arid lands of western North America, but only ash species are available in some canyons where this butterfly lives. *Octotoma* (hispidine chrysomelids), e.g., *O. plicatula* and *O. marginicollis*, were not included because their leafmining larval stages are specialists on non-ash species, even though the adult beetles are believed to do much of their adult feeding on *Fraxinus* species (Shawn Clark, in litt.).

We did not find mention of any specialist parasitoids, predators, or pathogens that we could confidently state were dependent on an ash herbivore. The recently described *Mymaromella pala* Huber & Gibson (Mymarommatidae) is known only from ash log collections, but its presumed host is a bark-residing psocid (Huber et al., 2008) likely to dwell on other trees as well. Gagné (1989) regards *Contarinia thalactri* to be a phytophagous inquiline in the galls of *Dasineura tumidosae*. However, beyond this inquiline record, we did not find mention of any other indirectly ash-specialized insects.

DISCUSSION

Imperilment Risk Ratings

It is our estimate that no less than 98 species of invertebrate herbivores would be appreciably affected by an elimination or massive reduction in abundance of North America's 16 native *Fraxinus*. For these herbivores we estimate endangerment risks as Very High (n = 5), High (n = 75), High to Moderate (n = 15), and Moderate (n = 3) (Fig. 21). Forty-five of the species-level taxa listed in Table 4 are identified as "at risk" for the first time. Eighteen (6%) of the taxa identified by Gandhi and Herms (2010) had their imperilment status upgraded; twenty six (35%) of the species listed in their treatment as being of high to moderate endangerment risk are dropped from consideration (Appendix 3). A key message deriving from this expert-based approach is that researchers should use caution when gleaned host records from dated literature, the internet, and especially secondary and tertiary resources. We found records (and especially older host records) to be rife with invalid taxa, erroneous identifications, instances where a presumed ash specialist was not phytophagous, cases where presumed ash specialists were generalists (type I errors), cases where presumed oligophagous or generalist herbivores were in fact specialists (type II errors), and cases where exotic or extralimital taxa were included.

As noted previously, we discounted the ecological importance of introduced (exotic) plants, e.g., lilac, privet, and olive, as alternative hosts that could support sufficiently large populations to ensure a taxon's long-term survival in North America. This seems to be a defensible position if one were to invoke the precautionary principle in assessing risk. But, we also recognize that it is possible that some invasive plants (such as *Ligustrum*) could play a role in the survival of some native Oleaceae specialists were EAB to eliminate much of the *Fraxinus* in a region.

The Very High risk rating – given to just five lepidopterans – was reserved for ash specialists believed to be at risk or in decline due to other causes. *Marmara basidendroca* and *M. corticola* (both Gracillariidae) are both specialized stem

miners known only from a restricted area in Upstate New York. *Philtraea latifoliae* (Geometridae) feeds exclusively on *Fraxinus latifolia* and is known only from a few counties in central California (Buckett, 1970). *Sphinx canadensis*' rating was raised to Very High because it is principally associated with *F. nigra*, an ash that is highly susceptible to EAB infestation (Leah Bauer pers. comm.) and which is predicted to be increasingly at risk due to climate change (Liang and Fei, 2014). *Sphinx franckii* is already uncommon and northern populations are in decline (Wagner, 2012).

For perspective on the importance of ash and the emerald ash borer, it is useful to compare ash decline with what is known about American chestnut (*Castanea dentata* [Marsh.] Borkh.) and its dependent herbivore fauna. Opler (1978) listed seven species of Lepidoptera that may have gone extinct as a result of losing this once ecologically dominant forest tree. One of these seven moths has since been rediscovered (*Synanthedon castaneae* [Busck]) (Anagnostakis et al., 1994), and another listed species, *Tischeria perplexa* Braun, may not be a valid species given that other Fagaceae-feeding *Tischeria* from the eastern United States are not chestnut specialists (Braun, 1972)⁴. Thus, five is a better estimate of the number of moth species that have been lost from the North American fauna⁵ due to American chestnut decline. If one compares the number of extinct moths restricted to chestnut (n = 5) to the at risk ash-feeding Lepidoptera listed in Table 4 (n = 32), one is immediately struck by the magnitude of the threat posed by the introduction and spread of EAB. North America has not faced a threat of this magnitude to its native insect herbivore biodiversity from an exotic species over the course of the last two centuries. We believe that this is because

⁴ Three other *Tischeria* occur on *Castanea dentata* – one of which, *T. castaneaeella*, is believed to be quite closely related to *T. perplexa*, the purported *Castanea dentata* specialist. All three of the extant *Tischeria* that fed on chestnut are breeding on red oaks. Given the above, it is DLW's belief that *T. perplexa* will prove to be a taxonomic synonym.

⁵ As a caveat, it is worth noting that no one has systematically sampled introduced *Castanea* or related native *Castanea*, and especially Alleghany chinquapin (*C. pumila*), which co-occurred with American chestnut; nor have workers surveyed nut-producing stands of *C. dentata* in Ohio, Maine, and elsewhere for the missing species.

Fraxinus represents a phylogenetically and or chemically isolated biological island that is too far removed from its allied genera (e.g., *Chionanthus*, *Forestiera*, exotic *Ligustrum*, and Oleaceae) for these plants to serve as refuges for *Fraxinus* specialist herbivores over ecological and evolutionary time.

Data Gaps

Host ranges for virtually all of the taxa in this study remain incompletely known. Targeted herbivore surveys of the 16 North American *Fraxinus* would be valuable, especially for understudied ash species and those currently under threat from EAB or soon to be attacked as the beetle's range expands. In particular, southern ash are poorly studied as they tend to grow in swamps and all nine western ash species require further research; almost nothing is known of *F. albicans*, *F. berlandieriana*, *F. cuspidata*, *F. gooddingii*, and *F. papillosa*. Likewise, the importance of other native Oleaceae, especially *Forestiera*, as hosts for ash-feeding herbivores is in need of study. Of critical importance to the evaluation of imperilment risk is the possibility that other native Oleaceae may be susceptible to the emerald ash borer. Only very recently did researchers learn that *Chionanthus* is also susceptible to attack (Entomology Today, 2014). Other Oleaceae species such as *Osmanthus* Lour., a genus of trees found in black water streams of the southern United States, remain virtually unstudied. While the susceptibility of other native Oleaceae to EAB is of no commercial relevance, it is a matter of considerable conservation significance.

We suspect that modern systematic analyses employing molecular markers will reveal additional cryptic species that are ash specialists (especially in the western United States where species-level taxonomic studies lag). One interesting example that surfaced over the course of our studies involves the sizable and charismatic great sphinx (*S. chersis*). COI barcodes suggest the hawkmoth is two species, with the populations from southeastern Arizona representing an as yet undescribed species that Chris Schmidt (in litt.) believes is closely related to *S. mexicana*. Conversely, some taxa in our treatment may have been over split taxonomically. The mirid genus with 14 *Tropidosteptes* species is in need of

revision, i.e., some names in Table 4 may prove to be synonyms (Michael Schwartz pers. comm.).

In summary, we recognized 98 species of herbivores as being threatened by the loss of *Fraxinus* in the United States and Canada. No doubt, additional ash specialists will be identified in the coming decades. Knowledge of herbivores feeding on ash is severely lacking in the southern and western United States; very little is known of the phytophagous insects feeding on six western *Fraxinus* species (*F. anomala*, *F. cuspidata*, *F. dipetala*, *F. gooddingii*, *F. greggii*, and *F. papillosa*). Gall midges (Cecidomyiidae), curculionid weevils, mites, thrips, and other taxonomically challenging arthropods can be expected to yield additional *Fraxinus* specialists. The latter two taxa seem especially likely to include ash specialists because their taxonomy is nascent and no systematic continent-wide surveys have been carried out. Across all taxa, molecular markers can be expected to reveal new cryptic specialist herbivores, especially in those taxa where the species-level taxonomy has proven difficult.

CONCLUSION

For the purposes of our ecological assessment we embraced the precautionary principle. The body of our assessment is, at its essence, a doomsday scenario: what might transpire if North America lost all of its *Fraxinus* or if ash numbers dwindled to a point where ash lost functional value in North American wildlands. Presently, EAB is spreading at a dramatic pace. We hope a growing number of parasitoids, pathogens, and predators will soon reduce the beetle's hyperabundance and rate of spread, and that some subset of ash species, genotypes, age classes, etc. will prove resistant to EAB. However, should the beetle cause catastrophic losses of ash, as many as 150 U.S. plant community types (16 of which are regarded as imperiled or critically imperiled) could be severely compromised. *Fraxinus* has a surprisingly rich, specialized, beautiful, and noteworthy invertebrate fauna, including hercules beetles, rhinoceros beetles, and hawkmoths – some of our continent's most magnificent invertebrates. By our assessment, the magnitude of North American invertebrate

biodiversity loss could greatly exceed that associated with American chestnut blight. The number of plant communities likely to be affected, the number of herbivores at risk (nearly 100 species), and the charismatic nature of the fauna in peril, argue for continued and increased efforts to bring the emerald ash borer under control.

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APPENDIX 1. Contacted forest managers, plant ecologists, land managers, and wildlife biologists

State	Contact	Affiliation	Area of Expertise/Comments
Connecticut	May, Dale	CT-Department of Environmental Protection (DEEP)	retired wildlife biologist; specialist on game species
	Tallamy, Doug	University of Delaware	Professor of Entomology and Wildlife Ecology; author of “Bringing Nature Home”
Indiana	Dunbar, Richard	Indiana Department of Natural Resources (IND-NR)	Northeast Region Ecologist; Division of Nature Preserves
	Homoya, Mike	Indiana Department of Natural Resources (IND-NR)	Botanist; Division of Nature Preserves
Michigan	Shuey, John	The Nature Conservancy (TNC)	Director of Conservation Science
	Kashian, Dan	Wayne State University	Professor of Biological Sciences; forest ecologist
	McCullough, Deborah	Michigan State University	Professor of Entomology; forest entomologist
	Reznicek, Anton	University of Michigan	Assistant Director of University of Michigan Herbarium; plant systematist; plant ecologist
	Bissell, James	Cleveland Museum of Natural History	Curator of Botany; Coordinator of Natural Areas (50+ preserves)
Ohio	Boone, Daniel	Bartlett Tree Experts	Certified arborist and field botanist
	Hausman, Constance	Cleveland Metropolitan Park District	Plant and Restoration Ecologist
	Gardener, Richard	Ohio Department of Natural Resources (ODNR)	Chief Botanist (ODNR); ecologist
	McCormac, James	ODNR- Ohio Division of Wildlife	non-game wildlife biologist
	Reinier, John	Cleveland Metropolitan Park District	Wetland Ecologist
	Semroc, Judy	Cleveland Museum of Natural History	Conservation Specialist
Ontario	Catling, Paul	Agriculture and Agri-food Canada	Research Scientist; botanist
	Gill, Bruce	Canadian Food Inspection Agency	Research Scientist; entomologist; invasive species biologist
	Oldham, Michael	Ontario Natural Heritage Information Centre (NHIC)	Botanist; herpetologist
	Waldron, Gary	University of Guelph	School of Environmental Sciences; tree specialist
Wisconsin	Wilterding, John	Olivet College	Professor of Biology and Chair of the Department of Natural and Physical Sciences; entomologist

APPENDIX 2. Contacted taxonomic authorities and principal experts for arthropod records.

Taxon	Family	Taxonomic Authority	Affiliation	Position/Area of Expertise
Acari	Eriophyiidae	Ochua, Ron	Systematic Entomology Lab, USDA Agriculture Research Service (ARS)	Research Entomologist
Acari	Tetranychidae	Ochua, Ron	Systematic Entomology Lab, USDA Agriculture Research Service (ARS)	Research Entomologist
Coleoptera	Brentidae	LaBonte, James	Insect Museum, Oregon Department of Agriculture	Museum Curator; Lead Taxonomic and Survey Entomologist
Coleoptera	Buprestidae	MacRae, Ted	Monsanto Company	Senior Research Entomologist & Project Leader
Coleoptera	Cerambycidae	Wescott, Rick	Insect Pest Prevention & Management Program; Oregon Department of Agriculture	Research Entomologist emeritus
Coleoptera	Cerambycidae	Alten, Ron	N/A	expert on western fauna
Coleoptera		Lingafelter, Steven	Systematic Entomology Lab, National Museum of Natural History, Smithsonian Institution	Research Entomologist
Coleoptera	Chrysomelidae	MacRae, Ted	Monsanto Company	Senior Research Entomologist & Project Leader
Coleoptera	Chrysomelidae	Clark, Shawn	Monte L. Bean Life Science Museum, Brigham Young University	Entomology Collections Manager
Coleoptera	Curculionidae	Riley, Ed	Texas A&M University Insect Collection	Associate Curator
Coleoptera	Curculionidae	Staines, Charles	Department of Entomology, National Museum of Natural History, Smithsonian Institution	Research Entomologist
Coleoptera	Curculionidae	Sullivan, Patrick	The Haden Collection, Sierra Vista, AZ	Executive Curator
Coleoptera	Curculionidae	Anderson, Robert	Canadian Museum of Nature	Research Scientist
Coleoptera	Curculionidae	Atkinson, Thomas	Insect Collection, University of Texas, Austin	Collections Manager
Coleoptera	Curculionidae	Burke, Horace R.	Department of Entomology, Texas A&M University	Professor emeritus
Coleoptera	Curculionidae	Clark, Wayne	Department of Entomology and Plant Pathology, Auburn University	Professor emeritus
Coleoptera	Curculionidae	Cognato, Anthony	A.J. Cook Arthropod Research Collection, Michigan State University	Associate Professor of Insect Systematics & Research Collection Director
Coleoptera	Curculionidae	O'Brien, Charles W.	University of Arizona	Research Entomologist
Coleoptera	Hispiinae	Staines, Charles	Department of Entomology, National Museum of Natural History, Smithsonian Institution	Research Entomologist

APPENDIX 2. (continued)

Taxon	Family	Taxonomic Authority	Affiliation	Position/Area of Expertise
Coleoptera	Scarabaeidae	Ratcliffe, Brett	Systematic Research Collections, University of Nebraska State Museum	Collection Curator, Professor of Entomology
		Sullivan, Patrick	The Haden Collection, Sierra Vista, AZ	Executive Curator
		Warner, Bill	California State Collection of Arthropods, California Department of Food and Agriculture (CDFA)	Research Associate
Coleoptera	various	Hespenheide, Henry	Department of Ecology and Evolutionary Biology, University of California Los Angeles (UCLA)	Professor Emeritus
		Quinn, Mike	affiliate of Texas A&M, University of Texas at Austin	expert on Texas fauna
		Schiff, Nathan	Center for Bottomland Hardwoods Research, USDA Forest Service	Research Entomologist
Diptera	Agromyzidae	Scheffer, Sonja Jean	Systematic Entomology Lab, USDA Agriculture Research Service (ARS)	Molecular Systematist
Diptera	Cecidomyiidae	Gagné, Raymond	Systematic Entomology Lab, National Museum of Natural History, Smithsonian Institution	retired Research Entomologist, current Collaborator
Hemiptera	Alyerodidae	Creel, Debra	USDA Agriculture Research Service (ARS)	Museum Specialist
		Blackman, Roger	Natural History Museum, London	Scientific Associate
Hemiptera	Aphididae	Miller, Douglass	Systematic Entomology Lab, USDA Agriculture Research Service (ARS)	retired Research Entomologist, current Collaborator
		von Dohlen, Carol	Utah State University	Professor of Biology
Hemiptera	Cicadellidae	McKamey, Stuart	Systematic Entomology Lab, National Museum of Natural History, Smithsonian Institution	Research Entomologist
Hemiptera	Coccoidea	Normark, Benjamin	University of Massachusetts, Amherst	Professor of Biology
Hemiptera	Derbidae	Watson, Gillian	California Department of Food and Agriculture (CDFA)	Senior Insect Biosystematist
		O'Brien, Lois	University of Arizona	systematist
		Wilson, Stephen	University of Central Missouri	Professor of Biology

APPENDIX 2. (continued)

Taxon	Family	Taxonomic Authority	Affiliation	Position/Area of Expertise
Hemiptera	Miridae	Schwartz, Michael	Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada	Research Entomologist
		Henry, Thomas	Systemic Entomology Lab, National Museum of Natural History, Smithsonian Institution	Research Entomologist
		Wheeler, Al	Clemson University	Adjunct Professor of Entomology
Hemiptera	Pentatomidae	Rider, Dave	North Dakota State University	Professor of Entomology
		Thomas, Donald	Subtropical Agriculture Research Center, USDA Agriculture Research Service (ARS)	Research Entomologist
Hemiptera	Psyllidae	Miller, Douglass	Systematic Entomology Lab, USDA Agriculture Research Service (ARS)	retired Research Entomologist, current Collaborator
Hemiptera	Tingidae	Henry, Thomas	Systemic Entomology Lab, National Museum of Natural History, Smithsonian Institution	Research Entomologist
		Miller, Laura	Pest Identification Laboratory, West Virginia Department of Agriculture	Taxonomic Entomologist
		Wheeler, Al	Clemson University	Adjunct Professor of Entomology
Hemiptera	various	Bartlett, Charles	University of Delaware	Associate Professor of Entomology and Wildlife Ecology
Hymenoptera	Tenthredinidae	Smith, David	Systemic Entomology Lab, National Museum of Natural History, Smithsonian Institution	retired Research Entomologist, current Collaborator
Hymenoptera	Eurytomidae	Gates, Michael	Systemic Entomology Lab, National Museum of Natural History, Smithsonian Institution	Research Entomologist
Lepidoptera	Geometridae	McFarland, Noel	N/A	authority on life histories of western moths
		Rand, Evan	N/A	Arizona moth expert
Lepidoptera	Gracillariidae	Davis, Don	National Museum of Natural History, Smithsonian Institution	Curator
		Fitzgerald, Terry	State University of New York (SUNY) at Cortland	Distinguished Professor of Environmental Sciences and Forestry
Lepidoptera	Noctuidae	Quinter, Eric L.	Follett Institute of Natural Sciences; University of Connecticut affiliate	retired collection manager

APPENDIX 2. (continued)

Taxon	Family	Taxonomic Authority	Affiliation	Position/Area of Expertise
Lepidoptera	Pyralidae	Hayden, James	Florida State Collection of Arthropods, Florida Department of Agriculture	Taxonomic Entomologist, Lepidoptera Curator
Lepidoptera	Sesiidae	Hansen, Jason	Michigan State University	Research Scientist
Lepidoptera	Sphingidae	Schmidt, Chris	Canadian National Collection of Insects Canadian Food Inspection Agency, Ottawa	systematist with Canadian Food Inspection Agency
Lepidoptera	Yponomeutidae	Tuttle, James P.	N/A	taxonomic expert
Lepidoptera		DeBenedictis, John	Bohart Museum, University of California Davis	Research Fellow
Lepidoptera		Epstein, Marc	Plant Pest Diagnostics Center, California Department of Food and Agriculture	Senior Insect Biosystematist
Lepidoptera		Landry, Jean-Francois	Canadian National Collection of Insects, Arachnids and Nematodes	Taxonomic Entomologist
Lepidoptera	various	Powell, Jerry	Essig Museum of Biodiversity, University of California- Berkeley	Director Emeritus
Lepidoptera	various	Sohn, Jay	Department of Entomology, National Museum of Natural History, Smithsonian Institution	Post-Doctoral Fellow
Lepidoptera	various	Jump, Peter	N/A	taxonomic expert
Lepidoptera	various	Wagner, David	University of Connecticut	Professor of Ecology and Evolutionary Biology
Leafminers and Gall-Formers	various	Eiseman, Charley	N/A	taxonomic expert
Thysanoptera	various	Creel, Debra	USDA Agriculture Research Service (ARS)	Museum Specialist
Thysanoptera	various	Hoddl, Mark	Department of Entomology, University of California at Riverside	taxonomic expert
Thysanoptera	various	Mound, Laurence	Ecosystem Sciences, Commonwealth Scientific and Industrial Research Organisation (CSIRO)	Honorary Research Fellow

APPENDIX 3. Misattributions from Published Literature and Online Sources

Taxon	Species	Previous Ranking	Current Ranking	<i>Fraxinus</i> Specialist?	Taxonomically Valid?	Herbivore?	Native to U.S.?	Comment(s)
Acari	<i>Eriophyes fraxini</i> Garm.	High	High		Invalid Taxonomy			Valid name: <i>Aceria fraxini</i> (Baker et al., 1996)
Acari	<i>Tetranychus homorus</i> Pritchard & Baker	High to Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				Polyphagous; hosts include <i>Carya</i> , <i>Fraxinus</i> , <i>Gossypium</i> , and <i>Poaceae</i> (INRA, 2014)
Coleoptera	<i>Anthicus nitidulus</i> LeConte	Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy	Not an Herbivore		Valid name: <i>Ischyropalpus nitidulus</i> ; mite predator (Landwer, 1977)
Coleoptera	<i>Apion porosicolle</i> Gemm.	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy			Valid name: <i>Apion cribricolle</i> ; recorded on deer weed, deer vetch, wild buckwheat and <i>Olea</i> (Bright, 1993)
Coleoptera	<i>Lytta sphaericollis</i> Say	Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy			Valid name: <i>Linsleya sphaericollis</i> ; larvae feed on grasshopper eggs, adults on <i>Fraxinus</i> , lilac and honey suckle (Church and Gerber, 1977; Pinto and Bologna, 1999)
Coleoptera	<i>Obridium rufulum</i> Gahan	Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				No North American cerambycids are known to be ash specialists (Ted McCrae in litt.)
Coleoptera	<i>Octotoma plicatula</i> (Fabricius)	High to Moderate	Further Research Required	Misattributed <i>Fraxinus</i> Specialist				Larvae feeds on <i>Campsis radicans</i> (Ed. Riley in litt.). Adults oligophagous but <i>Fraxinus</i> is a preferred host; beetle population potentially impacted by EAB (Shawn Clark in litt.)

APPENDIX 3. (continued)

Taxon	Species	Previous Ranking	Current Ranking	Fraxinus Specialist?	Taxonomically Valid?	Herbivore?	Native to U.S.?	Comment(s)
Diptera	<i>Colpodia teneritatis</i> Felt	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy	Not an Herbivore		Valid name: <i>Porricondyla teneritatis</i> ; mycophagous (Raymond Gagné in litt.)
Diptera	<i>Contarinia canadensis</i> Felt	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy			Valid name: <i>Contarinia canadensis</i> ; contamination record (Raymond Gagné, 1989; in litt.)
Diptera	<i>Dasineura</i> spp.	High	High		Invalid Taxonomy			Record from Solomon et al. (1993) refers to <i>D. apicata</i> ; (Raymond Gagné in litt.)
Diptera	<i>Lasioptera fraxiniflora</i> Felt	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy			Valid name: <i>Neolasioptera fraxinifolia</i> ; generalist, contaminant (Raymond Gagné, 1989; in litt.)
Diptera	<i>Lestodiplosis fraxinifolia</i> Felt	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist		Not an Herbivore		Generalist predator (Raymond Gagné in litt.)
Diptera	<i>Rhizomyia fraxinifolia</i> Felt	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				“Very definitely a generalist phyto- or saprophage” (Raymond Gagné in litt.)
Hemiptera	<i>Anormenis septentrionalis</i> (Spinola)	Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				“Feeds on a wide variety of woody and herbaceous plants” (Wilson and McPherson, 1981)
Hemiptera	<i>Leptoypha elliptica</i> McAtee	High- Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				Hosts are <i>Forestiera ligustrina</i> and <i>F. acuminata</i> (Wheeler, 2002)
Hemiptera	<i>Leptoypha ilicis</i> Drake	High to Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				Hosts are <i>Forestiera ligustrina</i> and <i>F. acuminata</i> (Wheeler, 2002)
Hemiptera	<i>Leptoypha mcateei</i> Drake	Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist				Hosts are <i>Osmanthus</i> and <i>Lyonia</i> (Drake and Ruhoff, 1965)

APPENDIX 3. (continued)

Taxon	Species	Previous Ranking	Current Ranking	Fraxinus Specialist?	Taxonomically Valid?	Herbivore?	Native to U.S.?	Comment(s)
Hemiptera	<i>Leptoypha nubilis</i> Drake	High to Moderate	High to Moderate		Invalid Taxonomy			Valid name: <i>Leptoypha minor</i>
Hemiptera	<i>Psyllopsis fraxinicola</i> Forst.	High	Not Imperiled				Exotic/ Introduced Species	European species (Hodkinson, 1988)
Hemiptera	<i>Thysanocnemis bischoffi</i> Blatchley	High	High to Moderate		Invalid Taxonomy			Valid name: <i>Lignyodes bischoffi</i>
Hemiptera	<i>Thysanocnemis helvola</i> LeConte	High	High to Moderate		Invalid Taxonomy			Valid name: <i>Lignyodes helvolus</i>
Hymenoptera	<i>Eurytoma</i> spp.	High	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist		Not an Herbivore		Wasps bulk reared & only associated with ash; species likely parasitoid (Keen, 1958; David Smith in litt.)
Hymenoptera	<i>Tethida cordigera</i> (Beauvois)	High	High		Invalid Taxonomy			Valid name: <i>Tethida barda</i>
Lepidoptera	<i>Manduca brontes</i> (Drury)	High to Moderate	Not Imperiled				Extralimital Species	Neotropical species recorded from Jamaica (Tuttle, 2007)
Lepidoptera	<i>Podosesia fraxini</i> (Lugger)	Moderate	Not Imperiled	Misattributed <i>Fraxinus</i> Specialist	Invalid Taxonomy			Color form of <i>Podesia syringae</i> ; oligophagous (Eichlin and Duckworth, 1988)