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Review

Review

Invasive Woody Plants and Their Effects on Arthropods in the United States: Challenges and Opportunities

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Abstract

Invasive plant introductions are increasing globally, and trends in human activity suggest these increases will continue. Although we know much about interactions between invasive herbaceous plants and arthropod communities, there is a dearth of knowledge examining interactions between invasive woody plants and arthropod communities. What information does exist shows that invasive woody plant relationships with mutualists (e.g., pollinators), herbivores, twig- and stem-borers, leaf-litter and soil-dwelling arthropods, and other arthropod groups are complex and hint at multiple factors influencing effects. These relationships warrant additional attention to allow better prioritization of species for research and regulatory review. Chinese tallow tree, e.g., is renowned for its attractiveness to honeybees, whereas reduced pollinator populations are found among other invasive woody plants such as privet. The unknown driving mechanisms and interactions that create these differences represent a substantial gap in knowledge and warrant additional research. Our objectives are to review current knowledge regarding invasive woody plants and their interactions with various arthropod groups in the United States, outline future research needs, and present a call to action regarding invasive woody plant research.

Key words: ecosystem impact, herbivore, invasive species, nontarget effect, trophic interaction

Global non-native species introductions and establishment has increased exponentially with human movement, a trend that shows no signs of slowing (Aukema et al. 2010, Lowry et al. 2013). Some non-native species—those with rapid, aggressive growth, a propensity to displace native species, threaten biodiversity, cause significant ecological or economic harm, and increase natural resource and agricultural management burdens—become classified as invasive species (Radosevich et al. 2007, Hooper et al. 2012). The costs of invasive species mitigation efforts approach (and probably exceed) $120 billion annually within the United States; a price tag denoting varying levels of control efficacy (Pimentel et al. 2005). Many of these non-native species are plants, and in many cases, eradication of invasive plants is not feasible and both public and private entities end up establishing long-term control programs to deal with the invader. Thus, these invaders often impose significant economic cost, as well as difficult-to-quantify ecological impacts on the local flora and fauna.

There is a wide breadth of literature surrounding the ecological impacts of non-native plants. Non-native plants have top-down and bottom-up effects on ecosystems through soil biota and nutrient alterations (e.g., Dickie et al. 2014), changes to native plant (e.g., Warren et al. 2017) and associated herbivore communities (Hartley et al. 2010), and effects on predators, parasites, and other wildlife through multitrophic interactions (Valtonen et al. 2006, Simao et al. 2010). Non-native plants can also affect human health as evidenced by giant hogweed's ability to cause phytophotodermatitis, where burns occur on people's skin after sun exposure on areas that had previously been in contact with giant hogweed leaves (Baker et al. 2017). The paucity of literature focused specifically on the impacts of non-native woody plants varies greatly by species, even though many are ubiquitous in managed and natural areas across the United States and are the focus of mitigation efforts.

The number of non-native woody species introduced can be estimated with some accuracy, as most of those currently established were introduced via the horticulture trade (Reichard and White 2001). Although some of these plants are well known for causing severe environmental impacts (e.g., Chinese privet; Hanula and Horn 2011a,b; Lobe et al. 2014), not all non-native woody plant species become invasive or have known detrimental impacts on the environment. In fact, only around 0.5–0.7% are currently invasive outside of their native range (Richardson and Rejmánek 2011). Several non-native woody species, such as *Nandina domestica* (Thunb.; Ranunculales: Berberidaceae), are now known to be invasive, and although they are not yet highly prevalent in natural systems, their frequency is increasing (EDDMapS 2020). For plants like these, we

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know very little—and in some cases, nearly nothing—about their potential ecological impacts.

The purpose of this article is to review the impacts of and interactions between invasive woody plants and arthropods in the United States to refine additional interactions such as landscape characteristics. We define 'non-native' as any organism with a native range outside of the United States and 'invasive' as a non-native organism that has recorded detrimental impacts, whether they be economic or ecological. A broad literature search was conducted to identify invasive trees and shrubs with enough literature to conduct a thorough review, leading us to the 11 species detailed in this article. Individual literature searches were conducted within Web of Science for each of the 11 invasive woody species discussed in this review. These advanced searches consisted of all accepted historic scientific names for each species as given by The Plant List (www.theplantlist.org; Supp Box 1 [online only]). In total, 4,346 publications regarding these species have been published to date, though a subsequent search further refining publications by inclusion of the keywords 'invasion' and 'invasive' reduced the number of related publications by 88%, indicating that most publications are not focused on the economic and ecological impacts of these species and their establishment (Table 1). Each of these 11 species have been cultivated and sold in the United States for over 100 yr, with the average length of tenure to date being 193 yr (Table 1).

A History of Invasive Woody Plants in the United States

Although Spaniards recorded introductions of non-native plants as early as 1565 in what is now Florida (Huxley 1978), colonial settlement lead to more persistent plant introductions. Although the first list of U.S. invasive species appeared in 1672 (Ewan 1969), indicating that awareness of non-native flora encroaching on native ecosystems was growing, introduction of non-native species continued. Roughly 50 yr following the first invasive species list, the first prominent botanical garden in the United States was established in Philadelphia by John Bertram and in 1737 Robert Prince's Flushing, NY nursery trading company was established (Lewis 1976). Since then, the horticultural industry has transformed into a multi-billion-dollar industry that continues to produce, promote, and sell some of the plants outlined in this article. For example, Norway maple (*Acer platanoides* L.; Sapindales: Sapindaceae), Chinese privet (*Ligustrum sinense* Lour.; Lamiales: Oleaceae), and 'Bradford' pear (*Pyrus calleryana* Decne.; Rosales: Roseaceae) all aggressively invade natural and managed forests (Burch and Zedaker 2003, Culley and Hardiman 2007, Chang et al. 2011) but are still sold at local nurseries, retail stores, and home improvement stores throughout the United States. These early documentations of non-native species activities provide us with more accurate timeline estimates for introductions, establishment, spread, and impacts of additional non-native, widely sold, woody horticultural selections.

Influential People in Early Non-native Plant Introductions

A variety of individuals are featured prominently throughout the history of non-native woody plant introductions in the United States. Some of these individuals including Joseph Rock and Frank N. Meyer (USDA Plant Introduction Section) and David Fairchild (USDA Section of Foreign Seed and Plant Introduction) were charged by federal agencies to explore foreign lands for plants that would be useful and grow well in the United States (Hodge and Erlanson 1956). These common botanical exploration practices resulted in several successful horticulture and agriculture industries (e.g., bamboo, avocado; Bernstein 1938). Additional plant introductions were made by acclimatization societies; informal and formal groups of people who brought plants and animals to the United States from their home countries specifically to make their new residence feel more like their native land (Lockwood et al. 2013). There are often variable lag times between establishment and impacts of invasive plants (Crooks and Soulé 1999). For example, (Kowarik 1995) found the average lag time of invasive plants in Germany to be 147 yr. These lag times negatively affect risk forecasting in relation to non-native woody plant invasions and indicate that there are probably many issues yet to come as a result of continued introductions.

Currently, 10 of the 11 species featured in this review have been added to individual state noxious weed lists, but none have been added to the federal list, which uses the definition of 'any plant or plant product that can directly or indirectly injure or cause damage to crops (including nursery stock or plant products), livestock, poultry, or other interests of agriculture, irrigation, navigation, the natural resources of the United States, the public health, or the environment' (U.S. Code § 7702 2020). There is considerable variance in the number of species listed for regulation from state to state,

Table 1. Summary of literature reviewed for each target species including the amount in 'invasion ecology' literature

Species (common name)	States designated invasive or noxious	Year (person) introduced	Number of total pubs (number of 'invasive' pubs)
Ailanthus altissima (tree-of-heaven)	AZ, CA, CT, MA, ME, MN, NH, NM, OR, PA, VT, WA, WI	1784 (William Hamilton)	700 (264)
Melia azedarach (chinaberry)	TX	Late 18th century (Thomas Lamboll)	1,225 (21)
Triadica sebifera (Chinese tallow)	FL, LA, MS, TX	1770s (John Bradby Blake)	359(193)
Albizia julibrissin (Mimosa)	N/A	1808 (Andres Michaux)	328 (19)
Acer platanoides (Norway maple)	MA, ME, MN, VT	1756 (John Bartram)	668 (101)
Pyrus calleryana (Callery pear)	OH	1908 (George Compere)	149 (14)
Ligustrum sinensis (Chinese privet)	FL, TN	1850s (Robert Fortune)	128 (81)
Rhamnus cathartica (common buckthorn)	MA, NH, VT, CT, WI, MT, MN	Prior to 1806 (undetermined)	173 (112)
Elaeagnus (autumn, Russian olives)	AZ, CO, CT, MA, ME, MI, NH, NM, TN, UT, WA, WI, WV, WY	Undetermined	541 (114)
Schinus terebinthifolia (Brazilian peppertree)	FL, TX	Undetermined	75 (30)

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with some such as Massachusetts listing over 130 species, whereas others such as Rhode Island and Georgia having no noxious weed list established.

Current Knowledge

Although invasive species in general cause millions of dollars in annual economic damages in the United States (Holmes et al. 2009), there is a scarcity of literature on the subject of invasive woody plant species, especially regarding interactions with arthropod communities. Since 1864, more than 6,000 papers have been published on the topic of invasive species. More than one-third of those have been published since 2015, and of those, over half have been published specifically about invasive plants (Web of Science; Supp Box 1 [online only]), indicating increasing concern over this ecological challenge. By comparison, a simple Web of Science topic search for 'forestry' yields over 36,000 publications. Our Web of Science search of applicable invasive species literature shows that a small fraction of research on most of the target species covered within this review is related to their invasive potential (Table 1).

Invasive Trees

Tree-of-Heaven (*Ailanthus altissima* (Mill.) Swingle; Sapindales: Simaroubaceae)

Tree-of-heaven is an invasive deciduous tree, native to China, that has spread throughout the eastern United States along roadsides, rights-of-way, and other disturbed areas (Kowarik and Säumel 2007). Pierre Nicholas le Cheron d'Incarville, a French Jesuit Father, shipped tree-of-heaven seeds to Philip Miller at the Chelsea Physic Garden in London in 1751. The progeny of this introduction was later shared with William Hamilton, the son of the original 'Philadelphia lawyer' Andrew Hamilton, who brought the trees to The Woodlands, his private arboretum in Philadelphia, PA, in the 1780s (Spongberg 1993). The trees were prized for their fast growth, appealing form, and high tolerance for physical damage and industrial pollution (Swingle 1916). This pollution tolerance was considered not only from an aesthetic standpoint, but also from a medicinal perspective as they were purported to protect individuals from 'malarial miasma'. As a result, they were widely planted, although they were not recorded as invasive until roughly 1965 (Kasson et al. 2013). As of 2008, tree-of-heaven was present in over 214,000 acres of southern forests and is even more common and widely spread in the Northeast and in California, the points of original introduction (Fryer 2010; Fig. 1).

Tree-of-heaven exudes allelopathic chemicals from its roots, which prevent surrounding flora from germinating (Heisey 1990a,b). These trees are extremely prolific, as females may produce over 52 million seeds in their lifetime (Wickert et al. 2017). Although this reproductive capacity was known in the late 1800s (Millspaugh 1892), the tree was still widely planted in managed landscapes and is still sold online today. Control efforts have been periodically attempted, but not in great enough magnitude to suppress populations as both mechanical and chemical treatments may be required for elimination (Burch and Zedaker 2003). As a partial control effort, tree-of-heaven has been added to state noxious weed listings in AZ, CA, CT, MA, ME, MN, NH, NM, OR, PA, VT, WA, and WI (Table 1).

Although tree-of-heaven's economic impacts are difficult to calculate, its ecological impacts are seen in interactions with native and non-native arthropods. For example, when tree-of-heaven reached southern Texas, the Ailanthus webworm moth (*Atteva aurea* Fitch 1856; Lepidoptera: Attevidae), which is native to Central America, expanded its range and is now found across eastern North America (Wilson et al. 2010). Recently, 'an unusual pest in large numbers on *Ailanthus altissima*' was recorded by Pennsylvania Game Commission Wildlife Education Specialist David Lynch with subsequent voucher specimen submission to the Pennsylvania Department of Agriculture (Barringer et al. 2015). These specimens were identified as spotted lanternflies (*Lycorma delicatua* White; Hemiptera: Fulgoridae) (SLF) and, since the initial discovery, live SLF have been detected in 13 states (Center for Environmental and Research Information Systems 2020) and cost the agriculture industry millions of dollars. Expansion of SLF populations is positively correlated with the range of tree-of-heaven (Urban 2019) and ongoing research aims to determine whether this pest can reproduce on other tree species (Song et al. 2018).

Chinaberry (*Melia azedarach* L.; Sapindales: Meliaceae)

Chinaberry, also known as Persian lilac tree or Pride of India, is a deciduous tree native to northwestern India (Bohnenstengel et al. 1999). In the late 18th century, Thomas Lamboll introduced Chinaberry to his Charleston, SC garden, with future progeny received by Thomas Jefferson in 1778 where several additional plants sprouted within a decade (Chappell 2000, Monticello.org 2019). In 1930, Chinaberry was identified as a native host of SLF (Chu 1930). This knowledge has led researchers to consider what role it may play in expansion of SLF infestations (Urban 2019, Barringer and Ciafré 2020). Currently, Chinaberry is only listed as a noxious weed in Texas. Its quick growth yields ample wood for furniture-making, the berries are eaten by wildlife, and it has been long known that the roots possess both antibacterial and anthelmintic properties (Ramsay 1858, Neycee et al. 2012). Chinaberry leaves were historically used in packing to prevent clothes moths and other insect damage (Bohnenstengel et al. 1999) and as feed for select livestock (Wood et al. 2000), though the leaves are known to be poisonous to many other livestock species (Williams 1980). This use was probably derived in part from the high content of limonoid compounds similar to azadirachtin, an active ingredient in certain insecticides. The limonoid compounds present in Chinaberry are insect antifeedants, and are featured in especially high concentrations within Chinaberry seeds (Caboni et al. 2012), potentially pushing phytophagous organisms away from them and toward surrounding plants.

Chinese Tallow (*Triadica sebifera* (L.) Small; Malpighiales: Euphorbiaceae)

Chinese tallow is a deciduous tree native to China, and there is some dissension regarding its introduction; in one account Chinese tallow was introduced by John Bradby Blake around 1770 (Ellis 1773), whereas others posit that Andre Michaux did so sometime after 1781 (True 1938, Savage 1970). Even after multiple introductions, Chinese tallow was recommended for introduction by the U.S. Patent Office in 1848 (Porcher 1863), unaware of these previous establishments. Given the high sterol content of Chinese tallow seeds, the Foreign Plant Introduction Division (now the Agricultural Research Service) of the U.S. Department of Agriculture worked diligently to establish the species in Louisiana and Texas for the soap and candle making industries (Howes 1949). Louisiana, Texas, Mississippi, and Florida have added this species to their noxious weed lists (Table 1).

Several studies suggest that Chinese tallow is detrimental to plants and aquatic organisms in surrounding native communities (Jones and McLeod 1989, Webster et al. 2007, Cotten et al. 2012)

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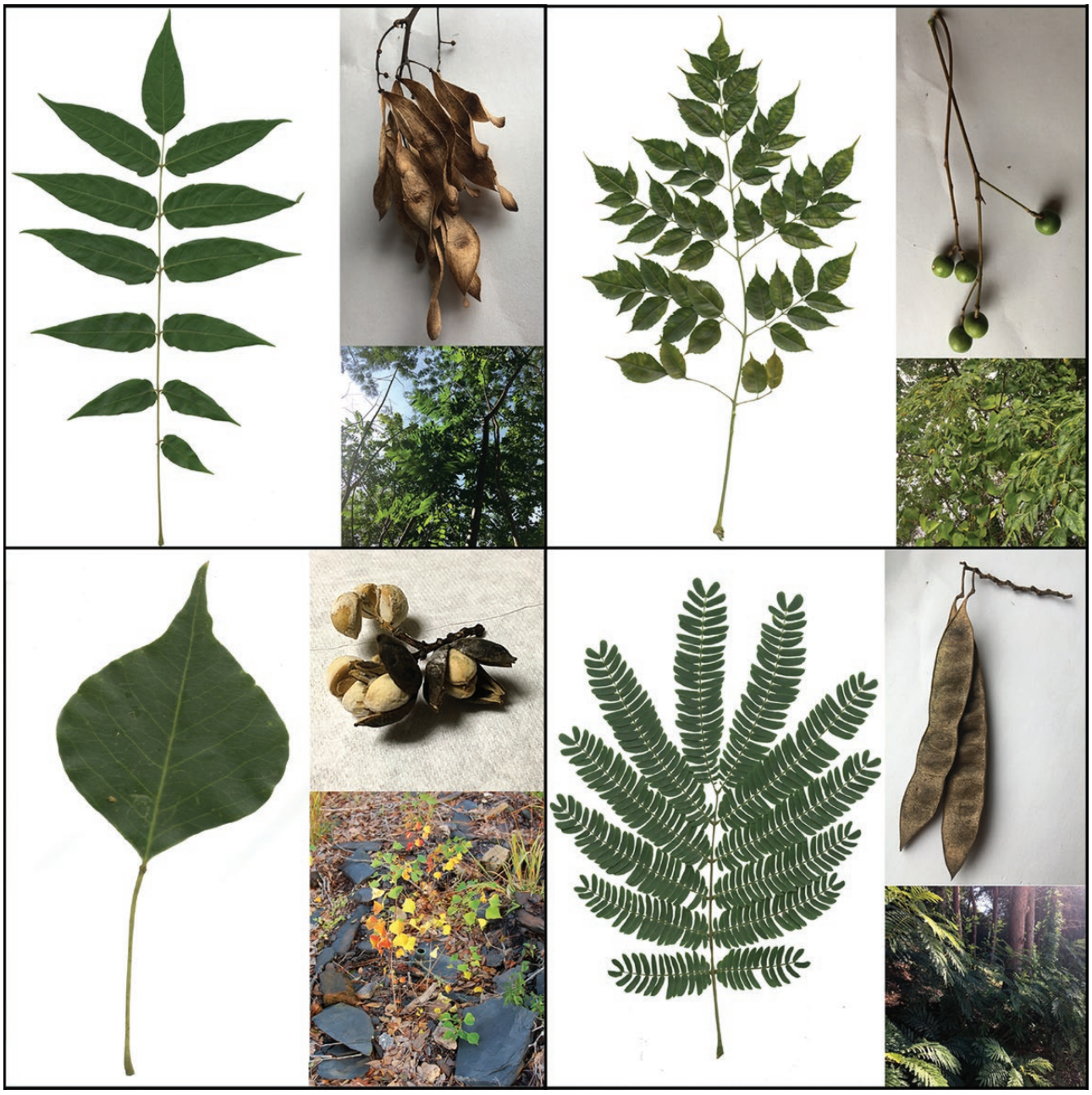

Fig. 1. Leaves (left), fruit (top right), and invaded site (bottom right) of tree-of-heaven (top left), Chinaberry (top right), Chinese tallow (bottom left), and mimosa (bottom right). Photographs courtesy of Sara Lalk, with assistance from Bridget Blood, Calvin Norman, and Crystal Strickland.

although they yield some benefits to the pollinator community. Chinese tallow is almost exclusively insect pollinated and both native generalist bee species and non-native European honeybees (*Apis mellifera* L., Hymenoptera: Apidae) readily use the flowers.

Mimosa (*Albizia julibrissin* Durazz., 1772 Non sensu Baker, 1876; Fabales: Fabaceae)

Mimosa is a deciduous tree that produces pink-white flowers in the summer and leguminous seed pods in the fall. Beginning with its introduction from the Middle East by French botanist Andres Michaux in 1808 (Bartram 1808), mimosa was eventually planted at Monticello for Thomas Jefferson because of its beautiful summer flowers. Often considered a beloved garden fixture, the wood can be used for furniture making, the bark as an insect repellent, and the seeds as an oilseed crop (Nehdi 2011). Mimosa has also been touted as a viable forage material for goats but shown to be less palatable and productive than some natives like black locust (*Robinia pseudoacacia* L.; Fabales: Fabaceae) (Animut et al. 2007).

Although mimosa is predominantly valued for its horticultural use and aesthetic beauty, it is susceptible to a variety of native and non-native pests (e.g., mimosa webworm, *Bruchidius* beetles, fusarium wilt, *Fusarium oxysporum* Schlecht. emend. Snyder & Hansen; Hypocreales: Nectriaceae, etc.), which can lead to an abundance of unsightly dead trees and increased removal costs (North and Hart 1983, Stipes 2001, Chang et al. 2011). Despite these issues, it remains a prolific spreader due to copious production of highly viable seeds and its ability to resprout from cut stumps (Pitman 2008). Furthermore, the utilitarian values of the wood, bark, seeds, and greenery are rarely exploited for modern industrial applications

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or other measurable use within the United States. To date, *Albizia julibrissin* is not featured in any state noxious weed list (Table 1).

Norway Maple (*Acer platanoides* L.; Sapindales: Aceraceae)

Norway maple is a deciduous tree distinguishable by its opposite branch arrangement and distinctive milky sap exuded by broken petioles and buds. This European native has been prized for its wide variety of color and form, evident by the 100+ cultivars available for purchase in the United States, but no nonhorticultural value is suggested for this species. In 1756, renowned botanist and administrator of the Chelsea Physic Garden in London, Philip Miller, sent John Bartram a shipment that included Norway maple seeds (Le Rougetel 1986). Ever since Bartram's receipt of these seeds, the species has been a widely celebrated and extensively cultivated horticultural fixture in temperate regions of the United States (Nowak and Rowntree 1990; Fig. 2.

Following the loss of American elm (*Ulmus americana* L.; Rosales: Ulmaceae) and chestnut trees [*Castanea dentata* (Marsh.) Borkh.; Fagales: Fagaceae] to Dutch elm disease and chestnut blight respectively, Norway maples were planted as street tree replacements due to their ability to thrive in a wide range of environments and established abundance in nurseries (Shatz et al. 2015). Norway maple is capable of aggressively establishing within intact, healthy forests and reducing native plant biodiversity (Webb et al. 2000). It is able to outcompete native species and reduces the understory in stands where it is the dominant species (Martin 1999). This aggressive planting and subsequent escape from cultivation also contributed to the establishment of the Asian longhorn beetle [*Anoplophora*

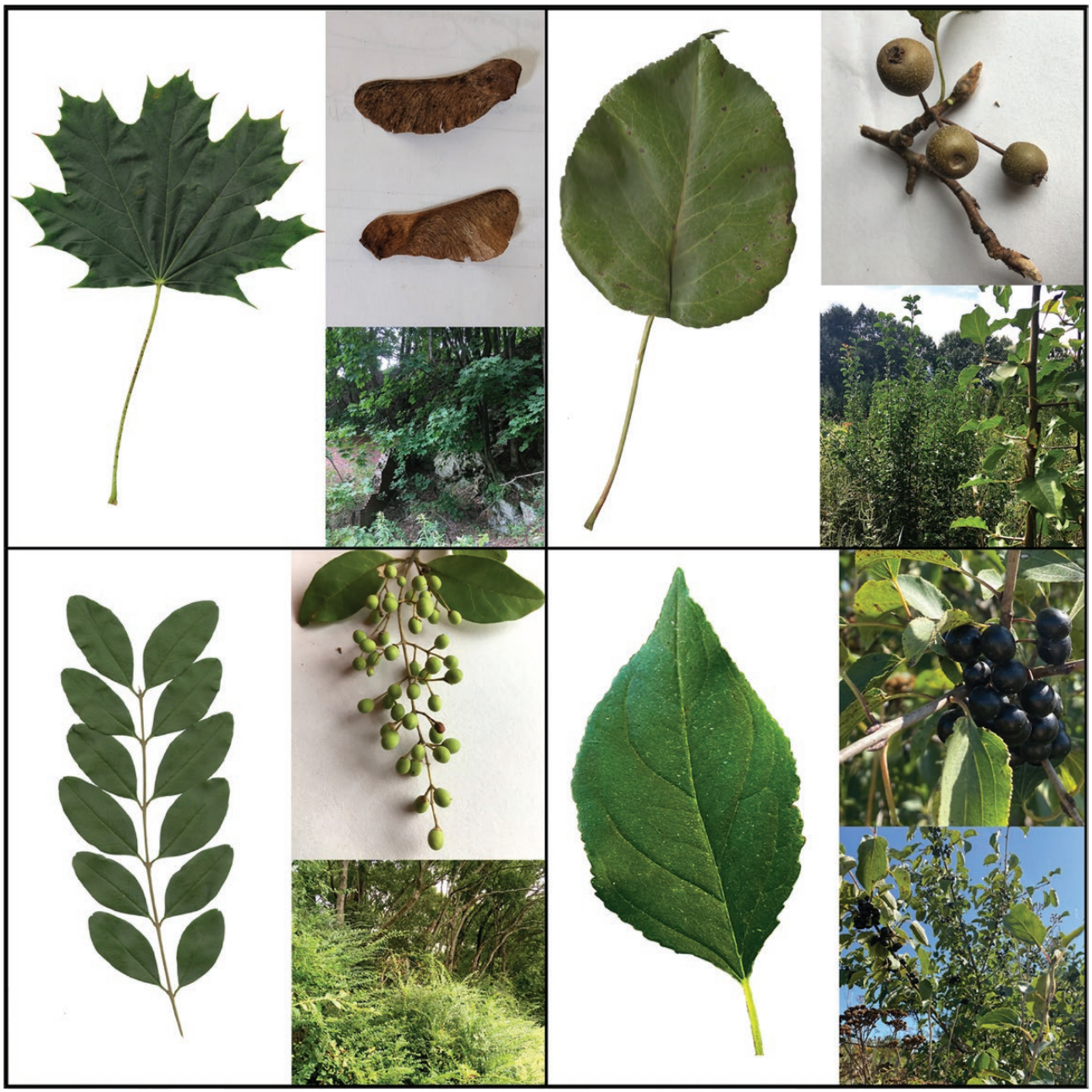

Fig. 2. Leaves (left), fruit (top right), and invaded site (bottom right) of Norway maple (top left), Callery pear (top right), Chinese privet (bottom left; immature fruit), and common buckthorn (bottom right). Photographs courtesy of Sara Lalk, Charles Decker, and Ashlee Lehner.

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glabripennis (Motschulsky, Coleoptera: Cerambycidae)] in Worchester, MA (Freilicher et al. 2008), as there is clear preference and improved fecundity for Asian longhorn beetle in these trees (Smith et al. 2001). Norway maple is currently listed as a noxious weed in MA, ME, MN, and VT (Table 1).

Callery Pear (*Pyrus calleryana* Decne.; Rosales: Roseaceae)

Callery pear is a deciduous tree bearing clusters of showy white flowers in early spring and small brown fruits in the late summer and fall. Its introduction from Asia is uncertain; some report it as being introduced by George Compere, Deputy Quarantine Officer of the California State Commission of Horticulture (Compere 1913), whereas others report that it was brought over by Frank Meyer with the USDA Foreign Plant and Seed Introduction division (Culley 2017). Callery pear trees show exceptional resistance to fire blight (*Erwinia amylovora* (Burr.) Winslow et al.; Enterobaterales: Erwiniaceae) and were initially brought to the United States to use to confer fire blight resistance to European pears, (*Pyrus communis* L.; Roseales: Roseaceae), to help the pear industry. Some selections were attractive options as landscape trees and ornamentals due to their unpalatability to herbivores, ability to tolerate harsh conditions, and aesthetic value. Although the most popular cultivar, 'Bradford', is sterile and cannot cross with another 'Bradford' pear, it can cross with any other *Pyrus*, with the resultant progeny eventually reverting to its wild state as a thorny, dense tree that causes damage to equipment, people, and pets (Culley and Hardiman 2007, Culley 2017). Callery pear produces hundreds of flowers, each one capable of producing up to 10 seeds in a single season which have an average germination rate of 87% (Culley and Hardiman 2009).

Although Callery pear is regarded as more insect and disease resistant than other ornamental pears, it can experience low to moderate herbivory by generalist insects and disease from damaging pathogens like fire blight (Momol et al. 2000, Matter et al. 2012). Although Callery pears show some fire blight resistance, notable lesions still develop on their twigs following inoculation with this bacteria (Bell et al. 2003). The bacteria may then be harbored and vectored by visiting pollinators creating other, yet unknown, issues (McArt et al. 2014). Moderate levels of herbivory by generalists, including grasshoppers, have been shown to increase the Callery pear's growth rate and spread (Gawkins 2019), making these interactions even more environmentally detrimental. Despite all this, the species has only been recently added to the OH noxious weed list (Table 1).

Invasive Shrubs

Chinese Privet (*Ligustrum sinense* Lour; Lamiales: Oleaceae)

Chinese privet grows as a shrub to small tree, forming dense, multistemmed, semideciduous thickets (Maddox et al. 2010). Differing dates of Chinese privet introduction are reported; Robert Fortune was credited with introducing the plant in either 1852 (Dirr 1998) or 1855 (Earle 1902). The spread of this escaped ornamental is most successful in forests with low overstory coverage, deep leaf litter, and basic soil pH (Hagan et al. 2014). Further success is found within disturbed areas characterized by urban development and high housing density (Atasoy 2017), and seed dissemination is facilitated by birds and some mammals. Chinese privet is only listed as a noxious weed in FL and TN (Table 1).

For humans and livestock, ingestion of components of the plant can cause a variety of symptoms including nausea, headache, vomiting, abdominal pain, and more (Westbrooks and Preacher 1986). Removal of privet can be challenging, and though herbicide control and hand-pulling seedlings is effective, prevention of initial colonization is the best approach (Maddox et al. 2010). Successful removal and exclusion of privet leads to increases in butterfly, bee, and beetle abundance and diversity near the forest floor (Ulyshen et al. 2020b; Hanula and Horn 2011a,b; Lobe et al. 2014), and these benefits persist for at least 5 yr following removal. This is probably due to the effects of Chinese privet litterfall on available N as well as lower lignin and cellulose, increasing decomposition rates in stands where it dominates (Mitchell et al. 2011).

Common Buckthorn (*Rhamnus cathartica* L.; Roseales: Rhamnaceae)

A deciduous shrub native to Europe, common buckthorn, was introduced to the United States probably for medicinal uses (Kurylo and Endress 2012), which transitioned to ornamental hedge planting. No common consensus exists regarding the initial introduction of this species, though it was known to be common in hedgerows in Philadelphia, PA, by 1806 (Coxe 1806). Buckthorn is tolerant of a wide array of environmental conditions and is a prolific invader as the bird-dispersed seeds have a high germination rate (Knight et al. 2007).

Buckthorn invasion reduces the growth and survival of native saplings in invaded sites and pushes the community structure toward more shade-tolerant species (Fagan and Peart 2004). Common buckthorn is an aggressive invader and quickly outcompetes natives to form monocultures that limit native plant establishment and survival, and contain lower biomass than uninvaded areas, thereby reducing carbon sequestration (Mascaro and Schnitzer 2007, 2011). Experimental removal of buckthorn results in higher native seedling establishment in previously invaded sites (Frappier et al. 2004) and increased biodiversity of insects (Schuh and Larsen 2015). Common buckthorn is listed as a noxious weed in MA, NH, VT, CT, WI, MT, and MN (Table 1).

Russian and Autumn Olives (*Elaeagnus angustifolia* L. and *E. umbellata* Thun.; Roseales: Oleaceae)

Both Russian and autumn olive are large, deciduous to semievergreen shrubs native to Asia that typically bear thorns (Fig. 3). Russian olive is native to southern Europe and western Asia and has been cultivated in England since the 16th century (Bean 1919), whereas autumn olive was described by Swedish botanist Carl Peter Thunberg sometime between 1775 and 1776 in Japan (Thunberg 1784).

These shrubs can grow up to 20 feet tall with highly fragrant yellow flowers and bird-disseminated fruits that range from red-pink (autumn olive) to whitish-yellow (Russian olive). European honey bees are reported as the main pollinator of Russian olive (Pan et al. 2011), whereas generalist pollinators such as *Bombus* (Hymenoptera: Apidae) and *Andrena* (Hymenoptera: Andrenidae) are reported as the main pollinators of autumn olive (Soley 2013).

Russian and autumn olives fix nitrogen (Gardner 1958), produce high volumes of seed, and resprout easily following mechanical control and burning, increasing their survival rates in inhospitable environments and making them difficult to control. They can quickly create dense monocultures, which shade out understory plants, and although they can be seen as beneficial to wildlife and pollinators in some respects (Borell 1971, Pendleton et al. 2011), they have been shown to increase nitrogen loading in streams leading to additional ecological damage (Goldstein et al. 2009, Mineau et al. 2011). It is unknown how these effects compare to ecosystem and pollinator

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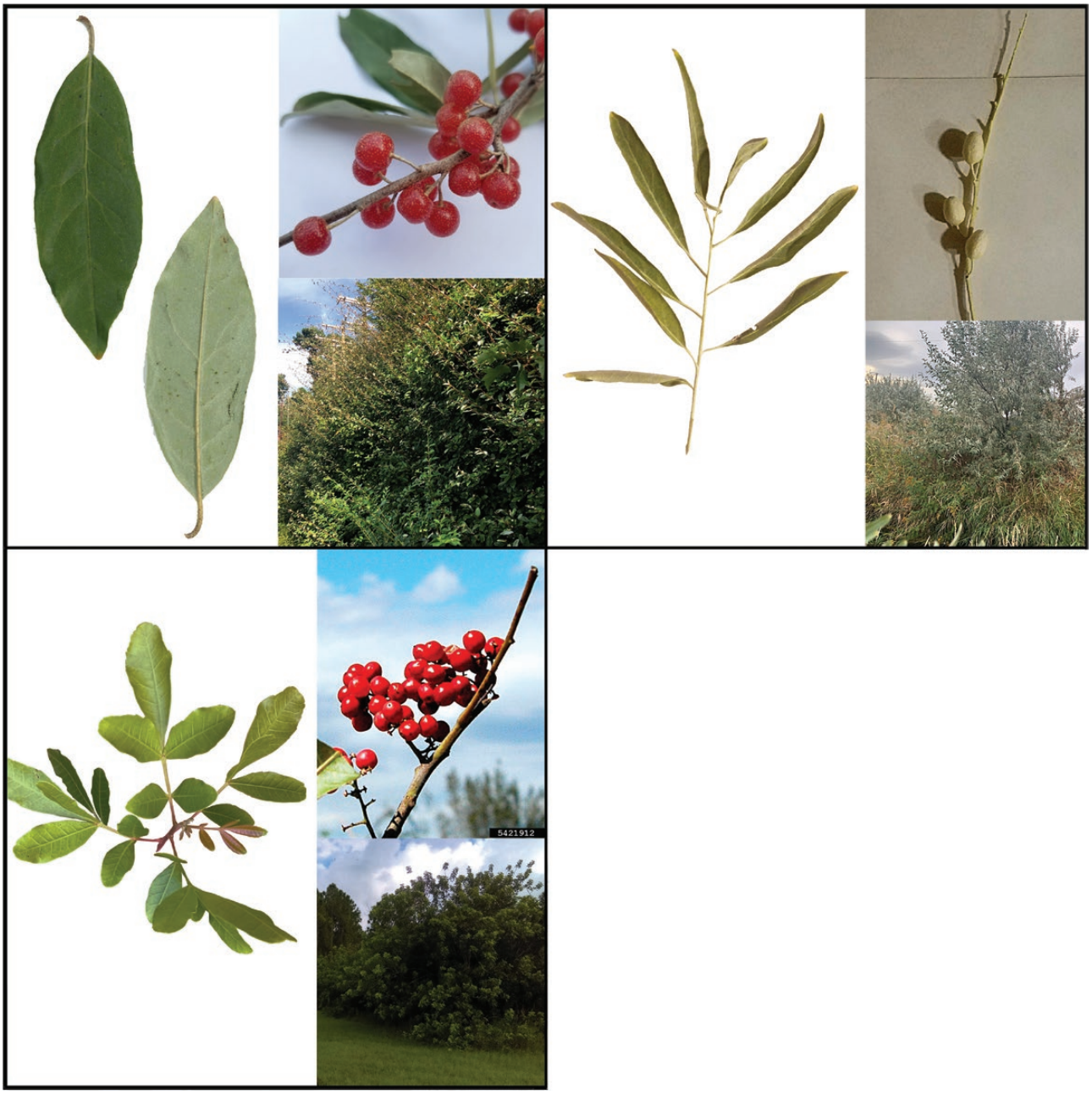

Fig. 3. Leaves (left), fruit (top right), and invaded site (bottom right) of autumn olive (top left), Russian olive (top right), and Brazilian peppertree (bottom left). Photographs courtesy of Sara Lalk, Robbie Doerhoff, Alex Kayfish, Joshua Botti-Anderson, and James H. Miller, USDA Forest Service, Bugwood.com.

services, which would otherwise be filled by native species in these areas. These species are included in the noxious weed lists of 14 states; AZ, CO, CT, MA, ME, MI, NH, NM, TN, UT, WA, WI, WV, and WY (Table 1).

Brazilian Peppertree (*Schinus terebinthifolia* Raddi; Sapindales: Anacardiaceae)

Brazilian peppertree is an evergreen tree native to subtropical and tropical South America, sharing the same family as poison ivy, poison oak, and poison sumac. It was introduced to FL in the mid-1800s as an ornamental and for Christmas decorations due to its dark green leaves and bright red berries (Williams et al. 2007). It is a frequent invader of disturbed habitats and is considered one of the most aggressive non-native shrubs in FL (MacDonald et al. 2008). It quickly outcompetes native plants and forms a dense monoculture, shading out understory plants and competing with other shrubs and trees.

Brazilian peppertree has negative effects on native communities and humans alike. For example, two native plants (*Bidens alba* L.; Asterales: Asteraceae and *Rivina humilis* L.; Caryophyllales: Petiveriaceae) grown with irrigation containing Brazilian peppertree extracts had lower germination and dry weight compared with those grown with extracts from native oak species (Morgan and Overholt 2005). Much like other members of the Anacardiaceae, Brazilian peppertree contains an aromatic sap that, if contacted by humans, can cause dermatitis (Morton 1978). Brazilian peppertree is only included in noxious weed lists for FL and TX (Table 1).

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Brazilian peppertree is dioecious, producing thousands of small white flowers on axillary clusters. The major pollinator of Brazilian peppertree is a small syrphid fly (*Palpada vinetorum* F.; Diptera: Syrphidae), but other Dipterans, honey bees and other hymenopterans, butterflies, and beetles are also known to visit the flowering trees (Cesário and Gaglianone 2013). Nectar from Brazilian peppertree may be important for honey bees during fall months, although the direct effects of the plant's nectar and pollen on honey and other bees are not well studied.

Interactions Between Non-native Woody Plants and Native Arthropods

Arthropods are arguably one of the most important fauna groups on the planet, comprising all or parts of nearly every trophic level, contributing billions of dollars annually to agriculture and natural resource systems, acting as bioindicators, and having significant impacts on global human health (van Straalen 1998, Losey and Vaughan 2006, Maleque et al. 2009). As such, the disruption of arthropod communities can alter ecosystem health and function and can cause widespread cascading effects, yet despite the importance of these issues, there is conflicting evidence regarding the impacts of non-native plants on native arthropods.

Some non-native plants can quickly outcompete native vegetation, creating a monoculture of dense trees, shrubs, and vines that are of little benefit to most native fauna. Changes to native plant communities may affect herbivores, leading to bottom-up effects on associated predators and parasites (e.g., Price et al. 1980) and top-down effects to soil biota and surrounding native plants (Ehrenfeld 2003, Haddad et al. 2009). However, the direction and magnitude of these effects are inconsistent. Some studies show that herbivore populations on non-native plants, including trees and shrubs, are lower compared with native plants, but predator populations tend to be higher on those non-native plants (Harvey and Fortuna 2012). For example, Chinese tallow supports relatively lower proportions of herbivores compared with native woody plants but a higher proportion of predators and a higher species richness of those predators (Hartley et al. 2010). Others report similar predator loads on non-native and native species (Engelkes et al. 2012, Parsons et al. 2020).

These varying interactions among native arthropods and invasive woody plants are governed by flora, fauna, and ecosystem characteristics. Specifically, the phylogenetic classification of each species and their relative phylogenetic relationship with surrounding native flora and fauna, trophic guild, and behavior (e.g., oligolectic pollinator) probably mediate interactions among these communities (Pyšek et al. 2014). Several hypotheses exist to explain the success or failure of invasive species in relation to their phylogenetic relationship with native species. For example, Darwin's naturalization hypothesis states that areas with a high abundance of closely related species are less likely to be invaded than areas with a low abundance of closely related species (Strauss et al. 2006, Enders et al. 2020). These interactions have not been studied in invasive woody plant systems.

Furthermore, a non-native species may act as a direct and/or indirect passenger or driver of invasion (MacDougall and Turkington 2005). As passengers, arthropods may be affected by the invasion of a non-native species, which may affect other arthropods in the community. One meta-analysis of 87 articles examining arthropod communities in invasive plant systems found a significant decrease in arthropod abundance in 62% of the papers (Litt et al. 2014). As drivers of invasion, the behavior of arthropods increases the success of the invasive plant (Lockwood et al. 2013). For example, moderate herbivory has been shown to increase the growth and spread of Callery pear (Gawkins 2019). Very little literature exists, however, examining invasive woody plants as drivers or passengers of disturbance and change (Madritch and Lindroth 2009, O'Leary et al. 2018, Linders et al. 2019) and even less is available examining specific driving mechanisms for invasive woody plants in the United States (Lobe et al. 2014).

Pollinators

Some invasive woody plants, like Chinese privet, have notably detrimental impacts on pollinator communities and removal of the invasive plant yields rapid improvement in the health and diversity of those communities (e.g., Hanula and Horn 2011a, Hanula et al. 2016). Conversely, other invasive trees such as Chinese tallow are well regarded for their benefits to certain pollinators (Hartley et al. 2004). These differences may be due to characteristics of both the plant and pollinator. For example, some pollinators, especially polylectic species, readily incorporate non-native plants into their host repertoire (Harmon-Threatt and Kremen 2015) and may benefit from the presence of invasive plants selected for their flowering properties. Other bees, especially mono- and oligolectic species, are less able, or unable, to add non-natives to their host range and are thus negatively affected by severe alteration of local plant communities by invasive plants.

Indirectly, the presence of invasive plants may alter the native plant community through pollinator competition, causing cascading effects when pollinators prefer invasive species over natives. However, the direction and magnitude of these interactions varies. For example, the presence of non-native asters increases pollination services to native plants by attracting additional pollinators (Tepedino et al. 2008), whereas other plants, e.g., purple loosestrife (Brown et al. 2002), outcompete natives for pollination services and, therefore, outcompete native plants to quickly create a monoculture. However, these studies have been conducted with herbaceous and not woody species. Although there is conflicting evidence, most studies suggest that invasive species tend to disrupt mutualisms between plants and pollinating arthropods (Traveset and Richardson 2006, Morales and Traveset 2009).

It is important to note that the current knowledge base regarding pollinator interactions with invasive plants is derived from nonwoody species observations. What is known of invasive woody plants reviewed in this article, such as glossy buckthorn (Godwin 1943, Charles-Dominique et al. 2012), Callery pear (Makimura et al. 2015), Russian olive (Pan et al. 2011), and Brazilian peppertree (Cesário and Gaglianone 2013), is simply that they are pollinated by insects. Additionally, most of these studies have been performed in the invasive species' native ranges, allowing even less information about pollinators of these woody plants in the contiguous United States.

Herbivores

Insect herbivores may be negatively affected by the establishment of non-native plants when they compete with preferred native food sources (Simao et al. 2010). Conversely, non-native plants may have positive effects on arthropod food webs, and some have been shown to benefit herbivores through higher fitness of arthropods (e.g., Cogni 2010) as well as associated predators and parasites through increased prey abundance. Overall, however, invasion by non-native plant species tends to reduce abundance and diversity of specialist herbivores and has little effect on generalist herbivores (Carvalheiro et al. 2010). Non-native woody horticultural plants are often chosen

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for commercialization because many are undesired or unpalatable to herbivores.

Herbivore pressure on non-native invasive plants differs among plant species and over time and are especially important in invasion characteristics of invasive woody plants due to their direct impacts on growth, spread, and placement within food webs. For example, herbivory on Chinese tallow tree was significantly lower in the early stages of plant introduction, contributing to release from natural enemy pressure and rapid spread of the invasive plant. However, herbivory increased significantly in later periods following introduction, reducing the earlier benefit to the plant (Siemann et al. 2006). Moderate herbivory by generalist grasshoppers on Callery pear increased the species' growth and contributed to its spread (Gawkins 2019). Although compensatory growth in woody plants as a response to moderate herbivory is common (Reichenbacker et al. 1996), this release from specialist herbivores and increased growth response with moderate pressure from generalists lend support for the enemy release hypothesis and the evolution of increased competitive ability hypothesis for some invasive woody species (e.g., Vilà et al. 2005, Jogesh et al. 2008, Williams and Sahli 2016). However, additional driving mechanisms are probably present and understudied.

Twig- and Stem-Boring Insects

Most native twig- and stem-borers (Coleoptera: Buprestidae, Curculionidae, Cerambycidae; Hymenoptera: Siricidae) are rarely considered primary pests and tend to invade trees that are stressed or weakened by other biotic or abiotic factor (e.g., the pigeon horntail (*Tremex columba* L.; Hymenoptera: Sircidae); Stillwell 1967), although some of our most damaging invasive insect species are wood borers themselves (Coleman et al. 2012, Herms and McCullough 2014, Hughes et al. 2017). These insects are sometimes first in the line of decomposers, often introducing decay fungi and bacteria that degrade lignin and cellulose (Jacobsen et al. 2017), and other times competing with decay fungi to slow the decomposition process (Skelton et al. 2019). These insects and their associated fungi are often generalists, able to use multiple genera, or even families, of woody trees and shrubs (Kühnholz et al. 2001).

Because of their role in decomposition (Ulyshen 2016), the interactions of wood borers with invasive woody plants are critical from a nutrient cycling perspective. Despite their importance in the ecosystem, little to no literature exists examining woodboring insect responses to invasive woody plants. We know that native wood borers are able to add non-native trees to their host range (e.g., Long et al. 2009, Haavik et al. 2013) and some work has been done regarding Asian long-horned beetle use of Norway maple (Freilicher et al. 2008), but little else is known regarding interactions among invasive woody plants and twig- and stem-borers.

Leaf Litter and Soil Arthropods

Arthropods in leaf litter and soil serve important roles in the decomposition and cycling of nutrients back into the soil for uptake by plants and trees (Hassall et al. 1987). These important arthropod groups have top-down impacts on soil biota, pH, soil nutrients, and soil moisture and act as a trophic base in many ecosystems (Anderson 1975). It makes sense, then, that different types of leaf litter would affect these arthropod communities. Specifically, succession of arthropods in the process of leaf litter composition probably changes with plant species due to differences in leaf phytochemistry, which is evident in some invasive woody plants like Japanese barberry, which results in lower leaf litter arthropod diversity and species richness (Clark and Seewagen 2019).

Leaf-litter and soil-dwelling arthropods also have differing responses to the encroachment by invasive trees. In a study examining tree-of-heaven, honeysuckle (*Lonicera maackii* Rupr. (Maxim); Dipsacales: Caprifoliaceae), and buckthorn leaf litter, evenness and diversity were similar to that of leaf litter surrounding native trees, but community composition differed significantly under invasive trees (Woodworth et al. 2020). Short-term impacts of the encroachment of invasive trees may represent a pulse of resources for arthropods, though over time native trees tend to support healthier leaf litter and soil communities (e.g., Heimpel et al. 2010, Lobe et al. 2014). It is important to note that decay rates of invasive woody plants differ highly among species and ecological context, so the benefit-to-cost ratios are not consistent across all invasive woody plants (Ulyshen et al. 2020a). Although some work has been done examining the impacts of disturbance and invasive species on soil-dwelling arthropods and annelids (Coyle et al. 2017), it is clear that additional research is needed to investigate the impacts of invasive woody plants on leaf litter-dwelling arthropods.

Opportunities and a Call to Action

Scientists have been sounding the alarm on the global issue of invasive species for years, yet we still know very little about certain aspects of the overall problem. Ecological impact of woody invasive is, unfortunately, one of those aspects. Why we lack this knowledge is a debatable question, but probably stems from the fact that woody invasive plants rarely encroach on high-value agricultural systems, instead establishing in natural areas and managed forests where their impacts are less easily quantifiable. Some are not perceived as detrimental or are associated with positive ecosystem services (Potgieter et al. 2019), and some even have positive relationships with wildlife (Gleditsch and Carlo 2011). Nonetheless, we identified several key knowledge gaps that deserve further research and attention.

Impacts on Flora and Fauna Communities

There are significant gaps in knowledge regarding how invasive woody plants affect biodiversity and ecosystem functioning and how they themselves function in different habitats. For example, do invasive plants represent an 'herbivore-free space', thus driving impacts in other trophic levels? Is there a shift in community composition, and if so, what is that shift, and how does it affect other trophic levels? In many cases, non-native woody plants gradually crowd out or overtake existing vegetation in ecosystems in which they establish (Richardson 1998). Certainly, for a few highly impactful invasive plant species, we do know something about the extent of those species' influence (e.g., Chinese privet, Lobe et al. 2014), although for others such as Chinese and Japanese wisteria (*Wisteria floribunda* (Willd.) DC. and *W. sinensis* (Sims) DC.; Fabales: Fabaceae), Japanese honeysuckle (*Lonicera japonica* Thunb.; Dipsacales: Caprifoliaceae), English ivy (*Hedera helix* L.; Apiales: Araliaceae), Oriental bittersweet (*Celastrus orbiculatus* Thunb.; Celastrales: Celastraceae), and other invasive woody vines, there is little literature on their impacts and even less on their interactions with arthropods. For many invasive woody plants, especially those in natural or noncrop areas, we know very little about their impacts—in fact, for many invasive woody plants, we know little more than presence/absence data.

Furthermore, several anthropogenic factors—including climate change and urbanization—compound the effects of invasive plants on arthropod communities (Bradley et al. 2010, Giejsztowt et al. 2020). Climate change increases the frequency and intensity of abiotic disturbances such as flooding, drought, and hurricanes, all of which disturb habitats and may increase their susceptibility to the establishment of invasive plants (Bradley et al. 2010). Habitat fragmentation through urbanization and conversion of forested land to agriculture also creates

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disturbed, undeveloped, and abandoned sites, which are easily colonized by invasive plants (Werner and Raffa 2000, Martinson and Fagan 2014). How these factors affect invasive woody plant and native arthropod interactions is unknown and additional research is warranted. It is imperative that we create a baseline from which to examine environmental changes due to invasive woody plants and that we continue researching the economic and ecological impacts of invasive plant encroachment into natural and managed areas.

Impacts on Ecosystem Services

The impacts and contributions of pollination and other ecosystem services and mutualisms are staggering: pollination contributes approximately $361 billion annually worldwide (Hanley et al. 2015), and other arthropod ecosystem services such as dung burial and pest control have been estimated to be as high as $60 billion per year in the United States alone (Losey and Vaughan 2006). Although invasive woody plants flower and undoubtedly affect pollinators as evidenced above, we know little about these ecosystem service interactions and their direct and indirect effects. Some species, like Chinese tallow, have been planted specifically as floral resources for pollinators, especially honey bees (Hartley et al. 2004). However, now that many non-native woody plants are naturalized, we know almost nothing about how this flower resource affects pollinator populations longitudinally. Although invasive woody plants may be providing a benefit in some cases (e.g., flowers when others are not available) or contribute to biodiversity (Schlaepfer 2018), they may also be a less-nutritious food source or competing with native plants for pollination services (Brown et al. 2002).

We also know little regarding how invasive woody plants interact with and affect native decomposing arthropods. The first decomposers to arrive at these non-native woody plants are probably twig- and stem-borers, which are known to attack stressed trees and act as the final straw (Jacobsen et al. 2017). Following seasonal senescence or tree mortality, arthropods in the soil and leaf litter then continue the decomposition process and cycle nutrients back to the ecosystem (Reichle 1977). These arthropod communities often form the base of ecosystems and interact with multiple trophic levels, providing myriad ecological benefits through decomposition, nutrient cycling, and pest control (e.g., Nichols et al. 2008).

No baseline exists from which to measure changes to native arthropod communities in the habitats most likely to experience encroachment by invasive plants. Research into the effects of non-native woody plants on these decomposer communities is essential to understanding multitrophic effects and impacts on ecosystem services.

Driving Mechanisms

Plants promoted for horticultural purposes often possess certain growth characteristics, including ease of establishment, rapid growth and colonization, and high fecundity (Richardson and Rejmánek 2011). These same characteristics help some escaped non-native plants become invasive and contribute to their outcompeting native flora. To that end, some of the mechanisms behind invasive woody plant spread seem intuitive, yet these have rarely been studied in invaded areas. We posit that a larger problem is the influence of humans; namely, that people continue to cultivate, purchase, plant, and in some cases promote invasive woody plants on the landscape.

There is no hope of large-scale successful management if invasive plants are continually being introduced into the environment. Some blame for this current situation goes to industry for continually producing known invasive species (Reichard and White 2001; however, as profit-driven businesses, these entities are making what sells. Some of the onusalls upon the shoulders of scientists and educators, as many home and landowners are simply not aware that certain species are invasive or that native alternatives to invasive woody plants exist. In many cases, these private citizens are just buying and planting what their neighbors have, what they consider aesthetically pleasing, or what is being promoted by retailers—another entity not without fault in this situation. Some might ask why states do not outright ban the sale of invasive woody plants—this would theoretically put a halt to this issue. However, regulatory actions are not a straightforward matter, and doing so takes a great deal of time, understanding, and—in some cases—compromise. The processes behind these determinations and bans are different for each agency and locality (e.g., Buerger et al. 2015) and their review falls outside the scope of this article, although their efficacy has been explicitly detailed and analyzed for a subset of Midwestern states (Buerger et al. 2015). These policies and processes directly affect industry groups and, therefore, support and buy-in from all of these groups is needed. Currently, we lack data on how these policies might affect our economy as well as stakeholder perceptions of invasive trees and shrubs.

The growing and continued demand for global trade, resource conservation, and economic feasibility of invasive control operations leaves scientists and practitioners with a responsibility to continue to strive for greater efficacy in the stewardship of our environment, both for ourselves and for future generations. It is unlikely—at least in the near future—that invasive woody plants will not continue to be sold, planted, and established in natural and managed systems. Knowing the impacts of these actions is the first step to creating successful management plans, and although broad patterns may emerge, there are likely to be species-specific interactions and implications in many of the aforementioned research areas.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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