



Alien plants and insect diversity

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Alien plants are ubiquitous

Although plants always have naturally redistributed around the globe, the increased temporal and spatial mobility of humans has resulted in an extraordinary increase in the rate of plant movements (Vitousek, Mooney, et al., 1997). Additionally, wherever we have purposefully landscaped our surroundings, we have heavily favored alien species of plants (Lambdon et al., 2008; McKinney, 2001, 2004; Reichard & White, 2001; van Kleunen et al., 2015). Thousands of plant species have been moved from their parent continent either purposely for agriculture, lumber production, horticulture, and restoration plantings or accidentally as hitchhikers. An estimated 13,168 plant species (about 3.9% of global vascular flora) have been introduced beyond their native ranges as a result of human activity (van Kleunen et al., 2015). Although some of these species have joined native plant communities without substantial changes to species abundance and composition, many others have become invasive, outcompeting native plant communities (Dehnen-Schmutz & Touza, 2008; Richardson & Rejmánek, 2011). For example, at least 3300 introduced plant species have become invasive in North America (Qian & Ricklefs, 2006), 300 in Europe (Keller et al., 2011), and 2700 in Australia (Webber et al., 2014), and, by now, all areas in the world are invaded by at least one alien plant species (Nuwer, 2014; Pyšek et al., 2020). Despite management efforts, invasive plants are increasing in abundance, especially in protected areas (Pyšek et al., 2020). Many native ecosystems with diverse species of plants and animals are rapidly being converted into novel assemblages, creating one of the most ubiquitous threats to biodiversity today (Dolan et al., 2011; Johnson, 2007; Radeloff et al., 2015).

In horticultural and ecological circles, concern often has focused only on alien plants that are invasive, assuming that if a plant is not invasive, it does

not cause ecological problems. This assumption has led land managers and the public to consider these species as acceptable choices for landscaping, agroforestry, and restoration. However, plants represent the first trophic level wherever they occur. In the United States of America (USA) alone, approximately 54.6 million hectares are in residential landscapes dominated by ornamental plants (Nickerson et al., 2007). If ornamental plants do not provide appropriate resources for herbivores, large areas may no longer serve as habitat. In addition, ornamental plants could become invasive in the future. Many invasive plants experienced a lag phase for decades or more before they began to spread or were recognized as invasive (Crooks, 2005; Essl et al., 2011). For example, at least 118 species of alien trees have naturalized in Puerto Rico and compete with native trees in natural stands (Francis & Liogier, 1991). Other ornamental plants, such as crepe myrtle (*Lagerstroemia indica*), Callery pear (*Pyrus calleryana*), burning bush (*Euonymus alatus*), and cool-season European turf grasses, often dominate managed landscapes in North America.

In many ecosystems, alien flora can be substantial components of floral diversity. By extrapolating data from USDA Forest Service inventory plots, Miller et al. (2008) estimated that 9% of forests in the southeastern USA are covered by just 33 common invasive plant species. In some island systems, alien plants now represent 50%–70% of the species in the ecosystem (Vitousek, D'Antonio et al., 1997). Yet, relatively few species are needed to alter an ecosystem. For example, cheatgrass (*Bromus tectorum*) has replaced sagebrush communities and the associated insects throughout more than 210,000 km² in the western USA (Bradley et al., 2018). Species such as kudzu (*Pueraria montana*), various privets (*Ligustrum* spp.), Amur and Tatarian honeysuckle (*Lonicera maackii* and *Lonicera tatarica*), common reed (*Phragmites australis*), Himalayan blackberry (*Rubus armeniacus*), and common buckthorn (*Rhamnus cathartica*) in North America provide additional examples of how single species can transform diverse native plant communities into near monocultures of invasive plants over millions of hectares. These alien plants dominate vegetative biomass and reduce taxonomic, functional, and phylogenetic diversity, further exacerbating their effects (reviewed in Sofaer et al., 2018). Plant invasions can alternative plant communities so thoroughly that arthropod populations dependent upon those communities can be devastated.



Alien plants affect arthropods

Every literature review of the subject to date has concluded that, more often than not, alien plants negatively influence arthropods in some way (e.g., richness, abundance) (Bezemer et al., 2014; Litt et al., 2014; Tallamy

et al., 2021; van Hengstum et al., 2014; Yoon & Read, 2016). However, arthropod responses to alien plants are not uniform, with some studies showing no effect and a few showing positive influences. Not surprisingly, the equivocal nature of these responses has led to controversy over how much alien plants actually affect arthropod populations. When comparing the results of studies examining the influences of alien plants on arthropods, an important source of variation is the functional or feeding group considered and the degree of association with native plants. Arthropods are associated with plants in a number of contexts: as folivores, wood eaters, detritivores, pollinators, frugivores, and seed eaters; as herbivores with chewing or sucking mouthparts; as species that use plants as a structure for foraging or as cover; and as host-plant specialists or generalists. These contexts are not equivalent and cannot be lumped when reporting results. In this chapter, we explore how the changes associated with invasions by alien plants influence different functional groups of arthropods, with concomitant effects on communities and ecosystems. We focus mainly on insects, but also include some insights about noninsect taxa (e.g., spiders [Araneae]).

Effects on herbivorous insects

The degree to which widespread alien plants contribute to declines of herbivorous insects is a function of how well such plants meet the nutritional needs of these insects. Decades of research have demonstrated that the vast majority of phytophagous insects are behaviorally and physiologically restricted to the few native plant lineages for which they have developed specialized adaptations to circumvent plant defenses (Ehrlich & Raven, 1964; Forister et al., 2015; Mitter et al., 1988; Strong et al., 1984; Tallamy et al., 2021). When native host plants are displaced by alien species, phytophagous insects typically do not recognize the novel host for feeding or oviposition, or they may be unable to overcome novel plant defenses (Bezemer et al., 2014; Litt et al., 2014; Tallamy, 2004; van Hengstum et al., 2014; Wagner & Van Driesche, 2010).

All herbivorous insects do not interact with plants in the same way. Insects with chewing (mandibulate) mouthparts (e.g., Lepidoptera) typically are more susceptible to defensive compounds in leaf vacuoles than are insects with sucking (haustellate) mouthparts (e.g., Hemiptera). Sucking insects tap into poorly defended xylem or phloem fluids and may be more likely to find alien plants to be acceptable hosts than chewing insects (Burghardt & Tallamy, 2013), although this idea has not been formally examined. If insect

herbivores that chew are less able to consume novel plants, there is a reason for concern when alien plants replace native hosts, given that there are more than 4.5 times as many mandibulate insect herbivores as haustellate species (Tallamy et al., 2021). Leaf mining and galling arthropods also have highly specialized relationships with plants (Forister et al., 2015) and, thus, may be even more negatively affected by novel hosts (Burghardt & Tallamy, 2013; López-Núñez et al., 2017).

Because plants in closely related lineages often share defensive chemicals and phenology, herbivorous insects that specialize on a particular plant group are more likely to accept alien congeners or con-familial species within that lineage than species that do not share an evolutionary history with native host plants (Burghardt et al., 2010; Burghardt & Tallamy, 2013; Connor et al., 1980; Hill & Kotanen, 2009; Lombardero et al., 2012; Pearse & Altermatt, 2013). However, the ability to accept related alien plants is not universal. When comparing insect use of congeneric pairings in a common garden experiment in Delaware, USA, alien congeners of native plants reduced insect abundance and richness by 68%, on average (Burghardt et al., 2010; Burghardt & Tallamy, 2013).

Herbivorous insects with a narrow diet breadth are less likely to develop on evolutionarily novel plants than insects with broader diets (Bertheau et al., 2010; Pearse, 2011). More insect species are host-plant specialists than generalists, with 76% of species associating with just one family of plant hosts (Forister et al., 2015). But, even when we focus only on populations of generalist herbivorous insects, species richness and abundance of these taxa are substantially lower on alien plants compared to native plants (Ballard et al., 2013). In addition, generalist herbivores often are locally specialized on particular plant lineages and thus may act more like specialists than we would expect based on host lists accumulated across their range (Fox & Morrow, 1981; Tallamy et al., 2010).

Of the insect taxa in global decline (Dirzo et al., 2014; Fox et al., 2014), Lepidoptera is by far the best studied for diet breadth. Globally, nearly 70% of caterpillar species develop on a single plant family (Forister et al., 2015). Novotny et al. (2004) determined that the average caterpillar species in New Guinea rainforests feeds on no more than three plant species, with over 90% of these caterpillars concentrated on a single plant host (see Novotny et al., 2002). Thus, the displacement of native plants by alien taxa is likely to contribute to declines in Lepidoptera (Ballard et al., 2013; Burghardt et al., 2010). Richard et al. (2019), for example, found that invaded hedgerows in the mid-Atlantic states of the USA supported 68% fewer

Lepidoptera species, 90% fewer caterpillars, and 96% less caterpillar biomass when compared to uninvaded hedgerows.

Another important factor is that native plants differ greatly in their ability to host phytophagous insects (Narango et al., 2020; Tallamy & Shropshire, 2009). Studies comparing alien plants to native plants that support very few phytophagous insects are less likely to find differences in phytophagous insect communities than studies comparing alien plants to native plants that host dozens of species. In the mid-Atlantic region of North America, for example, oaks (*Quercus* spp.) host 557 Lepidoptera species, whereas tulip trees (*Liriodendron tulipifera*) host only 21 species and yellowwood (*Cladrastis kentukea*) does not serve as host for any Lepidoptera (Tallamy & Shropshire, 2009). Comparing the magnitude of changes resulting from plant invasions in these disparate communities can lead to inappropriate inferences.

Although both woody and herbaceous alien plants can decrease the overall abundance of herbivorous insects, woody plants have stronger effects (Daehler, 2005; van Hengstum et al., 2014). Native woody plants generally support more species of phytophagous insects (Tallamy & Shropshire, 2009). Herbivorous insects that feed on well-defended plant tissues (e.g., leaves, buds, seeds) are less likely to be able to include alien plants in their diets than insects that use undefended tissues (e.g., fruits, nectar, wood). Although this hypothesis has never been tested formally, several species of introduced wood borers (e.g., emerald ash borer: *Agilus planipennis*, sirex woodwasp: *Sirex noctilio*, Asian long-horned beetle: *Anoplophora glabripennis*) and bark beetles (Coleoptera: Scolytinae) have easily included North American trees in their diets (Baranchikov et al., 2008; Eskalen et al., 2013; Fraedrich et al., 2008; Haack et al., 2010; Paap et al., 2018).

Effects on pollinating insects

Alien plants often are perceived as valuable to pollinators. However, alien plants negatively affect pollinators when they eliminate or reduce the abundance of the required food plants (Martin, 1999; Pyšek & Pyšek, 1995; Stout & Morales, 2009). Of more than 4000 species of native bees in North America, over one-third are highly specialized on one plant genus and can only rear young on the pollen produced by members of that genus (Cane, 2021; Fowler, 2020a, 2020b; Fowler & Droege, 2020). Thus, where alien plants replace native flower resources in natural areas or are favored in managed landscapes, specialist bees are unlikely to reproduce at those sites.

Native bees do visit some invasive plants, particularly when their bloom time fills a phenological gap in native flower resources (reviewed by Stout & Morales, 2009). However, dominance by a single plant species has

detrimental effects on bees and butterflies if their active flying and foraging seasons occur outside the periods of these blooms (Fowler, 2020a, 2020b; Fowler & Droege, 2020). This argument also holds for trees, such as *Eucalyptus* species, that are widely planted in shade coffee and forestry agroecosystems around the world (Tallamy, *pers. obs.*).

In general, we know little about which insects will accept novel hosts (Pearse et al., 2013) and there is a danger of overestimating the ability of pollinators to use alien plants and underestimating the negative effects of plant invasions on native pollinators. For example, in one area of northern California, Graves and Shapiro (2003) found that 34% of butterfly species oviposit or feed on alien plant hosts. Yet, the butterfly species in this region that cannot make this shift could suffer population declines due to encroachment by alien plants.

Effects on predatory arthropods

Predatory arthropod communities (which include predatory insects, as well as noninsect taxa such as spiders, harvestmen [Opiliones], and mites [Acari]) exhibit variation in their responses to plant invasion (reviewed in Litt et al., 2014). Predicting how predatory arthropods respond to plant invasion requires a complex understanding of a taxon's prey preferences, foraging behavior, interactions among other predators within the same or adjacent trophic levels, as well as how the taxon's prey may respond to the invasion of alien plants (Harvey et al., 2010). As such, there is a need for exploring multitrophic interactions (López-Núñez et al., 2017) that identify changes in predator–prey dynamics in landscapes where alien plants are prevalent.

Although diet breadth in this functional group is not as narrow as it is for herbivores, predatory arthropods generally are assumed to be prey limited (Foelix, 2010; Price et al., 2011). As such, plant invasion may exhibit bottom-up influences on predatory arthropods through changes in the presence, abundance, or availability of prey. Several studies highlight this relationship where changes in prey density or activity result in concomitant effects on densities of predatory arthropods (Bassett et al., 2012; de Groot et al., 2007; Emery & Doran, 2013; Ernst & Cappuccino, 2005; Gerber et al., 2008; Lau, 2013; Samways et al., 1996; Štrobil et al., 2019; Tang et al., 2012; Topp et al., 2008). When presented with limited prey in an invaded landscape, predator assemblages may reduce diet breadth (Carvalho et al., 2010; Hansen et al., 2009; Mitchell et al., 2021) or switch to a more abundant

prey source (Gratton & Denno, 2005; Kappes et al., 2007; Schreck et al., 2013). In a Mid-Atlantic forest understory dominated by garlic mustard (*Alliaria petiolata*), deHart and Strand (2012) documented that wolf spiders (Araneae: Lycosidae) and harvestmen shifted their prey preferences from springtails (Collembola) that were less abundant in invaded forests to caterpillars that fed on garlic mustard. However, wolf spiders also consumed ants (Hymenoptera: Formicidae), harvestmen, and smaller instars of their own species, requiring a shift to intraguild predation and cannibalism to supplement their diet (deHart & Strand, 2012).

Changes in vegetation structure created by plant invasion also may influence predatory arthropods through changes in foraging behavior, movement, or microclimate. Increased litter loads or ground cover following plant invasion may improve environmental conditions for some predatory arthropods (Ellis et al., 2000; Lindsay & French, 2006; Pehle & Schirmel, 2015; Schirmel, 2020; Wolkovich et al., 2009) or increase prey availability (Ralston et al., 2017), but also may reduce mobility when foraging (Bultman & DeWitt, 2008; Crist et al., 2006; Samways et al., 1996; Wolkovich et al., 2009; Wu et al., 2009). The direction and magnitude of these effects depend on the foraging strategy of the predator and the structural changes created by the alien plant. Simao et al. (2010) hypothesized that the structural simplicity in monocultures of Japanese stiltgrass (*Microstegium vimineum*) reduced web-building structure for spiders. In contrast, structural features created by spotted knapweed (*Centaurea maculosa*) in the Great Plains of North America were associated with increased densities of web-building spiders, as well as increased prey capture (Pearson, 2009).

Parasitoids inhabit and kill their hosts to complete their life cycle. These species have more specialized diets than other predatory arthropods and likely exhibit a bottom-up response to plant invasion (Harvey, 2005; Price et al., 2011). Like predatory arthropods, the abundance and diversity of parasitoids decrease in invaded landscapes, following decreased availability of prey (López-Núñez et al., 2017; Simao et al., 2010). During development, larval parasitoids may be affected by novel chemicals consumed by hosts, leading to delayed development, reduced fecundity, or survival (Fortuna et al., 2012; Harvey & Fortuna, 2012; Harvey & Gols, 2011; Ode, 2006). Fortuna et al. (2012) documented that caterpillars performed poorly when they consumed an alien congener, leading to longer development times and lower survival for the associated parasitoid. However, parasitoids that infested the caterpillar during its pupal stage were not affected (Fortuna et al., 2012).

Effects on detritivorous insects

Detritivore is a relatively broad term that includes organisms that consume dead plant material or microorganisms (i.e., bacteria and fungi) associated with detritus (Brussaard et al., 1997; Clarholm, 1985). If alien plants are unrecognized or unconsumed by plant-feeding insects, alien plant biomass can accumulate, presenting detritivores with an abundant but novel resource.

When presented with increased litter loads from alien plants, detritivores generally increase in abundance (67% of studies reviewed in Litt et al., 2014). Past studies document higher decomposition rates in litter from alien plants compared to native vegetation (Bassett et al., 2010; Ehrenfeld, 2003; Huenneke et al., 1990; Mayer et al., 2005; Standish, 2004; Ulyshen et al., 2020; Vitousek, 1990; Woodworth et al., 2020), which stem from changes in litter characteristics. Woodworth et al. (2020) documented differences in litter chemistry between native and alien plants, where alien litter had more nitrogen and less carbon, which could benefit decomposers. Increased litter cover can alter habitat conditions through changes in soil moisture (Lindsay & French, 2006; Wolkovich, 2010), temperature (Pehle & Schirmel, 2015; Vilardo et al., 2018), and pH (Alerding & Hunter, 2013; McGrath & Binkley, 2009). In addition, alien plants may change the timing of the detrital supply. For example, purple loosestrife (*Lythrum salicaria*) decomposes earlier in North America compared to native sedges and cattails (Grout et al., 1997), potentially reducing available litter loads for detritivores in the spring. Numerous information gaps remain in understanding the implications of alien plants on decomposers, including changes in rates of decomposition and ecosystem function (Prescott & Zuckswort, 2016; Zhang et al., 2019). Although beneficial in the short-term, labile litter loads from invasive plants can result in rapid declines in native detritivores, which may be more accustomed to more recalcitrant but stable litter loads (Blossey et al., 2001; Woodworth et al., 2020).

Although the densities of detritivores can be higher in invaded plant communities (Litt et al., 2014), abundance may not correlate with diversity. As we discuss for herbivores above, novel plant litter resources can favor the colonization of generalists (Ellis et al., 2000; Gergócs & Hufnagel, 2016; St. John et al., 2011). This is especially true in situations where litter loads facilitate the dominance of alien isopods (Isopoda) and other detritivores that increase mineralization rates or decomposition (David & Handa, 2010; Ellis et al., 2000; Hoback et al., 2020; Mitchell & Litt, 2016; Vilardo et al., 2018). Springtails and oribatid mites (Acari: Oribatida) are considered

powerful drivers in litter decomposition (Perez et al., 2013; Seastedt, 1984) and respond quickly to changes in soil chemistry and litter quality (Alerding & Hunter, 2013; Gergócs & Hufnagel, 2016). As such, these taxa may serve as indicators for changes in ecosystem services following plant invasion.

Effects on ants

Ants often are separated from other functional groups due to the versatility in their diet – most taxa encountered at the surface level are omnivorous (Brussaard et al., 1997; Folgarait, 1998; Whitfield & Purcell, 2021). As such, ant responses to plant invasion are highly variable; in a literature review, Litt et al. (2014) summarized a decline in ant richness and abundance in 47% of studies and an increase in only 7%. Invasive plants may alter vegetation structure, which can impede ant movement or increase foraging bouts (Kajzer-Bonk et al., 2016; Lenda et al., 2013; Wolkovich et al., 2009).

Ants can benefit from alien plants if ants recognize these novel seeds as a food source. Predation on seeds of alien plants by native ants varies. For example, multiple species of New World harvester ants (*Pogonomyrmex* spp.) avoid alien grass seeds (e.g., *B. tectorum*) over native seeds in both Patagonian Steppe and sagebrush steppe communities (Aput et al., 2019; Ostoja et al., 2009; Robertson & Robertson, 2020; Schmasow & Robertson, 2016). However, in coastal sage scrub communities, harvester ants prefer seeds of alien stork's-bill (*Erodium cicutarium*) over native con-familials (Briggs & Redak, 2016). On the other hand, ants may facilitate seed dispersal of alien plants (Pearson et al., 2018, but see Pearson et al., 2014). Seed morphology can help provide insights into dispersal and invasion success. Most native plants dispersed by ants produce seeds with elaiosomes – fleshy, lipid-rich structures exterior to seeds that serve as an attractant (Rico-Gray & Oliveira, 2007). This pattern also holds for alien plants, as has been shown for species from genera such as *Acacia* (Gibson et al., 2011; Marchante et al., 2010), *Carduus* (Alba-Lynn & Henk, 2010; Ortiz et al., 2021; Pearson et al., 2014; Pirk & Lopez de Casenave, 2017), *Centaurea* (Jensen & Six, 2006), *Cirsium* (Alba-Lynn & Henk, 2010), and *Euphorbia* (Berg-Binder & Suarez, 2012). Seed size and shape also are important. Small, narrow seeds and seeds dispersed by wind are commonly accepted by ants (Loesberg & Meyer, 2021; Penn & Crist, 2018; Wandrag et al., 2021). Seeds with awns can impede transport; ants in Australia dispersed invasive grass seeds that lacked awns and readily accepted native grass seeds when awns were removed (Wandrag et al., 2021).

Plant invasion also may affect ants indirectly through prey responses, especially where ants use other insects for honeydew. Kajzer-Bonk et al. (2016) reported that ant densities in Southern Poland decreased by more than 50% in fields invaded by alien goldenrods (*Solidago* spp.), which was correlated with declines in specialist caterpillars and their native host plants. In contrast, Lescano and Farji-Brener (2011) documented increased activity of *Brachymyrmex* and *Dorymyrmex* ants associated with increased densities of aphids (Hemiptera: Aphidoidea) on alien thistles (*Carduus thoermeri* and *Onopordum acanthium*) in the Patagonian Steppe. Lescano et al. (2012) also explored ant–aphid relationships, but included an additional parameter – refuse dumps of leaf-cutting ants (*Acromyrmex lobicornis*), which increased thistle biomass and aphid densities, leading to increased ant activity. In this scenario, the activity of native ants could improve conditions for invasive plants to grow and develop, leading to concerns about ants facilitating invasion success.

Given that ants represent an ecologically diverse and important taxonomic group, research focused on a mechanistic understanding of plant invasion and ant responses can yield insights about the potential success of restoration efforts. This is especially true in scenarios where ants contribute to the spread of a novel plant (Briggs & Redak, 2016; Gibson et al., 2011; Ortiz et al., 2021; Pirk & Lopez de Casenave, 2017) or where ants impede restoration through the predation of native seeds (Linabury et al., 2019; MacDougall & Wilson, 2007; Mitchell et al., 2021; Ostoja et al., 2009).

Effects on community composition and food webs

The dominance of alien plants and the concurrent loss of native plant hosts can lead to local extirpation of arthropods, with concomitant changes in the composition of the arthropod community, food webs, and ecosystem function (Bezemer et al., 2014; Chew, 1981; Gratton & Denno, 2006; Mitchell, 2019; Narango et al., 2017; Richard et al., 2019; Sunny et al., 2015). These changes are further complicated because many arthropods perform multiple roles (e.g., larvae could be herbivores, whereas adults are pollinators).

Any reduction in the abundance and diversity of insect herbivores is likely to cause a subsequent reduction in the insect predators and parasitoids of those herbivores. Although the logic here is irrefutable and has some support (Harvey, 2005; Narango et al., 2018), relatively few studies have attempted to measure natural enemy reductions where invasive plants are common. Predaceous arthropods decreased in only 44% of the studies

examined by Litt et al. (2014), which could reflect changes in the typical prey of spiders, the most abundant arthropod predators in terrestrial ecosystems. Web-spinning spiders are generalist predators that target flying insects, which are more often produced in detritus than on living plants. In contrast, the vast majority of parasitoids are highly specialized on particular host lineages (Forbes et al., 2018; Smith et al., 2006; Vinson, 1998); declines in these native plants could lead to more substantial effects.

Arthropods also comprise a large and important part of the diet of many animal species, such that the influences of alien plants can be very wide-reaching. For example, Tallamy and Shriver (2021) hypothesized a link between large-scale decreases in bird populations and declines in insects, in part because of the increased dominance of alien and ornamental plants. Specifically, they demonstrated substantial declines in population size for bird species that rely on insects in their diet for some part of their life history (Tallamy & Shriver, 2021).

In invaded landscapes, detritivores may supplant herbivores as the dominant functional group in invertebrate communities. Redirecting energy from living plants (“green food web”) to detritus (“brown food web”) can have profound influences on trophic dynamics (Gratton & Denno, 2006; Levin et al., 2006; McCary et al., 2016; Mitchell, 2019). Understanding how arthropod food webs respond to changes in the litter may yield avenues for restoring ecosystem services lost following plant invasion.



Impacts through pests and diseases associated with alien plants

Although biosecurity measures help reduce risks (Nahrung et al., 2023), there are repeated examples of serious plant diseases and insect pests accompanying the introduction of alien plants. These pathogens and pests, in turn, directly alter the composition of native plant communities, with potential implications for insects that depend on native plants. The horticultural and agricultural plant trade has been a leading pathway for invasive pests and pathogens (see Chapter 9). An early example was the introduction of the chestnut blight (*Cryphonectria parasitica*) with the commercial sale of Chinese chestnut (*Castanea mollissima*). Chestnut blight completely transformed >70 million km² of eastern deciduous forests in North America by destroying viable populations of the iconic American chestnut (*Castanea dentata*). The functional loss of American chestnuts is believed to have resulted in the complete extinction of five insect herbivores that specialized on *Castanea*

(Wagner & Van Driesche, 2010). Although the effects of blight on nonspecialist taxa are unknown, *Castanea* is a member of the Fagaceae, an extraordinarily important source of nutrition for hundreds of species of insects (Narango et al., 2020). As such, the loss of the American chestnut likely negatively affected the abundance and diversity of forest insects throughout the tree's range. Similarly, the importation of Chinese (*Ulmus parvifolia*) and Siberian elm (*Ulmus pumila*) as ornamental trees to Europe may have played an important role in the introduction of Dutch elm disease, three *Ophiostoma* fungal pathogens that have devastated native elms and the insects that depend on them in European and North American forests and urban plantings.

Other important examples include oaks in North America and Great Britain, which currently are threatened by the introduction of several serious diseases, including sudden oak death syndrome, bacterial leaf scorch, acute oak decline, and oak wilt, all of which were introduced via nursery stock. These diseases already have killed more than 1 million oaks in California (Alexander & Swain, 2010). Any reduction in oak diversity or abundance is concerning from a conservation perspective because oaks in North America host over 950 species of Lepidoptera (Shropshire & Tallamy, n.d.). These Lepidoptera provide the primary source of nourishment for the nestlings of 96% of terrestrial bird species (Kennedy, 2019) and thus contribute more insect energy to local food webs than any other plant genus in North America (Narango et al., 2020).

In addition to plant diseases, alien plants can be sources of alien insects. The viburnum leaf beetle (*Pyrrhalta viburni*) likely was imported to Canada with ornamental European cranberry bushes (*Viburnum opulus*) (Becker, 1979). Hemlock woolly adelgid (*Adelges tsugae*) was imported with ornamental Japanese hemlocks and has completely destroyed most southern populations of eastern hemlock (*Tsuga canadensis*) in North America along with associated insect populations (Havill et al., 2014). The Japanese beetle (*Popillia japonica*) is less destructive, but far more wide-ranging in terms of the number of native plants it affects. Japanese beetles were introduced to North America in soil surrounding imported *Iris* bulbs and this insect is now a pest on more than 300 plant species (USDA, 2015), competing with native insects requiring those resources.



Conclusions

Although alien plants can provide ephemeral resources for some insects (e.g., generalist pollinators, some generalist insect herbivores) (Rodríguez et al., 2019), a review of the literature suggests that alien plants typically have detrimental effects on native insect herbivores, as well as the predators and parasitoids that depend on them (Narango et al., 2017; Richard et al., 2019; Rodríguez, Cordero-Rivera et al., 2020; Rodríguez, Novoa, et al., 2020). This is particularly true for specialist herbivores, especially caterpillar species, for which restricted host ranges are the norm. Detritivores also can be negatively affected, particularly when novel phytochemical defenses are retained in leaf litter for long periods. Although many alien plants provide some ecological benefits, those benefits must be weighed against the serious costs to pollination, food webs, nutrient recycling, and other services to accurately determine the net effect of a plant invasion on insect communities.

Arthropods fill diverse functional roles, and the changes resulting from invasive plants and alien ornamentals that we describe here can have widespread and compounding effects at the population, community, and ecosystem levels. In many cases, the specific mechanisms driving the documented changes are still sizable information gaps, especially the implications of alien plants on arthropod reproduction and survival, species interactions, and trophic relationships. Fortunately, the negative impacts of alien plant invasions on insect communities often are reversible (Braschi et al., 2021; Maoela et al., 2016; Robertson et al., 2011); when invasive plants are removed or controlled, the native trophic balance can return remarkably quickly. Using native plants in landscaping and horticultural applications has important conservation implications, even at small spatial scales. Continuing to build our understanding about different functional groups of arthropods can guide restoration and management efforts to mitigate the loss of species and ecosystem function (see Chapter 10 for further details).

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