



# Do non-native plants contribute to insect declines?

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**Abstract.** 1. With evidence of significant global insect declines mounting, urgent calls to mitigate such declines are also increasing. Efforts to reverse insect declines will only succeed, however, if we correctly identify and address their major causes.

2. One potential cause that has received little mention is the global spread of non-native plants as invasive species, agroforestry products, and ornamental plants.

3. Here we (a) review the theory predicting that most insect herbivores are evolutionarily constrained to use a fraction of available plant lineages; (b) document the extent to which nonnative plants have displaced native plant communities around the globe; (c) examine the evidence that non-native plants reduce insect abundance and diversity; and (d) suggest guidelines for measuring the impact of non-native plants on insect populations.

4. We conclude that host range expansions to non-natives do occur among many insect herbivores but not at the frequency required to prevent insect declines when non-native plants replace native plant communities. Accordingly, we suggest that curbing the spread and use of non-native plants at local, national, and international scales will be a necessary and effective way to reduce some insect declines.

**Key words.** Host plant specialization, insect declines, invasive species, native plants, non-native plants, plant/insect interactions.

## Introduction

Over 30 years ago, E.O. Wilson made general but dire predictions about the ecological consequences of global insect declines that included the loss of flowering plants, terrestrial food web collapse, and its associated loss of animal diversity, as well as the end of rapid nutrient cycling (Wilson, 1987). Although the biomass of some groups may be declining less than others (e.g. moths: Macgregor *et al.*, 2019; aquatic insects: van Klink *et al.*, 2020), accumulating evidence from Germany (Hallmann *et al.*, 2017), England (Conrad *et al.*, 2006), Costa Rica (Janzen & Hallwachs, 2019), the Netherlands (van Strien *et al.*, 2019), North America (Cameron *et al.*, 2011; Forister *et al.*, 2019), and other places, as well as global assessments (Dirzo *et al.*, 2014;

van Klink *et al.*, 2020) suggest that insect declines may no longer be theoretical musings. Habitat loss, climate change, industrial agriculture, light pollution, and pesticides have all been blamed for insect declines and, undoubtedly, all of these have played a role (reviewed by Forister *et al.*, 2019; Wagner, 2020). Because so many factors may be simultaneously reducing insect populations, David Wagner (2020) has likened the cause of insect declines to ‘death by a thousand cuts’.

Curiously, one potential cut that has received relatively little attention in the literature on insect declines, and was not considered at all in recent recommendations by Harvey *et al.* (2020) and Samways *et al.* (2020) for how to reverse insect declines, is the indirect impact non-native vegetation has on insect herbivore populations and, by extension, the populations of all arthropod and vertebrate insectivores that depend on them. To be sure, insect conservationists have long noted the importance of habitat containing appropriate native host plants (Majer, 1987; Panzer & Schwartz, 1998; Wagner & van Driesche, 2010), but the widespread replacement of native host plants with non-native species has yet to penetrate the growing literature on insect declines in any meaningful way. The degree to which this has

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been a serious omission in the quest to understand and subsequently mitigate insect declines is the subject of this review.

Given that: (a) there are so many species of insect herbivores that rely on particular plant lineages and, in turn, support a vast global richness of insect predators and parasitoids; (b) evolutionarily novel non-native vegetation is predicted to be poor at sustaining large and diverse populations of insect herbivores; and (c) non-natives have so widely diluted coevolved native plant communities in both human-dominated and 'natural' landscapes, we examine the evidence for and against the hypothesis that long term changes in the species composition of plant assemblages have contributed to local and global declines in the abundance and diversity of the insect communities dependent upon those assemblages.

### Theoretical considerations

The hypothesis that non-native plants contribute to insect declines depends largely on the premise that host plant specialization in phytophagous insects, which represent the majority of insect diversity (Strong *et al.*, 1984; Mitter *et al.*, 1988) is the rule rather than the exception. Decades of research supports this view: the majority of plant-feeding insects have restricted relationships with plants that allow recognition and use of a just few closely related plant lineages (Ehrlich & Raven, 1964; Forister *et al.*, 2015). When native plants are displaced in the landscape by non-native species, phytophagous insects typically do not recognise the novel host for feeding or oviposition, or may be unable to overcome novel plant defenses (Tallamy, 2004; Wagner & van Driesche, 2010; Bezemer *et al.*, 2014; Litt *et al.*, 2014; van Hengstum *et al.*, 2014). The concurrent loss of native plant hosts and dominance of non-native plants can lead to local extirpation of phytophagous insects and thus to changes in the composition and structure of local food webs (Chew, 1981; Gratton & Denno, 2006; Bezemer *et al.*, 2014; Sunny *et al.*, 2015; Mitchell, 2018).

#### Host specialization

Insect-plant host relationships have been the focus, if not the impetus, for coevolutionary theory, starting with Ehrlich and Raven's (1964) seminal observations on host plant associations in the order Lepidoptera (butterflies, skippers, and moths). Ehrlich and Raven (1964) postulated that recognition of secondary plant compounds served as a primary driver for the distribution and diversity exhibited by phytophagous insects on their respective plant hosts. Consumption of plant tissues reduces host fitness and drives selection for the development of chemical, physical, or phenological defenses against herbivory, which consequently drives selection for phytophagous insects to develop traits to detect and tolerate plant defenses over time (Dethier, 1954; Fraenkel, 1959; Ehrlich & Raven, 1964; Holloway & Hebert, 1979). Coevolutionary theory assumed that such stepwise, reciprocal adaptations between insects and their hosts led to the specialised relationships we see today.

Although this line of reasoning dominated the literature for years, additional studies suggested that such stepwise, coevolutionary relationships may actually be rare (Janzen, 1980; Jermy, 1984). It was argued that herbivory by insects conferred variable effects on host plant fitness (Jermy, 1984; Crawley, 1989; Mauricio & Rausher, 1997; Fine *et al.*, 2004) and the presence of secondary metabolites in plant tissues may not be a response to herbivore attack (Owen, 1990; Harvey & Purvis, 1991). Furthermore, most plant lineages are hosts for numerous herbivores, which would dilute selection pressures for defense against any specific attacker (Feeny, 1970; Feeny, 1976; Auerbach & Simberloff, 1988; Lau & Strauss, 2005; Agrawal *et al.*, 2006; Pearse & Hipp, 2009). It has also been suggested that host specialization is not a product of coevolution at all; instead, specialised adaptations to particular plants, particularly cryptic coloration, is the result of selection pressures from predation and parasitism in space and time (Bernays, 1988; Bernays & Graham, 1988; Jermy, 1988; Bernays & Cornelius, 1989; Dyer, 1995). Finally, nutritional quality, digestibility, and availability of host plants, not just plant defenses, may play a significant role in the host plant preferences of phytophagous insects (Awmack & Leather, 2002). Nevertheless, coevolutionary theory served as a foundation to demonstrate associations between phytophagous insects and their hosts, with the need for further expansion and empirical evidence on larger scales (Janzen, 1980; Jermy, 1984; Futuyma & Agrawal, 2009).

Regardless of their evolutionary causes, insects have developed adaptations to the phytochemistry, nutritional value, phenology, and physical traits of specific plant lineages (Futuyma & Moreno, 1988; Jaenike, 1990; Jermy, 1993; Mayhew, 1997; Futuyma & Agrawal, 2009). This correlation permits some phytophagous insects to utilise novel congeners and confamilial species as hosts (Huang & Renwick, 1993; Janz & Nylin, 1998; Becerra & Venable, 1999; Winkler & Mitter, 2008). Beyond consumption, ovipositional preferences/behaviours are influenced by competition, predation and parasitism loads, chemical signatures, host plant dispersion, the species composition of surrounding neighbours, and evolutionary experience at local scales (Fox & Morrow, 1981; Jermy, 1984; Jaenike, 1990; Larsson & Ekbohm, 1995; Nylin *et al.*, 2000; Dulaurent *et al.*, 2012). Thus, host specificity in native phytophagous insects may be viewed as a function of phylogenetic history, plant defenses, and ecological experience within specific environments.

#### Host specialization: Scope and scale

Understanding diet breadth in phytophagous insects is paramount in the context of interactions with non-native plants, as an insect's ability to recognise non-native species in the landscape as novel hosts will depend largely on its evolutionary experience. The diet of most insects is constrained to a single plant family in any one habitat or location, with dietary specialization even narrower both in many temperate lineages and hyper-diverse tropical lineages (e.g. Asteraceae, Fabaceae, Forister *et al.*, 2015; Forister & Jenkins, 2017). In fact, diet specialization increases with decreasing latitudes, concurrent with theories of increased plant and animal diversity in the tropics (Hillebrand, 2004; Dyer *et al.*, 2007; Anstett *et al.*, 2016).

For example, in rainforests ecosystems of Papua New Guinea, the majority of phytophagous insects (>90%) specialise at the genus level (Novotny *et al.*, 2002). This result is important as the potential for non-native plants to be recognised as novel hosts by insects may depend on what native confamilials are present in the landscape (Forister *et al.*, 2015). Due to such specificity, the displacement of native plants by non-native species may have profound effects on phytophagous insect populations everywhere.

Of the taxa in global decline (Dirzo *et al.*, 2014; Fox *et al.*, 2014), by far the best studied taxon for diet breadth is Lepidoptera. Caterpillars are generally restricted to host plants at the genus or family level (Ehrlich & Raven, 1964; Futuyma, 1976; Thompson, 1998). Novotny *et al.* (2004) determined that the average caterpillar species in New Guinea rainforests feeds on three or fewer plant species; over 90% of these caterpillars are concentrated on a single plant host (but see Novotny *et al.*, 2002). Globally, nearly 70% of caterpillar species develop on a single plant family (Forister *et al.*, 2015). Thus, the displacement of native plants with non-native taxa is likely to contribute to declines in Lepidoptera.

#### Recognition and utilization of novel hosts

Although most phytophagous insects develop host specificity through evolutionary relationships with native plants, there are nonetheless uncommon cases where native insects utilise non-native plants as novel hosts (Bezemer *et al.*, 2014; Litt *et al.*, 2014; van Hengstum *et al.*, 2014; Sunny *et al.*, 2015). Because non-native plants are typically underutilised by native herbivores, it is generally assumed that they are 'released' from top-down pressures imposed by specialist herbivores that otherwise inhibit plant performance (i.e. Enemy release hypothesis, Hierro *et al.*, 2005; Keane & Crawley, 2002). However, the opposite may also be occasionally true; non-native plants may lack defenses that repel native insects and thus become more susceptible to herbivore attack (e.g. agricultural crops, Colautti *et al.*, 2004; Maron & Vilà, 2001). In cases where native phytophagous insects recognise susceptible non-natives, insects may expand their host range (Carroll & Boyd, 1992; Parker & Hay, 2005; Strauss *et al.*, 2006; Carroll & Fox, 2007; Hull-Sanders *et al.*, 2007), and even impede non-native plant performance (Parker *et al.*, 2006; Suwa & Louda, 2012).

The most likely pathway to host range expansion to non-native plants is phylogenetic similarity with native host plants (Janz & Nylin, 1998; Thompson, 1998; Winkler & Mitter, 2008; Harvey *et al.*, 2010; Forister & Wilson, 2013; Chupp & Battaglia, 2014). Non-native congeners or confamilials that are similar in foliar chemistry and nutrition, phenology, and morphology, may occasionally serve as novel hosts for herbivorous insects and support higher diversity and abundance than non-native, non-congeners (Burghardt *et al.*, 2010; Clem & Held, 2015; Narango *et al.*, 2017). However, novel use of congeners may increase larval mortality, extend development or pupation time, reduce biomass, and reduce fitness compared to that on native hosts (Bowers *et al.*, 1992; Graves & Shapiro, 2003; Zuefle *et al.*, 2007; Castells & Berenbaum, 2008;

Keeler & Chew, 2008; White *et al.*, 2008; Brown & Zuefle, 2009; Ding & Blossey, 2009; Müller, 2009; Harvey *et al.*, 2010; Gillespie & Wratten, 2011; Fortuna *et al.*, 2012; Knerl & Bowers, 2013).

Although some insects attempt to reproduce on non-native plants, such attempts can become ecological traps when the use of novel hosts results in mortality or reduced fitness (deJonge *et al.*, 2017; Forister & Scholl, 2012; Nakajima *et al.*, 2013; Schlaepfer *et al.*, 2005; Steward *et al.*, 2019; Sunny *et al.*, 2015). For example, butterflies in the family Pieridae (whites, sulphurs, and yellows) exhibit preference for host plants in the mustard family (Brassicaceae, Ehrlich & Raven, 1964). Radiation in this family occurred through the development of a nitrile-specifier protein that detoxifies glucosinolate, a metabolite commonly encountered in mustard plants (Wheat *et al.*, 2007); glucosinolate and its derivatives are believed to dictate oviposition and feeding preference for Pierid taxa (Huang & Renwick, 1993; Huang *et al.*, 1994; Müller, 2009). Although Pierid butterflies recognise non-native crucifers as hosts based on phytochemical markers, not all confamilials serve as hosts; invasive plants such as garlic mustard (*Allaria petiolata*), field penny-cress (*Thlaspi arvense*) and Turkish rocket (*Bunias orientalis*) inhibit development and survival in *Pieris* caterpillars (Chew, 1981; Huang *et al.*, 1994; Porter, 1994; Haribal & Renwick, 1998a; Graves & Shapiro, 2003; Keeler & Chew, 2008; Harvey *et al.*, 2010; García-Robledo & Horvitz, 2011; Fortuna *et al.*, 2012; Steward *et al.*, 2019). Similarly, swallowworts (*Vincetoxicum* spp.) are confamilials of milkweeds (*Asclepias* spp.) and have become invasive in parts of the northeastern United States. Similar phytochemistry between swallowworts and milkweeds can lead monarch butterflies (*Danaus plexippus*) and milkweed beetles (*Chrysochus auratus*) to fatally mistake these chemically protected plants as hosts (Haribal & Renwick, 1998b; deJonge *et al.*, 2017). The degree to which *Vincetoxicum* act as ecological traps for these taxa is likely to become more pronounced as the plants become dominant and displace milkweeds in the landscape (DiTomasso & Losey, 2003; Casagrande & Dacey, 2014; Sunny *et al.*, 2015).

Alternatively, some herbivores have benefitted from the introduction of novel hosts. Rattlebox moths (*Utetheisa ornatrix*) exhibit higher oviposition rates and fitness on non-native congeners compared to their native hosts (Cogni, 2010). Several skippers and butterflies (e.g. common sootywing, *Pholisora catullus*, large marble, *Euchloe ausonides*, and anise swallowtail, *Papilio zelicaon*) benefit from the introduction of novel congeners in California, especially where anthropogenic factors have led to the loss of native host (Graves & Shapiro, 2003). Similarly, the palamedes swallowtail (*Papilio palamedes*) use less suitable but abundant camphor trees (*Cinnamomum camphora*) following outbreaks of disease on its preferred host (Chupp & Battaglia, 2014) and the federally protected *Manduca blackburni* now uses tree tobacco in Hawaii (Rubinoff & San Jose, 2010). Although the potential exists for phylogenetically related plants to be recognised by phytophagous plants as novel hosts, it is by no means a guarantee (Burghardt *et al.*, 2010); well after a century of colonization, non-native *Piper* trees were devoid of specialists that should have established from adjacent, native congeners (Novotny *et al.*, 2003).

Given the close evolutionary link between herbivorous insects and their host plants, when nonnative plants dominate ecosystems, either through invasion or cultivation, they inevitably displace the host plants that are necessary to support sustainable insect populations. How well native insects perform on non-native plants is one important variable determining non-native plant impacts on insect declines.

### Do non-native plants reduce insect populations?

To posit that non-native plants, either as invasive species, agroforestry crops, or widely planted ornamentals, are contributing to global or local insect declines, there must be clear evidence that insects directly requiring plant resources have lower fitness when using non-native plants, do not recognise them as viable host plants, or avoid them altogether. It is also necessary that reductions in herbivore numbers caused by non-native plants are not mitigated by density-dependent effects such as reduced competition. These questions have been an active area of research as they relate to the impacts of invasive plants and have been reviewed extensively several times in the last decade (Bezemer *et al.*, 2014; Litt *et al.*, 2014; van Hengstum *et al.*, 2014; Yoon & Read, 2016). As predicted by theory (reviewed above), studies have repeatedly shown that phytophagous insect host plant affiliations are constrained by plant evolutionary history (Ødegaard *et al.*, 2005; Weiblen *et al.*, 2006; Janz, 2011) and that when native host plants are reduced within or removed from landscapes, insect herbivore populations on the whole are smaller and less diverse. For example, in one of the most rigorous meta-analyses available, Yoon and Read (2016) examined the impact of non-native plants on Lepidoptera larval performance, survival, oviposition preference, abundance, and species richness in 76 studies. With few exceptions, caterpillars had higher survival and were larger when reared on native host plants, and plant communities invaded by non-native species had significantly fewer Lepidopterans and less species richness. Moreover, in 3 of 8 cases examined, non-native plants functioned as ecological traps, inducing female Lepidoptera to lay eggs on non-native plants that did not support successful larval development.

Non-native plants can also indirectly alter the abundance of native insects on native plants via their effects on the quality, abundance, and/or diversity of native plants (Powell *et al.*, 2013), or on the structure of their habitat (Bezemer *et al.*, 2014). Not only to invasive plants replace edible plant biomass with inedible vegetation (a direct impact), they also typically devastate the diversity of native plant communities on a local scale, which is the scale at which ecosystems function (Powell *et al.*, 2013). Although this is an indirect effect, the global scale of plant invasions is so huge (see below) that the impact on insect populations is likely to be enormous as well.

Although each of the above reviews concluded that non-native plants negatively impacted insects more often than not, insect responses to non-natives were not uniform, with some studies showing no effect and a few showing positive impacts from non-native plants. For example, in a review of 89 studies, Litt *et al.* (2014) found that phytophagous arthropod populations decreased in 48% of the studies but increased in 17%. Similarly,

Bezemer *et al.* (2014) reviewed studies that found non-native plants to be toxic to native insects (e.g. Keeler & Chew, 2008; Ding & Blossey, 2009) as well as cases where non-natives were acceptable host plants (e.g. Harvey *et al.*, 2010). Not surprisingly, the equivocal nature of these responses has led to controversy over how much non-native plants actually affect insect populations.

There are two reasons to urge caution when interpreting the reports of host range expansions to non-native plants that are scattered across the literature. First, these reports do not represent a balanced survey of host use across all species. When host range expansions in particular species are detected, it is news-worthy and they are published. In contrast, examples of insects unable to use introduced plants are predicted by theory and therefore not newsworthy, studied, or written up for publication. Who, for example, would study whether monarch butterflies could develop on Crepe myrtle (*Lagerstromia indica*) and what journal would publish such foregone results? Because of their exceptional nature, there is a danger of overestimating the prevalence of non-native host use and worse, underestimating the negative impacts of non-natives on insect populations.

Host range expansions are exceptions, which means more species cannot use non-natives for growth and reproduction than can. In one area of northern California, 34% of the butterfly species rely on non-native hosts because their closely related native hosts have been extirpated (Graves & Shapiro, 2003). Yet even in this most celebrated example of insects expanding to non-native plants, it is likely that 66% of the butterflies in this region would be expected to suffer population declines where their hosts are declining due to encroachment by non-natives.

An important source of variation in the results of studies examining non-native plant impacts on insects is the context of the host plant associations studied. Insects 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; and as host plant specialists or generalists. Non-of these contexts are equivalent and thus they cannot be lumped when reporting results. That is, the context in which the impacts of non-native plants on insects are examined is critical to the ramifications of the results. When the context within which studies were performed is considered, the following patterns emerge;

- 1 Insects with chewing (mandibulate) mouthparts are typically more susceptible to defensive secondary metabolites contained in leaf vacuoles than are insects with sucking (haustelate) mouthparts that tap into poorly defended xylem or phloem fluids (Verhoeven *et al.*, 2009). Thus, sucking insects find novel non-native plants to be acceptable hosts more often than do chewing species. Indeed, failure to recognise that all members of the second trophic level do not interact with plants in the same way has been a source of misinterpretation and controversy in many studies of non-native plants. Not surprisingly, some studies of detritivorous invertebrates (e.g. Sax, 2002) and frugivorous birds (e.g. Gleditsch & Carlo, 2011) found no negative impact from invasive plants, while studies of insect folivores and the insectivores that eat them (e.g. Flanders *et al.*, 2006; Burghardt

**Table 1.** Species richness of phytophagous insects with mandibulate and haustellate feeding modes.

Taxon	Mandibulate	Haustellate	Reference
Lepidoptera	157 424 spp		Van Nieuwerkerken <i>et al.</i> , 2011
Coleoptera			
Chrysomelidae	40 000 spp		Jolivet & Hawkeswood, 1998
Cerambycidae	36 000 spp		Wang, 2017
Buprestidae	14 700 spp		Bellamy, 2002
Thysanoptera		5641 spp	Mound, 2013
Hemiptera			
Auchenorrhyncha		40 000 spp	Dietrich, 2009
Sternorrhyncha		16 000 spp	Gullan & Martin, 2009
Total	248 214 spp	62 641 spp	

*et al.*, 2010; Narango *et al.*, 2018; Richard *et al.*, 2018) usually find large impacts. Considering that there are more than 4.5 times as many mandibulate insect herbivores as haustellate species (Table 1), there is reason for concern when non-native plants replace native hosts; the largest guild of insect herbivores is also the most vulnerable to non-native plants and the most valuable to insectivores.

- Although both woody and herbaceous non-natives decrease the overall abundance of insects, the impact of woody species is stronger (Daehler, 2005; van Hengstum *et al.*, 2014). This could be because woody native species, on average, support more species of phytophagous insects (Tallamy & Shropshire, 2009), so their displacement by non-natives will have greater impacts.
- Because plants in closely related lineages often share defensive chemicals and phenology with native hosts, insects are more likely to accept non-native congeners or con-familial species as novel hosts than non-natives that do not share an evolutionary history with native host plants (Connor *et al.*, 1980; Hill & Kotanen, 2009; Pearse & Hipp, 2009; Burghardt *et al.*, 2010; Lombardero *et al.*, 2012; Burghardt & Tallamy, 2013; Pearse & Altermatt, 2013). Acceptance of related non-natives by insects is far from universal, however. A highly controlled common garden experiment comparing insect use of 18 congeneric pairings found that non-native congeners of native species reduced insect abundance and species richness by 68% (Burghardt *et al.*, 2010; Burghardt & Tallamy, 2013).
- Insects with a narrow diet breadth (host plant specialists) are less likely to develop on evolutionarily novel non-natives than are insects with broader diet breadth (Bertheau *et al.*, 2010; Pearse, 2011). Because there are far more species of host plant specialist than generalists (Forister *et al.*, 2015), generalists will not prevent serious declines in species richness and abundance when native plants are replaced by non-natives. Even when populations of generalists are compared on native and non-native plants, non-natives cause significant reductions in species richness and abundance (Ballard *et al.*, 2013). In fact, despite evidence of broad host plant use, generalists are often locally specialised on particular plant lineages and thus may function more like specialists than host lists accumulated across their range suggestion (Fox & Morrow, 1981; Tallamy *et al.*, 2010).
- Any reduction in the abundance and diversity of insect herbivores will cause a concomitant 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), 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). These results could reflect the typical prey of spiders, the most abundant arthropod predators in terrestrial habitats. Web-spinning spiders are generalist predators that target flying insects more often produced by detritus and aquatic habitats than living plants. No studies have traced the fate of parasitoid communities linked to phytophagous insects when native plants are replaced by non-natives. Yet the vast majority of parasitoids are highly specialised on particular host lineages (Vinson, 1998; Smith *et al.*, 2006; Forbes *et al.*, 2018). It follows, then, that if a host lineage decreases in abundance due to non-native plants, so will its parasitoid complex.
- Studies comparing native plants that support very few phytophagous insects to non-native plants are less likely to find differences in phytophagous insect communities than studies comparing non-natives to native plants that host dozens of species. Native plants differ by orders of magnitude in their ability to host phytophagous insects (Tallamy & Shropshire, 2009). In the mid-Atlantic region of North America, for example, oaks (*Quercus* spp.) host 557 Lepidoptera species, while tulip trees (*Lireodendron tulipifera*) host only 21 species and Yellowwood (*Cladrastus kentuckea*) does not serve as host for any Lepidoptera. Thus, a comparison of the impacts of a congeneric non-native such as Norway maple will depend a great deal on the choice of native plants with which it is compared.
- Insects that feed on well-defended living tissues such as leaves, buds, and seeds are less likely to be able to include non-natives in their diets than are insects that develop on undefended tissues like wood, fruits, and nectar. Although this hypothesis has never been formally tested, the ease with which introduced wood borers like emerald ash borer (*Agrilus planipennis*), *Sirex* woodwasp (*Sirex noctilio*), Asian long-horned beetle (*Anoplophora*

*glabripennis*), the polyphagous shot hole borer (*Euwallacea* sp), redbay ambrosia beetle (*Xyleborus glabratus*), and many other species of introduced bark beetles have included North American trees in their diets, as well as the extraordinary polyphagy of frugivores like the brown marmorated stinkbug (*Halyomorpha halys*) support this notion (Baranchikov *et al.*, 2008; Fraedrich *et al.*, 2008; Haack *et al.*, 2010; Eskalen *et al.*, 2013; Paap *et al.*, 2018).

### How pervasive are non-native plants?

Given the poor performance of most insect herbivores on non-natives, the widespread use and invasive behaviour of many non-native plants increases the potential scale of impact on insect abundance and diversity. Although plants have always distributed themselves around the globe, the increased temporal and spatial mobility of humans has resulted in an extraordinary increase in the rate of plant movements (Vitousek *et al.*, 1997a) and most species' introductions have happened in the last 200 years (van Kleunen *et al.*, 2018). Habitat is rapidly being converted from coevolved native ecosystems into novel assemblages of plants and animals, making the conversion of native plant communities into plant assemblages dominated by non-native species one of the most ubiquitous threats to biodiversity today (Johnson, 2007; Radeloff *et al.*, 2015). The introduction of non-native plants has completely transformed the composition of present-day plant communities in both natural and human-dominated ecosystems around the globe (McKinney, 2004; Dolan *et al.*, 2011) and the magnitude of introductions is staggering. An estimated 13 168 plant species (about 3.9% of global vascular flora) have been introduced and naturalised beyond their native ranges as a result of human activity (van Kleunen *et al.*, 2015) with more than 3300 species of non-native plants established in the continental U.S. alone (Qian & Ricklefs, 2011). Where they are abundant, non-native plants can dominate plant biomass, and also reduce native plant taxonomic, functional and phylogenetic diversity, and heterogeneity, further exacerbating their impact (Walker *et al.*, 2009; Rejmánek *et al.*, 2013; Beaury *et al.*, 2019; Padullés Cubino *et al.*, 2019). The global dominance of non-native plants species in natural and human-dominated systems is due to introductions from three primary sources: *invasion, agriculture & agroforestry products, and horticultural ornamental plants.*

#### Plant invasion

Invasive plants are regarded as a major threat to biodiversity and ecosystem function (Czech *et al.*, 2000; Pyšek *et al.*, 2020). The dispersal and spread of invasive plants has been driven by global trade networks and colonialism (Chapman *et al.*, 2017; van Kleunen *et al.*, 2018). At least 1/6 of the globe is highly vulnerable to plant invasions which includes areas of biodiversity hotspots (Stohlgren *et al.*, 2003; Early *et al.*, 2016).

In many ecosystems, invasive 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 SE U.S. forests are covered by just 33 common

invasive plant species. New technology has facilitated surveys over larger spatial areas; for example, using remote sensing, Bradley *et al.* (2015) found that in a 28 000 km<sup>2</sup> area in northern Nevada, monocultures of non-native cheatgrass (*Bromus tectorum*) expanded from 14% of the area to 29% in less than 30 years. Even in protected lands, invasive flora is a major threat to ecological function and few areas are completely free of invaders (Pyšek *et al.*, 2020). For example, in some island systems, invasive species can be 50–70% of the species in the ecosystem (Vitousek *et al.*, 1997b). Despite management efforts, evidence points toward invasive plants increasing in abundance, especially in protected areas (Pyšek *et al.*, 2020).

Introductions of non-native plants can introduce other non-native organisms that alter the composition of native plant communities and thus the insects that depend on them. The horticultural and agricultural plant trade has been a leading pathway for invasive pests and pathogens. For example, the commercial sale of Chinese chestnut (*Castanea mollissima*) introduced chestnut blight (*Cryphonectria parasitica*), which completely transformed >70 million km<sup>2</sup> of eastern deciduous forest by the loss of the iconic American chestnut (*Castanea dentata*) and is believed to have caused the extinction of five specialist insect herbivores that fed on *Castanea* (Wagner & van Driesche, 2010); the blight's effects on non-specialist taxa are unknown. Similarly, Hemlock woolly adelgid (*Adelges tsugae*) was imported with ornamental Japanese hemlocks and has destroyed most southern populations of eastern hemlock (*Tsuga canadensis*) populations along with the insects dependent upon them (Havill *et al.*, 2014).

#### Agriculture and agroforestry

The need for fast-growing colonizing trees in agroforestry and restoration (e.g. *Acacia* and *Albizia*) has also increased the use of non-native species, many of which have escaped to dominate nearby native forests (Schroth *et al.*, 2004). At least 25% of the world's planted forests are composed of non-native tree species (Lombardero *et al.*, 2012); for example, one fourth of Portugal's forestland (900 000 hectares) is planted in *Eucalyptus* (Ames, 2017). At least 118 exotic tree species have naturalised in Puerto Rico and compete with native species in natural stands (Francis & Liogier, 1991); the African rubber tree, *Funtumia elastic*, a species that is invasive in >30 countries and completely dominates secondary forests of many tropical Pacific islands, is now one of the most common trees in Puerto Rico (Rejmánek & Richardson, 2013) as well. Grassland communities are also vulnerable to invasion by non-native plants, particularly from adjacent agricultural land. Aided by purposeful introductions for cattle as well as excess nutrients from agriculture, grasslands around the globe are six times more likely to be dominated by non-native plants than are other ecosystems (Seabloom *et al.*, 2015).

#### Horticulture

Because of the popularity of non-native plants in landscaping, horticulture is a major source of non-native plants in both

cultivated and natural ecosystems (van Kleunen *et al.*, 2015). Non-native plants tend to be aggregated in areas with high human densities (McKinney, 2001), high international trade, and robust horticultural industries, highlighting the importance of these regions for facilitating introductions to wider geographical areas (van Kleunen *et al.*, 2015; Dawson *et al.*, 2017). There are estimates that 50–70% of invasive and naturalised species are a direct result of intentional horticultural introductions (Dehnen-Schmutz & Touza, 2008; Richardson & Rejmánek, 2011). Even though many invasive plant species are regulated in the U.S. and included on ‘do-not-plant lists,’ these problematic taxa are abundantly sold in horticulture; 61% of non-native plants on the invasive species list are still sold in all lower 48 states (Beaury *et al.*, 2020). Gardens retain ideal conditions and stable sources of non-native species that have the potential to become invasive if climate or environmental conditions shift (Dukes & Mooney, 1999; Smith *et al.*, 2020).

One land use with high dominance of non-native species is in urbanised areas which are predicted to cover 5–20% of earth’s habitable land mass by 2030 (Seto *et al.*, 2012). Non-native plants are particularly abundant in urban areas because of the strong preference of non-native plants in horticulture (McKinney, 2004; Dolan *et al.*, 2011; Avolio *et al.*, 2015). Moreover, non-natives frequently escape cultivation into disturbed and fragmented areas which characterise urban areas (Vilà *et al.*, 2007; van Kleunen *et al.*, 2019).

Because of these and other factors, the majority of flora are non-native in most cities (Qian & Ricklefs, 2006; Avolio *et al.*, 2015, 2018; Zeeman *et al.*, 2017). For example, more than 40% of plant species are non-native in the most urbanised areas of New York and New Jersey (Aronson *et al.*, 2014). Although urban areas are often characterised by habitat loss relative to natural areas, if the plant biomass that is retained or replaced is strongly dominated by non-native species, this further amplifies the loss the native habitats within the developed matrix (Niinemets & Peñuelas, 2008; Goddard *et al.*, 2010; Lerman & Warren, 2011; Aronson *et al.*, 2014; Lepczyk *et al.*, 2017; Avolio *et al.*, 2018) as well as further degradation of adjacent natural areas due to invasion (Maskell *et al.*, 2006; Duguay *et al.*, 2007).

In horticulture and ecological circles alike, concern has focused primarily on invasive species with the assumption that if a plant is not invasive, it does not cause ecological problems. Indeed, the majority of ornamental species have not become invasive (Reichard & White, 2001), leading land managers and the public to deem these species acceptable for plantings. There are two problems with this reasoning. First, ornamental plants that are distributed by the millions across landscapes represent the first trophic level wherever they are planted. Even if they never develop invasive behaviour, they have not replaced the ecological functions of the native plants that used to support insect populations. Second, there is no guarantee that an ornamental species that is well-behaved today will not become invasive in the future. Many invasive plants experienced a lag phase during which they were benign or overlooked members of plant communities before being recognised as invasive (Essl *et al.*, 2011). Altered conditions and increased introductions from climate and land use change may further enable species to escape cultivation and become invasive; thus, non-native plant

dominance is predicted to increase in magnitude over the next decades (Hellmann *et al.*, 2008; Bradley *et al.*, 2012; Smith *et al.*, 2020).

## Designing robust experiments

One cannot accurately determine the role of non-native plants in insect declines if the experiments purportedly measuring how non-native plants impact insect abundance and diversity are not designed properly. To our knowledge there have been no studies explicitly designed to measure impacts of non-native plants on insect populations over ecological time frames and/or across landscape-level spatial scales. At present, we can only extrapolate from the results of existing short-term studies performed at local spatial scales, often with one or more design limitations.

We suggest the following 10 guidelines should be considered when designing or interpreting robust investigations of the impact of non-native plants on insect populations:

- 1 Experimental designs should carefully choose appropriate control sites to reveal more meaningful results. Consider experiments where insect specialists have not already been reduced in richness and /or abundance or extirpated altogether such as urban ecosystems or islands that have experienced human perturbations for centuries. Comparing impacts of non-native plants on communities that are already depauperate can lead to the false conclusion that non-native plants do not seriously reduce insect diversity and abundance. Similarly, comparing insect communities between invaded sites and sites from which invasive plants have been removed is only appropriate if natural communities of native plants that support rich communities of insects (not all do) have first been allowed to regenerate or have been otherwise restored to natural levels of plant diversity, abundance, and biomass within the removal treatments. Such would be difficult to achieve in areas with an overabundance of white-tail deer, for example.
- 2 Do not conflate pollinators and other flower visitors with insect folivores. Although many pollinators are plant specialists, most pollinators and nearly all flower visitors are generalist feeders, and plant preferences are far more generalised than that of insect herbivores. Thus, the presence of pollinators and flower visitors on non-natives does not mean such plants serve as suitable hosts for leaf-eaters.
- 3 Care should be taken not to restrict comparisons to solely native and non-native congeners instead of representative native and non-native species assemblages. There is little phylogenetic filtering in the human-altered ecosystems to which insect populations are subjected. Congeneric comparisons are unnaturally conservative and will lead to underestimates of the impacts of non-native plants.
- 4 Results are more robust when immature stages of insect development are measured in comparisons of native and non-native plants but can be decidedly more ambiguous when adult numbers are measured, when adults are more generalised feeders than immatures, or when they are simply sheltering on non-host species. Results can also be

- misleading when late instar larvae are found on plants that are unable to support the development of early instars. If an insect does not complete its development on a plant from first instar on, that plant should not be considered a viable host alternative.
- 5 When examining impacts of non-native plants on insects, results are most easily interpreted when the focal organisms are insect herbivores, the organisms directly dependent on plant quality. Generalist predator, parasitoid or detritivore communities should not be considered acceptable surrogates for evaluating the herbivore communities that directly interact with plants. Counts of predatory arthropods collected on plants would be misleading if species are deriving most of their nutrition from non-plant food webs.
  - 6 Because insect adaptations to plant defenses are species-specific and diverse, it is important to make species the functional taxonomic unit of comparative experiments. Work that considers responses at the family or ordinal level is far less meaningful, difficult to interpret, and often produces equivocal results. Moreover, studies that look only at abundance or biomass, and fail to consider species diversity, can miss drastic faunal changes. This may be the most common shortcoming in the existing literature.
  - 7 The impact of non-native plants on insect populations should be investigated in both natural, managed, and working agricultural landscapes. Managed, non-agricultural landscapes (e.g. urban, timber, etc.), which now occupy nearly half of the conterminous U.S. and enormous parts of Europe, can and must support viable insect populations in the future if we are to curb the loss of insects, so understanding how non-natives impact insects in such landscapes is essential. Similarly, agricultural lands must be made more insect friendly by returning native plant communities wherever possible as nearly half of terrestrial earth is now in some form of agriculture (Kremen & Merenlender, 2018)
  - 8 Because both native and non-native plants vary by orders of magnitude in their ability to support insect herbivores, native vs non-native comparisons are often oversimplified. The identity of native and non-native species chosen for an experiment, as well as the species composition of the matrix in which they reside, may heavily influence the results. The most accurate comparisons will thus employ realistic assemblages of both productive and unproductive native and non-native species in a given system.
  - 9 The spatial arrangement of the experimental plants will also impact results and should be controlled or accounted for in all treatments. A native plant surrounded by non-natives may support a different insect community composition and abundance than a native surrounded by other natives (Clem & Held, 2018). The converse may also be true. Similarly, host plants surrounded or adjacent to different landscape matrices (e.g. urban, forest, agriculture) may support different insect communities due to variation from rates of colonization and dispersal.

- 10 As above, establish the link between individual and population-level performance. Although ample correlative data exist showing smaller insect populations where non-native plants dominate, experiments designed to measure whether impacts on individual fitness cause population declines over time are still lacking.

### Concluding remarks

Understanding insect declines requires a careful review of the evidence that (1) insect populations in many parts of the world are, in fact, declining and (2) such declines are being driven by several anthropogenic causes. Whether insects are declining in undisturbed natural areas is still a matter of debate (e.g. Harris *et al.*, 2019; Janzen & Hallwachs, 2019; Crossley *et al.*, 2020), but there is less controversy about declines caused by light pollution, development, industrial agriculture, and pesticides in human-dominated landscapes (Wagner, 2020). In this review, we have presented evidence that non-native plants, both invasive species and widely used ornamental plants, have disrupted specialised evolutionary relationships between insect herbivores and their native host plants over such large areas that non-natives should also be considered a threat to insect populations.

When deciphering the contribution non-native plants have made to global insect declines, the question should not be ‘Can we document single species use of non-native plants?’ but rather ‘How do the majority of species and thus insect populations in aggregate respond to the replacement of native host plants with non-native plants?’ The preponderance of evidence suggests that more insect species than not suffer when the abundance and diversity of native host plants are reduced by non-native species, and that mandibulate folivores, the most speciose insect taxa, suffer more than less speciose insects with sucking mouthparts. The reduction of mandibulate folivores such as caterpillars has outsized negative impacts on animal diversity for two reasons; (1) caterpillars are critical dietary components of most terrestrial birds species and their loss from food webs directly reduces bird fitness (Narango *et al.*, 2017, 2018), and (2) caterpillars serve as hosts for insect parasitoids, perhaps the most speciose guild of metazoan animals on the planet (Forbes *et al.*, 2018).

Critical gaps in our knowledge remain. For example, we know little about how to extrapolate the results of local studies to non-native plant biomass at larger spatial scales, and to our knowledge, few studies have compared patterns across different ecosystems and biomes using systematic methodology. Similarly, we know little about the impacts of non-native plants on insect populations over long ecological time scales. To address the variance in sensitivity to non-native plants, we need a better understanding of how various insect guilds and functional groups differ in their responses. Finally, our knowledge of the impacts of non-natives on different trophic levels and food webs is scanty at best.

Despite these knowledge gaps, enough evidence already exists to implicate non-native plants as a factor in insect declines, and one that can be mitigated by property owners and managers worldwide relatively easily. Non-native plants are not the ecological equivalents of native plants, yet they have replaced native



plant communities as ornamental species, agroforestry products, and invasive species across the globe. Given that more than 160 million hectares of arable land are nonnegotably dedicated to non-native crop plants in the U.S. alone (USDA NASS, 2019), how we respond to the increasing abundance of non-native plants in areas outside of agriculture may determine how well we can sustain ecologically vibrant insect herbivore populations, as well as the myriad bird and parasitoid species that depend on them in the future. We suggest that curbing the spread and use of non-native plants at local, national, and international scales will be a necessary and effective way to reduce insect declines.

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## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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