Diversity

Do Alien Plants Reduce Insect Biomass?

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Alien plants, defined here as species whose evolutionary history occurred elsewhere, are replacing native vegetation in natural ecosystems and anthropogenic landscapes throughout North America (Williamson 1996; Mooney & Hobbs 2000; Pimentel et al. 2000). At least 5000 alien plant species have been introduced to the United States, either intentionally or by accident. Hundreds are now well established in natural ecosystems, but many more reside as ornamentals in managed gardens. Some species are aggressively invasive and disperse rapidly by wind, water, and animal transport, whereas others with no invasive characteristics are planted each year in millions of suburban hectares from which native plants have been removed. A number of biotic and abiotic consequences of the large-scale replacement of native vegetation have been recognized (e.g., Randall 1996; Cox 1999; Levin 2002). However, one potentially important impact that has received little empirical attention concerns the replacement of native plants that are palatable to a diverse array of specialist and generalist insect herbivores with alien species predicted to be partially or entirely unpalatable to most native phytophagous insects.

Several researchers have examined the relationship between phytophagous insects and alien plants from the phytocentric perspective of how insects affect the fitness of such plants (reviewed in Keane & Crawley 2002). Others have shown that the diversity of invertebrates in a habitat is reduced by alien species (Olckers & Hulley 1991; Samways et al. 1996), but no one has explicitly designed a study to measure the impact of alien plants on the production of native insect biomass. Such studies are essential to the management of natural and anthropogenic landscapes for biodiversity because phytophagous insects play a critical role in transferring energy from plants to higher trophic levels (Wilson 1987). An estimated 37% of all animal species are insects that eat green plants (Weis & Berenbaum 1989), and these, or the predatory and parasitic insects that eat them, comprise essential parts of the diets of innumerable species of reptiles, amphibians, birds, and mammals. To understand the level of biodiversity that can be supported in landscapes consisting entirely or in part of alien plant species, one must first understand how native herbivores adjust to the loss of native vegetation. Here I briefly review the theory predicting that native insect specialists and generalists respond to alien plants in very different ways. I then outline the questions we need to answer to better our understanding of how alien plants may be affecting higher trophic levels.

There are three reasons to suspect that alien plants negatively affect native phytophagous insects. First, many of the alien plants now in North America did not come from a random sample of all plants that evolved elsewhere; rather, they are a subset specifically selected for their unpalatability to insects. An important trait historically favored by the ornamental industry is that a plant be "pest free" (Dirr 1998). Many pest-free ornamentals have escaped cultivation and are now naturalized over wide areas (Mack & Erneberg 2002). Some of the worst offenders in this category are, for example, *Melaleuca, Lonicera,* and *Eleagnus* species, and, most recently in the U.S. Northeast, *Polygonum perfoliatum* and *Miscanthus sinensis*.

Second, the success of alien plants in novel landscapes is often credited to their escape of the natural enemy complex of the homeland—the enemy release hypothesis (Williamson 1996). Definitive tests of the enemy release hypothesis have not been conducted (Keane & Crawley 2002), but the literature is replete with evidence that the number of herbivores associated with alien plants in exotic habitats is only a small fraction of the historical complex of natural enemies. In Europe, for example, the Eurasian genotype of *Phragmites australis* supports over 170 species of phytophagous insects, whereas only 5 species of native herbivores use this plant in North America (Tewksbury et al. 2002). *Eucalyptus stellulata* is attacked by 48 species in Australia (Morrow & La Marche 1978) but only 1 in California (Strong et al. 1984). Flowerhead herbivory by dipteran specialists on 13 species of Asteracae is 480 times higher in Britain, where these plants are native, than in New Zealand, where they have been introduced (Fenner & Lee 2001).

Third, theory and decades of empirical support predict that most phytophagous insect species should be

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restricted to eating vegetation only from plant lineages with which they share an evolutionary history (e.g., Erhlich & Raven 1965; Strong et al. 1984; Bell 1987). Physical and chemical defenses developed by plants typically are broken only when herbivores develop specialized adaptations. At least 90% of all phytophagous insects are specialists that have evolved in concert with only one or a few plant lineages (Bernays & Graham 1988). Such restricted interactions typically require evolutionary (as opposed to ecological) time spans to develop (Kennedy & Southwood 1984) and have honed the ability of these insects to track their hosts in time and space, to circumvent physical and chemical defenses through behavioral and physiological adaptations, and to convert their host's tissues to insect biomass quickly and efficiently (Strong et al. 1984). The evolution of specialized abilities to eat the tissues of one particular plant lineage usually, in turn, decreases an insect's ability to eat other plants that differ in phenology, chemistry, or physical structure (Erhlich & Raven 1965). By definition, native insects have shared little or no evolutionary history with alien plants (although some may have interacted with a species in a common genus) and thus may not possess the adaptations required to use these plants as nutritional hosts. Consequently, theory predicts that the solar energy harnessed by alien plants is largely unavailable to native specialists, at least in ecological time, and therefore will be unavailable to all consumers that include these insects in their diets.

The theoretical predictions above form the basis of the enemy release hypothesis, one popular explanation for the competitive success of alien species (Williamson 1996). Two critical assumptions of this hypothesis are (1) that host-switching onto an introduced plant by specialist herbivores of native congeners will be rare, and (2) that generalist herbivores will have a greater impact on—that is, eat more of—native plants competing with the introduced species than on the introduced species itself. Together, these assumptions predict that alien plants will support a smaller load of specialist insect herbivores than will native congeners and a smaller load of generalists than will native plants in general. In their review of the evidence for and against these assumptions, Keane and Crawley (2002) found that most discussions of the negligible degree to which native insects use alien plants as hosts are based only on anecdotal evidence. Five studies (Connor et al. 1980; Bowers et al. 1992; da Ros et al. 1993; Creed & Sheldon 1995; Jobin et al. 1996) document some level of host switching by specialists from native congeners of the introduced plant, but specialists typically comprised a small percentage of the insect fauna on the introduced species ($\bar{x} = 22\%$, ranging from 11% to 67%). A recent comparison between a native and introduced *Piper* in Papua New Guinea recorded no *Piper* specialists using the alien species 140 years after its introduction (Novotny et al. 2003). Only one study has compared

herbivory by specialists on natives and their alien congeners. Although leaf-miner specialists of oak have added alien *Quercus accutissima* to their host list in Florida, leaf-miner densities are significantly lower on this alien oak (Auerbach & Simberloff 1988).

Similarly, no one has addressed explicitly the question of whether generalist insects do as well on alien plants as on natives. However, the comparison has been quantified for other purposes in nine studies. In five comparisons there was more herbivory by generalists on natives than on introduced plants (Southwood et al. 1982; Olckers & Hulley 1991; Schierenbeck et al. 1994). Three comparisons showed no difference (Southwood et al. 1982; Burki & Nentwig 1997; Novotny et al. 2003), and one suggested greater herbivory on the introduced plant (Southwood et al. 1982). Clearly, the degree to which both specialist and generalist insect herbivores grow and reproduce on alien plants remains an open question.

It is possible that, even if specialists or generalists cannot use aliens to the degree that they use native plants, insect productivity is so high that it typically exceeds the needs of animals that consume them. That is, insect consumers may be limited by factors other than food. If this is so, any given habitat may be able to accommodate a substantial number of alien plants before there is a negative impact on insect consumers in that habitat. If insectivorous birds are typical of other insectivores, however, insect productivity does not seem to outpace the needs of insect predators. Numerous studies have linked bird fitness to the quality and quantity of their insect food supplies (e.g., Burke & Nol 1998; Marra et al. 1998; Zanette et al. 2000).

Several questions must be answered to fully understand how native insects adjust to the loss of native vegetation. First, to what degree can specialist herbivores grow and reproduce on alien plants that are close relatives of their native host plants? Closely related plants often share major classes of secondary metabolic compounds that determine their smell, taste, and toxicity for phytophagous insects. Thus, specialist herbivores that have adapted to the chemistry of one plant species are more likely to be able to exploit a close relative of that species, even if their lineage has never actually interacted with the relative. The potential for specialists to adopt evolutionarily novel relatives of their native host plants is the central tenet of host-specificity testing in weed biological control programs (Pemberton 2000).

Many of the alien plants now established in North America are congeners of native North American plants. If aliens can serve as functional hosts for insects that have specialized on their native congeners, the production of insect specialists in areas with large populations of alien plants may not differ from that of specialists in areas comprised entirely of natives. Moreover, in some cases, alien plants have carried one or more of their own insect specialists with them to North America. The imported

willow leaf beetle (*Plagiodera versicolora*) and the mimosa webworm (*Homadaula anisocentra*) are good examples. These alien specialists are now as much a part of North America as are their alien host plants and must be considered in measures of insect productivity associated with those plants. The degree to which introduced insects support diverse guilds of predators and parasitoids is unknown. There is growing evidence, however, that the fauna of parasites and pathogens associated with alien insects is depauporate (Torchin et al. 2003).

Second, to what extent do generalist insect herbivores eat alien plants? It is estimated that only 10% of all phytophagous insects have the physiological and behavioral ability to grow and reproduce on unrelated plants in several different families (Bernays & Graham 1988). Though less diverse than specialists, such generalists can be enormously successful in converting plant tissues to insect biomass. Generalists may often be more common than specialists and thus may provide more biomass to higher trophic levels (Futuyma & Gould 1979; C. Elzinga & B. Farrell, personal communication). It is possible, then, that if generalists use alien plants as hosts with the same frequency and success that they use native plants, the total production of insect biomass in a habitat composed in part or entirely of alien species may not differ from that produced in a habitat lacking such plants. Moreover, because introduced insect generalists may lack the natural enemy complex associated with native generalists (Hawkins et al. 1999), their presence in a community invaded by alien plants could additively lead to higher levels of phytophagous insect productivity than in pristine natural areas.

It is also necessary to learn how the percentage of aliens in the landscape affects the response of generalists and specialists toward these plants. The proximate host range of a phytophagous insect is determined as much by behavioral constraints associated with host selection as by physiological constraints on digestion and tissue detoxification (Courtney et al. 1989). Host selection, in turn, can be influenced by the encounter rate. In habitats with ample numbers of suitable native hosts, phytophagous insects have the opportunity to discriminate against aliens during oviposition or feeding choices. If aliens are encountered frequently, however, discriminating becomes more costly and more eggs or trial feeding may occur on them. Loading a habitat with aliens can, in a sense, be likened to no-choice cage experiments used to test host specificity in prospective biocontrol agents. Such tests are criticized because they often lead to the "selection of unnatural hosts" (Clement & Cristofaro 1995). The opposite prediction can also be made. Habitats with a low percentage of alien plants may support high densities of insects that are forced by competition to accept aliens as hosts more often than they would in the absence of competition. Obviously, experimentation is required to determine which of these scenarios is currently operating.

Finally, to what extent do changes precipitated in the food supply by alien plants affect members of higher trophic levels? Terrestrial birds, for example, may be particularly vulnerable to plant-induced reductions in insect populations because 96% of all terrestrial birds in North America rear young on insect protein (Dickinson 1999). To date, studies have focused on the use of aliens as nest sites (Whalen & Dilger 1995; Schmidt & Whalen 1999), but the effect of aliens on foraging time and on fledgling number, size, and survivorship has yet to be quantified. Furthermore, with the notable exception of purple loosestrife (*Lythrum salicaria*) invasions, we know little about how the replacement of native vegetation with alien species affects insectivorous mammals, reptiles, and amphibians (Blossey 1999). Given the pervasiveness of alien plants in North America and the speed with which they continue to replace native vegetation, addressing such questions should become a priority among funding agencies and researchers alike.

Acknowledgments

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