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Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America

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Abstract Alien invasive insects such as gypsy moth, hemlock woolly adelgid, and emerald ash borer continue to disturb the mixed deciduous and hemlock forests of eastern North America by causing wide-scale defoliation, decline and/or mortality of their hosts. Some of the most devastating species are spreading in "defense free space", causing extensive mortality of hosts that are inherently susceptible, perhaps due to their lack of coevolutionary history with the invader. These disturbances have altered the dynamics of canopy gaps, coarse woody debris, biogeochemical cycling, and ecological interactions among organisms in terrestrial and aquatic systems, with consequent effects on forest composition, structure, and function. Populations of indigenous species specialized to particular habitats and/or host trees are most likely to decrease, while some generalist and opportunistic species may increase in invaded forests, including exotic plants as their facilitation by alien insects sparks an "invasional meltdown". Although poorly documented, alien insects may induce positive feedback effects on ecological processes and interactions. For example, effects of herbivory on foliar chemistry may indirectly alter tri-trophic interactions of indigenous herbivores on their shared hosts, slow rates of terrestrial nutrient cycling, and decrease productivity of aquatic habitats based on allochthonous inputs. Tactics used to eradicate or suppress alien insects in forests such as insecticide applications, biological control, and silvicultural prescriptions can also have ecological impacts. As alien insects continue to establish and spread in forests of eastern North America, their already pervasive effects on ecological interactions and ecosystem processes will continue to magnify.

Keywords Invasive species · Invasional meltdown · Defense free space · Disturbance · Nutrient cycling · Gap ecology · Forest succession · Nontarget effects

Introduction

During the last two centuries, the number of alien phytophagous insect species that have established in forests of North America has increased exponentially (Mattson et al. 1994; Liebhold et al. 1995; Niemelä and Mattson 1996). Some have been especially devastating, either alone or in conjunction with pathogenic symbionts, causing wide-spread mortality of their hosts that has substantially altered forest

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structure and ecosystem processes. For example, gypsy moth (*Lymantria dispar* L.) and beech scale (*Cryptococcus fagisuga* Lind.) with its pathogenic fungal associates have severely impacted oak (*Quercus* spp.) (Davidson et al. 1999) and beech (*Fagus grandifolia* Ehrh.) (Houston 1994; Morin et al. 2007) stands, respectively, throughout New England. Smaller European elm bark beetle (*Scolytus multistriatus* Marsh.) historically has been the most important vector of Dutch elm disease (Hanula and Berisford 1984), which decimated American elm (*Ulmus americana* L.) throughout North America (Barnes 1976; Karnosky 1979). Hemlock woolly adelgid (*Adelges tsugae* Annand) has caused wide-spread mortality of eastern [*Tsuga canadensis* (L.) Carr.] and Carolina hemlock (*Tsuga caroliniana* Engelm.), which are keystone species in riparian areas in the Appalachian forests (Orwig et al. 2002; Ellison et al. 2005; Small et al. 2005). Balsam woolly adelgid [*Adelges piceae* (Ratzeburg)] has devastated Fraser fir [*Abies fraseri* (Pursh) Poir.] in high altitude forests of the southern Appalachian Mountains (Pauley and Clebsch 1990; Hollingsworth and Hain 1991). More recent and still relatively localized introductions causing wide-spread morality of their hosts include emerald ash borer (*Agrilus planipennis* Fairmaire) (Cappaert et al. 2005; Poland and McCullough 2006), viburnum leaf beetle [*Pyrrhalta viburni* (Paykull)] (Weston et al. 2007), and redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff) and its fungal symbiont (*Raffaelea* sp.) (Hanula et al. 2008). Other emerging threats that have the potential to impart severe impacts on forests of eastern North America include Asian longhorned beetle [*Anoplophora glabripennis* (Motschulsky)] (Townsend Peterson and Sachetti-Pereira 2004), and European woodwasp (*Sirex noctilio* Fabricius) (Ciesla 2003; Haugen and Hoebeke 2005).

Release from natural enemies has been considered a key factor in facilitating success of alien insects as they establish and spread readily in “enemy free space” (Liebhold et al. 1995). However, if indigenous host plants are highly susceptible to alien insects because their lack of coevolutionary history with the herbivore has left them without effective targeted defenses, then release from bottom-up regulation also may be critical in the establishment, spread, and ultimate impact of exotic herbivores. Wide-spread tree mortality can result as range expansion of alien insects occurs in “defense free space”. This appears to be the case with some of the most devastating alien invaders, which threaten to functionally extirpate their host plants. For example, there is experimental evidence that North American hosts naïve to the alien insect are more susceptible than are their coevolved congeners in the case of balsam woolly adelgid and North American firs (Witter and Ragenovich 1986), beech scale and North American beeches (Houston 1987), hemlock woolly adelgid and eastern North American hemlocks (Havill et al. 2006), and emerald ash borer and North American ashes (*Fraxinus* spp.) (Rebek et al. 2008).

To date, more than 400 alien phytophagous insect species have established in North American forests, and nearly every genera of woody plant endemic to eastern North America has at least one alien insect and/or pathogen associated with it (Mattson et al. 1994, 2007). About 75% of the alien herbivorous insect fauna currently established in North American forests is endemic to Europe (Niemelä and Mattson 1996; Mattson et al. 2007). Pathways of introduction have been unintentional such as infested wood packing or soil and plant material (Work et al. 2005; Haack 2006; McCullough et al. 2006), and intentional as biocontrol agents (Elkinton and Liebhold 1990). As “biological pollutants” and anthropogenic disturbance agents, alien invasive phytophagous insects have caused widespread economic and ecological damage in urban and forested areas of North America (Wallner 1996). The economic impact has been estimated at billions of US dollars each year through loss of forest products, reforestation efforts, management efforts, removal and disposal of hazard trees in urban areas, and loss of livelihood of local communities (Pimentel et al. 2000; Sydnor et al. 2007).

Significant and diverse direct and indirect ecological impacts of alien insects have been documented (Lovett et al. 2006). For example, effects of widespread gypsy moth defoliation (Fig. 1) can range from relatively short-term alteration of the forest floor environment to longer-term effects of tree decline and mortality on successional trajectories. Other alien insects such as emerald ash borer selectively kill individual trees resulting in formation of small but widely distributed canopy gaps, ultimately removing their host taxa from invaded communities (Fig. 2). In turn, these disturbances clearly have the potential to unleash a cascade of indirect effects on ecological processes and

Fig. 1 Wide scale defoliation by gypsy moth triggers short term changes in light, temperature, and moisture regimes on the forest floor, alters nutrient cycles, and exerts longer term effects on competitive interactions and successional trajectories

Fig. 2 Ash mortality induced by emerald ash borer results in isolated but widely distributed canopy gaps, coupled with extirpation of ash species from invaded forests

interactions that reverberate throughout the forest ecosystem.

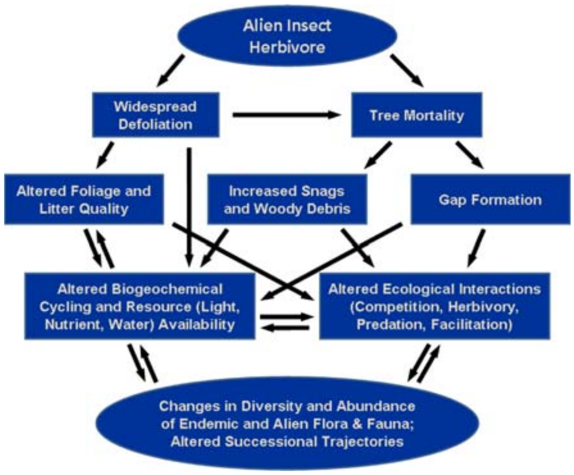

Fig. 3 Generalized conceptual model depicting cascading direct and indirect effects of alien insect herbivores on ecological processes and interactions that ultimately impact community composition and successional trajectories in eastern North American forests

The last two decades have seen an increase in studies addressing the economic and ecological impacts of alien insects in forests, and the publication of several important reviews (e.g. Liebhold et al. 1995; Chornesky et al. 2005; Ellison et al. 2005; Lovett et al. 2006; Kenis et al. 2009). Perhaps the best documented ecological impacts of alien insects in eastern North American forests are those of gypsy moth and hemlock woolly adelgid on community composition and nutrient cycling (Lovett et al. 2006). A diverse potpourri of isolated studies has documented an array of additional ecological impacts, but few of these have been characterized comprehensively, and a full accounting of impacts of alien insects on forest ecosystems remains elusive.

The objective of this review is to elucidate potential direct and indirect ecological impacts of alien herbivorous insects in the mixed deciduous and hemlock forests of eastern North America. To address the following questions, we employ the framework of Parker et al. (1999) for classifying impacts of invasive organisms, emphasizing effects on ecological processes (e.g. on disturbance regimes such as gap formation, and rates of resource availability and acquisition), as well as community and population level impacts. How can alien insects directly alter abiotic conditions and ecological processes? How can these changes cascade through forest ecosystems as indirect effects on ecological interactions, community structure, and successional trajectories? What are the direct and indirect impacts of management activities targeted at alien insects? A conceptual overview of our synthesis is outlined in Fig. 3. By necessity, much of this review is focused on illuminating knowledge gaps and hypotheses for testing.

Impacts of alien insects on ecosystem processes

Formation of canopy gaps

Several alien insect species have caused extensive tree mortality in eastern forests, including gypsy moth, hemlock woolly adelgid, and beech scale (Liebhold et al. 1995; Ellison et al. 2005; Lovett et al. 2006), and more recently emerald ash borer (Herms et al. 2004; Poland and McCullough 2006), which has caused nearly 100% mortality of ash near its point of introduction in southeastern Michigan (Gandhi et al. 2008). Gap formation resulting from decline and mortality of oak and beech, resulting from gypsy moth defoliation (Davidson et al. 1999; Jedlicka et al. 2004) and beech bark disease (Houston 1975; Morin et al. 2007; Runkle 2007), respectively, is particularly well documented. By inducing the decline and mortality of host trees, alien herbivorous insects cause the formation of canopy gaps (Rabenold et al. 1998; Runkle 2005), with their size and frequency being dependent upon host dominance, density, distribution, and mortality levels. The ecological significance of gap formation for community structure and successional trajectory is especially important in eastern forests where wildfire frequency is naturally low and has been further suppressed by management activities (Runkle 1982, 1990, 1998, 2000; Shang et al. 2007).

Gap dynamics induced by alien insects are likely to differ from those generated by gradual decline and senescence of canopy trees or abiotic disturbance events such as windthrow. In the mixed deciduous forests characteristic of eastern North America, natural decline and mortality of aging trees generates gradual but ongoing formation of small gaps, while storms can generate episodic formation of numerous gaps, which can vary in size depending on the intensity of the disturbance (Runkle 1990; Canham et al. 2001; Nagel and Svoboda 2008). Gap formation caused by alien insects is also likely to be episodic. However, decline and mortality of trees in response to insect infestation is more likely to be species-specific and generally slower, with dead trees remaining standing longer as snags (Krasny and DiGregorio 2001). In the Allegheny hardwood forests of New York impacted by beech bark disease and gypsy moth, the area covered by gaps increased from 20 to 32% over 6 years (Krasny and DiGregorio 2001).

Gap formation caused by alien insects (and other disturbance agents) alters the forest microenvironment including light, moisture, and temperature regimes (Twery 1990; Stadler et al. 2006), and increases edge-effects, patchiness, and habitat heterogeneity (Canham et al. 1990; Webb 1999; Gandhi et al. 2007). For example, hemlock decline and mortality caused by hemlock woolly adelgid increased canopy gaps and levels of light reaching the forest floor (Orwig and Foster 1998), which decreased soil moisture within 3 years (Orwig et al. 2008). Such alterations in microhabitat conditions can alter understory vegetation dynamics (Orwig and Foster 1998; Rabenold et al. 1998; see section "Impacts on Native Understory Plants").

Impacts on woody debris dynamics

As host trees experience greater mortality over time, dead standing trees (snags) eventually fall and become downed-woody debris (DWD), which provides important habitat for many animal and plant species (Gandhi et al. 2007; Owens et al. 2008). DWD, including fine—(small branches and roots) and coarse—(tree trunks and branches) woody debris, increases structural and chemical heterogeneity of the forest floor (Harmon et al. 1986).

Few studies have addressed rates and volume of woody debris generated by mortality caused by alien insects. The rate and manner of tree fall (e.g. uprooted trees disturb the adjacent soil environment to a greater degree than do trees that snap above ground) and decomposition will likely differ depending on tree species and rate of mortality (e.g. slower decline caused by defoliation vs. more rapid mortality caused by wood-borers), presence of decay agents such as fungi and other saproxylic insects, topography, and prevalence of wind- and ice-storms (Gandhi et al. 2007). For example, beech trees killed by beech bark disease fell at a rate that tripled over 6 years, while oaks killed by gypsy moth fell at a rate that remained constant over the same period (Krasny and DiGregorio 2001). Species-specific rates of tree-fall suggest that invasive insects can alter the dynamics of snags and downed woody debris. It remains to be seen, however, how increased habitat heterogeneity and other ecological impacts of woody debris generated by alien insects compare with those created by abiotic disturbances such as wind- and ice-storms (Gandhi et al. 2007).

Impacts on biogeochemical cycling

In a seminal paper, Mattson and Addy (1975) proposed that phytophagous insects can act as regulators of primary productivity by influencing patterns of nutrient cycling. The boreal forest of North America has long been subjected to expansive outbreaks of indigenous defoliating insects including forest tent caterpillar (*Malacosoma disstria* Hübner) and spruce budworm [*Choristoneura fumiferana* (Clemens)] (Mattson et al. 1991). Eastern deciduous forests, however, did not experience episodic defoliation on a wide scale prior to introduction of gypsy moth (Mattson et al. 1991). Subsequent studies have confirmed the potential for gypsy moth defoliation to alter biogeochemistry of both terrestrial and aquatic ecosystems through increased inputs of DWD, green litter fall, frass, and their corpses (Lovett et al. 2002).

Expansive defoliation can transfer substantial quantities of foliar nitrogen in green leaf fragments and frass to the forest floor before it can be reallocated within the plant prior to leaf senescence (Schowalter et al. 1986; Lovett et al. 2002). Furthermore, Lovett and Ruesink (1995) found that highly labile carbon in gypsy moth frass stimulated microbial growth resulting in immobilization of more than 90% of nitrogen in soil samples within 10 days, which could potentially reduce availability of nitrogen to trees, at least in the short term. Similar results were found for nitrogen in frass of gypsy moth that had consumed oak foliage labeled with ^{15}N. Nitrogen in the frass was mobilized more quickly than nitrogen in leaf litter, rendering it largely unavailable to plants (Christenson et al. 2002). In a Pennsylvania oak forest, gypsy moth defoliation increased quantities of nitrogen, potassium, and phosphorus in litter fall, and decreased quantities of calcium (Grace 1986). The seasonality of the nutrient pulse was also altered as most litter (including frass and leaf fragments) fell in early summer when larvae were feeding, rather than in early autumn during natural leaf abscission. In addition to effects imposed by defoliation, canopy gap formation resulting from tree mortality can also alter patterns of nitrogen and carbon cycling (Scharenbroch and Bockheim 2008a, b).

Effects of alien insects on biogeochemical cycles also have been detected at the level of the watershed (Swank et al. 1981; Ellison et al. 2005; Lewis and Likens 2007). Grady et al. (2007) found that 66 watersheds in western Virginia had reduced concentrations of dissolved silica from 1988 to 2003. Abiotic factors such as pH, precipitation, and water discharge were not correlated with changing amounts of silica. However, the reduction in silica levels did coincide with initiation of gypsy moth outbreaks in that region. The authors hypothesized that defoliation increased light availability and nitrate concentrations in the streams, which, in turn, stimulated populations of benthic diatoms, leading to greater extraction of silica from the water. Webb et al. (1995) reported that gypsy moth defoliation affected the pH and buffering capacity of streams, and increased nitrate levels almost tenfold. This potentially may have consequences for aquatic animals, as high nitrate levels have been shown to adversely affect the behavior, morphology, and survival of amphibian larvae (Marco et al. 1999).

It can be hypothesized that the extensive defoliation characteristic of gypsy moth outbreaks may trigger positive feedbacks that decrease productivity of terrestrial and aquatic ecosystems for several years (Choudhury 1988; Schweitzer et al. 2005). For example, herbivory has been shown to decrease the rate of decomposition of litter derived from the damaged leaves (Findlay et al. 1996), as well as increase foliar concentrations of secondary metabolites and decrease foliar nutrient concentrations in the years following defoliation (Schultz and Baldwin 1982; Tuomi et al. 1984; Bryant et al. 1993). Higher secondary metabolite concentrations and carbon:nitrogen ratios in green foliage have been associated with decreased rates of litter decomposition and nitrogen mineralization (Horner et al. 1988; Hättenschwiler and Vitousek 2000), which can decrease nutrient availability and uptake by trees. In turn, soil nutrient limitation can elevate foliar concentrations of carbon-based secondary metabolites (Mattson 1980; Herms and Mattson 1992), which may further inhibit decomposition, thereby decelerating rates of nutrient cycling (Schweitzer et al. 2005). Such feedback effects should relax over time as delayed defoliation-induced effects on host quality subside over subsequent years (Haukioja 1990).

Indirect effects of herbivory on litter quality may also impact the productivity of allochthonous aquatic habitats by decreasing the quality of the leaf detritus upon which their food webs are founded, including streams (Irons et al. 1991) and tree-holes (Walker et al. 1997; Strand et al. 1999). In some cases, defoliation can also increase the quality of leaf litter. Following severe defoliation by gypsy moth during spring, oak trees generally refoliate during summer.

Hutchens and Benfield (2000) found that this second flush of foliage had higher ratios of protein to fiber than did the first flush leaves, resulting in their faster decomposition in streams.

Altered patterns of terrestrial and aquatic nutrient cycling have been well documented in hemlock stands impacted by hemlock woolly adelgid (Ellison et al. 2005). Hemlock mortality accelerated nitrogen mineralization and nitrification rates (Jenkins et al. 1999; Orwig et al. 2008), elevated nitrate and cation levels in soil water (Yorks et al. 1999), and increased dissolved organic carbon and nitrogen in through-fall (Stadler et al. 2006). Following adelgid-induced hemlock decline and mortality, Small et al. (2005) reported up to 140% increase in density of black birch (*Betula lenta* L.) seedlings and saplings, which have higher concentrations of foliar nitrogen and produce higher quality litter than does hemlock foliage (Cobb and Orwig 2002). Hemlock woolly adelgid may also exert ecologically significant impacts on hydrological cycles. For example, Ford and Vose (2007) concluded that wide-spread mortality of eastern hemlock will decrease annual stand-level transpiration by about 10%, and decrease winter and spring stand-level transpiration by about 30%, resulting in persistent increases in discharge by forest streams.

Impacts of alien insects on biotic populations and communities

Impacts on canopy composition

Decline and mortality of indigenous tree species caused by alien phytophagous insects has altered forest community composition and successional trajectories (Campbell and Sloan 1977; Runkle 2005). Shifts in forest species composition following defoliation by gypsy moth have been well documented in eastern North America (Campbell and Sloan 1977; Davidson et al. 1999). Several studies found that growth of oaks declined in the year following defoliation, while the growth of less favored hosts such as maples (*Acer* spp.) and ashes increased, probably due to release from competitive suppression (Muzika and Liebhold 1999; Naidoo and Lechowicz 2001). Furthermore, there is evidence that oak mortality increased the importance of shade-tolerant species that are less preferred by gypsy moth, such as maples, beech, and cherries (*Prunus* spp.) (Campbell and Sloan 1977; Nowacki and Abrams 1992; Muzika and Twery 1995; Fajvan and Wood 1996; Jedlicka et al. 2004). Beech bark disease has decreased the density of American beech in the overstory while, at least in some cases, increasing its density in the understory, probably via strong basal sprouting of infested mature trees (Houston 1975; Morin et al. 2007; Runkle 2007).

Forests infested with hemlock woolly adelgid have also experienced a shift in canopy composition, with black oak (*Q. velutina* Lam.), sassafras [*Sassafras albidum* (nutt.) Nees], red maple (*Acer rubrum* L.), black birch, yellow birch (*B. alleghaniensis* Britton), and American beech gaining in importance in the canopy layer as hemlock declined (Small et al. 2005). Successional responses were site-specific, with black oak gaining greater dominance on xeric ridges and ledges, and other species on mesic sites in ravines (Small et al. 2005).

Ironically, in several cases, endemic tree species that increased in dominance as alien insects killed their competitors have themselves in recent years become threatened by the next wave of alien invaders. For example, wide-scale mortality of American elm caused by Dutch elm disease led to increased dominance of ash in eastern North American forests (Barnes 1976), which are now threatened by emerald ash borer. It has been hypothesized that following the chestnut blight epidemic, American chestnut [*Castanea dentata* (Marsh.) Borkh.] was replaced in riparian areas of the Appalachians by hemlocks (Ellison et al. 2005), which are now threatened by the hemlock woolly adelgid. Oak trees increased in density in the eastern United States early in the twentieth century, in part due to the demise of American chestnut (Muzika and Liebhold 2001), only to become the preferred host of gypsy moth.

Impacts on native understory plants

The forest understory is also directly affected by defoliation and gap formation caused by alien insects, and the consequent increase in light penetration and temperature (e.g. Kasbohm et al. 1996). In New England, increased growth of black birch, red maple, and oak seedlings in the understory was observed in response to hemlock decline (Orwig 2002). Hemlock mortality also increased cover of hay-scented fern [*Dennstaedtia punctilobula* (Michx.) T. Moore], which can form a dense herbaceous layer that inhibits tree regeneration following disturbance (Penrod and McCormick 1997). Populations of other bryophytes have also been observed to increase as hemlock mortality increased light availability in the understory (Cleavitt et al. 2008).

Following mortality of Fraser fir due to balsam woolly adelgid, the cover of woody shrubs such as blackberry (*Rubus canadensis* L.) increased, whereas the cover of various herbaceous species, including some bryophytes, decreased (DeSelm and Boner 1984). Similarly, in the Great Smoky Mountains, the density of blackberry increased, while that of herbaceous plants such as woodfern [*Dryopteris campyloptera* (Kunze) Clarkson] and oxalis (*Oxalis acetocella* Linnaeus) decreased, as did density of shade-adapted shrubs such as hobblebush (*Viburnum alnifolium* Marsh.) and mountain cranberry [*Vaccinium erythrocarpum* (Michx.)] (Rabenold et al. 1998).

The herbaceous plant layer can exert strong control over ecological processes in temperate forest ecosystems (Zak et al. 1990; Gilliam 2007). Hence, these studies suggest that effects of alien insects on canopy species will invariably cascade to the forest floor, leading to reorganization of the understory community with important implications for forest successional trajectories.

Impacts on invasive plants

It has been hypothesized that alien forest insects, including hemlock woolly adelgid (Orwig and Foster 1998) and emerald ash borer (Herms et al. 2008), can facilitate the establishment and spread of invasive plants by creating canopy gaps that increase light availability while relaxing interspecific competition for space and resources, thereby igniting an “invasional meltdown” (Simberloff and Von Holle 1999). Many invasive plant species are not highly tolerant of shade and are more common at forest edges where light is not as limiting (Knapp and Canham 2000; Parendes and Jones 2000; Hunter and Mattice 2002). Furthermore, disturbances that open the canopy have been shown to facilitate establishment of alien plants in the forest interior (Horvitz et al. 1998; Snitzer et al. 2005; Webster et al. 2005; Glasgow and Matlack 2007; Eschtruth and Battles 2009). McEwan et al. (2009) speculated that gypsy moth may also facilitate the spread of invasive shrubs in North America by selectively feeding on native species.

Although few studies have directly investigated facilitation of invasive plants by alien herbivores, increased incidence and cover of invasive plants has been documented in stands impacted by hemlock woolly adelgid (Orwig 2002; Eschtruth et al. 2006), with interactions between canopy disturbance and propagule pressure being the most important factors affecting the distribution of exotic plants (Eschtruth and Battles 2009). Increased abundance of exotic plants may prevent recruitment and establishment of indigenous species, and thus alter successional trajectories within invaded forests (Levine et al. 2003), while exerting feedback effects that further alter community composition (e.g., Gómez-Aparicio and Canham 2008). While not yet well documented, alien invasive insects clearly have the potential to exert pervasive indirect effects that cascade through forest communities through facilitative effects on invasive plants.

Impacts on native fauna

Alien herbivorous insects may impact indigenous animals by decreasing (or, in some cases, increasing) the distribution and abundance of plants on which they depend for at least part of their life-cycle (Koh et al. 2004). The effect may be especially strong for herbivorous insects that specialize on host plants strongly impacted by alien herbivores. Wagner (2007) catalogued at least 21 species of monophagous Lepidoptera that specialize on North American ash species that will be threatened by the demise of North American ash due to emerald ash borer. Specialist herbivores of eastern hemlock and Fraser fir are similarly threatened by hemlock woolly adelgid and balsam woolly adelgid, respectively. To date, there has been little synthesis of the natural history of the community of organisms associated with tree species threatened by alien insects and pathogens. Such research is urgently needed before these trees become rare or locally extirpated, resulting in biotic impoverishment.

Alien insects may also decrease the abundance of native phytophagous insects through competitive interactions (Scriber 2004). Work and McCullough

(2000) assessed the response of forest Lepidoptera to defoliation by gypsy moth in Michigan. While most native species appeared to be resilient to the gypsy moth outbreak, the populations of a subset of species associated with oak (a favored gypsy moth host) were negatively affected during the year of the outbreak, possibly because of interspecific competition for food. Gypsy moth defoliation also temporarily decreased populations of native Lepidoptera in West Virginia; however, the effects were small relative to annual fluctuations in caterpillar density due to factors such as weather (Sample et al. 1996).

Alien herbivorous insects may exert indirect effects on the population and community structure of indigenous fauna by altering their habitat and food supply. For example, balsam woolly adelgid reduced the dominance of endemic fir trees by about 50% and drastically opened the canopy in the Appalachian forests. In response, populations of birds that forage in the canopy and sub-canopy of the fir forests decreased, whereas populations of bird species more characteristic of disturbed habitats increased (Rabenold et al. 1998). Similarly, populations of birds that are habitat specialists of hemlock forests, such as Acadian flycatcher [*Empidonax virescens* (Vieillot)], have been adversely affected by extensive adelgid-induced hemlock mortality (Tingley et al. 2002; Becker et al. 2008). In contrast, populations of other birds increased in infested hemlock stands, including the hooded warbler [*Wilsonia citrina* (Boddaert)], a species of regional concern that benefited from a dense black birch understory created by hemlock mortality (Tingley et al. 2002), and opportunistic species such as the wood thrush [*Hylocichla mustelina* (J.F. Gmelin)] that benefited from increased numbers of dead trees and canopy gaps (Becker et al. 2008).

During outbreaks, gypsy moth larvae represent a super-abundant food source for predators such as native cuckoos (*Coccyzus* spp.) that specialize on hairy caterpillars, and Barber et al. (2008) observed a shift in cuckoo distributions during outbreaks, with more cuckoos in areas where gypsy moth was epidemic. As predators respond spatially and temporally to populations of alien insects, predation pressure on indigenous species may change in complex ways.

Stress imposed on oaks by severe gypsy moth defoliation decreases or eliminates acorn production (Kasbohm et al. 1996), which is an important food source for many species of wildlife (Ostfield et al. 1996; McShea 2000; McShea et al. 2007). Effects of gypsy moth defoliation on acorn production have been shown to reduce the reproductive success of small mammals including white-footed mice (*Peromyscus leucopus* Rafinesque) and eastern chipmunks (*Tamias striatus* L.), alter the foraging patterns of white-tailed deer [*Odocoileus virginanus* (Zimmerman)] (Ostfield et al. 1996), and shift the dietary choices of black bear (*Ursus americanus* Pallas) (Kasbohm et al. 1996). Gypsy moth defoliation also increased the rate of nest predation of forest birds, possibly by increasing nest visibility (Thurber et al. 1994). Conversely, longer-term habitat changes including increased availability of snags and opened canopy may create more nesting habitat for many bird species (Bell and Whitmore 2000).

Gypsy moth density may be indirectly tied to acorn production through effects of acorn availability on mice populations, which are key predators of gypsy moth. In a fascinating experiment, Jones et al. (1998) manipulated the availability of acorns in the forest by removing them from some plots and distributing the collected acorns in other plots. Where the acorn supply was experimentally increased, mouse populations increased dramatically, as did predation of gypsy moth pupae by mice. Where acorn density was experimentally lowered, mouse populations decreased and gypsy moth predation declined. Hence, it is possible that gypsy moth outbreaks could be prolonged if defoliation-induced reductions in acorn production have positive feedback effects on gypsy moth survival through effects on mice.

Indirect negative interactions between alien and endemic insect herbivores mediated by host trees and natural enemies have also been documented. In Michigan, Redman and Scriber (2000) found that gypsy moth defoliation decreased growth and survival of native swallowtail butterflies (*Papilio canadensis* Rothschild & Jordan) on quaking aspen (*Populus tremuloides* Michx.) by inducing reductions in host quality. Further, tiger swallowtail larvae experienced higher rates of parasitism in the vicinity of high gypsy moth populations. The generalist parasitic wasp was likely attracted in greater numbers by the presence of gypsy moth. This study suggests that alien herbivorous insects can indirectly exert both top–down and bottom-up impacts on native fauna. Preisser and Elkinton (2008) documented competitive interactions between two alien insect specialists of hemlock: hemlock woolly adelgid and elongate hemlock scale (*Fiorinia externa* Ferris). The densities of both species were reduced by 30% in mixed-species relative to single-species trials. Interestingly, foliage growth was greater in the mixed-species treatment, indicating that the presence of elongate hemlock scale (a less damaging species on hemlock trees) can mitigate some of the adverse effects of hemlock woolly adelgid.

Not all interactions between alien and native insects are negative. For example, Hammons et al. (2009) found that feeding on ripening fruits by the exotic scarab Japanese beetle (*Popillia japonica* Newman) facilitated subsequent feeding by native scarab beetles. Gypsy moth defoliation has been shown to facilitate colonization of oaks by twolined chestnut borer [*Agrilus bilineatus* (Weber)], probably by compromising tree defenses to this phloem-feeding wood borer (Dunbar and Stephens 1975; Wargo 1977).

Ecological impacts of management practices for controlling alien insects

Impacts of chemical control

Direct and indirect effects of alien insects on forest ecosystems can be considered to extend to the tactics used to manage them. For example, aerial applications of the biopesticide *Bacillus thuringiensis kurstaki* (*Btk*) used to eradicate and suppress gypsy moth infestations can have nontarget effects on indigenous Lepidoptera (Herms 2003; Scriber 2004). In West Virginia, a single aerial application of *Btk* to suppress gypsy moth decreased the diversity and abundance of endemic butterflies and moths for one season (Sample et al. 1996). Similar effects were observed in Virginia (Rastall et al. 2003). In Oregon, where three applications of *Btk* were made during the same season to eradicate small populations of gypsy moth, caterpillar diversity was lower 3 years after application, although overall numbers of caterpillars rebounded within 1 year (Miller 1990). The short residual activity of *Btk* in the field (considered to be only a few days) is thought to minimize effects on nontarget Lepidoptera. However, Johnson et al. (1995) found that foliage treated with *Btk* applied with ground equipment at a high labeled rate remained toxic to swallowtail butterfly (*P. glaucus* L.) larvae for 30 days following application. Conversely, nucleopolyhedrosis virus (NPV) applied to suppress gypsy moth in West Virginia had no detectable adverse effects on populations of native Lepidoptera (Rastall et al. 2003), or in laboratory studies on mammalian predators of gypsy moth such as white-footed mouse, short-tailed shrew [*Blarina brevicauda* (Say)], and Virginia opossum (*Didelphis marsupialis* L.) (Lautenschlager et al. 1977).

Diflubenzuron is a growth regulating insecticide that interferes with exoskeleton formation of immature insects during the molting process. It is considered more effective than *Btk* for suppressing gypsy moth, but is not used as widely because it impacts a much broader diversity of insects with effects that persist much longer (Eisler 1992). Aquatic arthropods, including insects and crustaceans, are especially sensitive, but aerial applications of diflubenzuron also have been shown to decrease the abundance and diversity of numerous taxa of terrestrial forest insects, with effects persisting beyond the year of application (Martinat et al. 1988; Butler et al. 1997). Residues can persist on foliage throughout the season, and soil and aquatic arthropods have been impacted by senesced leaves that abscise in autumn (Griffith et al. 2000). In a study on litter- and soil-dwelling arthropods in a West Virginia forest, spiders (Araneae) and mites (Acari) were not affected by application of diflubenzuron, but populations of springtails (Collembola) were decreased (Perry et al. 1997).

Effects of aerial insecticide applications on nontarget insects may also extend to higher trophic levels by decreasing their food supply. For example, in a study in which *Btk* applications caused significant declines in Lepidoptera larvae, populations of 18 of 27 insectivorous birds also declined (Strazanac and Butler 2005). However, effects on most bird species were temporary, with all but two recovering fully within 3 years following the treatments (Strazanac and Butler 2005). Another study found that when caterpillar populations were decreased by aerial application of diflubenzuron, birds consumed fewer caterpillars and spent more time foraging for food (Cooper et al. 1990).

Impacts of biological control

Classical biological control, the introduction of natural enemies from the endemic range of the alien herbivore, is considered a corner-stone of integrated pest management. However, there have been cases when these “enemies of the enemy” have turned against nontarget indigenous fauna with unintended consequences (Hawkins and Marino 1997). For example, high rates of parasitism by the alien tachinid fly, *Compsilura concinnata* Meig, which was introduced to eastern North America more than 100 years ago to control gypsy moth, has been implicated in the decline of North American silk moths (Saturniidae) in New England, including *Hyalophora cecropia* (Linnaeus) and *Callosamia promethea* (Drury) (Boettner et al. 2000). Kellogg et al. (2003) reported similar effects of this parasitoid on experimental populations of luna moth (*Actias luna* L.). As might be expected, these impacts on North American silk moth populations appear to vary regionally (Selfridge et al. 2007).

There is some evidence that introduced biocontrol agents can competitively exclude indigenous parasitoids. For example, comparison of surveys of parasitoids of endemic Lepidoptera conducted between 1915–1929 and 1999–2005 in Massachusetts revealed that the tachinid fly, *Lespesia frenchii* (Williston), was a common parasitoid of the silk moth *C. promethea* and eastern tent caterpillar (*Malacosoma americanum* Fabricius) early in the twentieth Century. However, this indigenous parasitoid species was not recovered in the latter survey when parasitism by the alien *C. concinnata* was common (Parry 2009). Interestingly, in New York, where *C. concinnata* parasitism rates are much lower, *L. frenchii* was reared from its native Lepidoptera hosts in similar frequencies in 1915–1929 and 1999–2005 (Parry 2009).

Impacts of silvicultural treatments used to manage alien insects

Host trees are sometimes removed from forested landscapes and destroyed in an attempt to eradicate alien species, as was the case for the emerald ash borer eradication program (Herms et al. 2004; Poland and McCullough 2006), or to salvage logs from trees killed by alien species (Orwig and Kittredge 2005), which can alter microhabitat conditions and successional trajectories. For example, logging of hemlock woolly adelgid-infested trees in New England increased soil compaction, pH, nitrification rates, scarification, and biomass of woody debris, while increasing dominance of black birch, brambles (*Rubus* spp.), sedges (Cyperaceae), and hay-scented fern (Kizlinski et al. 2002; Orwig and Kizlinski 2002). Hausman et al. (2008) reported that removal of ash trees from a natural area to eradicate emerald ash borer increased soil compaction, possibly facilitating colonization of the newly formed gaps by invasive plants.

Thinning and pre-salvage harvesting of living trees have also been evaluated as tactics for preemptively decreasing forest susceptibility to invasion by alien insects. One study assessed the impact on salamanders of selective pre-salvage harvesting of green hemlock trees in anticipation of hemlock woolly adelgid invasion (Brooks 2001). Although populations of eastern redback salamander (*Plethodon cinereus* Green) decreased in harvested areas, the effects were ephemeral as populations rebounded within a few years (Brooks 2001). Muzika et al. (2004) assessed the effects of thinning of oaks to reduce vulnerability of forests to gypsy moth on small mammal populations in West Virginia. Mice (*Peromyscus* spp.) were found in higher numbers in thinned than in unthinned control stands, while populations of masked shrew (*Sorex cinereus* Baird) and redback vole [*Clethrionomys gapperi* (Vigors)] were not affected. Comparable studies on other taxa (invertebrates and vertebrates) are notably absent.

Synthesis and conclusions

Alien insect herbivores, and the programs to manage them, clearly have the potential to unleash a diverse cascade of direct and indirect effects on ecosystem processes and ecological interactions that can alter community composition and successional trajectories of eastern North American forests (Fig. 3). Direct effects can range from widespread defoliation (e.g. gypsy moth) to formation of isolated but widely distributed gaps caused by species-specific tree mortality (e.g. emerald ash borer). Effects of gypsy moth and hemlock woolly adelgid on the abiotic environment, nutrient cycling, and community composition are the most comprehensively documented (Lovett et al. 2006), but a diverse array of additional direct, indirect, and feedback effects have also been documented or can be hypothesized (Kenis et al. 2009).

The impact of some of the most devastating alien species that cause wide-spread tree mortality, such as hemlock woolly adelgid (Havill et al. 2006) and emerald ash borer (Rebek et al. 2008), is magnified by the low level of resistance in their hosts, possibly because their lack of coevolutionary history has rendered them effectively defenseless. These alien invaders threaten to decimate their hosts on a continental scale as they continue to spread in "defense free space." More studies are required to document the effects of extensive host tree mortality on the native fauna that depend on them for food and shelter. Such studies would generate a better understanding of the threat of host extirpation on co-extinction of their specialized fauna.

Tree mortality creates canopy gaps and increases woody debris (both standing and fallen), which in turn affects the physical environment and biogeochemical cycling (Stadler et al. 2006), and ultimately community composition (Runkle 2005). Canopy gaps caused by alien insects may exert ecological impacts that differ qualitatively from those caused by natural tree decline and senescence, which tend to form more slowly, or those caused by disturbances such as wind and ice storms, which do not selectively remove individual taxa from the community (Gandhi et al. 2007). The dynamics and effects of gaps caused by extensive species-specific tree mortality should be more thoroughly investigated.

Defoliation and tree mortality induced by alien insects may generate a cascade of indirect effects on ecological interactions. For example, gypsy moth defoliation can substantially decrease acorn production by oak, which in turn can reduce small mammal populations by decreasing their food supply (Ostfield et al. 1996; McShea et al. 2007). Gypsy moth defoliation has also been shown to increase the rate of nest predation of forest birds, possibly by increasing nest visibility (Thurber et al. 1994). Although poorly documented, feedback effects of herbivory and tree mortality caused by alien insects may be pervasive. For example, changes in foliage and litter quality induced by defoliation (e.g. Findlay et al. 1996) may trigger positive feedbacks on nutrient cycles that could decrease the productivity of terrestrial and aquatic ecosystems over several years (e.g. Choudhury 1988; Schweitzer et al. 2005), as well as alter competitive (Redman and Scriber 2000) and facilitative (Hammons et al. 2009) interactions between endemic and alien herbivores. Some studies also suggest widespread potential for alien insects to facilitate the establishment and spread of exotic plants by altering resource availability and competitive interactions (e.g. Eschtruth et al. 2006; Eschtruth and Battles 2009), thereby unleashing an "invasional meltdown" (Simberloff and Von Holle 1999).

An increasing body of evidence suggests that tactics used to eradicate and suppress alien species also can have direct and indirect effects on forest communities. Aerial insecticide applications have been shown to temporarily suppress endemic nontarget fauna (Sample et al. 1996), with effects that can extend to higher trophic levels (Strazanac and Butler 2005). There is evidence that some generalist parasitoids released as biological control agents have exerted long-term negative effects on indigenous fauna (Boettner et al. 2000; Parry 2009). Tree removal associated with eradication programs (Hausman et al. 2008) and salvage logging of stands impacted by invasive insects (Kizlinski et al. 2002; Orwig and Kizlinski 2002) also has the potential to alter forest communities and ecosystem processes. Additional research is required to fully characterize the costs and benefits of programs to manage invasive forest insects.

The mixed deciduous and hemlock forests of eastern North America have experienced large-scale disturbance during the last two centuries, resulting in habitat destruction, isolation, and fragmentation (Russell and Davis 2001). Combined with ongoing climate change, the addition of alien herbivorous insects to the "disturbance potpourri" will almost certainly continue to increase the strain on the stability and resilience of North American forests (Mattson 1997; Dale et al. 2009). However, major knowledge gaps remain regarding short and long-term direct and indirect effects of alien invasive insects on structure and function of forest ecosystems. Future research may focus on longer-term assessments of impacts of alien herbivorous insects across various abiotic conditions, taxa, and ecosystems; provide models for predicting and mitigating some of these adverse impacts at the landscape level (e.g. Dale et al. 2009); and document the benefits (and costs) of quarantine, eradication, and containment measures for preventing the establishment and spread of alien invasive insects.

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