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Source: The Journal of the Torrey Botanical Society, 143(4) : 367-385

Published By: Torrey Botanical Society

URL: <https://doi.org/10.3159/TORREY-D-15-00049.1>

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A review on the invasion ecology of Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) a case study of ecological impacts at multiple scales¹

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Abstract. Invasive species are of global importance because of their impacts on ecological communities, habitat structure, native community dynamics, and ecosystem processes and function. Scientists and conservation managers are increasingly focusing on the biological impacts of invasive species and on devising management practices that emphasize the health of ecosystems based on measured biological processes. Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) is a highly successful invasive shrub in forests of eastern North America. The scientific literature surrounding this species has grown in the past several decades as researchers have investigated *L. maackii* impacts across multiple ecological scales. In this review we synthesized literature on (a) the key traits related to this species' invasion success, (b) the impacts this invasive species has at various ecological scales, (c) the outcomes of restoration efforts for this species, and (d) the connections of this weed to invasion ecology theories. *Lonicera maackii* impacts are complex and vary across ecosystems and spatial scales; we report findings from studies demonstrating a wide range of effects on species composition, community structure, ecosystem function, and successional trajectories. We end by providing a working ecological framework that may help guide future research and conservation efforts.

Key words: Ecosystem processes, invasion ecology, invasion theory, restoration impacts, terrestrial-aquatic linkages

Invasive species are considered to be one of the most important threats to biodiversity and ecosystem function across the globe (Ruesink *et al.* 1995, Wilcove *et al.* 1998), with the economic costs estimated to be as high as approximately \$120 US billion/yr (Pimentel *et al.* 2005). Invasive plants have prompted a great deal of interest with particular focus on quantifying the effects invaders have on plant communities (other articles in this special issue, Levine 2000, Collier *et al.* 2002, Crooks 2002, Callaway and Ridenour 2004). Effects ascribed to invasive plants include modification of habitat structure, changing ecosystem processes, and decreasing native biodiversity (Hejda *et al.* 2009). Many states in the USA have rules about invasive plants, and efforts to manage activities for invasives are widespread and include

cooperative weed management areas and invasive plant boards.

From both a management and scientific perspective, there is a clear need to identify invasive species and ensure they are thoroughly studied and have well-established, empirical evidence of ecosystem effects (Gurevitch and Padilla 2004, Sagoff 2005). For example, tamarisk has been classified as an invasive in southwestern USA and previous research suggested this plant reduced water availability through increased evapotranspiration rates (ETR; Thomas 1963). More-recent studies have indicated that the ETR of riparian, invaded forests with tamarisk is the same, regardless of tamarisk density, and the impacts of tamarisk varies among sites (Stromberg and Chew 2002, Stromberg *et al.* 2009). Invasion implies high abundance of a particular problematic species, and although this can be easily measured in the field (and is visually obvious), some have argued that exotic species have been too quickly “demonized” or “vilified” as “invasive” before their effects on ecosystems are fully understood (Stromberg and Chew 2002, Gurevitch and Padilla 2004, Borrell 2009, Stromberg *et al.* 2009, Davis 2011). The native vs. exotic paradigm has started shifting, and scientists continue to focus on quantifying the biological impacts of particular species (Chew and Hamilton 2010, Thompson and Davis 2011) to inform management practices that positively influence the ecosystem's health, based

¹ The authors thank Anastasia Stolz for her confocal photos of *L. maackii* and her *P. serotina* images and to Meg Maloney and Erin Rowekamp for their photos of *Anaxyrus americanus* and *T. migratorius*. This work was supported in part by the Office for Graduate Academic Affairs, University of Dayton, through the Graduate Student Summer Fellowship Program, and by the National Science Foundation (DEB 1352995).

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doi: 10.3159/TORREY-D-15-00049.1

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Received for publication September 1, 2015, and in revised form December 28, 2015; first published August 1, 2016.

on measured biological processes (Borrell 2009, Stromberg *et al.* 2009).

Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder.) is a highly successful invasive shrub in the eastern deciduous forest. Concern over this species is widespread and, in fact, legal limitations exist in some states (USDA 1999). Initial research on this species provided an outstanding background on the invasion biology of *L. maackii* (Luken 1988, Luken and Goessling 1995, Luken *et al.* 1995, Hutchinson and Vankat 1998, Deering and Vankat 1999, Gould and Gorchoff 2000). Since then, an extensive body of empirical evidence has been developed that documents this plant's (a) suite of invasive traits, (b) success as regulated by landscape characteristics, and (c) significant impacts at multiple ecological scales. This burgeoning scientific literature makes *L. maackii* an ideal species to serve as a model of invasion impact; however, no recent consolidation of the empirical evidence has, to our knowledge, been made.

In this article, we synthesize the available literature to provide a framework for understanding the ecological effects of *L. maackii* and to help direct future research and management practices. We begin by describing how anthropogenic activities and the life-history traits of *L. maackii* contributed to its invasion success in the USA. We then summarize findings from empirical studies that identify key traits that regulate the invasion of *L. maackii* into vulnerable habitats and describe the effects this invasive plant has at various ecological scales. We end by connecting *L. maackii* to invasion ecology theories and identify directions for future research that will strengthen and advance plant invasion biology.

***Lonicera maackii* Advantageous Life-History Traits.** DISPERSAL MECHANISMS. Long-distance dispersal and propagule pressure are key characteristics that contribute to the success of invasive plant populations (Gosper *et al.* 2005, Davies and Sheley 2007). For example, Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus) propagule pressure was found to be 556.6 and 144.5 plants/m² in riparian and upland forests, respectively (Eschtruth and Battles 2011). Camphorweed (*Heterotheca latifolia* Buckley) dispersal was found to be related to wind patterns in the Georgia piedmont area (USA), with expansion increasing at a rate of 4.8 km/yr (Plummer and Keever 1963). Arguably, anthropogenic activities—especially

during the industrial revolution and globalization eras—have been the most effective dispersal agents, spreading invasive weeds across oceans and continents (Meyerson and Mooney 2007). The initial introduction of common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) to the USA is believed to have occurred at coastal ports along the Atlantic ocean, with dispersal of this invasive promoted by the use of ship ballast to fill marsh sites used for railroad development (Saltonstall 2002). High propagule pressure combined with long-distance dispersal vectors and anthropogenic activities are a potent combination for the success of invasive plants.

Lonicera maackii is a good model of long-distance dispersal and abundant propagule production in invasive plants. These shrubs have large fruiting events (Fig. 1a) and produce seeds that can germinate in various light, temperature stratification, and soil conditions (Luken and Goessling 1995, Hidayati *et al.* 2000). We have also documented the presence of *L. maackii* berries submerged in streams with and without *L. maackii* in the riparian forest (Fig. 1b; R.E.M. and R.W.M., personal observation)—suggesting stream corridors are vectors for the spread of *L. maackii* propagules. Bartuszevige and Gorchoff (2006) found some native birds (*e.g.*, *Turdus migratorius*; American robin) eat and disperse viable *L. maackii* seeds *via* defecation. Castellano and Gorchoff (2013) found that 68% of *L. maackii* seeds were still viable after passing through the intestinal system of *Odocoileus virginianus* (white-tailed deer). Although the fruits of this species are a poor source of nutrition for wildlife (Ingold and Craycraft 1983), these animals contribute to the long-distance dispersal of *L. maackii* and may specifically support dispersal to edge habitats (Bartuszevige and Gorchoff 2006, Castellano and Gorchoff 2013).

RAPID GROWTH AND ENVIRONMENTAL PLASTICITY. Rapid growth and plasticity in response to changing environmental conditions are characteristic traits of successful invasive species. For instance, mile-a-minute (*Polygonum perfoliatum* L.) is an invasive Asian vine well known to grow quickly, as indicated by its common name (Oliver 1996). Fogarty and Facelli (1999) demonstrated the invasive European shrub Scotch broom (*Cytisus scoparius* (L.) Link) grows faster than, and successfully outcompetes, South Australian natives varnish wattle (*Acacia verniciflua* A.



FIG. 1. *Lonicera maackii* fall fruit production in (a) terrestrial, and (b) stream-run habitats. (c) Freeze-resistant leaves in mid-December 2009, and (d) senesced leaf litter in a headwater stream in southwestern Ohio, USA. Photos taken by R.E.M.

Cunn), myrtle wattle (*Acacia myrtifolia* (Sm.) Willd.), and beaked pincushion tree (*Hakea rostrata* F. Muell. Ex Meisn.). A Hawaiian study that surveyed more than 60 invasive and native plants found that invasives spent less energy producing leaves and had greater specific leaf area, CO₂ assimilation, and N and P levels than natives did (Baruch and Goldstein 1999). These results also indicate that invasive plants have phenotypic plasticity, which, in turn, may facilitate their success in novel habitats. Invasive plants are commonly thought to grow faster than native weeds do, this trait is usually accompanied by the plant's ability to use resources well, with greater phenotypic and genetic plasticity than natives have (Daehler 2003).

Lonicera maackii has a highly competitive growth pattern, which is an important phenotypic characteristic that helps facilitate its success in new habitats. This woody shrub produces numerous stem shoots and grows rapidly as an immature stem, then shifts resource allocation toward height growth and reproduction in its mature stage

(Deering and Vankat 1999). When upright stems are clipped, they resprout readily (Luken and Mattimiro 1991, Deering and Vankat 1999), which adds to this plant's already "bushy" appearance and contributes to a dense *L. maackii* canopy that decreases light availability to the herb layer. This plant is also known to exhibit growth plasticity in different habitats (Luken *et al.* 1995, 1997b). Compared with spicebush (*Lindera benzoin* (L.) Blume), *L. maackii* was found to successfully use a range of light levels (1, 25, and 100% of full-sun photosynthetic photon flux density) more effectively for growth and photosynthesis and to exhibit higher branch plasticity and stomatal density (Luken *et al.* 1997b). Seedling establishment can occur in a variety of light conditions, and shrubs located in open habitats produce significantly greater numbers of fruits than do those in shaded habitats (Luken and Goessling 1995, Luken and Thieret 1996, Lieurance 2004). The net primary productivity and aboveground biomass of *L. maackii* in open, high-sunlit habitats are substantially greater compared with shrubs located in low-

light woodland communities (Luken 1988, Lieurance 2004). The unique growth plasticity of *L. maackii* leaves and branches across light environments provides this shrub a competitive edge in a variety of habitats.

PHENOLOGY. Invasive plant species' phenologies have been shown to vary, compared with natives in the invaded habitat. Japanese barberry (*Berberis thunbergii* DC.), an invasive in the eastern deciduous forest, leafs out nearly 1 mo earlier than do native shrubs and demonstrates significantly greater photosynthetic capacity than native plant species do (Xu *et al.* 2007). An invasive biennial herb, garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande), has a competitive edge in early spring because its leaves emerge earlier than native herbs do and because it achieves high photosynthetic rates (Myers and Anderson 2003). Tree-of-heaven (*Ailanthus altissima* (P. Mill.) Swingle) is another invasive plant that leafs out in early spring, stores high concentrations of photosynthate in its leaves and stems, and is efficient at photosynthesis, making this plant highly competitive early in the growing season (Fryer 2010). A combination of early leaf emergence and efficient photosynthetic processes are important characteristics that promote the success and spread of invasive plant species.

Lonicera maackii has an extended growing season in comparison with other plants. Leaf development and expansion occurs 2 to 3 wk earlier, and the final leaf abscission is later than native species (McEwan *et al.* 2009a). Another competitive edge is that the leaves are freeze resistant and are still present on shrubs during early winter (Fig. 1c; McEwan *et al.* 2009a). As stated earlier, *L. maackii* propagule production is copious in the fall, and berry formation begins in early fall and will stay attached well into winter (R.E.M. and R.W.M., personal observation; Fig. 1a). Massive flower production occurs in midspring (Luken and Thieret 1996), and these flowers are a resource for pollinators (Goodell *et al.* 2010, McKinney and Goodell 2011). The combination of previously described growth characteristics and phenology gives *L. maackii* a competitive edge that increases its ability to outcompete native flora.

ALLELOPATHY AND RESISTANCE TO HERBIVORY. Some invasive plant species have been shown to exhibit biochemical effects on predators through the production of allelochemicals (Theoharides

and Dukes 2007). These chemicals are secondary plant compounds that typically suppress the growth, survivorship, and reproductive capabilities of competitors (Hiero and Callaway 2003). A meta-analysis of common invasive plants in China found 75% of the most noxious invasive weeds displayed evidence of allelopathic effects (Ni *et al.* 2012). Stinson *et al.* (2006) found evidence that the antifungal phytochemistry of *A. petiolata* can indirectly disrupt the mutualistic relationship between hardwood trees and mycorrhizal fungi, which can result in a reduction of tree-seedling regeneration in forest communities. Allelochemicals also affect microbial communities (Callaway and Ridenour 2004), suggesting invasive plants may alter those communities and nutrient cycling in terrestrial and aquatic systems.

A series of studies were conducted that established evidence of the *L. maackii* allelopathic effects on plants. Cipollini *et al.* (2008c) identified 13 secondary metabolites present in *L. maackii* leaves and demonstrated that luteolin and apigenin derivatives were the main allelopathic chemicals present in leaf extracts. *Lonicera maackii* root and shoot extracts have been shown to reduce germination of several native herbaceous plants, including jewelweed (*Impatiens capensis* Meerb.), and tall thimbleweed (*Anemone virginiana* L.) (Dorning and Cipollini 2005, McEwan *et al.* 2010, Cipollini and Flint 2013). McEwan *et al.* (2010) also demonstrated *L. maackii* leaf and fruit extracts had differential effects on four grass and forb species. *Lonicera maackii* fruit extracts suppressed all forb and grass seed germination in tall fescue (*Festuca arundinacea* Schreb, known synonym, *Schedonorus arundinaceus*), a dwarf white impatiens hybrid (*Impatiens walleriana* Hook. f. known synonym buzzy lizzy), garden coreopsis (*Coreopsis lanceolata* L.), and Kentucky bluegrass (*Poa pratensis* L.), whereas leaf extracts only suppressed seed germination of *I. walleriana*. Other experimental studies have focused on the effects of *L. maackii* extracts on the morphology, fecundity, reproduction, and growth on Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.) (Cipollini and Dorning 2008, Cipollini *et al.* 2012). Mouse-ear cress grown in *L. maackii*-conditioned soils exhibited decreased survivorship and an 11-day delay in flower production; however, seed production and mature leaves were larger and more abundant compared with those grown in unconditioned soils (Cipollini and Dorning 2008). Schradin and

Cipollini (2012) conducted a study to identify positive or negative feedbacks on *L. maackii* growth compared with the native northern bush honeysuckle (*Diervilla lonicera* Mill.) grown in different soil types and to determine whether growth patterns were due to soil abiotic or biotic conditions. Soil type (sandy and loamy) and conditioning and soil biota influenced the sign and strength plant-soil feedbacks. For example, *L. maackii* grew approximately two times more in its own conditioned, sandy soil (*L. maackii*-conditioned) compared with unconditioned soil, resulting in a positive feedback. Soil sterilization resulted in negative feedback, decreasing *L. maackii* growth in sandy soil. Alternatively, there was negative feedback on *D. lonicera* growth when grown in its own soil, with feedback effects neutralized when the soil was sterilized. Cipollini *et al.* (2012) also conducted a study to determine whether *L. maackii* and the invasive herb *A. petiolata* had similar allelopathic effects on *A. thaliana*. Results indicated that *L. maackii* leaf extracts reduced reproduction and growth of *A. thaliana*, whereas there were few effects from *A. petiolata*. Bauer *et al.* (2012) cautioned that allelopathic impacts are dependent on context, based on their field study, which suggested soil microorganisms and different native species are important factors that influence net allelopathic effects. These collective findings suggest the chemistry of *L. maackii* can have an effect on native plant communities, and strong evidence suggests it has allelopathic effects in some experimental settings; however, more research is needed to understand how allelopathic effects are manifested in the invasion biology of *L. maackii* in the field.

Evidence suggests that *L. maackii* has some traits that confer resistance to herbivory in its introduced range. McEwan *et al.* (2009b) investigated the antiherbivory potential of *L. maackii* on the invasive generalist gypsy moth caterpillar (*Lymantria dispar*; Erebidae). Caterpillar relative consumption and growth rates were significantly reduced when provided with only *L. maackii* as a food resource. The development time of the caterpillars was also inhibited when fed *L. maackii*, and all larva died before molting to the next stage. Cipollini *et al.* (2008c) found indications that the moth generalist beet armyworm (*Spodoptera exigua*; Noctuidae) had reduced feeding when given food sources made with *L. maackii* leaf

extracts compared with control food. Lieurance and Cipollini (2013a) conducted a study to identify how juvenile *L. maackii* shrubs responded to herbivory under conditions of environmental stress. They found that, at low light and nitrogen levels, *L. maackii* tolerance and resistance to herbivory was still high. These findings suggest *L. maackii* has strong resistance to natural predators, which may be another competitive strategy for this invasive species.

***Lonicera maackii* Invasion Effects at Various Ecological Scales.** EFFECTS ON PLANT COMMUNITIES. As invasive species encroach and proliferate in habitats, they modify substrate, resources, and ecosystem processes, which can result in substantial changes in plant and animal communities taxonomically and functionally (Randall 1996, Shea and Chesson 2002, Vilà *et al.* 2011). Empirical evidence suggests *L. maackii* invasion has substantial negative impacts on native plants. Forests with this invasive shrub have significantly less herb fecundity, fitness, and growth (Gould and Gorchov 2000, Miller and Gorchov 2004). Collier *et al.* (2002) found that herb abundance and richness significantly decreased under *L. maackii* shrubs compared with away locations and with stands that had longer *L. maackii* residence times. *Lonicera maackii* exhibited strong aboveground competition, where removal of its shoots increased seedling and herbaceous growth (Gorchov and Trisel 2003), survivorship (Cipollini *et al.* 2008a, Gorchov and Trisel 2003), and species richness (Musson and Mitsch 2003). The presence of *L. maackii* shrubs may also decrease recruitment of secondary forests because native seedlings experience greater herbivory because of the lack of protective herbaceous cover under *L. maackii* shrubs (Meiners 2007). White *et al.* (2014) found when *L. maackii* abundance increased in riparian zones, native tree seedling and sapling densities decreased. Invaded forests are predicted to experience alterations in species interactions and species composition, ultimately affecting community structure, function, and successional trajectories (Hutchinson and Vankat 1997, Luken *et al.* 1997a, Hartman and McCarthy 2008).

ANIMAL COMMUNITY IMPACTS. Effects of invasive plants on animals are an important motivating factor for managers of natural areas and for the public. Pyšek *et al.* (2012) found nearly 70% of studies reported nonnative invasive species vegetation

negatively affected animal communities. Most invasive plants are pollinated by generalists, which can affect native plant-pollinator mutualistic relationships (Richardson *et al.* 2000, Traveset and Richardson 2006). For example, ornamental jewelweed (*Impatiens glandulifera* Royle), an Asian invader in central Europe, attracts native bee pollinators because its nectar is more nutrient rich than that of the native flowers, resulting in decreased fitness and abundance for the native flowers (Chittka and Schürkens 2001). Ballard *et al.* (2013) found arthropod abundance, biomass, and richness was substantially reduced on nonnative plants compared with native plants, suggesting nonnative plants may affect food resources (e.g., arthropods) that support higher trophic levels. These studies highlight the importance of research on invasive plant impacts on animal communities.

Lonicera maackii has substantial effects on food resources for fauna, resulting in alterations in food-web dynamics and disease-vector population dynamics. Goodell *et al.* (2010) found *L. maackii* serves as a resource for pollinators and was related to increased pollinator visits and pollen deposition of the native herb largeleaf waterleaf (*Hydrophyllum macrophyllum* Nutt.) despite *L. maackii* shading effects (McKinney and Goodell 2011). Alternatively, McKinney and Goodell (2010) found spotted geranium (*Geranium maculatum* L.) pollination visits and seed set were reduced in the presence of *L. maackii*, suggesting *L. maackii* has differential impacts on pollinators. Loomis *et al.* (2014) found spider taxa and guilds were more abundant in honeysuckle-present plots, with more than double the vertical colonization of spiders compared with honeysuckle-absent plots, suggesting the complex branch architecture of *L. maackii* is important for spider communities. However, Buddle *et al.* (2004) reported ground-dwelling predator spider communities were less diverse in narrow riparian forests and hedgerows compared with wider forests buffers because of decreased habitat complexity and ground cover, which the authors suggested may have been due to the presence of *L. maackii* in these habitats. In a similar study, Loomis *et al.* (2014) found other arthropod orders (e.g., Diptera, Hymenoptera, Coleoptera) were more diverse and vertically covered more shrub area in honeysuckle-present plots than honeysuckle-absent plots. Christopher and Cameron (2012) found *L. maackii* invasion did not affect arthropod community diversity; howev-

er, invaded plots supported greater Acari (mites and ticks) abundance than did noninvaded plots. These studies demonstrate *L. maackii* has differential effects on arthropod communities, influencing resources and habitat substrate for arthropod use.

Lonicera maackii can also have consequences on human-related disease vectors. This shrub has been demonstrated to affect *Ochlerotatus triseriatus* (known synonym: *Aedes triseriatus*; Culicidae), which is the disease vector for the La Crosse encephalitis virus (Conley *et al.* 2011). In fact, Conley *et al.* (2011) found the oviposition of this disease-vectoring mosquito decreased with *L. maackii* density, suggesting *L. maackii* alters the landscape by decreasing the amount of habitat (e.g., tree holes) available for oviposition. A different study found *L. maackii* may be a facilitator of the West Nile Virus mosquito vector *Culex pipiens* (Culicidae; Shewhart *et al.* 2014). Mosquito eggs exposed to *L. maackii* leaf and flower leachates had the highest larval survivorship compared with native leaf leachates, and only larvae exposed to *L. maackii* leachates reached adulthood (Shewhart *et al.* 2014). In a study observing the effects of *L. maackii* on tick-borne diseases, it was found white-tailed deer visited *L. maackii*-invaded areas more frequently, which supported a greater number of lone star ticks (*Amblyomma americanum*) that were infected with a bacterial pathogen from the ehrlichiosis group (*Ehrlichia* spp.) compared with areas in which *L. maackii* was removed (Allan *et al.* 2010). These studies suggest *L. maackii* may affect mosquito- and tick-vector habitats and population dynamics, ultimately affecting the incidence of human disease.

Lonicera maackii invasion across the forest-to-urban gradient has substantially affected the survivorship of avian species fledglings and the nesting-habitat availability (Borgmann and Rodewald 2004, Rodewald 2009, McCusker *et al.* 2010, Rodewald *et al.* 2010). Forests with dense *Lonicera* spp. invasion had increased densities of understory bird species (e.g., *T. migratorius*), especially for overwintering birds, when *Lonicera* spp. fruit production was high; however, densities of upper-canopy birds (e.g., *Contopus virens*, eastern wood-pewees) decreased in these forests (McCusker *et al.* 2010). Nest predation is one of the most important threats to avian fledgling success; therefore, it is important for birds to

select appropriate nesting habitats (Martin 1992). Borgmann and Rodewald (2004) found avian nest success of *T. migratorius* and *Cardinalis cardinalis* (northern cardinal) was lower in invasive *Lonicera* spp. and multiflora rose (*Rosa multiflora* Thunb.) locations along an increased urban gradient compared with native woody species. Rodewald (2009) discovered an increase in *Empidonax vireescens* (Acadian flycatcher) brood parasitism was positively related to the number of stems around the nest. Stems were associated with *L. maackii* invasion, suggesting its “bushy” growth pattern creates perching sites for brown-headed cowbirds (*Molothrus ater*) to view nests, increasing opportunities for brood parasitism to occur. Rodewald *et al.* (2010) suggest *L. maackii* presence results in an ecological trap for avian species. *Lonicera maackii* is suspected to be an ephemeral ecological trap for *C. cardinalis* because of its unique leaf phenology. Birds may preferentially build nests in *L. maackii* shrubs to hide nests from predators because of the early leaf out this plant exhibited in the spring compared with native plants; however, *L. maackii* shrubs lack the habitat complexity needed for nesting sites, which, in actuality, makes nests more susceptible to predation and results in a decrease in overall bird annual production (Rodewald *et al.* 2010). Research has yet to identify if *L. maackii* influences bird plumage color, an important trait for mate selection; however, a study conducted by Witmer (1996) found that *E. vireescens* tail bands change from yellow to orange when Morrow’s honeysuckle (*Lonicera morrowii* A. Gray) fruits were consumed. These studies indicate *L. maackii* shrubs provide poor habitat for avian fauna, creating an ecological trap that reduces avian success.

The invasion of *L. maackii* can also initiate behavioral changes in animals, resulting in alterations in foraging behavior and predation risk. *Peromyscus leucopus* (white-footed mouse) was found to increase in risky behavior (*e.g.*, foraging) in *L. maackii* stands (contingent upon food availability and moon light), most likely because of the high canopy cover *L. maackii* provides in the shrub layer (Mattos and Orrock 2010). Similar findings were observed for other nocturnal mammals (*e.g.*, opossums and raccoons), with mice preferring to forage under *L. maackii* shrubs on cloudless nights (Dutra *et al.* 2011). Rodent granivores also preyed on *L. maackii* seeds more

than they did native roughleaf dogwood (*Cornus drummondii* C.A. Mey.) during the spring (Mattos *et al.* 2013). These studies indicate some granivores and mesopredators may be positively influenced by the presence of *L. maackii*; however, more research is needed to identify how the presence of this shrub may influence behavior.

There has been some research related to how *L. maackii* may mediate amphibian communities. Watling *et al.* (2011c) investigated how invaded *L. maackii* plots in a deciduous forest altered the understory microclimate (temperature and humidity) and amphibian community. Plots invaded by *L. maackii* had a lower mean daily temperature and amphibian species richness and evenness and experienced a shift in the amphibian community composition. In a study focused on the interaction of predators and *L. maackii* chemistry on amphibian larvae, artificial pools were created in invaded and noninvaded plots (Watling *et al.* 2011b). Pools were lined with soil that was or was not chemically influenced by *L. maackii* growth and allowed to fill up with natural rain water. It was found that *Anaxyrus americanus* (American toad) larvae development was significantly faster in pools containing leaf litter and soil from *L. maackii*. Hickman and Watling (2014) also found *A. americanus* tadpoles exhibited increased risk-prone behaviors, such as increased surfacing and swimming behavior in *L. maackii* leachate, regardless of the presence of predator chemical cues. These findings indicate *L. maackii* chemically alters amphibian habitat, indirectly altering risk-prone behavior and making these animals more susceptible to predators.

Odocoileus virginianus is an important ungulate known to reduce tree seedling and herbaceous regeneration (Tilghman 1989, Rooney and Dress 1997), forest habitat structure (McShea and Rappole 1992, Fuller 2001), and food-web interactions (Rooney and Waller 2003). Several studies have indicated there is an important relationship between *L. maackii* and *O. virginianus*. Deer are known to eat *L. maackii* berries, and Castellano and Gorchov (2013) found 68% of seeds were still viable after passing through the deer gut, suggesting this ungulate can be an important dispersal vector of *L. maackii*. Christopher *et al.* (2014) demonstrated both *L. maackii* presence and *O. virginianus* browsing decreased annual and spring perennial abundance. A *L. maackii* × *O. virginianus* interaction effect revealed *O. virginianus*

reduced perennial abundance regardless of *L. maackii* presence or absence. In a study examining the interactive effect of *L. maackii* and *O. virginianus* on litter arthropod communities, no interactive effect was found on arthropod diversity and total abundance, but there was a significant interaction effect on the abundance of Acari (Christopher and Cameron 2012). *Lonicera maackii* led to a decrease in *Aranea* spp. (orb-weaver spiders) abundance, whereas there was an increase in Acari abundance, suggesting *L. maackii* and deer may have indirectly affected arthropod communities (Christopher and Cameron 2012). Future research is needed to understand how the interactive role of *L. maackii* and *O. virginianus* can affect higher trophic levels and ecosystem processes.

MICROBIAL COMMUNITY IMPACTS. Invasive species affect soil and aquatic microbial communities, which are crucial to organic matter processing and nutrient cycling, resulting in alterations in ecosystem processes and function (Kourtev *et al.* 2002, Hawkes *et al.* 2005, Gessner *et al.* 2007, Claeson *et al.* 2014). Invasive plants tend to support different microbial communities, when compared with native plants, coupled with unique leaf characteristics (*e.g.*, increased nitrogen), which result in alterations in decomposition and nutrient transformation. Arthur *et al.* (2012) reported *L. maackii* leaf-litter breakdown was five times faster, had greater nitrogen, and less lignin concentrations than native white ash (*Fraxinus americana* L.) and hickory *Carya* Nutt. spp. Through the decomposition process, *L. maackii* leaf litter maintained microbial communities that were distinguishable from the community present on native species (Arthur *et al.* 2012). Ali *et al.* (2015) found that *L. maackii* leachate added to sterilized soil caused a 1.5-fold increase in mycorrhizal infection of *I. capensis* compared with sterilized soil, generally increasing *I. capensis* growth; however, when leaf extracts were added to live soil, there was a decrease in mycorrhizal infection of *I. capensis* and overall growth. In a plant-soil feedback study that examined changes in arbuscular mycorrhizal fungi abundance associated with invasive species, *L. maackii* reduced arbuscular mycorrhizal fungi on native plant roots indirectly *via* soil legacy effects and directly when grown in conjunction with *L. maackii* (Shannon *et al.* 2014). These findings suggest *L. maackii* leaves support unique microbial communities and leachate alters soil

communities, affecting ecosystem function and processes. Further research is needed to fully understand how these microbial effects may manifest as alterations of ecosystem function.

***Lonicera maackii* Invasion and Landscape Ecology.** Plant species invasions have been strongly linked to land use and characteristics of the landscape matrix in which the potentially invadable habitat is embedded (Hutchinson and Vankat 1998, Bartuszevige *et al.* 2006, Johnson *et al.* 2006). For instance, Johnson *et al.* (2006) reported a relationship between invasive species colonization and site features such as soil pH. Edge effects can also strongly influence resource availability within a given site. Bartuszevige *et al.* (2006) and Yates *et al.* (2004) found the amount of edge in the landscape surrounding habitat patches was a strong determinant of invasion and small forest patches are susceptible to edge effects well into their interiors. Intensive land use is well-known to have a lasting influence on the vegetation composition of forests (Bellemare *et al.* 2002, Foster *et al.* 2003), including the facilitation of invasive species establishment (Johnson *et al.* 2006). Moreover, if the historical land use creates an “extinction debt” of native species (Vellend *et al.* 2006), invasive species may exploit the resources that were made available in this “empty niche” (Hiero *et al.* 2005).

Lonicera maackii is a good model species for understanding and demonstrating the landscape ecology of plant invasion. Landscape features have been shown to influence the invasion biology of this species, and anthropogenic features are particularly important. For instance, Bartuszevige and Gorchov (2006) and Hutchinson and Vankat (1997) both demonstrated this species’ presence in forest patches was positively related to the distance to the nearest town. White *et al.* (2014) found *L. maackii* was indicative of areas that were more urbanized and less associated with forested areas. Borgmann and Rodewald (2005) found that *L. maackii* cover was best explained by an increase in urban land cover, and that *L. maackii* was more pervasive in urban forests compared with rural ones. Flory and Clay (2005, 2009) demonstrated the density and germination success of *L. maackii* increased closer to roadways and in forests at early and midsuccessional stages in central and southern Indiana, USA. In a study conducted in Louisville, KY, USA, *L. maackii* was shown to be less

successful in terms of stem density within forest patches located outside 10 km from the center of the city, compared with those within that distance (Trammell and Carreiro 2011). Pennington *et al.* (2010) found *L. maackii* was a dominant species in urban riparian systems, and McNeish *et al.* (2012, 2015) found that *L. maackii*-dominated riparian zones affected aquatic ecosystems, suggesting accumulated impacts at the watershed scale may be more severe.

***Lonicera maackii* Effects on Ecosystem Processes.** Ecosystems are open systems, susceptible to subsidies and allochthonous flows of resources from adjacent habitats (Baxter *et al.* 2005, Leroux and Loreau 2008). Invasive species can substantially alter ecosystem processes, such as nutrient cycling, decomposition, and energy transformation, within and across ecosystems. Kudzu (*Pueraria montana* (Lour.) Merr.) is an invasive, nitrogen-fixing legume found in the southeastern USA, which significantly increased net N mineralization, nitrification, and nitric oxide emissions from invaded soils by more than 100% (Hickman *et al.* 2010). Mineau *et al.* (2012) found the riparian invasive tree Russian olive (*Elaeagnus angustifolia* L.) substantially increased terrestrial organic-matter subsidies and retention of leaf organic matter in a stream system, resulting in an estimated 14% decrease in stream ecosystem efficiency (ratio of ecosystem respiration to organic matter input). In a meta-analysis of 199 articles presenting data related to invasive species effects, it was found that, although presence of invasive species tends to result in a decline of local native species, many plant invasions result in increased ecosystem function (Vilà *et al.* 2011).

Several studies have demonstrated *L. maackii* can affect a variety of terrestrial and aquatic ecosystem processes and functions. For example, Trammell *et al.* (2012) found total foliar biomass was 1.5 times lower in invaded *L. maackii* forests; however, *L. maackii* foliar biomass was 16 times greater in those plots, compared with less-invaded forests. This study suggests *L. maackii* may negatively affect production of native tree and shrub species. In a tree-ring study, Hartman and McCarthy (2007) found upper canopy trees had reduced radial growth in forested sites with dense *L. maackii* compared with noninvaded sites. *Lonicera maackii* affects organic matter processing and availability in terrestrial and aquatic habitats as

described *via* five leaf breakdown experiments in which *L. maackii* leaf breakdown was up to approximately four times faster than that of several native leaf species (Arthur *et al.* 2012, McNeish *et al.* 2012, Poulette and Arthur 2012, Trammell *et al.* 2012, Fargen *et al.* 2015). In an aquatic leaf-pack study, *L. maackii* leaves supported greater and a more-complex microbial growth, possibly because of the increased number of trichomes, which created a more-complex leaf-surface topography at the microscale, compared with black cherry (*Prunus serotina* leaves Ehrh.; Fig. 2; R.W.M., unpublished data). *Lonicera maackii* leaf deposition into streams is quite high (Fig. 1d; McNeish *et al.* 2015); therefore, there may be impacts on the scaling of aquatic leaf processing from the reach to the watershed level.

Lonicera maackii may also have substantial effects on water and nutrient transformation and availability. In a terrestrial leaf-pack study, *L. maackii* released nitrogen faster compared with sugar maple (*Acer saccharum* Marshall) leaf litter (Trammell *et al.* 2012). Poulette and Arthur (2012) found *L. maackii* increased N loss in mixed honeysuckle-hickory leaf packs up to approximately two times more than any other honeysuckle-native leaf-pack combination. A through-fall study demonstrated there was decreased through-fall volume under *L. maackii* shrubs and cation concentrations increased up to three times (McEwan *et al.* 2012). *Lonicera maackii* has been shown to have a higher transpiration rate compared with other shrubs, using an estimated 10% of ground and surface water (Boyce *et al.* 2011). Rapid uptake of surface water, coupled with high leaf N concentration and loss during decomposition, may support a positive nutrient feedback loop for *L. maackii* shrubs, resulting in an impact on forest production and water and nutrient transformation and availability in terrestrial and aquatic habitats.

Management and Restoration of *Lonicera maackii*-Invaded Habitats. DETECTION AND MANAGEMENT. Early detection of invasive species is an important proactive approach to management (Moody and Mack 1988). The USA National Invasive Species Council developed guidelines for early detection and rapid response of invasive species (USDOI 2015). Early detection allows for preemptive eradication of nascent foci before these small populations combine into

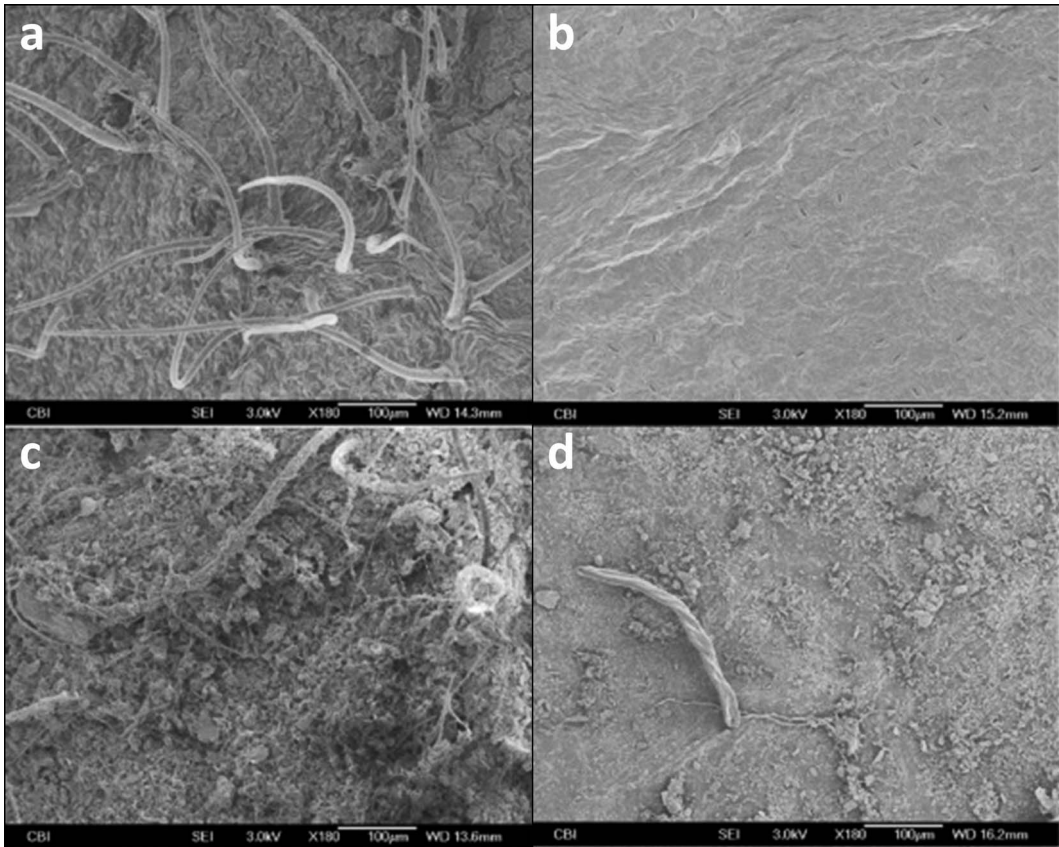


FIG. 2. Scanning electron microscope images of fresh (a) *L. maackii*, and (b) *P. serotina* leaves depicting trichome density and aquatic microbial and fungal growth on (c) *L. maackii*, and (d) *P. serotina* leaves anchored in a headwater stream for three days. Pilot study was conducted summer of 2010 with *L. maackii* and *P. serotina* leaf packs anchored in a small headwater stream for 7 days. Photos were taken by Anastasia Stolz.

larger populations and become more difficult to control (Moody and Mack 1988). Simberloff (2003) discusses the importance of early detection and rapid response of invasive species, highlighting several successes in the eradication of invasives, such as *Acacia karroo* (*Vachellia karroo* (Hayne) Banfi & Galasso) in Western Australia and tansy ragwort (*Senecio jacobaea* L.) in New Zealand. For example, killer alga (*Caulerpa taxifolia* (Vahl) C. Agardh) is a tropical alga that has invaded the coasts along several countries, including France, Italy, and Spain. This invasive alga was first sighted in a small coastal area outside Monaco in 1984; however, no management efforts were made until the population spread along thousands of hectares (Simberloff 2003). Wilfong *et al.* (2009) demonstrated that satellite Landsat 5 Thematic Mapper™ and Landsat 7 ETM+ imagery, coupled with the

unique, seasonal timing of leaf abscission of many invasive plants compared with native species, can be used to facilitate detection of invasive species. These studies highlight that early detection methods and preemptive efforts are pivotal in the quest for managing plant invaders.

A suite of studies have identified practical detection and treatment methods that are useful for management of *L. maackii*. Environmental remote-sensing images can be used to detect and map locations of invasive species in a cost-effective manner (Huang and Asner 2009). The extended leaf phenology of *Lonicera maackii* allows for detection in early spring and late fall using image differencing of satellite photos (Wilfong *et al.* 2009). A combination of images with fine spatial resolution, data from TM satellites, and ground truthing (field observations)

can potentially be one of the most-effective methods for early detection of *L. maackii* (Johnston *et al.* 2012, Shouse *et al.* 2013).

Several eradication studies have been conducted to identify the most effective way to manage *L. maackii*. Schulz *et al.* (2012) found seasonal stem cutting, followed by an application of 18% glyphosate, resulted in a 75–85% reduction of *L. maackii* individuals, whereas stem cutting, followed by spraying of regrowth shoots with 1% glyphosate approximately 40 days later, was less effective, resulting in up to 56% of *L. maackii* individuals killed. Rathfon and Ruble (2007) tested four removal-treatment methods: foliar application, streamline basal bark application, full basal bark application, and stump cutting with a chemical application. Foliar applications were effective in controlling 70–90%, whereas basal bark applications did not give consistent results and were thus considered unreliable. Stump cutting coupled with chemical application was most effective against larger *L. maackii* shrubs, which resulted in more than 90% control of *L. maackii* shrubs. In a study examining the rationale of 1 yr vs. annual treatment of *L. maackii*, annual treatment of *L. maackii* via stump cutting treated with glyphosate coupled with pulling plants was up to approximately six times more effective than a one-event treatment (Loeb *et al.* 2010). Hartman and McCarthy (2004) found that stump cutting with a treatment of glyphosate and stem injection with EZ-Ject Lance (EZ-ject, Omaha, NE) were both highly effective at killing *L. maackii* shrubs (> 94%). These collective studies suggest that best-management practices for *L. maackii* is an application a chemical herbicide immediately after stump cutting and repeating the process on an annual or semiannual basis; although, a more cost-effective method may be to use foliar applications.

In addition to human-induced efforts, there has been some natural dieback of invasive honeysuckle species reported in several states throughout the Midwest, USA (Boyce *et al.* 2014). In recent years, some *L. maackii* shrubs have exhibited dieback because of the presence of a honeysuckle leaf blight fungus (*Insolibasidium deformans*: Basidiomycete; Boyce *et al.* 2014). This fungus affects individuals of the *Lonicera* genus and is widespread throughout northcentral and northeastern USA and the UK (Riffle and Watkins 1986, Beales *et al.* 2004). Symptoms of *I. deformans* start in spring when lesions on new leaves develop,

eventually causing leaves to brown and premature senescence (Riffle and Watkins 1986, Beales *et al.* 2004). In a recent survey of *L. maackii* shrubs conducted around Cincinnati, OH, USA, 61.8% of *L. maackii* stems were dead, which was approximately 58% more than found in reports from 1989 (3.2%; Boyce *et al.* 2014). Thus far, there has been no studies, to our knowledge, on biocontrol agents for *L. maackii*; however, a study by Waipara *et al.* (2007) demonstrated herbivore and pathogen damage was low on Japanese honeysuckle (*Lonicera japonica* Thunb.) in New Zealand and suggested further research on natural enemies in the native *L. japonica* range is necessary for the development of biocontrol agents.

Lonicera maackii populations may be susceptible to forest litter and allelopathic effects from native plant species. Wilson *et al.* (2013) conducted a study to identify forest characteristics related to *L. maackii* invasion. Findings indicated increased oak (*Quercus* L.) leaf-litter depth was negatively associated with the presence of *L. maackii*. Rietveld (1983) found the allelochemical juglone, commonly found in the walnut (*Juglans* L.) family, had negative effects on *L. maackii*. In that study, varieties of herbaceous and woody plant species, including *L. maackii*, were exposed to different juglone concentrations (0–10⁻³ M). There was a significant decrease in *L. maackii* seed germination (92–43%), radical growth (8–0 mm), and shoot elongation (20–1 cm) when exposed to increasing juglone concentrations. These studies are important because they identified forest characteristics that may increase forest community resistance to *L. maackii* invasion.

LONICERA MAACKII MANAGEMENT IMPACTS ON FLORA AND FAUNA. Several studies have documented the effects on removal and managing *L. maackii* on plant and animal communities. Runkle *et al.* (2007) found that 7–8 yr after *L. maackii* removal, plant cover, tree seedling density, and species richness increased—suggesting removal of *L. maackii* can enhance plant ground cover and affect ecosystem productivity and function. Hartman and McCarthy (2004) conducted a removal and non-removal study to identify how removal of *L. maackii* affected native seedling survivorship. They found 3 yr after *L. maackii* removal, seedling survivorship was greater compared with plots in which *L. maackii* was present; however, seedling survivorship varied among genera. Removal of *L. maackii* shrubs also resulted in an increase in the

abundance of *P. leucopus*, an important generalist rodent (Shields *et al.* 2014). McNeish *et al.* (2015) found removal of *L. maackii* from the riparian zone of a stream significantly increased in-stream light availability, terrestrial organic matter contribution to the stream, and aquatic macroinvertebrate density, compared with a nonremoval stream reach, indicating management of *L. maackii* in terrestrial habitats can affect adjacent aquatic systems. In a similar study, Fargen *et al.* (2015) found removal of riparian *L. maackii* did not influence in-stream leaf-litter decomposition; however, *L. maackii* leaf-litter packs supported lower macroinvertebrate abundance compared with native *A. saccharum* litter packs.

Connections to Invasion Theory. Several theories have been developed to address how and why some nonnative species become overabundant, successfully outcompete natives, and eventually become classified as invasive. For example, the empty niche hypothesis (ENH) presumes a nonnative can become successful when there is open habitat for the organism to colonize, proliferate, and spread outside its native range (Shea and Chesson 2002). The enemy release hypothesis (ERH) details the idea a nonnative becomes invasive when a natural enemy (*e.g.*, specialist consumer) is not present in the new range, and thus, the nonnative has essentially escaped from its natural enemy (Keane and Crawley 2002, Colautti *et al.* 2004). The novel weapons hypothesis (NWH) states invasive plants may bring with them, into “recipient” communities, new biochemistries that provides an advantage, and through generations, this alteration may become selected for and increase in strength (Callaway and Ridenour 2004). Some invasive plants are known to exhibit increased allelochemical production outside their native range, which may serve as a “novel weapon,” providing a competitive edge against native species (Vivanco *et al.* 2004, Ni *et al.* 2012). The evolution of increased competitive ability theory postulates that, with the removal of natural enemies, an invasive plant will shift resources from defense to growth to improve its competitive ability (Blossey and Notzold 1995). Another major ecological theory—invasional meltdown—predicts that the success and establishment of one invasive species may facilitate and/or increase the establishment of other invasive species (Simberloff and Holle 1999,

Simberloff 2006). For example, the European buckthorn (*Rhamnus cathartica* L.) and the *Lumbricus terrestris* (European earthworm) may have cofacilitated one another in North America, and their coinvasion may have facilitated several other invasive pests and insects (Heimpel *et al.* 2010). These theories are often studied and considered separately; however, there is evidence that many of these theories may apply to single species, and the theories themselves are conceptually linked, which highlights the importance of exploring these theories in tandem (Hiero *et al.* 2005, Joshi and Vrieling 2005).

The invasion biology of *L. maackii* is a good model for understanding the overlap and interconnection of some important invasion theories. For instance, the success of *L. maackii* has been linked to both the NWH and the ERH. Several studies presented in the Forest Community Impacts and Resistance to Herbivory sections above suggested *L. maackii* may have allelopathic effects, inhibiting native plant germination, growth, and development and suppressing insect survivorship (Dorning and Cipollini 2005; Cipollini *et al.* 2008b, c; McEwan *et al.* 2009b, 2010). *Lonicera maackii* generally experiences low levels of arthropod herbivory (Lieurance and Cipollini 2012) but has been commonly observed to be browsed by *O. virginianus* (Castellano and Gorchoy 2013). Cipollini *et al.* (2008c) identified secondary compounds in *L. maackii* leachate that decreased insect herbivore consumption and native seed germination, suggesting allelochemistry may in part explain why *L. maackii* is so successful and lending support to the NWH. Lieurance and Cipollini (2013b) also studied the herbivory effects of the specialist North American honeysuckle sawfly (*Zaraea inflata*: Cimbicidae) and the generalist caterpillar *Spodoptera frugiperda* (fall armyworm: Noctuidae) on *L. maackii*, grape honeysuckle (*Lonicera reticulata* Raf.), blackhaw (*Viburnum prunifolium* L.), and *L. japonica* (Japanese honeysuckle Thunb.) in field and laboratory settings. *Lonicera maackii* had significantly less foliage damage and was not affected by the sawfly specialist, which preferred *L. reticulata* over *L. maackii* when given a choice (Lieurance and Cipollini 2013b). The generalist caterpillar fed equally on all *Lonicera* species, but, in laboratory assays, effects on *L. maackii* were more strongly observed (Lieurance and Cipollini 2013b). These findings lend support to the NWH and ERH because (a) *L. maackii*

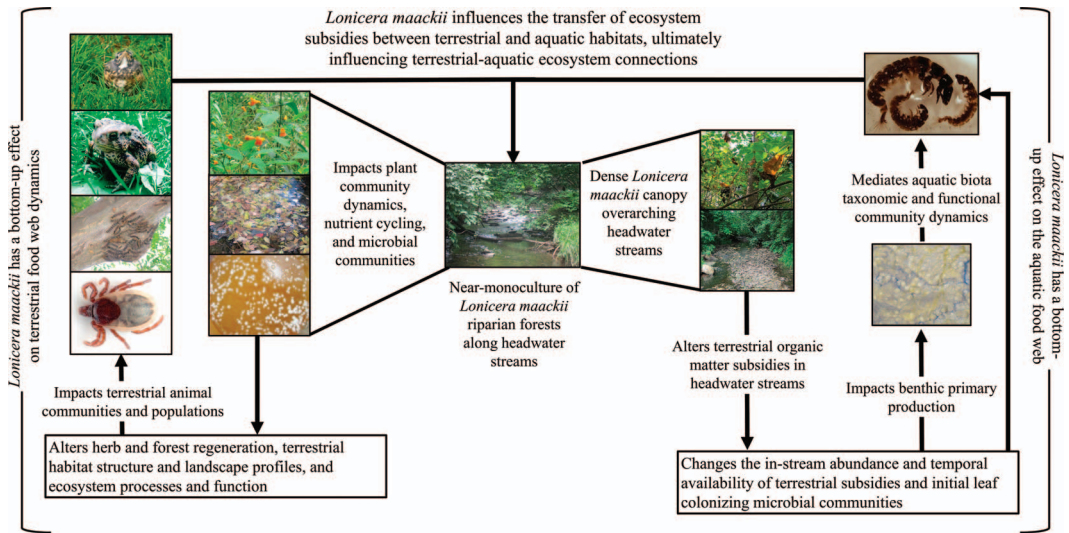


FIG. 3. Predictive framework for *Lonicera maackii* impacts across ecosystems at multiple ecological scales.

produces allelochemicals that negatively affect native plants and arthropods, (b) herbivory is quite low on *L. maackii*, and (c) this invasive can escape from specialist and generalist insect herbivores, which hinder native honeysuckle and confamilars. These findings also suggest strong potential for the evolution of increased competitive ability hypothesis, particularly given the rapid growth rate and phenotypic plasticity of *L. maackii*. Observations by the authors from forests in Ohio and Kentucky, USA, suggest invasional meltdown may also be occurring with *L. maackii* invasion because control sites often display a profusion of *A. petiolata* growth, and some areas of heavy invasion by *L. maackii* are underlain by an invasion of winter creeper (*Euonymus fortunei* (Turcs.) Hand.-Maz.).

Future Directions and Considerations. In this review, we have synthesized empirical literature that demonstrated the effects of *L. maackii* across various ecological scales, ecosystem processes and function, and restoration efforts. *Lonicera maackii* has been shown to (a) suppress local plant species survivorship, growth, and reproduction; (b) decrease primary productivity and enhance the ecosystem processes of decomposition and nutrient turnover; (c) increase risk-prone behavior and decrease reproductive success of certain animals; (d) provide needed protection from predators and supply seeds as a food resource for granivores; (e) provide support for human disease vectors; and (f) support high vertical diversity of certain arthropod

communities. These findings lend support to the hypothesis that *L. maackii* effects are complex and vary across ecosystems and multiple ecological scales (Fig. 3), suggesting this invasive has a diversity of impacts on species interactions and composition, community structure and successional trajectories, and ecosystem function and processes.

Lonicera maackii transforms aquatic and terrestrial ecosystems via alterations of terrestrial subsidies, habitat structure, community composition, and ecosystem function (Fig. 3). The presence of *L. maackii* along stream habitats (or potentially along other water bodies) resulted in a substantial change in the pool of resources in the aquatic system that support aquatic food webs and ecosystem processes (McNeish *et al.* 2015). Many aquatic macroinvertebrates have a terrestrial adult phase (*e.g.*, mosquitoes and blackflies), and impacts on the population dynamics of aquatic-insect life stages, which may result in a bottom-up effect on secondary production present in the terrestrial habitat, and serves as an important food resource for terrestrial vertebrates (Lounibos 2002, Baxter *et al.* 2005, Burdon and Harding 2008). Co-occurring with *L. maackii* impacts in aquatic systems are similar effects in terrestrial systems. *Lonicera maackii* alters plant community composition and microbial communities, affecting the pool of resources available in terrestrial systems, ultimately influencing amphibian, avian, and arthropod communities (Gould and Gorchov

2000; Miller and Gorchov 2004; Watling *et al.* 2011a, b; Loomis *et al.* 2014). Because of the presence of *L. maackii* along water bodies, we expect impacts as this invasive plant crosses the terrestrial-aquatic interface, which will have major implications on a watershed scale (Fig. 3). This framework of *L. maackii* impacts should be considered when managing for this invasive species, so that adjacent habitats and communities are not adversely affected.

The research synthesized in this review has assisted in developing a broad framework to explain *L. maackii* effects across ecological scales (Fig. 3) and has elucidated several avenues for future research. Several studies have suggested an allelopathic mechanism is in part linked to the success of this invasive plant; however, more work is necessary to determine direct and indirect effects on native plant and herbivore communities and to provide more evidence for the NWH and ERH. Restoration efforts have identified removal of *L. maackii* positively affects native plant communities, but it would be interesting to expand research efforts to understand how various management efforts (*e.g.*, cutting and removal *vs.* defoliation) affect resources that support animal communities. For example, McNeish *et al.* (2015) suggested *L. maackii* branch architecture is responsible for delayed and reduced availability of in-stream leaf-litter resources that serve as aquatic food and habitat substrates, which suggests cut and removal efforts may be more beneficial compared with defoliation methods for aquatic ecosystem health. Finally, a link has been identified between *L. maackii* and human disease vectors; however, very few studies have been conducted in this area. Continued emphasis on synthesizing effects of widespread species, such as *L. maackii*, is critical for building generalizable frameworks for invasion effects and guiding research and management efforts.

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