

A REVIEW OF IMPACTS BY INVASIVE EXOTIC PLANTS ON FOREST ECOSYSTEM SERVICES

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Abstract.—Many of our forest ecosystems are at risk due to the invasion of exotic invasive plant species. Invasive plant species pose numerous threats to ecosystems by decreasing biodiversity, deteriorating ecosystem processes, and degrading ecosystem services. Literature on Kentucky's most invasive exotic plant species was examined to understand their potential impacts on natural and semi-natural systems. This review suggests that many of the targeted species possess the ability to alter ecosystem processes and functions. However, the impacts on these services are still emerging, are often vague, and lack empirical data. Thus, further research on species-level impacts and the mechanisms facilitating the impacts of exotic plants on ecosystem services is sorely needed.

INTRODUCTION

Ecosystem services, defined as the complex interplay of conditions and natural cycles through which ecosystems sustain and fulfill humanity (Daily and others 2001), are essential to human well-being. Forest ecosystems play a vital role in performing a suite of processes and functions that produce resources for consumption and other uses. For example, forests play a critical role in delivering drinking water to more than 180 million people in the United States and support nutrient exchanges necessary for biological communities (Smail and Lewis 2009). Forests provide the pathways for water capture, transport, and evaporation as it circulates throughout various systems at multiple scales (Hornberger and others 1998). Forest-derived processes also serve integral functions in determining plant and animal community compositions by influencing light levels, soil conditions, nutrient availability, and physical structures (Boettcher and Kalisz 1990, Vitousek and others 1997, Smail and Lewis 2009). Furthermore, forests play globally important roles in influencing other large-scale ecosystem patterns and processes such as the carbon and nutrient cycles (Bowman and others 2009).

Infiltration of invasive exotic species (IES) into forested environments may disrupt forest ecosystem processes and functions by displacing native species (Collier and others 2002, Huebner 2003). In addition, species that become community dominants may alter environmental conditions and resource availability of market and non-market products and services (Gordon 1998). This disruption is accomplished when IES differ from native biota in specific species traits such as nutrient cycling, chemistry, and phenology (Ehrenfeld 2003). However, not all invading species are equal in their ability to alter larger-scale processes. It seems reasonable that IES with the ability to become community dominants will contribute the greatest alterations to existing ecosystem services (Gordon 1998). In view of the multitude of IES entering forest ecosystems, identifying which species pose the greatest threats is important when considering effective management schemes.

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Incorporating the ecosystem services approach into conservation management is becoming increasingly prevalent through better understanding of the connections between ecosystems and their associated products and processes (Patterson and Coelho 2009). While much effort has gone into the quantitative valuation of these goods and services, knowledge gaps persist in understanding how IES impact ecosystem services (Pejchar and Mooney 2009). A comprehensive analysis of existing literature may provide insight into how much we understand the impacts caused by IES on ecosystem services in eastern forests. Such an exercise could help ecologists, social scientists, and natural resource managers to discover hidden taxes on ecosystem services and could assist in developing effective IES management strategies (Webster and others 2006, Pejchar and Mooney 2009). In this paper we examined the extent and prevalence of the impact of IES on ecosystem services.

METHODS

To accomplish this goal, we synthesized peer-reviewed data on IES impacts on three targeted ecosystem services (regeneration, nutrient dynamics, and hydrology) and provided examples from the literature for extended discussion. Due to the large number of species that exist in the eastern forests, a comprehensive review of all IES requires tremendous time and effort. Thus we reviewed manuscripts concerning the 26 most detrimental IES, as identified by the Kentucky Exotic Pest Plant Council (KY-EPPC) (Table 1). These species are listed as the most severe threat to Kentucky because they possess the characteristics of invasive species and displace native vegetation. Many of these 26 species are documented as invasive in states containing central hardwood forests. Other species, such as *Lonicera japonica*, *L. maackii*, and *Alliaria petiolata* have become highly invasive in both disturbed areas and closed-canopy forests throughout much of the United States (Nuzzo 1999). We conducted literature searches on all 26 species to examine evidence for their ability or potential to alter ecosystem services. Examples of other species impacting targeted forest ecosystem services throughout different regions of the world were also provided.

Table 1.—Most severe invasive plants in Kentucky and their documented impacts on ecosystem processes.

Scientific Name	Common Name	Invasive Species Effects on Ecosystem Processes		
		Regeneration	Nutrient Dynamics	Hydrology
<i>Ailanthus altissima</i>	Tree-of-heaven	(Huebner 2003); (Gomez-Aparicio and Canham 2008)	(Gomez-Aparicio and Canham 2008)	--
<i>Alliaria petiolata</i>	Garlic mustard	(Hochstedler and others 2007; Meekins and McCarthy 1999; Stinson and others 2006)	(Rodgers and others 2008)	--
<i>Carduus nutans</i>	Musk thistle	(Floyd and others 2006)	--	--
<i>Celastrus orbiculata</i>	Oriental bittersweet	--	--	--
<i>Conium maculatum</i>	Poison hemlock	--	--	--
<i>Coronilla varia</i>	Crown vetch	(Brown 1995)	--	--

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(Table 1 continued)

Scientific Name	Common Name	Invasive Species Effects on Ecosystem Processes		
		Regeneration	Nutrient Dynamics	Hydrology
<i>Dioscorea oppositifolia</i>	Chinese yam	--	--	--
<i>Elaeagnus umbellata</i>	Autumn olive	(Orr and others 2005)	(Goldstein and others 2009; Orr and others 2005)	--
<i>Euonymus alatus</i>	Burning bush	--	--	--
<i>Euonymus fortunei</i>	Winter creeper	--	--	--
<i>Festuca arundinacea</i>	Kentucky 31 fescue	(Spyreas and others 2001; Tunnell and others 2004)	--	(Self-Davis and others 2003)
<i>Lespedeza cuneata</i>	Sericea lespedeza	(Brandon and others 2004)	--	--
<i>Ligustrum sinense</i>	Privet	(Morris and others 2002)	--	--
<i>Lonicera japonica</i>	Japanese honeysuckle	(Dillenburg and others 1993; Yurkonis and Meiners 2004)	--	--
<i>Lonicera maackii</i>	Bush honeysuckle	(Cipollini and Dorning 2008; Flory and Clay 2009; Hutchinson and Vankat 1997; Meiners 2007)	(Collier and others 2002; Demars and Boerner 1997)	--
<i>Lythrum salicaria</i>	Purple loosestrife	(Blossey and others 2001)	(Gutknecht and others 2006)	--
<i>Melilotus alba</i>	White sweet clover	(Wolf and others 2004)	(Wolf and others 2004)	--
<i>Melilotus officinalis</i>	Yellow sweet clover	(Van Riper and Larson 2009)	--	--
<i>Microstegium vimineum</i>	Japanese grass	(Adams and Engelhardt 2009; Baiser and others 2008; Horton and Neufeld 1998; Oswalt and others 2007)	(Ehrenfeld and others 2001; McGrath and Binkley 2009)	--
<i>Miscanthus sinensis</i>	Chinese silver grass	--	--	--
<i>Phragmites australis</i>	Common reed	--	--	--
<i>Polygonum cuspidatum</i>	Japanese knotweed	--	--	--
<i>Pueraria lobata</i>	Kudzu	--	--	--
<i>Rosa multiflora</i>	Multiflora rose	--	--	--
<i>Sorghum halapense</i>	Johnson grass	--	--	--
<i>Stellaria media</i>	Chickweed	--	--	--

RESULTS

REGENERATION

Sustainable timber production in the eastern United States depends upon continued regeneration of high-value tree species. Survival of tree seedlings is a necessary component because current seedling stock must mature to economically viable timber. Many native woody species are dependent upon mutualistic relationships with native plants, animals, and fungi for their growth and survival (Callaway and others 2008). Natural regeneration regimes are known to be altered by invading plant species that utilize various mechanisms to dominate understory environments and outcompete desired species for available resources (Hutchinson and Vankat 1997, Stinson and others 2006). Moreover, invading species may change disturbance regimes or resource supply rates, resulting in large, even cascading impacts (Adams and Engelhardt 2009).

Overall, 50 percent of the species listed as a severe threat by the KY EPPC have been documented to threaten regeneration through direct resource competition, altering resource availability, or a suite of other mechanisms (Table 1). For example, *Rosa multiflora* and *L. maackii* were shown to invade forest edges, openings, and disturbed understories by outcompeting native woody species, resulting in simplified biological communities (Meiners 2007). *L. maackii* was proven to have influenced landscape-level species composition by invading along forest-edge environments throughout a wide range of light environments (Hutchinson and Vankat 1998). In another study, results suggest that *Elaeagnus umbellata* utilizes allelopathy as a mechanism to impact the regeneration of several common successional species such as *Acer saccharinum*, *Populus deltoides*, and *Platanus occidentalis* (Orr and others 2005). This experiment showed the emergence of all three native tree species was suppressed when aqueous extracts derived from soil, leaf litter, and live leaves of *E. umbellata* were introduced. In Southern forests, *Microstegium vimineum* was shown to reduce native woody species regeneration by invading disturbed environments in moist forests (Oswalt and others 2007). In this study, regression models showed *M. vimineum* percent cover had a strong negative relationship with native woody species density. This species was shown to successfully invade areas with both low and high light conditions (Horton and Neufeld 1998) and responded positively to several harvest treatments (Oswalt and others 2007), making it a direct threat to woody species regeneration throughout the central hardwoods region and beyond.

Successful invasion into mesic temperate forests also appears to be facilitated by disequilibrium in native communities or the ability of invasive plants to disrupt existing ecological associations among native species (Stinson and others 2006). Most vascular plants form mycorrhizal associations with arbuscular mycorrhizal fungi (AMF), on which they are highly dependent (Smith and Read 2008). Invasive plants not dependent on such associations can invade sites and degrade AMF densities in the soil. *A. petiolata*, a nonmycorrhizal plant, was shown to suppress the growth of native tree seedlings by impairing native mycorrhizal mutualisms (Smith and Read 2008). This particular study provided empirical evidence that dominant native hardwood species, *A. saccharum*, *A. rubrum*, and *Faxinus americana* showed reduced growth and survival rates when grown in soils where *A. petiolata* had invaded.

While these examples illustrate that invasive plants can inhibit regeneration of several native woody species, knowledge gaps exist for many invasive exotic plants regarding their influence on regeneration processes. Research is needed on the following questions: 1) Which mechanisms yield the greatest alteration to community structure and regeneration regimes; 2) Which species exhibit what type of mechanism; and 3) Which species are capable of causing a large-scale ecosystem change?

NUTRIENT DYNAMICS

In total, only 25 percent of the species have been documented to alter nutrient dynamics (Table 1). Nutrient availability to primary producers is a key ecosystem function which appears to be sensitive to changes in the composition of plant communities (Mack and D'Antonio 2003). Invading species possessing specific traits capable of altering soil nitrogen (N) pools, as well as a suite of other soil conditions, are likely to influence soil processes (Corbin and D'Antonio 2004). Alterations to nutrient dynamics within soils may further drive species composition changes and affect net primary production, producing dramatic changes in biodiversity. Adverse ecological impacts on nutrient dynamics arise when IES occupy large areas or occur in high densities. Certain traits of exotic plants may cause alterations to the soil-based community or ecosystem-level processes by augmenting atmospheric N fixation or increasing rates of N losses (Corbin and D'Antonio 2004). Such soil alterations may favor fast-growing invasive species throughout a variety of environments. For instance, soils directly beneath *M. vimineum* were shown to contain elevated levels of pH and nitrification rates when compared to soils beneath the native *Vaccinium pallidum* (Ehrenfeld and others 2001). In this study, leaf litter from *M. vimineum* was shown to decompose at a rate different from that of surrounding native species, causing reduced N immobilization. *M. vimineum* populations were also shown to utilize low light levels to enhance carbon gain while combining small biomasses of N-rich roots and N-poor litter to change soil surface conditions (Horton and Neufeld 1998). Rodgers and others (2008) also suggested IES enhance invasibility by creating positive feedback cycles through soil alterations. By comparing various species compositions and soil horizon developments at sites in five northeastern forests, Rodgers and others (2008) reported *A. petiolata* consistently and significantly elevated N, phosphorus (P), calcium, and magnesium availability, and soil pH, in invaded plots. These apparent traits may be an important competitive advantage within undisturbed communities throughout deciduous forests, enabling ecosystem-level modifications in community structure.

Nitrogen-fixing is another trait that allows IES to invade and potentially alter ecosystem processes and services. The ability of *E. umbellate* to produce nonpoint source pollution by enhancing stream nitrate levels was documented by Goldstein and others (2009). This particular study examined the relationship between *E. umbellate* cover in a watershed and stream quality. *E. umbellate* is an N-fixing invasive shrub that has become naturalized in the eastern United States. Percentage of *E. umbellate* cover is positively correlated with mean stream nitrate concentrations. *E. umbellate* reached a critical density threshold in a watershed in southern Illinois, allowing it to produce watershed-scale impacts. This examination provides supporting evidence that ecosystem-level impacts from invasive exotic plant species are possible if species are present in critical abundance. Wolf and others (2004) observed lower nitrogen availability and mineralization in soil patches invaded by the N-fixing exotic *Melilotus alba* in montane grasslands in Colorado. Although this study was not conducted in eastern forests, these findings illustrate the potential impacts of N-fixing exotics.

Other studies provide additional support to the few examples identified for the targeted species in this study. For example, a study in New Zealand suggested that novel interactions between an invasive shrub, *Coriaria arborea*, and soil symbionts in floodplain systems produced soil alterations favorable to invaders and simplified communities (Bellingham and others 2009). The invasive shrubs were shown to alter soil N:P ratios, favoring invasion and limiting P available to native species. In another example, Jordan and others (2008) observed how three species of invasive grasses—*Euphorbia esula*, *Bromus inermis*, and *Agropyron cristatum*—modified soil microbiota by further invasion by conspecifics in the Great Plains region of North America.

Concern is growing over the impacts caused by IES on nutrient dynamics in soils. These examples offer

insight into how IES alter nutrient dynamics important for ecosystem function. Given the challenges that IES pose to ecosystems, it is important to investigate: 1) Which IES are capable of producing ecosystem-level changes in nutrient dynamics; 2) How long do these impacts last; and 3) will soil alterations be sustained even after the removal of IES?

HYDROLOGY

Forest hydrology cycles produce many diverse goods and services through a combination of multiple complex inputs and conditions (Hornberger and others 1998). This supporting ecosystem service often has no direct market value yet is vital to ecosystems worldwide (Wilson and Carpenter 1999). Examples of native plant species that alter hydrology through changes in evaporation rates (Breshears and others 1998), surface runoff (Lacey and others 1989), and water table levels (Jackson and others 2000) exist throughout the literature.

However, the existing studies that documented the impact of IES on hydrology are very limited. Out of our 26 targeted species, only *Festuca arundinacea* was documented for its impact on hydrologic systems. In this study *F. arundinacea* was compared with four other species and was shown to be more effective at reducing runoff volumes and increasing infiltration. Investigations into how IES may impact hydrology are uncommon, and those that do exist are mostly focused on areas dryer than eastern forests. For example, catchments invaded by *Eucalyptus* species in South Africa recorded flow reductions up to 22 percent, severely impacting downstream industries dependent on this resource (Le Maitre and others 2002). *Eucalyptus* tree species have higher net evaporation rates than natives in this region and extract more groundwater. Quantifying the water loss to South African industries justified spending millions of dollars on invasive management controls (Le Maitre and others 2002).

Since invasive herbaceous and woody plants often have different maximum rooting depths, they may influence underground water resources differently (Jackson and others 2000). Herbaceous plants generally have much shallower rooting depths than shrubs or trees in eastern forests (Canadell and others 1996). Therefore, herbaceous species invading forests could potentially have an effect on forest hydrological regimes if such species become prominent over large areas. Gaining specific knowledge of whether Kentucky's most severe invasive plant species can alter water resources will help to quantify their impacts on this resource. As invasive species expand in abundance and distribution, this information may become increasingly important in light of increases in future water resource demands.

Given the abundant stream channels and adjacent riparian environments found throughout the central hardwoods region, understanding what impacts IES may exert on these systems is crucial. Natural riparian zones are characterized as diverse, dynamic, and complex biological interfaces (Mulla 2003). They serve a myriad of roles as ecosystem regulators by controlling energy and material fluxes and by maintaining critical habitat (Naiman and Decamps 1997). Furthermore, riparian zones may be sensitive to environmental and biological change. While none of the targeted species are documented to disrupt these systems, they could potentially alter riparian processes and subsequent riparian functions. Several knowledge gaps need to be addressed regarding IES impacts on hydrology: 1) Which IES exhibit significant differences in water consumption; 2) Do IES with different water utilization rates produce measurable alterations to hydrologic regimes; and 3) Do IES alter riparian processes and functions?

DISCUSSION

Although numerous studies have attributed exotic plant invasions to losses in community structure and dominance, fewer report alterations to key ecosystem functions and processes. Identifying the mechanisms from which these impacts arise provides information for predicting which species are most likely to exert large impacts (Wilgen and others 1996, Levine and others 2003). Overall, our findings suggest insufficient data were available for many invasive species important to the central hardwoods region. Invasions to forest ecosystems may directly or indirectly alter the ability of forests to carry out important functions, leading to changes in plant community composition and structure that ultimately alter or disrupt ecosystem services.

This review revealed a suite of mechanisms by which invasive plants degrade ecosystem services by altering biotic and abiotic conditions. Forests in eastern North America are being rapidly invaded by myriad IES, which disrupt native understory and canopy species. Without clear empirical tests of the importance of their effects, the evidence for justifying management control efforts on many species may be insufficient. Further investigation into the mechanisms and densities necessary for ecosystem-level change is critical to understanding the impacts on ecosystem services and producing justifiable IES management schemes.

Invasive exotic species have been shown to alter, disrupt, and degrade many ecosystem services throughout the eastern United States and across the world. By invading intact forests, riparian zones, or disturbed habitats, they have the ability to alter the environmental and biological conditions around them, often leading to further invasions. As consumption of natural resources continues to rise, understanding how to minimize the expanding impacts of IES on resource development will be critical. Resources such as timber, water, food, and fibers are dependent on the natural conditions where they are produced.

Research assessing the impacts of IES on ecosystem services is still emerging and our understanding of the impacts to some ecosystem services is not fully developed. Further research on predicting factors that influence invasion, comparing invader and native traits, and evaluating environmental impacts is needed (Pejchar and Mooney 2009). Moreover, research is needed to assess large-scale replacement of plant functional types (e.g., herbaceous versus woody, N-fixing versus non-fixing species), which has the potential to alter regeneration, soil nutrient dynamics, and hydrology in forest ecosystems.

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