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RESEARCH ARTICLE

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Effects of Riparian Invasive Nonindigenous Plants on Freshwater Quantity and Ecological Functioning in Mesic Temperate Landscapes

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ABSTRACT: As invasive nonindigenous plants colonize streamside ecosystems, they can transform ecological functioning by replacing native species, altering interspecific interactions, and reducing biodiversity. As a result of the intimate relationship between the riparian areas and their associated freshwater ecosystems, alteration of the riparian community may be reflected in the freshwater ecosystem. Research conducted in arid climates repeatedly has demonstrated that invasive nonindigenous plants can reduce water quantity, but far fewer studies have investigated the effects on water quantity and aquatic ecosystem functions when nonindigenous plants invade mesic temperate riparian areas. We identified 35 studies published since 1981 documenting impacts to freshwater ecosystems in mesic temperate climates attributable to invasions of riparian areas by nonindigenous plants. These studies revealed impacts on water quantity and on ecosystem function related to water temperature, edaphic characteristics, and physical and chemical alteration in allochthonous inputs. However, our assessment of the results found great variability in hydrological and ecological responses, with the strongest evidence for changes to (1) the timing of allochthonous organic matter inputs, (2) organic matter decomposition rates in aquatic ecosystems, and (3) aquatic community structure. In addition, in watersheds densely colonized by nitrogen-fixing invasive species, stream eutrophication is likely to occur. Because of the variability in the existing research results, more studies need to be focused specifically on invaded mesic temperate riparian ecosystems. Furthermore, more research is needed to consider the impact of additional problematic plant species that have yet to be studied, the correlation between invasive plant density and aquatic ecosystem response, the relationship between the length of time a plant community has been invaded and the aquatic community's reaction, and if invasive plant management and native species reintroduction can help restore the aquatic ecosystem.

Index terms: invasive plants, literature review, riparian ecosystems, temperate landscapes, water quality

INTRODUCTION

Ecological services provided by freshwater riparian ecosystems are important in both arid and mesic environments. Because alterations to riparian plant communities have been shown to affect freshwater ecosystems in terms of character and function, many studies have been conducted to identify impacts related to the replacement of indigenous riparian plant species by nonindigenous invaders. This review considers studies that have sought to identify connections between invaded riparian plant communities and various aspects of the freshwater ecosystems associated with them (Vitousek 1986; Walker and Smith 1997; Gordon 1998; Schmitz and Jacobs 2007).

Several excellent and comprehensive reviews have presented information about the ecological effects of nonindigenous plants, including effects related to water resources. Gordon (1998) reviewed invasive plant impacts in Florida. Schmitz and Jacobs (2007) assessed impacts on hydrology and riparian ecosystems in the semi-arid northwestern United States. Ehrenfeld (2003) examined effects on soil nutrient cycling. While all three reviews present useful information for aquatic ecologists and hydrologists, none offers insights into the effects that invasive plant species are having on freshwater ecosystems in mesic temperate regions.

Our search for studies that addressed this topic revealed a number of limitations in the research findings currently available. Notably, most research about the effects of nonindigenous terrestrial plants on freshwater ecosystems has been conducted in arid or Mediterranean climates (Le Maitre et al. 2015). Many of these studies in xeric regions focus on the potential for invasive plants to increase transpiration in riparian zones and deplete already limited water supplies. Conversely, in mesic climates, water for human use and maintaining habitat integrity is adequate or even overly abundant; therefore, in mesic environments ecological concerns tend to overshadow water quantity concerns. Despite this difference in water availability between mesic and xeric ecosystems, the majority of studies conducted in temperate mesic climates to document the effects of nonindigenous plants on water quantity have measured differences in transpiration regimes, an aspect more applicable to arid and xeric sites. Relevant aspects of water quantity on mesic sites (including the effect of invasive plants on stream base flow, soil water, groundwater levels, runoff, recharge, and the fate of precipitation with

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regard to interception by vegetation) are considerably less studied.

This review focuses specifically on studies conducted in temperate well-watered landscapes. In these regions the effects of colonization by nonindigenous species within floodplains are of greater concern to ecosystem functioning and water quality than to the reduction in water quantity associated with invasions in arid ecosystems. As a result, studies about riparian invasives in mesic temperate ecosystems have focused largely on ecosystem functioning and water quality and the majority of this review consolidates research related to these topics.

The largest body of research we identified is directed at the impact of invasive plants—either singly or in mixed assemblages—on allochthonous inputs, especially leaf litter, and the cascading effects on decomposer, macroinvertebrate, and fish communities. Chemical impacts of the allochthonous inputs of invasive plants have also been considered in research about water quality. By changing soil fertility, nutrient cycling, and soil chemistry in the riparian ecosystem, the presence of invasive plants can alter chemical inputs to streams. Most such changes that have been studied involve nutrients leaching from soils.

Separate from studies of the effects of allochthonous inputs are studies that examine changes caused by invasive plants to physical characteristics of the floodplain. Alterations in vegetative cover can affect the amount of exposed soil and modify rates of stream bank erosion and siltation. Additionally, physical characteristics affect the dynamics of sediment and nutrient capture, retention, and stability. All of these changes, in turn, can affect stream channel characteristics, fluvial geomorphology, and ultimately water quality.

Studies documenting physical changes in streambed shading and water temperatures also contribute to the larger category of water quality. Changes in water temperature are often concomitant with restructuring fundamental trophic structures in aquatic communities. Such restructuring can then lead to changes in food web functionality, at which point water quality may be affected.

In organizing the findings from 35 studies, we first divided impacts on freshwater ecosystems caused by invasive plants into those that affected water quantity and those that affected water quality and ecosystem functioning. We then further dissected impacts on water quality and ecosystem functioning into four categories: (1) shading and stream temperature, (2) streambed and riparian edaphic factors, (3) physical changes to allochthonous inputs, or (4) chemical changes to allochthonous inputs. We were able to identify at least one published study that considered each of these impacts; in some cases, a body of research has developed regarding a few individual species and types of impacts.

We listed alphabetically by author and enumerated sequentially those studies that assess impacts of nonindigenous plants on aquatic ecosystems (Table 1). We categorized the hydrological and ecological impacts that were studied, identified the plant species that were studied in relation to those impacts, and referenced the relevant studies enumerated in Table 1 (Table 2).

In this review, we use the words native and indigenous interchangeably. All invasive plants evaluated in this review are nonindigenous to the locations they were studied.

WATER QUANTITY

Invasive plants alter hydrologic regimes by changing the rate or timing of evapotranspiration, runoff and recharge, and baseflow. The origin of these impacts can be attributed to differences between invasive and indigenous species' transpiration rates, phenologies, photosynthetic tissue biomass, rooting depth, or a combination of characteristics working synergistically (Levine et al. 2003).

Most investigations that have measured invasive species' impact on water quantity have been conducted in arid climates such as the southwestern United States (Zavaleta 2000; Doody et al. 2011; Hultine and Bush 2011), South Africa (Le Maitre et al. 2015), and Australia (Doody and Benyon 2011; Doody et al. 2014). However, in subtropical Florida, the woody broad-leaved paperbark tree (*Melaleuca quinquenervia* (Cav.) S.F. Blake) increased community transpiration when the tree invaded native sawgrass swards (*Cladium jamaicense* (L.) Pohl). Transpiration increased because of *Melaleuca*'s greater leaf area and its evergreen growth (Woodall 1981, cited in Gordon 1998). In a tropical Hawaiian wet forest, Cavaleri et al. (2014) compared transpiration rates of co-occurring native and nonnative trees growing in four plots.

Table 1. List of research studies documenting impacts of nonindigenous riparian invasive plants on associated aquatic ecosystems. The specific invasive plants and freshwater impacts documented in these studies are summarized in Table 2.

1	Alonso et al. (2010)
2	Barker (2011)
3	Bottollier-Curtet et al. (2011)
4	Boulton et al. (1997)
5	Braatne et al. (2007)
6	Burkle et al. (2012)
7	Caffrey (1999)
8	Calder and Dye (2001)
9	Cavaleri et al. (2014)
10	Child et al. (1992)
11	Church et al. (2004)
12	Dangles et al. (2002)
13	DeMeester and Richter (2010)
14	Fargan et al. (2015)
15	Freund et al. (2013)
16	Gerber et al. (2008)
17	Goldstein and Willard (2008)
18	Goldstein et al. (2009)
19	Hladyz et al. (2011)
20	Lecerf et al. (2007)
21	Maerz et al. (2005)
22	McEwan et al. (2012)
23	McNeish et al. (2012)
24	McNeish et al. (2015)
25	McNeish et al. (2018)
26	Mineau et al. (2011)
27	Reinhart and VandeVoort (2006)
28	Roon et al. (2016)
29	Royer et al. (1999)
30	Swan, et al. (2008)
31	Talmadge and Kiviat (2002)
32	Urgenson (2006)
33	Vanderklein et al. (2014)
34	Watling et al. (2011)
35	Woodall (1981)

Table 2. Plant species studied and the riparian aspects measured in relation to the presence of those species in the research studies cited. The numbers in the matrix refer to the research studies listed in Table 1.

Invasive plant species	Water quantity	Water temperature	Edaphic aspects	OM quantity	OM timing	OM decomposition	Terrestrial invertebrates	Chemical inputs
Acer platanoides (Norway maple)				27		27		
Ailanthus altissima (tree of heaven)						1*, 30		
Buddleja davidii (butterfly-bush)						3		
Elaeagnus angustifolia (Russian olive)						29		11, 26
Elaeagnus umbellata (autumn olive)								11, 17*, 18
Fallopia japonica (Japanese knotweed)	33		10, 31, 32	32		5, 12*, 20	16, 21	32
Heracleum mantegazzianum (hogweed)			7					
Lonicera maackii (Amur honeysuckle)	22*, 25			24	22*, 23	2, 14, 23		22*, 25, 34*
Lythrum salicaria (purple loosestrife)							6*	
Melaleuca quinquenervia (paperbark)	35*							
Metrosideros polymorpha (‘Ōhi‘a lehua)	9*							
Microstegium vimineum (stiltgrass)								13*
Pinus nigra laricio (Corsican pine)	8*							
Pinus radiata (Monterey pine)		4						
Prunus padus (bird cherry)							28	
Rhamnus cathartica (buckthorn)					15	15		
Rhododendron ponticum		19				19		

OM: organic matter

*denotes studies not conducted in riparian zones

In two of the plots, all trees remained undisturbed. In the other two plots, the investigators removed the nonindigenous trees and measured transpiration from the remaining indigenous ‘ōhi’a lehua trees (*Metrosideros polymorpha* Gaudich.). Stand-level water use within the plots from which the invasive species were removed was half that of the plots where the nonindigenous trees remained. The investigators concluded that native-dominated forests free of invasive species can be conservative in overall water use, making a strong argument for invasive species control and preservation of native-dominated forests.

Only a few studies (four in this survey) directly assessed invasive plants’ impacts on stream volumes in mesic temperate climates. In the very wet climate of Wales in the United Kingdom, nonindigenous conifer plantations intercept significant proportions of precipitation and return the moisture to the atmosphere through advective loss via strong and sustained winds. Such evaporation represents the major source of forest evaporation in this climate. In comparatively drier landscapes in England, studies confirmed that no precipitation reached the ground under nonindigenous Corsican pine (*Pinus nigra laricio* Maire) plantations during rain events that wet the soil profile thoroughly under native oak and heath vegetation (Calder and Dye 2001). Because Corsican pines intercept and evaporate more water than shorter vegetation in Great Britain, water yields, especially during the dry season or from drier portions of the watershed, may be altered by this vegetative replacement.

In North America, Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) has been studied intensively in the Midwestern United States. Honeysuckle has been shown to intercept and evaporate significantly more precipitation during the growing season than native shrub understories (McEwan et al. 2012; McNeish et al. 2018). Moreover, the shrub has been shown to have a higher transpiration rate than that of native shrubs. In one study (Boyce et al. 2012), Amur honeysuckle increased stand transpiration 1–6% depending on invasive shrub density. Honeysuckle transpired an estimated 10% more shallow ground water and surface water than a native shrub understory at one site studied. Such enhanced transpiration can shorten the time water is present in ephemeral ponds and streams, causing adverse impacts on larval amphibians. In addition, heavy infestations of Amur honeysuckle may reduce soil moisture and adversely affect shallowly rooted forbs and seedlings.

Similarly, Vanderklein et al. (2014) demonstrated that a dense riparian stand of Japanese knotweed (*Reynoutria japonica* Sieb. & Zucc.) significantly lowered stream base flow, although the investigators were unable to determine if the plants were transpiring water directly from the stream, lowering shallow groundwater that was replenished by lateral movement from the stream, or a combination of both.

WATER QUALITY AND ECOLOGICAL FUNCTIONING

Changes to the riparian ecosystem can affect water quality and ecosystem functioning in many different ways, some of which act synergistically. For example, modifying the vegetation structure on a floodplain can change the extent to which a stream is shaded which, in turn, influences water temperature. In such cases, changes in water temperature can translate further into changes in trophic structure by shifting the composition of aquatic communities toward organisms with different thermal tolerances or altered dependence on autochthonous energy sources. The impact of these altered communities is then compounded by alterations in available allochthonous energy sources, which is another aspect affected by changes in riparian vegetation composition.

To the extent practical, we have organized the effects of riparian invasive plants on water quality and ecosystem functioning into four categories: (1) shading and stream temperature, (2) streambed and floodplain edaphic factors, (3) physical allochthonous input, and (4) chemical allochthonous input. However, because impacts often are interrelated and cascade throughout the aquatic ecosystem, we attempt to summarize higher-level perturbations where appropriate.

Shading and Stream Temperature

Depending on the physical structure of nonindigenous vegetation, shading and stream temperature may increase or decrease in response to colonization. In England, dense riparian colonization by nonindigenous common rhododendron (*Rhododendron ponticum* L.) casts deep shade over streams and lowers water temperature. The shading changed the aquatic community structure in these formerly exposed pasture streams from primarily autochthonous to allochthonous trophic pathways. In addition, the cooler water slowed decomposition of the resistant, low-nutrient rhododendron litter, leading to a depauperate aquatic community (Hladyz et al. 2011). Similarly, nonindigenous riparian pine (*Pinus radiata* D. Don) woodlands (and native deciduous forest stands) in New Zealand lowered water temperature compared to the temperature in pasture streams (Boulton et al. 1997).

In rural Massachusetts, USA, the most prevalent trend is the replacement of forest cover by invasive, nonindigenous shrub, vine, and low herbaceous vegetation. These plant forms do not provide the water supply protection afforded by forests, such as deep root systems, shading, slowed decomposition of allochthonous materials, and biological filtration through a tall, dense, and multistoried forest canopy (Massachusetts DCR 2011).

In a study of a third-order stream in Ohio with a riparian zone characterized by a dense Amur honeysuckle shrub subcanopy overshadowed by a taller native tree canopy, experimental removal of the nonindigenous shrubs significantly reduced canopy cover over the stream for several months following removal. Canopy cover ranged from 20% to 80% in the reach where the shrubs were removed whereas canopy cover ranged from 70% to 100% in a neighboring undisturbed stream reach. However, the investigators did not measure differences in water temperature between reaches (McNeish et al. 2015).

Streambed and Floodplain Edaphic Factors

The morphology of floodplain vegetation affects the extent to which water velocity is reduced and subsequently the amount of suspended sediment that drops out of the water column. Thus, the species of vegetation present can influence the detailed features of the floodplain through varying levels of sediment deposition (Schmitz and Jacobs 2007). Vegetation also affects erosion rates in riparian ecosystems. Plants with deep roots and high roughness more effectively stabilize soils and mitigate the erosive power of precipitation and high flows. When such vegetation is replaced by nonindigenous species with differing morphology or phenology, floodplains may become increasingly less or more vulnerable to erosion (Massachusetts DCR 2011).

In a comprehensive assessment of the impacts of invasive plants on watershed hydrology and riparian ecology in the arid northwestern United States, Schmitz and Jacobs (2007) concluded that sediment trapping and erosion are a function of any vegetation in a riparian zone and that they are naturally highly variable. Thus, to attempt to attribute specific sediment trapping characteristics to invasive plants in a riparian zone is misguided. Schmitz and Jacobs (2007) concluded that those studies that have compared the sediment trapping capacity of native vegetation to that of invasive species have not addressed the natural range of variability in riparian ecosystems in general.

Similarly, it is not at all clear that soil loss from streambanks dominated by nonindigenous species is a result of the characteristics of those species or is simply a reflection of the ability of some invasive species to take advantage of disturbed habitats. For example, Caffrey (1999) posited that dense stands of giant hogweed (*Heracleum mantagazzianum* Sommier & Levier) suppress and ultimately exclude indigenous herbaceous species that play an important role in bank stabilization. This replacement could result in erosion during winter floods, with large quantities of soil washed into the stream. Like giant hogweed, the sparse winter canopy of Japanese knotweed may leave bare soil exposed and vulnerable to erosion (Child et al. 1992; Urgenson 2006).

When a large flood occurred in Cornwall in the United Kingdom, observers noticed that the Japanese knotweed stands along the St. Austell River suffered both the greatest soil loss and greatest deposition. However, it was unclear if scoured areas provided favorable habitat for knotweed colonization or if knotweed-dominated areas eroded more easily. Scoured areas might collect vegetative knotweed propagules during floods, or erosion might stimulate rhizomes, resulting in prolific growth. Live knotweed canes dislodged by flooding might be transported downstream and take root in areas of fine alluvium or in areas denuded of other vegetation (pers. comm. cited in Talmadge and Kiviat 2002).

Alternately, knotweed could trap sediment during overbank flooding. At the same time, knotweed could increase the severity of flooding because the stiff canes can block flood channels, and more severe flooding could spread viable canes farther onto the floodplain. Thus, knotweed might alter sedimentation patterns in a stream by changing either erosion or deposition. Talmadge and Kiviat (2002) acknowledged that they were unable to find any quantitative data relating Japanese knotweed to an increase in bank erosion and stream turbidity and concluded that hard data are needed to document the impact of knotweed on erosion and deposition.

Physical Allochthonous Input

Among the most frequently hypothesized impacts of riparian invasive species on freshwater ecosystems are changes in the characteristics of allochthonous organic matter (OM) entering the water body. Because nonindigenous species potentially have phenological, morphological, and nutrient characteristics that differ from indigenous species, nonindigenous invaders could disrupt aquatic ecosystems attuned to indigenous plant community dynamics. The changes in allochthonous organic inputs produced by the invasion of nonindigenous species relate to (1) organic matter quantity; (2) timing of OM deposition; and (3) decomposition rate, palatability, and nutrient content. In turn, these direct changes could cascade through the aquatic ecosystem affecting aquatic community richness, abundance, diversity, and feeding guild relations. In addition, some studies have documented changes in the aquatic community related to changes in (4) terrestrial invertebrates that fall into water bodies and serve as prey for fish and predatory insects.

Organic Matter Quantity

Although it seems reasonable to assume that the differing morphological characteristics and growth habits of invasive species might influence the volume of organic matter delivered to aquatic ecosystems, only four studies assessed the differences. McNeish et al. (2015) and McNeish and McEwan (2016) compared leaf material in an Ohio stream reach bordered by a dense stand of Amur honeysuckle with that in a stream reach in which the honeysuckle understory had been removed. Honeysuckle's organic matter was significantly greater in the reach that had not been cleared, but unexpectedly, total leaf material in the streambed was significantly greater in the reach where honeysuckle had been removed, a difference driven by an increase in the input of leaves of indigenous species. Honeysuckle's dense canopy over the stream may have acted as a physical barrier or filter, preventing or delaying the entrance of abscised native leaves from the upper riparian canopy. Amur honeysuckle retains most of its leaves until late November–early December; therefore, this dense canopy may persist throughout the autumn. When honeysuckle was removed, so was this barrier, which allowed increased volumes of native material to drop into the stream (McNeish et al. 2015). Even with differences in overall allochthonous input, though, total and native leaf organic matter in-stream accumulation rates assessed on a weekly basis were not significantly different between reaches. As expected, honeysuckle leaf accumulation rates were significantly higher in the reach where the shrubs had not been removed. In Oregon, Urgenson (2006) documented an average 70% reduction in native litter input correlated with invasion by Japanese knotweed.

Reinhart and VandeVoort (2006) reviewed the impact of expanding colonization by Norway maple (*Acer platanoides* L.) in Montana, a tree that is also a common and expanding invasive species in temperate eastern North America. Norway maple may alter stream ecosystem function because of the increased volume of leaf OM entering streams. Leaf area index, a measure of canopy cover, was 225% greater in a stream reach dominated by Norway maple than in a neighboring native riparian reach. Consequently, leaf litter in a Norway maple–dominated reach was more than twice that in a neighboring native reach. The authors speculated that these increases in leaf OM volume may translate into differences in aquatic macroinvertebrates that use the leaf substrate, though they did not assess the differences.

Timing of OM Deposition

Given the seasonality and pulsed nature of subsidies, alterations of the temporal and spatial synchrony of resource availability to consumers across ecosystems are likely to result in ecological mismatches that can scale up from individual to community to ecosystem responses (McNeish et al. 2012; Larsen et al. 2016).

McEwan et al. (2012) demonstrated that leaf senescence of the co-occurring indigenous shrubs spicebush (*Lindera benzoin* (L.) Blume) and pawpaw (*Asimina triloba* (L.) Dunal) ended in mid-November, while Amur honeysuckle continued to senesce into December. McNeish et al. (2012) found that sycamore (*Platanus occidentalis* L.) and ash (*Fraxinus* spp.) leaves collected from a stream peaked during the first two weeks of November, whereas honeysuckle senescence peaked a week later and made up 23% of the in-stream leaf litter in early December.

Similarly, Freund et al. (2013) compared leaf senescence of the two most common riparian trees on a stream in central New York, the native green ash (*Fraxinus pennsylvanica* Marshall) and the nonindigenous common buckthorn (*Rhamnus cathartica* L.). Green ash leaves fell from September through mid-October, whereas common buckthorn contributed leaves for an additional month until mid-November.

Decomposition Rate, Palatability, and Nutrient Content

By far, most studies evaluating the impact of invasive species on freshwater ecosystems have compared litter quality and the decomposition rate of leaves of invasive plants with those of co-occurring indigenous plants. Most have also assessed the effects of these differences on detritivorous macroinvertebrate communities. Litter quality can be measured by (1) palatability, which is related to concentrations of tannins and polyphenols; and (2) nutrient content, which is most often measured by the C:N ratio. High levels of tannins and polyphenols and a high C:N ratio are associated with slow rates of decomposition and nutrient release (Stockan and Fielding 2013).

Our review of 14 studies demonstrates that it is not possible to generalize about the rate of leaf decomposition based solely on species origin. Leaves of some nonindigenous species decomposed more rapidly, some decomposed less rapidly, and some decomposed at the same rate as native co-occurring species. For example, in one study (Royer et al. 1999), leaves of Russian olive (*Elaeagnus angustifolia* L.) decomposed less rapidly than those of an indigenous species in one Idaho softwater stream, but in a second stream with harder water there were no differences in decomposition rates between olive leaves and those of a second indigenous species. Decomposition rate, then, was dependent on the composition of the leaf matter and the characteristics of the physical environment, but not on species origin.

Studies documented that the leaves of two nonindigenous species, tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) and Amur honeysuckle, consistently decomposed more rapidly than those of indigenous co-occurring species. Swan et al. (2008) working in an urban Appalachian Piedmont stream, and Alonso et al. (2010) working in an artificial lake in central Spain, found that tree-of-heaven leaves decomposed more quickly than those of several indigenous species. McNeish et al. (2012) demonstrated that Amur honeysuckle leaves decomposed more rapidly than those of indigenous species. Two other studies evaluated the impact of the more rapid honeysuckle leaf decomposition on aquatic macroinvertebrate communities and found different impacts. Fargen et al. (2015) found that aquatic macroinvertebrate numbers associated with honeysuckle leaf packs, especially invertebrates in the scraper functional feeding guild, were lower than those found in leaf packs composed of native species. In contrast, Barker (2011) found that the number of macroinvertebrates increased in association with honeysuckle leaves, though there were no differences in functional feeding guild structure.

Four studies examined the breakdown of Japanese knotweed leaves but returned disparate results. In a heavily invaded French Pyrenees mountain stream, knotweed leaf breakdown was more rapid than that of indigenous species, possibly because the large leaf biomass supported a large population of caddisfly (Trichoptera) shredders. In contrast, no such differences in breakdown rate or invertebrate effects were observed in a less heavily colonized British stream in the Pennines (Lecerf et al. 2007). Braatne et al. (2007) found no differences in the breakdown rate between knotweed and indigenous leaves in Wisconsin, a finding confirmed by Dangles et al. (2002).

Decomposition rates and aquatic invertebrate impacts varied considerably among other nonindigenous species. Reinhart and VandeVoort (2006) found that Norway maple decomposition did not differ from that of indigenous black cottonwood (*Populus trichocarpa* Torr. & A. Gray). Freund et al. (2013) found that leaves of nonindigenous common buckthorn senesced later and broke down more rapidly than those of indigenous green ash or elm (*Ulmus* spp.).

Bottollier-Curtet et al. (2011) compared leaf breakdown rates of five indigenous riparian species with five invasive species in a southwestern French stream. Four of the paired comparisons revealed no differences in breakdown rates between species, but in the fifth, nonindigenous butterfly-bush (*Buddleja davidii* Franch.) decomposed significantly more rapidly than indigenous black poplar (*Populus nigra* L.).

Alonso et al. (2010) found that leaves of the nonindigenous black locust (*Robinia pseudoacacia* L.), with the lowest C:N ratio (i.e., highest quality and palatability) among four species that they studied, decomposed least rapidly, but that the differences in decomposition rates did not translate into differences in aquatic macroinvertebrate communities.

Hladyz et al. (2011) examined the breakdown of very low quality nonindigenous common rhododendron leaves and found them to be extremely resistant to decomposition. This refractory allochthonous material depressed aquatic invertebrate richness and diversity in British streams flowing through riparian areas dominated by dense rhododendron thickets.

While they did not include nonnative species in their analyses, Lecerf et al. (2005) and Swan and Palmer (2004) independently concluded that riparian plant species richness may indirectly govern aquatic ecosystem functioning through complex trophic interactions. Because invasive species often overwhelm ecosystems they colonize and thereby reduce plant diversity, riparian communities dominated by one or a few invasive species could produce significant alterations in aquatic ecosystems. Such alterations in the vegetation might be reflected in changes in the aquatic macroinvertebrate communities, and especially in the functional feeding guild structure (Dangles et al. 2002; Reinhart and VandeVoort 2006; Freund et al. 2013).

Terrestrial Invertebrates

Streams and their adjacent riparian zones are closely linked by reciprocal flows of invertebrates. Terrestrial invertebrates flying above, falling into, or climbing on vegetation alongside bodies of water can provide up to half the annual energy input for fish such as salmonids, with deciduous, closed-canopy riparian vegetation providing the highest inputs (Baxter et al. 2005). By contrast, nonindigenous plants typically support a tiny fraction of the number of terrestrial invertebrates hosted by indigenous species (Tallamy 2007).

As a result, riparian areas dominated by a few invasive plant species could contribute significantly fewer terrestrial invertebrates to adjacent streams.

Roon et al. (2016) found that riparian nonindigenous European bird cherry (*Prunus padus* L.) supported four to six times less terrestrial invertebrate biomass on its foliage and contributed two to three times lower allochthonous subsidies relative to native deciduous trees in urban Alaskan streams. Greenwood et al. (2004) found similar overall reduction in terrestrial invertebrate inputs to streams whose southeastern Australian floodplains were dominated by invasive white-crack willow (*Salix* × *rubens* Schrank [*alba* × *fragilis*]). Riparian habitats invaded by Japanese knotweed were characterized by lower plant richness and supported lower overall abundance and richness of terrestrial invertebrates along several western European streams (Gerber et al. 2008). Invertebrate biomass in knotweed stands was less than half that of shrub and grassland habitat. Maerz et al. (2005) found equivalent reductions in central New York. All of these studies suggest that large-scale invasion by nonindigenous plants is likely to affect biodiversity and reduce the quality of riparian ecosystems for predators whose diets are largely composed of terrestrial arthropods.

In a particularly elegant study, Burkle et al. (2012) used experimental wetlands planted with nonindigenous purple loosestrife (*Lythrum salicaria* L.) to test the degrees to which floral density of this invasive plant trigger a chain of interactions. High loosestrife floral density attracted high levels of insect pollinators and, in turn, predatory adult dragonflies. High loosestrife floral density was also associated with increased dragonfly oviposition and subsequent high larval dragonfly abundance in the aquatic community. High floral density was also related to changes in zooplankton communities. Through changes in animal behavior and trophic interactions in terrestrial and aquatic ecosystems, this study illustrated the broad and potentially cryptic effects of invasive species.

Chemical Allochthonous Input

Dissolved Nutrients and Cations

Several studies have documented changes in soil water and streams bordering riparian areas colonized by two closely related nonindigenous nitrogen-fixing species of the genus *Elaeagnus*: autumn olive (*E. umbellata* Thunb.) and Russian olive. Church et al. (2004) found significantly greater nitrate (NO_3^--N) leaching (but not ammonium nitrogen [NH_4^+-N] leaching) during the dormant season from plots dominated by autumn olive than from old-field plots in southern Illinois.

Goldstein and Willard (2008) assessed the impact of autumn olive on soil water and groundwater. They found that soil water NO_3^--N concentrations were significantly higher under autumn olive than they were under open field vegetation. Groundwater nitrate levels were low. Soil water and groundwater NH_4^+-N levels were not different between vegetation types. Soil water base cations (i.e., magnesium, calcium, sodium) showed a positive correlation with nitrate concentrations, but there were no differences between vegetation types. Nevertheless, at the pH levels of these soils (5.43–5.59), the cation–nitrate correlation indicated significant leaching potential. Goldstein et al. (2009) measured stream nitrate and ammonium concentrations in 12 first-order ephemeral streams draining deciduous forest watersheds with autumn olive cover ranging from 10% to 35%. The degree of autumn olive cover was positively correlated with stream nitrate concentrations, but not ammonium concentrations. All three of these studies concluded that in watersheds where autumn olive is a common riparian plant nitrate leaching could have important water quality implications.

Mineau et al. (2011) assessed the ability of Russian olive to subsidize arid western US streams with nitrogen. They found that stream reaches invaded by olive had higher organic nitrogen concentrations and supported biofilms coating the stream substrates that were less limited by nitrogen compared with reaches flowing through grassland and sparsely vegetated shrublands. At low background inorganic N concentrations, invaded reaches also exhibited high demand for both NH_4^+-N and NO_3^--N compared to reference reaches. The results suggest that these streams have the potential to retain nitrogen and diminish the nutrient's downstream export and ecological effects, at least temporarily.

Three other studies assessed the impact of nonindigenous non-nitrogen-fixing species on nutrients and cations in soil, and then proposed (but did not investigate) pathways by which these impacts could affect water quality. Japanese knotweed resorbs 76% of its foliar nitrogen before senescence compared to 2% resorbed by co-occurring red maple (*Acer rubrum* L.) and 33% by willow (*Salix* spp.). Where colonization is extensive, the resorption by knotweed could reduce the nitrogen contribution to soils and aquatic ecosystems compared to that from indigenous vegetation (Urgenson 2006).

DeMeester and Richter (2010) found that another especially aggressively riparian invader, Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), accumulated half the annual nitrogen biomass and released significantly less nitrogen during decomposition compared to a diverse indigenous plant community. They concluded that stiltgrass invasion appears to diminish within-ecosystem nitrogen circulation through the understory vegetation.

McNeish et al. (2018) and McEwan et al. (2012) examined precipitation throughfall volume and chemistry and soil nutrients under and away from Amur honeysuckle shrubs in invaded Midwestern US forests. Honeysuckle significantly reduced the volume of rainwater reaching the forest floor and altered the chemistry of the water that did penetrate the foliage layer causing an increase in cation concentrations and a reduction in dissolved nitrogen. As a result, they concluded that Amur honeysuckle has the potential to cause significant alterations in nutrient cycling and riparian functioning.

Water-soluble Phytochemicals

Water-soluble phytochemicals produced by nonindigenous plants may represent novel elements of invaded ecosystems that could produce a variety of direct and indirect effects on indigenous organisms. Watling et al. (2011) coupled an exploration of the effects of Amur honeysuckle extract on the larvae of four indigenous Midwestern US amphibians with behavioral observations. The observational component was designed to determine if behavior could ameliorate the effects of exposure to the honeysuckle extract. The researchers reared the amphibian larvae in three aqueous media: extracts of Amur honeysuckle, mixed indigenous leaf litter, and water. Toad tadpoles reared in the honeysuckle extract were more likely to die than those reared in the mixed indigenous plant extract, but mortality rates for the other three amphibians were not different between treatments. Toad and frog tadpoles made more trips to the surface in the honeysuckle extract, consistent with a hypothesis that the honeysuckle extract may interfere with respiratory physiology. These results suggest that at least some tadpoles could compensate behaviorally for the negative effects of the honeysuckle extracts. It is unlikely that leaf extracts would reach concentrations in streams similar to those created in this experiment, although it is possible to imagine very high concentrations developing in shallow vernal pools favored by amphibians in riparian areas heavily invaded by Amur honeysuckle.

Custer et al. (2017) exposed aquatic macroinvertebrates to fruits and flowers of Amur honeysuckle in laboratory and field experiments. Results suggested that these plant parts presented a negative and potentially toxic subsidy to aquatic communities resulting in reduced survival and growth. The researchers were unable to identify the precise mechanism responsible but hypothesized that the effects could be related to inherent chemical toxicity, secondary effects associated with water chemistry changes, or secondary effects related to microbial community changes.

CONCLUSION AND RESEARCH NEEDS

While riparian zones are prone to colonization by invasive plants, only a few of the reviewed studies were able to attribute changes in freshwater or riparian ecosystems directly to the invasive plants themselves. In many cases, the research showed no quantifiable effects on measured parameters, while other studies yielded inconclusive or even contradictory results. The lack of consistency among the research findings suggest that a broader scope of environmental factors, which may be specific to a given location, must be taken into account before the impacts to these complex systems can be understood.

Our survey of the effects of nonindigenous riparian plants in mesic temperate landscapes documents that these plants differ in morphology, phenology, and other characteristics from indigenous species. However, the differences are highly variable across species. The fundamental challenge presented by nonindigenous plants, then, may not lie in their physiological differences from indigenous species, but instead on their colonization characteristics. Invasive nonindigenous plants, once established, tend to colonize densely and to exclude indigenous species by usurping growing space, nutrients, and sunlight. In so doing, they reduce the biodiversity of the ecosystem (Levine et al. 2003; Charles and Dukes 2008). Furthermore, through their dominance, the characteristics of these nonindigenous species can transform the ecological functioning of the entire ecosystem (Vitousek 1986). Thus, as demonstrated in several studies we reviewed (Dangles et al. 2002; Lecerf et al. 2007; Goldstein et al. 2009; Roon et al. 2016), higher colonization densities exhibit larger measurable ecological impacts.

In situations in which densely growing nonindigenous plants have different growth habits or exude toxic chemicals, the impacts can be direct, immediate, and readily apparent. However, if the invading plants have relatively similar physiological characteristics to the indigenous species they replace, slight differences in leaf decomposition rates or the timing of leaf senescence may cause impacts that are more difficult to measure or take longer to manifest. Therefore, the effects need to be evaluated for each species individually in the broadest ecological context possible (both spatially and temporally) because impacts to aquatic ecosystems may be difficult to measure if the riparian habitat is only recently or sparsely colonized.

The morphological, phenological, and physiological differences between indigenous and nonindigenous species have been shown to be important factors in hydrological and ecological changes. In their review of the impacts of invasive plants in the northwestern United States, Schmitz and Jacobs (2007) concluded that there is a substantial scientific basis to expect that invasive plants could affect watershed hydrology as well as riparian and freshwater ecology. However, they also documented great variability in hydrological and ecological responses to invasion and noted that the responses did not lend themselves to generalizations or exhibit distinct and predictable trends. Our review of published studies conducted in mesic temperate landscapes echoes these findings.

The strongest evidence in the research results we have compiled relates to effects that riparian invasive plants exert on the timing of allochthonous OM input, the decomposition rate of OM in aquatic ecosystems, and changes in aquatic community structure. In addition, there are consistent data suggesting that in watersheds densely colonized by nitrogen-fixing invasive species, stream eutrophication is likely.

This review revealed several research needs regarding the impacts of invasive plants on freshwater ecosystems. Considering the overwhelming and pervasive impact of invasive plants on riparian communities, relatively few studies have been conducted in temperate mesic landscapes. Furthermore, the effects of only two species, Amur honeysuckle and Japanese knotweed, have been investigated in repeated studies; many other prolific species have received much less or no attention. Many more nonindigenous species than those evaluated in the studies in this review are common on floodplains in mesic regions and their impacts need to be assessed, especially if site conditions or plant characteristics suggest that these species could affect aquatic ecosystems. Additionally, Ehrenfeld (2003) emphasized the need to determine the magnitude of the morphological or physiological differences between invasive and native plants that are necessary to alter ecosystem processes.

Another potentially significant gap is the lack of investigations that examine the ecological impacts caused by colonization over longer periods of time. The majority of studies included in this review were conducted during just a single growing season and none monitored effects within a freshwater ecosystem for more than a year (let alone a decade). Longer studies could reveal findings that further correlate riparian invasion by nonindigenous plants to any number of the aspects addressed; in particular, aspects related to aquatic food webs are likely to be affected. It seems reasonable to hypothesize that the fate of such specialized invertebrate communities would not be apparent until colonization by less palatable, nonindigenous plant species had significantly reduced allochthonous inputs of native OM for a number of years. If this is the case, effects on water quality related to aquatic community structure might only be measurable if the same stream ecosystem were monitored for many growing seasons in floodplains that were becoming increasingly invaded. Furthermore, studies that examine the effects of removing invasive plants from floodplains are unlikely to show a correlation with aspects of the food web until native plant species can be restored to previously invaded areas and aquatic communities are given time to rebound. The effects of nonindigenous invasion on any ecosystem are rarely (if ever) fully recognizable in short time spans because of the inherently complex and highly interconnected nature of such systems; there is little reason to think that freshwater ecosystems would be an exception.

Only a few studies have made direct correlations between nonindigenous plant colonization and changes in floodplain geomorphology, sediment regime, and nutrient cycling. When effects have been documented, they sometimes have been inconclusive, produced contradictory findings depending on location, and are species-specific. Additional research needs to be conducted to more clearly characterize the impact of nonindigenous colonization on floodplain physical processes. More research is also needed to document the densities to which nonindigenous plants must be reduced in invaded riparian ecosystems to yield changes in ecosystem functioning. Such required density reductions likely will differ among nonindigenous species, and mixed-species assemblages may be particularly difficult to assess. Where riparian communities have been altered by invasions, nonindigenous plant management followed by restoration of the indigenous plant community likely would restore pre-disturbance conditions, but our review of the literature revealed only one study of the effect of nonindigenous plant removal and restoration work (McNeish et al. 2015). As Schmitz and Jacobs (2007) pointed out, the most reliable assessments would come from highly controlled paired watershed experiments, but to date no such studies have been performed. Research results demonstrating improvements in aquatic ecosystem functioning when nonindigenous species are removed and replaced by natives would help to justify expensive stewardship and restoration activities.

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