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Authors: Fargen, Catherine, Emery, Sarah M., and Carreiro, Margaret M.

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RESEARCH ARTICLE

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Influence of *Lonicera maackii* Invasion on Leaf Litter Decomposition and Macroinvertebrate Communities in an Urban Stream

Catherine Fargen[1]

[1]Department of Biology
University of Louisville
Louisville KY 40292

Sarah M. Emery[1,2]
Margaret M. Carreiro[1]

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ABSTRACT: *Lonicera maackii* (Amur honeysuckle) is an aggressive alien shrub that invades many habitat types in the eastern United States, including riparian zones. The effects of *L. maackii* have been well documented in terrestrial ecosystems and can range from alteration of plant and insect communities to changes in ecosystem processes; however, the effects on aquatic ecosystems are less well known. Research on other invasive species has shown that replacement of native trees with exotic species can have significant influences on decomposition rates in nearby streams. This study investigated the direct and indirect effects of *L. maackii* invasion and management (removal) on leaf litter decomposition in an urban stream by placing leaf litter packs of *L. maackii* and the native *Acer saccharum* (sugar maple) in stream segments invaded by or managed for *L. maackii*. We found that *L. maackii* litter decomposed two times faster than *A. saccharum* litter, and that *A. saccharum* leaf litter supported a higher abundance of macroinvertebrates than *L. maackii*. Functional feeding groups of macroinvertebrates were also affected by the invasive species; significantly more scrapers were associated with *A. saccharum* litter, and predators were positively associated with both *A. saccharum* and invaded sites. Indirect effects of *L. maackii* presence along streambanks on leaf decomposition and macroinvertebrate communities were negligible, possibly due to overriding effects of urbanization on the stream. These results have important implications for stream ecosystems that run through terrestrial areas invaded by *L. maackii*, as stream diversity and nutrient retention are strongly influenced by allochthonous inputs.

Index terms: ecosystem function, invasive species, restoration, riparian, stream ecology

INTRODUCTION

Leaf litter decomposition, the process by which fallen plant matter breaks down physically and chemically, is an extremely important ecosystem process. Allochthonous leaf litter inputs (i.e., from land to aquatic systems), form the base of food webs in forested low order streams (Vannote et al. 1980). Additionally, leaf litter decomposition is an integral step in the cycling of many nutrients such as carbon, nitrogen, and phosphorus (Lindeman 1942; Triska et al. 1984; Meyer and Likens 1979).

The rate of leaf litter decomposition is controlled by many biotic and abiotic factors, most of which are well understood. For instance, the quality or chemical composition of leaves, as well as the community of organisms, such as macroinvertebrates, fungi, and bacteria, consuming the organic matter will partially determine how quickly decomposition occurs (Melillo et al. 1982; Covich et al. 1999). Environmental variables such as temperature, light, water chemistry, dissolved oxygen, and physical disturbance can also alter the decay rate (Webster and Benfield 1986; Gurtz and Tate 1988; Guo and Sims 2001; Gulis and Suberkropp 2003). Despite a good understanding of the role of individual factors on decomposition, the cumulative effects of multiple factors, especially those that change in response to anthropogenic influences, are not as well understood.

Research on invasive plant species introduced through human activities has shown that invasives can have significant, but variable, impacts on decomposition rates in both terrestrial (e.g., Bailey et al. 2001; Reinhart and VandeVoort 2006) and aquatic systems (e.g., Alonso et al. 2010; Freund et al. 2013). For instance, litter from invasive species often contains a different chemical composition than litter from native species, resulting in variation of decomposition rates. Godoy et al. (2010) investigated 19 co-familial native–invasive pairs and found overall slower terrestrial decomposition rates among leaf litter of invasive species. Similarly, Furey et al. (2014) found slower decomposition rates for invasives compared with natives in a survey of 29 plant species found in Argentinian woodlands. Other terrestrial studies have shown no significant difference in the decomposition rates between native and invasive plant litter (Hata et al. 2012). Still other studies have found that invasive litter decays more rapidly than native litter (e.g., Harner et al. 2009; Jaeger et al. 2013). For example, Allison and Vitousek (2004) compared the decay rates of five native and six invasive understory plants in terrestrial plots and found wide variation, with invasives decomposing more quickly than natives.

Fewer studies have examined invasive

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[2] Corresponding author: sarah.emery@louisville.edu; 502-852-5940

species effects on decomposition rates in aquatic ecosystems, but have generally still found mixed effects (e.g., Marano et al. 2013). For example, Swan et al. (2008) compared in-stream decomposition rates of six native riparian tree species to that of the invasive tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) and found consistently faster decomposition for the invasive. Similarly, an aquatic study in which litter from a native plant and invasive saltcedar (*Tamarix ramosissima* Ledeb.*)* were paired found faster leaf decomposition and lower abundance and diversity of macroinvertebrates associated with the saltcedar (Bailey et al. 2001). In contrast, a study by Serra et al. (2013) found that the invasive crack willow (*Salix fragilis* L.) decomposed more slowly than the native chacay (*Ochetophila trinervis* (Gillies ex Hook.) Poepp. ex Endl.), and a study by Reinhart and VandeVoort (2006) found no differences in decomposition rates in streams between the invasive tree *Acer platanoides* L. and the dominant native *Populus trichocarpa* Torr. & A. Gray ex Hook. These changes in decomposition are sometimes, but not always, linked to changes in aquatic invertebrate communities as well (e.g, Bailey et al. 2001; Reinhart and VandeVoort 2006; Lecerf et al. 2007; Serra et al. 2013). This variability in results highlights the importance of species-specific studies in order to understand impacts of invasives on ecosystem function.

Invasive plants can also alter decomposition rates and invertebrate communities indirectly by altering environmental factors such as light availability and habitat quality. Ashton et al. (2005) compared decomposition rates among various native and invasive plant litter species in uninvaded plots and plots invaded by *Alliaria petiolata* (M. Bieb.) Cavara & Grande (garlic mustard), *Lonicera japonica* Thunb. (Japanese honeysuckle), *Celastrus orbiculata* Thunb. (Asian bittersweet), *Elaeagnus umbellata* Thunb. (autumn olive), and *Rosa multiflora* Thunb. (multiflora rose). The study found faster terrestrial decomposition rates in invaded sites independent of plant litter type. The authors suggested that altered microbial communities and microclimates could drive differences. Another study in an aquatic environment showed some differences between saltcedar-invaded versus uninvaded sites in leaf litter decomposition rates, which were thought to have resulted from altered aquatic invertebrate communities (Kennedy and Hobbie 2004). Further, Reid and Barmuta (1999) compared stream reaches invaded by willows (*Salix* spp.) to reaches with only native *Eucalyptus* species and found altered benthic invertebrate communities due to altered light regimes, water chemistry, and patch quality.

One invasive plant that may have significant impacts on leaf litter decomposition dynamics in aquatic systems is *Lonicera maackii* (Rupr.) (Amur honeysuckle). *Lonicera maackii* is an invasive exotic shrub of Asian origin, which thrives in the eastern United States, especially in urban areas (Pennington et al. 2010; White et al. 2014). This species was originally planted as an ornamental and to aid in erosion control, and aggressively spreads by a number of means, most notably through birds that carry the seeds after consuming the plant's abundant berries. This plant is characterized by dense vegetation up to 5-m tall and shallow yet extensive root structures (NPS 2013).

Lonicera maackii has been studied for a number of years, and many of its effects on terrestrial systems are relatively well known. For instance, early leaf expansion, late leaf abscission, and dense canopy formation by *L. maackii* result in increased competition for light and decreased reproductive abilities of nearby and understory plants of other species (Miller and Gorchov 2004). Allelopathic chemicals in the leaf and root tissues of *L. maackii* have also been found to inhibit seed germination of native plants (Dorning and Cipollini 2006). Relatively high nitrogen content leaves and rapid decomposition rates of *L. maackii* in terrestrial systems can alter nutrient cycling dynamics (Blair and Stowasser 2009; Trammell et al. 2012). Trammell et al. (2012) suggested that *L. maackii* inhibits ecosystem production since forests invaded by *L. maackii* produced significantly less leaf biomass than comparable uninvaded forests. This study also found increased decay rates and nitrogen release associated with *L. maackii* leaf litter as compared to *Acer saccharum* Marsh. (sugar maple). Additionally, *L. maackii* can influence invertebrate communities through the production of phenolic metabolites that may deter terrestrial insect herbivores (Cipollini et al. 2008).

Despite the longstanding efforts to understand the terrestrial implications of *L. maackii* invasion, few studies have sought to determine its effects on aquatic ecosystems. Recently, however, ecologists have attempted to investigate these consequences. A study by Lewis and Brown (2010) compared leaf litter from *L. maackii* to that of three native species (sycamore (*Platanus occidentalis* L.), dogwood (*Cornus florida* L.), and redbud (*Cercis canadensis* L.)) in an invaded urban stream environment and found that *L. maackii* decomposed faster than the native species. McNeish et al. (2012) found faster in-stream *L. maackii* leaf litter decomposition rates and altered invertebrate communities compared to leaves of native ash (*Fraxinus* spp.), sycamore, and mixed leaf packs. To date, no published studies have examined both the direct and indirect effects of this species on aquatic decomposition and associated macroinvertebrate communities. The purpose of this study was to evaluate the direct and indirect effects of *L. maackii* invasion and removal by investigating decomposition rates of *L. maackii* and the native species *Acer saccharum* in stream segments adjacent to riparian areas invaded by *L. maackii* and in areas of recent *L. maackii* removal. The removal was part of a major restoration effort in an urban park woodland. We addressed three specific questions: (1) Do *L. maackii* and *A. saccharum* differ in their decomposition rates in stream ecosystems? (2) Does *L. maackii* invasion of streambanks indirectly alter decomposition rates for both species? And (3) do *L. maackii* and *A. saccharum* differ in their direct and indirect effects on macroinvertebrate communities?

METHODS

Study Site

Beargrass Creek is a network of three converging waterways (South Fork, Middle Fork, and Muddy Fork) in Jefferson

County, Kentucky, that drains 160 km^2 of surrounding watershed and empties into the Ohio River. This study took place in the Middle Fork of Beargrass Creek (MFBC; 38°14'14", 85°39'53"), a 3rd order stream with an average discharge of approximately 1.1 cms (USGS 2013). Upstream of the stretch used in this study, the MFBC subwatershed passes through suburban and urban lands, 33% of which consist of impervious surfaces (Beargrass Creek Watershed Council 2005). Despite the fact that the stream also runs through a series of city parks and protected lands, this stream is highly symptomatic of the urban stream syndrome (Walsh et al. 2005) and is listed as impaired on Kentucky's Division of Water 303d list (Kentucky Environmental and Public Protection Cabinet 2011). Portions of the streambank have been entirely paved, a Combined Sewage Overflow (CSO) system frequently leaks contaminants into the waterway, and high levels of surrounding impervious surface create incised channels, frequent flash floods, and increased chemical runoff (Beargrass Creek Watershed Council 2005). Still, MFBC has a small but resilient community of aquatic invertebrates, fish, and plants, and the local human community and park organizations have been working over the past several years to restore the biodiversity of the creek and surrounding riparian zones.

In 2005, the Louisville Olmsted Parks Conservancy initiated a $3.5 million project aimed at eliminating invasive species in several parks throughout Jefferson County. Since then, *L. maackii*, which became widely established in Cherokee and Seneca Parks after the 1974 tornado (Carreiro and Zipperer 2011), has been removed in about 98% of these two adjoining parks (Waltman pers. comm., 2013) through which a 7-km stretch of MFBC runs. To date, about 28% of the riparian areas along the MFBC remains invaded by *L. maackii* (Fargen 2013). At the start of this study, three segments of MFBC that run through *L. maackii* removal areas, as well as three nearby segments where *L. maackii* remains, were chosen to investigate the effects of *L. maackii* removal versus invasion. The shrub had been removed from these areas in the previous 1–2 years. Due to an early miscommunication with management, one of the initial *L. maackii* invaded sites had to later be reassigned as an *L. maackii* removal site, thus resulting in two invaded and four removal plots. All segments occurred in a 7-km stretch of stream running through highly invaded parkland affected by storm sewer input and CSOs. The native species, *A. saccharum,* was chosen to compare litter decomposition rates because it is also well represented in the study areas.

Experimental Design

Leaf litter of *A. saccharum* and *L. maackii* was collected during leaf senescence in November and December 2011, respectively, by placing bed sheets on the ground and gently shaking the branches to allow leaves to fall. Collected leaves were air dried for 3–8 weeks (dependent on initial collection time), and hand mixed occasionally to promote even drying.

Leaf packs were then made by weighing 5.00 ± 0.05 g of leaf litter from a single species and placing it in 5 mm polypropylene mesh bags (24 × 37 cm) (Associated Bag Company; Milwaukee, WI). For each species, 132 bags were prepared, for a total of 264 bags. Seven *A. saccharum* packs were tied to a nylon string and coupled with seven *L. maackii* packs to form one paired string. On 2 January 2012 (approximately three weeks after *L. maackii* leaf fall), three paired string replicates were set out in each site by securing them with zip ties to root bundles on the sides of the streambank. Two study sites were located in segments of the stream where the banks were heavily invaded by *L. maackii* and four sites where *L. maackii* had been removed (Figure 1). All stream sites were glides with exposed roots. Additionally, six control bags of each species were carried throughout the process but were not set out in the stream. These bags were taken back to the lab, oven dried at 60 °C, and weighed to estimate mean initial leaf mass by accounting for potential handling loss and by factoring in the air-dry to oven-dry mass conversion factor.

The mass loss rates between *A. saccharum* and *L. maackii* were expected to differ greatly due to chemical and physical differences in the leaves (Trammell et al. 2012), so collection dates for each species followed separate schedules. *Lonicera maackii* litter bags were incubated in the stream from 2 Jan–20 Feb, 2012, for a total of 49 days, while *A. saccharum* litter bags were incubated from 2 Jan–21 May, 2012, for a total of 140 days. One bag of *A. saccharum* from each of three replicate strings at each site was collected 16, 49, 75, 112, and 140 days after experiment initiation, and one bag of *L. maackii* from each replicate string at each site was collected 3, 6, 10, 16, 26, 35, and 49 days after deployment. When collected, mesh bags were placed in plastic re-sealable bags, transported to the lab over ice, and stored at 4 °C until processing. Additionally, environmental variables (i.e., light, temperature) were measured on one day at the end of the experiment to compare between-site conditions.

Leaf Litter Decomposition

In the lab, leaf litter was removed from mesh bags and gently rinsed over 4-mm and 121-µm sieves. Insects larger than 4 mm were selected and stored in ethanol for later identification. Material retained in the 4-mm sieve was placed in paper bags, oven dried at 60 °C for 48 hours and weighed. It was apparent upon collection that significant sediment infiltration had occurred in our samples, producing artificially high oven dry mass (ODM). Therefore, a subsample of each sample was removed, weighed in an aluminum pan, combusted at 550 °C for one hour, cooled in desiccators for four hours, and re-weighed. This value was used to calculate the ash-free dry mass (AFDM) and to standardize the percent organic mass loss at every interval to account for sediment deposition. Additionally, sediment samples were taken from the field sites and also dried at 60 °C and 550 °C to estimate the organic content in sediment. We then used a soil correction equation to isolate the fraction of organic content originating from leaf litter rather than sediment (Blair 1988).

Macroinvertebrates

Material that passed through the 4-mm

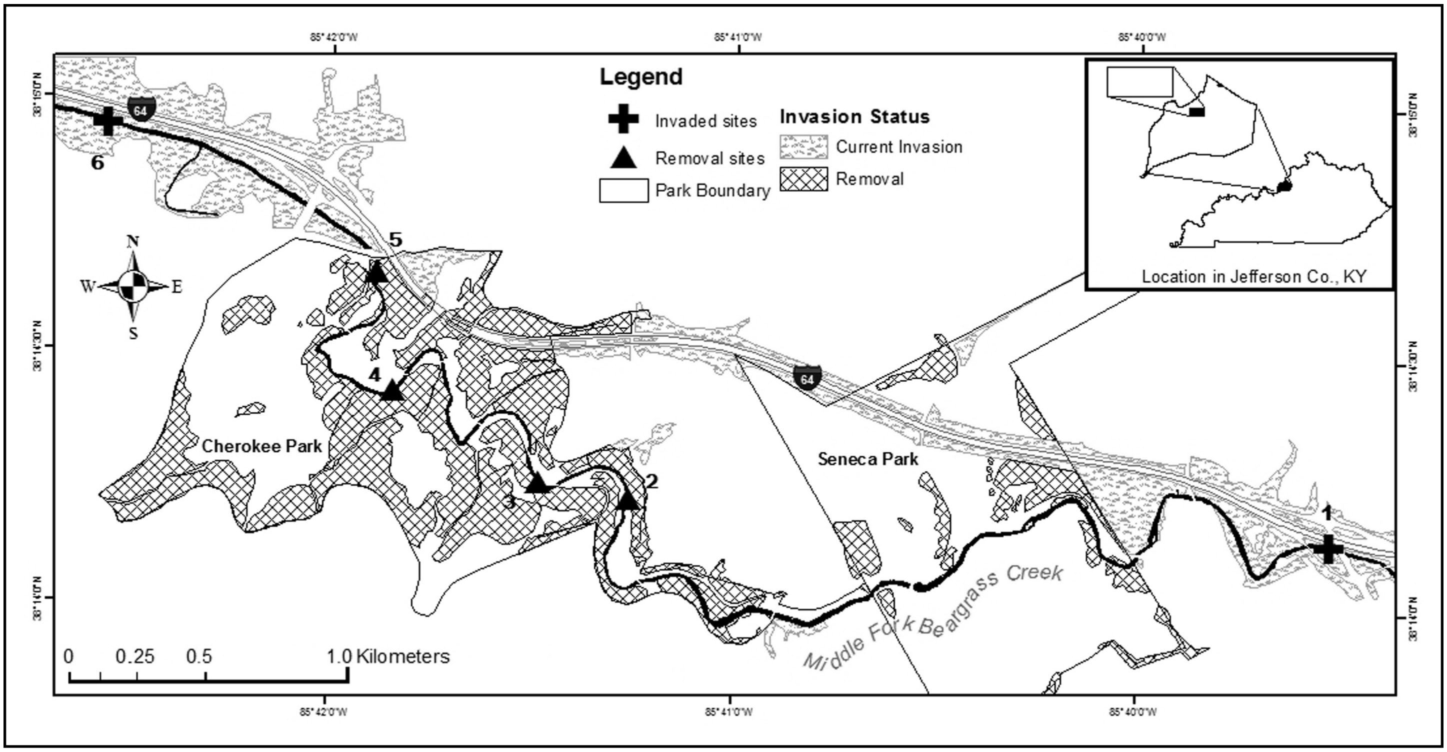

Figure 1. Map of numbered field sites along Beargrass Creek in Louisville, Kentucky. Features in this map were adapted from various maps made by Major Waltman and the Louisville Olmsted Parks Association, using the Louisville & Jefferson County Information Consortium (LOJIC) GIS library 1:20.137, 2013. Cartography by Catherine Fargen.

sieve and was retained by the 121-µm sieve was transferred to Whirl-paks® and stored in 70% ethanol. Once all collections were complete (both of arthropods >4 mm and those retained on 121-µm sieve) the material was transferred to petri dishes and sorted, identified under a dissecting microscope, and archived in glass vials. Invertebrates were identified to family (or lowest possible taxon) and assigned to functional feeding groups (FFG) based on Merrit et al. (2008) and Thorp and Covich (2001). If a taxon comprised more than one FFG, the FFG that the majority of species in the region belonged to was used (KDOW 2009; Johnson et al. 2013). Shannon diversity (H') and taxa richness were calculated for each replicate sample, and values from the three replicates per site per date were averaged for statistical analysis due to the loss of one sample in the lab (making site our experimental unit for these analyses).

Data Analysis

For each litterbag string at each site, the percent AFDM remaining for each litter type was plotted against time, and the first order exponential decay model was used to estimate the daily decomposition coefficients (k) (Peterson and Cummins 1973). A two-way mixed linear model was performed on the resulting k values using leaf litter species and stream invasion status as fixed factors and site as a random block term.

The data on average macroinvertebrate abundance, taxa richness, and Shannon diversity per replicate per site per collection day were analyzed using mixed linear models with variance components using stream invasion status and leaf litter species as fixed factors and days since deployment as a random covariate. These dependent variables were also analyzed on day 49, the last weekly sample day when both litter species were still present in litter bags, using ANOVA with litter species and invasion status as fixed factors. Additionally, abundances of each FFG were averaged per bag per replicate site per collection day and analyzed across all days and on day 49 using the same methods. Bonferroni corrections were not considered in order to minimize type II error, as suggested for many conservation studies, especially those with small sample sizes (e.g., Brosi and Biber 2009; Mudge 2013). Response variables were transformed [ln(x+1) or sqrt(x+1)] to better meet model assumptions. To compare macroinvertebrate community composition on day 49 (the last day when both litter types could be compared directly), we ran a PERMANOVA with leaf litter species and stream invasion status as factors. Community composition data were square-root transformed and the PERMANOVA was conducted on the Bray-Curtis similarity matrix. All statistical analyses were performed using SYSTAT (Version 12; SYSTAT 2007) or PRIMER (Anderson et al. 2008).

RESULTS

Lonicera maackii decomposed 70% faster than *A. saccharum,* based on comparing the AFDM k values calculated after 49 days of decay across all sites for *L. maackii* and across all sites after 112 days for *A.*

saccharum (species $F = 8.77$, $P = 0.006$; status $F = 0.49$, $P = 0.521$; species*status $F = 0.21$, $P = 0.654$; site $F = 0.99$, $P = 0.323$; Table 1) when *A. saccharum* had achieved an equivalent level of mass loss (92.1% for *A. saccharum* and 93.5% for *L. maackii* (Figure 2)). The average daily decay coefficients ranged from -0.019 to -0.072 for *A. saccharum* litter and -0.038 to -0.095 for *L. maackii* litter across all sites (Table 1). We found no evidence for effects of stream invasion status or interactive effects between litter species and stream invasion status on mass loss.

A total of 14,210 macroinvertebrates was collected and identified during the study, with 22% of individuals collected from *L. maackii* litter bags and 78% from *A. saccharum* litter bags. For both the entire study and for just the day 49 comparison, total macroinvertebrate abundance, taxa richness, and Shannon diversity did not vary with respect to litter species or site invasion status. Abundance and taxa richness increased over time, however (Tables 2, 3; Figure 3A, B). Members of Chironomidae, Oligochaeta, Asellidae, and Planariidae were by far the most widely represented taxa found in this study (Table 4). We found no significant differences in community composition at the family level between treatments (PERMANOVA – species: pseudo-$F = 0.75$, $P = 0.49$; status: pseudo-$F = 0.63$, $P = 0.58$; species*status: pseudo-$F = 0.35$, $P = 0.81$).

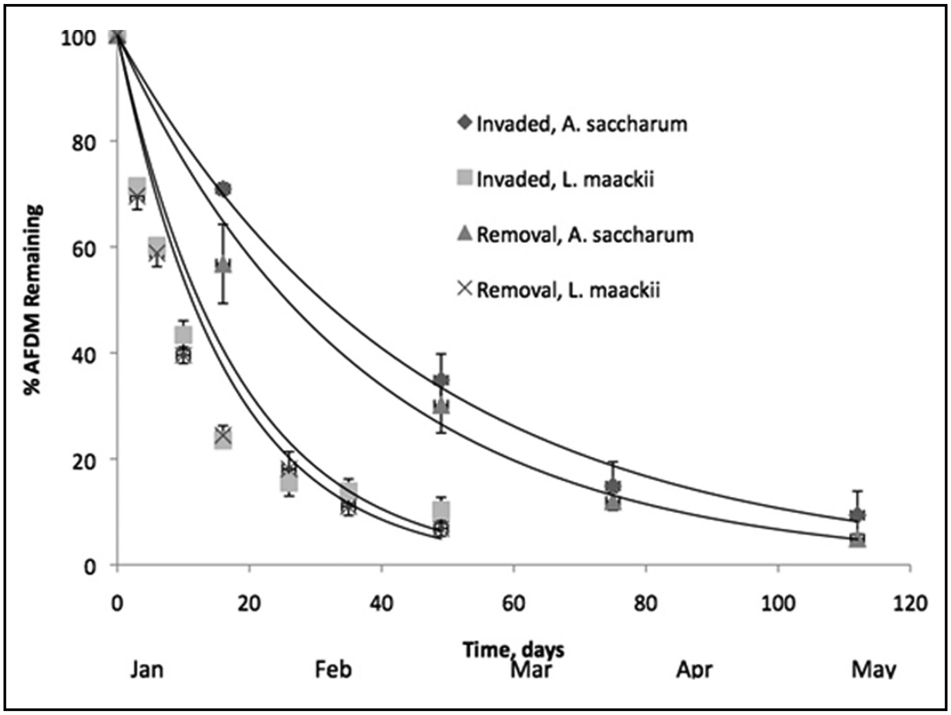

Figure 2. Mass loss curves (ash-free dry mass basis) for L. maackii and A. saccharum litters placed in Beargrass Creek alongside riparian sites invaded with L. maackii or where this invasive shrub had been removed one to two years previously. Error bars indicate ± 1 SE.

We determined that collector-gatherers were the most abundant FFG on both *A. saccharum* and *L. maackii* litter across all days, accounting for about 96% of all individuals (Figure 4A). Analyses of FFGs showed significant increases in numbers of collector-gatherers over time irrespective of litter species or site invasion status (Table 2, Figure 3C). Scrapers increased over time, and also showed significantly different responses to leaf litter species, with higher abundances on *A. saccharum* litter (Table 2, Figure 3E). There were no differences in numbers of collector-filterers or shredders over time or by treatment (Table 2). Predators responded to invasion status, and the interaction between invasion status and litter species, as well as time (Table 2, Figure 3D). Predators were on average six times more abundant in litter

Table 1. Average first order decay coefficients (-k as fraction AFDM loss per day) based on AFDM data corrected for sediment infiltration (see Methods) for litter bags deployed from 2 January to 20 May, 2012, in Middle Fork Beargrass Creek, Louisville, Kentucky. Site locations can be found in Figure 1.

Site	Stream Invasion Status	*Acer saccharum* Average from Day 0–112	*Lonicera maackii* Average from Day 0–49
1	Invaded	0.0442	0.0649
6	Invaded	0.0187	0.0384
2	Removal	0.0288	0.0954
3	Removal	0.0243	0.0450
4	Removal	0.0722	0.0675
5	Removal	0.0275	0.0553
Mean for All Invaded Sites		0.0315	0.0517
Mean for All Removal Sites		0.0382	0.0658

bags located in invaded sites compared to removal sites (5.86 versus 1.06 individuals/bag), with the largest abundances in *A. saccharum* litter bags (10.9 predators per bag in invaded sites, compared with 1.81 per bag in removal sites).

On the last day when both litter species were still present in bags, abundances of predators, scrapers, and shredders were all 3–4 times greater on *A. saccharum* litter compared to *L. maackii* litter, with predators also showing sensitivity to site invasion status (greatest abundance on *A. saccharum* litter in invaded sites; Table 3, Figure 4B).

DISCUSSION

This study showed that *L. maackii* litter decomposed approximately twice as quickly as *A. saccharum* litter, with mean residence times (1/k) of 19.5 versus 39.0 days, respectively. This trend is consistent with similar studies that found invasive *L. maackii* decomposed more quickly in aquatic environments than its various native counterparts (Lewis and Brown 2010; McNeish et al. 2012). This is unsurprising since the rate of decay between species depends largely on litter quality, and *L. maackii* is known to have a higher nitrogen and lower lignin content than *A. saccharum* (Trammell et al. 2012).

We found no evidence that streambank invasion by *L. maackii* affected decomposition rates of either species. While terrestrial studies have shown both positive and negative effects of *L. maackii* presence on leaf litter decomposition (e.g., Arthur et al. 2012; Trammell et al. 2012), to our knowledge, no prior studies have published information on the effects of riparian invasion by *L. maackii* on decomposition rates of other riparian zone species. However, we expected that in aquatic systems *L. maackii* could indirectly alter decomposition rates by altering both the biotic and abiotic environment, similar to *L. maackii* effects in terrestrial systems. For example, Trammell et al. (2012) cited potential influences on microclimate, soil chemistry, and decomposer communities as reasonable explanatory factors in their particular

Table 2. Mixed linear model statistics for abundance, taxa richness, Shannon diversity, and functional feeding groups across all days for litter bags deployed from 2 January to 20 May, 2012, in Middle Fork Beargrass Creek, Louisville, Kentucky. Significant factors ($P \le 0.05$) are in bold.

		Abundance		Taxa Richness		Shannon Diversity		Collector-Filterers		Collector-Gatherers		Predators		Scrapers		Shredders	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Time	1	**13.66**	**<0.001**	**26.58**	**<0.001**	1.1	0.364	0.4	0.757	**12.99**	**<0.001**	**9.12**	**<0.001**	**5.53**	**0.004**	2.08	0.125
Litter Species	1	0.37	0.547	2.04	0.164	1.02	0.321	0.07	0.801	0.27	0.61	4.02	0.054	**5.79**	**0.023**	2.07	0.161
Invasion Status	1	0.19	0.667	0.14	0.712	0.08	0.782	1.54	0.225	0.12	0.736	**12.85**	**0.001**	0.02	0.885	0.73	0.402
Invasion Status × Litter Species	1	0.03	0.859	0.32	0.859	0.03	0.868	0.84	0.367	0.01	0.927	**8.41**	**0.007**	0	0.999	1.78	0.192

Table 3. ANOVA statistics for abundance, taxa richness, Shannon diversity, and functional feeding groups, on Day 49 (20 Feb, 2012), the last weekly sampling date when both species were still present in litter bags placed in Middle Fork Beargrass Creek, Louisville, Kentucky. Significant factors ($P < 0.05$) are in bold.

		Abundance		Taxa Richness		Shannon Diversity		Collector-Filterers		Collector-Gatherers		Predators		Scrapers		Shredders	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Litter Species	1	1.82	0.214	3.44	0.101	0.14	0.722	0	0.999	1.56	0.246	**11.37**	**0.01**	**5.64**	**0.045**	**6.83**	**0.031**
Invasion Status	1	0.31	0.592	0.3	0.597	2.89	0.128	0.89	0.373	0.26	0.624	**19.06**	**0.002**	0.02	0.968	0.69	0.431
Invasion Status × Litter Species	1	0.05	0.832	0.37	0.56	1.84	0.212	0	0.999	0.03	0.86	**8.17**	**0.021**	0.28	0.614	0.37	0.561

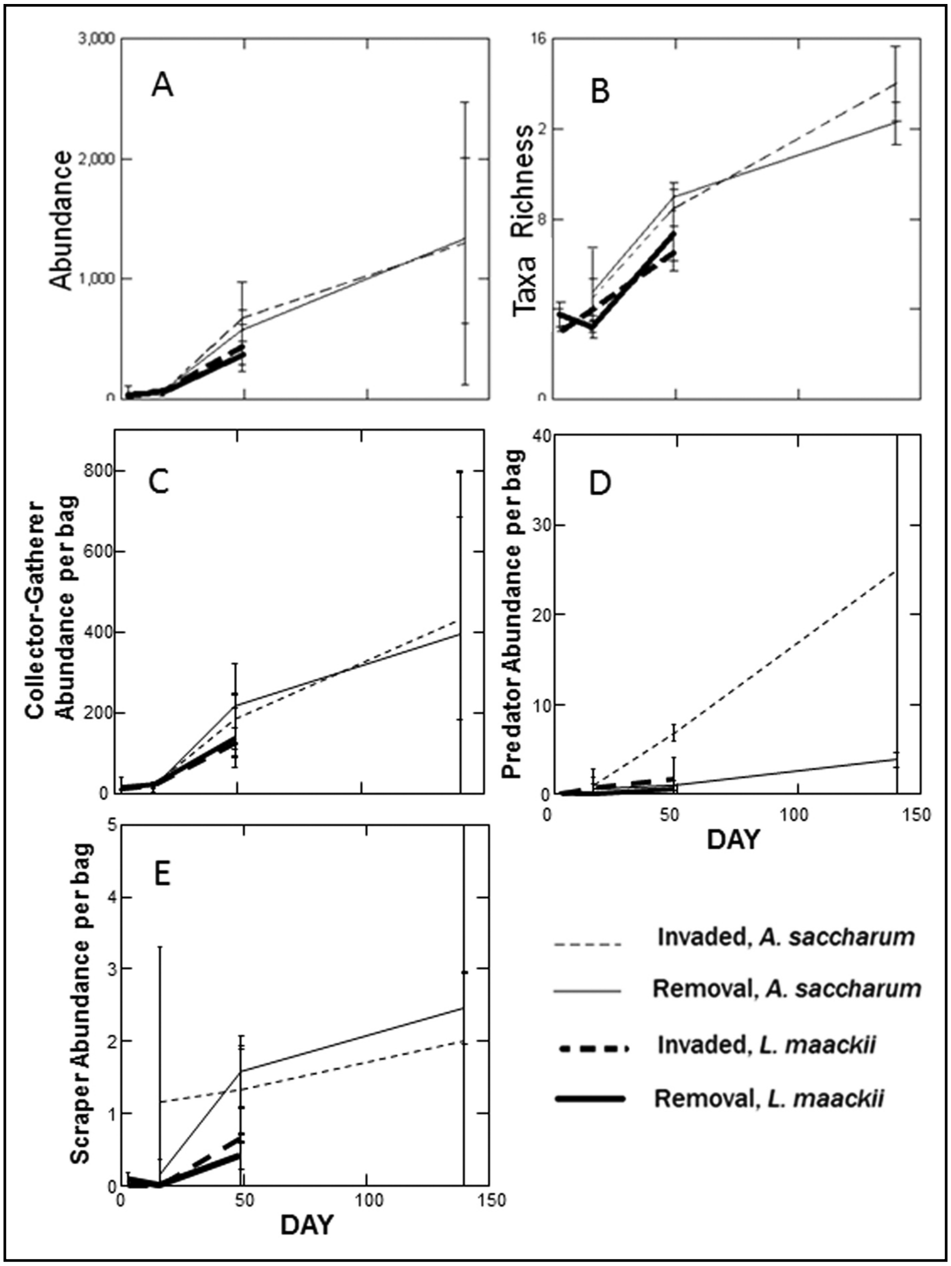

Figure 3. Time is the only significant factor influencing A) average macroinvertebrate abundance, B) average taxa richness, and C) collector-gatherer abundance per sample bag per site and litter type in Middle Fork Beargrass Creek, Louisville, Kentucky. Time as well as treatment influenced D) predator abundance, and E) scraper abundance. Day 0 is 2 Jan 2012. Error bars indicate ± 1 SE.

study. Arthur et al. (2012) attributed the effects of *L. maackii* to changes in microbial communities and potential changes in soil moisture. In riparian habitats, we expected that replacement of native trees with *L. maackii,* a low and overhanging shrub, could influence stream shading, altering both light and temperature. In general, decomposition is often slowed in cooler, shadier streams (Lagrue et al. 2011). However, light and temperature effects could have been undetectable due to the season in which our study was performed (winter), since leaves on *L. maackii* bushes and trees were not present for most of the study. Light and temperature measurements taken in June found significantly warmer air temperatures in removal versus invaded sites (26.8 °C versus 25.9 °C, respectively, $P = 0.04$; no differences in light), but this may not correspond to winter conditions. Alternatively, it is possible that lower inputs of native tree litter input along banks invaded by *L. maackii* would have left a legacy effect on the abundance or kinds of macroinvertebrates along these stream stretches.

As expected, we found that the per-date abundance and richness of macroinvertebrates across all sites and litter types increased with time. This was due to increases in collector-gatherers (especially Chironomidae, Oligochaeta, and Asellidae), the predators in Planariidae, and the scrapers in Physidae. These taxa were by far the most widely represented invertebrates found in this study and are tolerant to pollution associated with urban ecosystems (e.g., Lenat and Crawford 1994; Bacey and Spurlock 2007). We also found more scrapers and predators on *A. saccharum* litter compared to *L. maackii* litter over time, possibly due to extended colonization periods and changes in seasonal weather as *A. saccharum* decayed beyond the 49 days that it took the honeysuckle to decompose (Pond et al. 2003).

On the last day when both species were still present in litter bags, higher abundances of predators, scrapers, and shredders were supported in *A. saccharum* versus *L. maackii* litter. Shredders directly consume leaf litter and are known to show feeding preferences based on leaf litter chemistry, leaf toughness, and fungal colonization (Rong et al. 1995; Motomori et al. 2001; Bastian et al. 2007). Similarly, it has been documented that gastropods—which made up the largest group of scrapers in our study—are normally characterized as algal-feeders but can also process leaf litter (Brady and Turner 2010), and do show preferences for certain litter species over others (Lombardo and Cook 2002). *Acer saccharum* litter is tougher for shredders to consume, but also lacks allelopathic chemicals found in *Lonicera* tissues (Cippolini et al. 2008). In terrestrial systems, allelopathic compounds in plant tissues are known to reduce fungal colonization (e.g., Grove et al. 2012). Similarly, allochthonous inputs of allelopathic litter may support lower fungal colonization as well as directly repel shredders, resulting in reduced abundances of this FFG (Ervin and Wetzel 2003). Predator responses mim-

Table 4. Average number of each taxon per bag per site on day 49 and across all days. Functional feeding group (FFG) abbreviations are as follows: Collector-filterers (CF), collector-gatherers (CG), predators (P), scrapers (SC), and shredders (SH).

		Acer saccharum Litter in Invaded Site		*Acer saccharum* Litter in Removal Site		*Lonicera maackii* Litter in Invaded Site		*Lonicera maackii* Litter in Removal Site	
Taxon	**FFG**	**Day 49**	**Total**	**Day 49**	**Total**	**Day 49**	**Total**	**Day 49**	**Total**
Ancylidae	SC	0	0.17	0.25	0.17	0	0	0	0
Asellidae	CG	393.5	266.67	457.75	252.88	263	110.33	262.75	113.75
Cambaridae	SH	0	0	0	0.25	0	0	0	0
Chironomidae	CG	55	264.83	31.25	339.67	22.5	11	52.75	18.92
Coenagrionidae	P	9	4.83	0.5	1.67	3.5	1.83	0.25	0.08
Collembola	CG	1	7.83	0	1.75	0.5	2.83	0.25	1.67
Curculionidae	SH	0	0	0	0.08	0	0	0.25	0.08
Cyclopoidea	P	3	1	0.5	0.17	0.5	0.17	1	0.5
Elmidae	SC	0	0	0	0.08	0	0	0	0
Ephemeroptera	CG	0	0	0.25	0.08	0	0	0	0
Gammaridae	SH	5.5	11.17	6	2.33	0	0	1.25	0.42
Heptageniidae	SC	0.5	0.33	0	0	0	0	0	0
Hirudinea	P	0	4.5	0	0.33	1	0.33	0	0
Hydrachnida	P	0	1	0	0.92	0	0	0	0
Hydrobiidae	SC	0	0	0	0.08	0	0	0.25	0.08
Hydroptilidae	SC	0	0	0	0.17	0	0	0	0
Leptophlebiidae	CG	0.5	0.17	0.25	0.08	0	0	0.75	0.25
Lutrochidae	SH	0	0.17	0	0	0	0	0	0
Nematomorpha	P	0	0.17	0	0	0	0	0	0
Oligochaeta	CG	198	84.33	65.5	42.5	129.5	52.5	64.25	22.58
Physidae	SC	3.5	3.5	3	1.71	1.5	0.5	0.5	0.17
Planariidae	P	8.5	21.33	2	2.33	0	0	0.75	0.33
Planorbidae	SC	0	0	0.5	0.54	0.5	0.17	0.5	0.17
Pleuroceridae	SC	0	0.33	1	1.38	0	0	0	0
Psephenidae	SC	0	0.17	0	0.08	0	0	0	0
Psychodidae	CG	0	1	0	0	0.5	0.17	0.25	0.08
Ptilodactylidae	SH	0	0	0	0.08	0	0	0.25	0.08
Scirtidae	SC	0	0	0	0	0	0	0	0.08
Sphaeriidae	CF	0	0	0.25	0.63	0	0	0.25	0.08
Tipulidae	SH	0	0	0	0.17	0	0	0.25	0.08
TOTAL		678	675.83	571.5	655.25	423	179.83	386.5	159.5

icked these lower trophic level FFGs, most likely through trophic interactions (e.g., Johnson et al. 2013). It is notable that the predators were dominated by Planariidae (flatworms). In general, predators are lacking in many urban streams due to a lack of small soft-bodied prey items (Johnson et al. 2013). However, Planariids are known to feed on snail eggs (e.g., Lombardo et al. 2011), and so increases in scrapers could lead to increases in these predators. Our data are contrary to those found in a similar study (McNeish et al. 2012), which found higher densities of macroinvertebrates, especially collector-gatherers, on *L. maackii* rather than native leaf litter. The causes of these inconsistencies are not known, but could be due to different pre-existing invertebrate community assemblages, level of taxonomic resolution, and the different native litter types used. Although our stream system contained 10 out of the 14 invertebrate taxa found in the McNeish et al. (2012) study, we also found several additional taxa in low abundances that were not present in the other study.

The only evidence we found for indirect effects of *L. maackii* invasion on aquatic invertebrate communities was for preda-

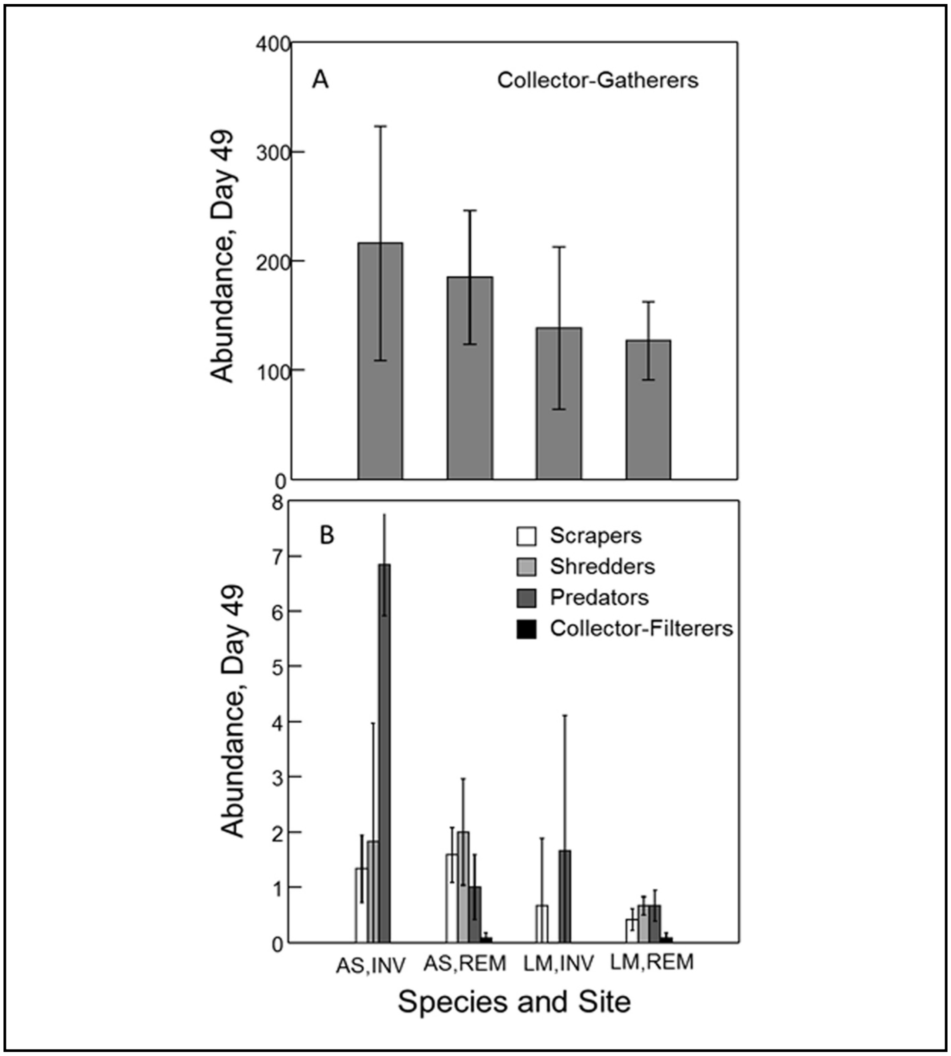

Figure 4. Average number of invertebrates per bag per site in Middle Fork Beargrass Creek, Louisville, Kentucky, grouped by functional feeding group on Day 49. Note very different scales on y-axis. AS = *Acer saccharum* litter, LM = *Lonicera maackii* litter, INV= sites invaded with *L. maackii*, REM = sites where *L. maackii* had been removed. Error bars indicate ± 1 SE.

tor abundances. Oddly, we found larger numbers of predators in invaded compared to managed habitats, but only on *A. saccharum* litter. Planarians are known to be only somewhat sensitive to pollution (e.g., Carmargo 1992), but the two invaded sites, 7 km apart in our study, were both upstream and downstream of all the managed sites (Figure 1), and so we expected that effects due to potential water chemistry differences would likely be cancelled out. Water temperature can influence planarian abundance (e.g., Roca et al. 1992; Durance and Ormerod 2010), so it is possible that removal sites were more exposed to direct sun earlier in the year and, therefore, warmer than ideal. Unfortunately, we lack water temperature data from before *Lonicera* leaf-out.

In addition to the fact that we conducted our study in winter when temperatures were cold and the *L. maackii* canopy was inactive for most of the duration of our study, lack of detectable indirect effects (effects of stream invasion status) in this study may be due to an overriding factor: urbanization. Urbanization influences hydrologic regimes and water chemistry in a number of ways that would mask the ability to detect a riparian plant colonization effect on stream litter decay. Increased impervious surface can lead to increased surface runoff, which alters streamflow patterns by increasing the frequency of high flows and altering base flow/storm flow dynamics. This, in turn, alters biological communities by decreasing suitable habitat (Konrad and Booth 2005). Higher nutrients in urban streams can increase microbial activity (Imberger et al. 2008), but pollution such as pavement sealant runoff can decrease invertebrate abundances and alter community assemblages (Bryer et al. 2010). A study by Chadwick et al. (2006) attempted to identify and quantify the biological, physical, and chemical effects of urbanization on stream ecosystem processes such as litter decomposition. The study concluded that effects of urbanization due to impervious surface, such as altered flow regimes and invertebrate biodiversity, can decrease leaf litter decay rates once impervious surface cover exceeds 30–40%.

CONCLUSION

Leaf litter decomposition is an essential ecosystem process that is responsible for supporting stream ecosystems and the cycling of nutrients. Therefore, factors that can change litter decomposition rates could have longstanding impacts throughout the rest of the aquatic food web. For instance, leaf litter that falls as a pulse into a stream in autumn in a deciduous forest typically supports the ecosystem throughout the winter months. However, if the rate of decomposition is increased such that organic matter leaves the system twice as quickly, as found in our study, then fewer resources could be available to invertebrates and subsequent trophic levels in the spring. Findings from our study show that the cumulative abundance of macroinvertebrates is lower on *L. maackii* litter, in part due to its relatively rapid decay. Streams with riparian zones densely colonized by this invasive shrub would be expected to have a low abundance of macroinvertebrates across a range in FFGs; this trend was detectable, even in this highly disturbed, urban stream. Anthropogenic influences such as increased impervious surface, increased nutrient inputs, and decreased riparian buffer zones have significantly influenced the leaf litter decomposition and associated invertebrate communities in stream ecosystems (Gulis and Suberkropp 2003; Chadwick et al. 2006; Krutzweiser et al. 2010), and the introduction of invasive plant species to riparian areas could have multiple cascading effects on aquatic structure and function. Managing *L. maackii* invasions in urban riparian habitats could help increase macroinvertebrate abundance over time, potentially increasing not only decomposition, but also other ecosystem services such as filtration, secondary production, and nutrient recycling as well (Lecerf and Richardson 2010).

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Catherine Fargen has a master's degree in Biology from the University of Louisville. She currently works for the US Geological Survey's Kentucky Water Science Center and has interests in stream ecology as well as surface and ground water quality.

Sarah Emery is an associate professor at the University of Louisville and broadly interested in biodiversity and the dynamics of terrestrial plant communities. Her current work focuses on plant–fungus interactions in Great Lakes sand dunes and agronomic systems. Other related interests include the role of dominant species in ecosystems, prairie and savanna restoration, and the management and population dynamics of exotic invasive species.

Margaret Carreiro is an associate professor at the University of Louisville and broadly interested in urban and suburban ecology, ecosystem ecology, soil ecology, and restoration ecology. Her current work focuses on impacts of invasive shrub honeysuckle and its management on plant communities, soil processes, and erosion in woodlands.

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