Removal of the Invasive Shrub, *Lonicera maackii* (Amur Honeysuckle), from a Headwater Stream Riparian Zone Shifts Taxonomic and Functional Composition of the Aquatic Biota

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Riparian plant invasions can result in near-monocultures along stream and river systems, prompting management agencies to target invasive species for removal as an ecological restoration strategy. Riparian plant invaders can alter resource conditions in the benthos and drive bottom-up shifts in aquatic biota. However, the influence of management activities on the structure and function of aquatic communities is not well understood. We investigated how removal of a riparian invader, *Lonicera maackii* (Amur honeysuckle), influenced aquatic macroinvertebrate community functional and taxonomic diversity in a headwater stream. We hypothesized that removal of *L. maackii* from invaded riparia would result in (H_1) increased aquatic macroinvertebrate abundance, density, and diversity; (H_2) a taxonomic and functional shift in community composition; and, in particular, (H_3) increased functional diversity. Aquatic macroinvertebrates were sampled monthly from autumn 2010 to winter 2013 in headwater stream riffles with a dense riparian *L. maackii* invasion and those where *L. maackii* had been experimentally removed. We found macroinvertebrate density was significantly higher in the *L. maackii* removal reach ($P < 0.05$) and that macroinvertebrate community structure and functional trait presence was distinct between stream reaches and across seasons ($P < 0.05$). The removal reach exhibited greater functional richness during spring and summer and had more unique functionally relevant taxa (20% and 85%) compared with the *L. maackii* reach (5% and 75%) during summer and autumn seasons. Our results suggest bottom-up processes link restoration activities in the riparian corridor and aquatic biota through alterations of functional composition in the benthic community.

Nomenclature: Amur honeysuckle, *Lonicera maackii* (Rupr.) Maxim.

Key words: Community, diversity, macroinvertebrate.

Taxonomic and functional diversity within ecological communities are shaped by biotic and abiotic conditions and influence broader ecosystem processes (Allison 2012; Webb et al. 2010; Xiao et al. 2012). Biotic interactions (e.g., competition, facilitation) and environmental "filter effects" (e.g., hydrologic and temperature gradients) influence community composition and trait presence from plot-to-global spatial scales (Gross et al. 2009; Lamouroux et al. 2002; McGill et al. 2006; Olden and Kennard 2010; Reich and Oleksyn 2004). Changes in environmental conditions can select for certain functional traits and influence species abundance in communities (Ackerly and Cornwell 2007; Allison 2012; Case 1981; Funk et al. 2008; Gross et al. 2009; Lamouroux et al. 2002; McGill et al. 2006; Webb et al. 2010). Developing a predictive framework for how forest management activities influence ecological communities depends on understanding how organisms with particular traits respond to changing resource conditions (Keddy 1992; Weiher and Keddy 2001).

Management Implications

Developing a predictive framework for how forest management activities influence ecological communities depends on understanding how organisms with particular traits respond to changing resource conditions. We provide evidence that riparian removal of the invasive shrub *Lonicera maackii* (Rupr.) Maxim. (Amur honeysuckle) is linked to the taxonomic and functional trait composition of aquatic macroinvertebrate communities. There are at least two important implications for management. First is the basic discovery that terrestrial invasion influences stream communities. Land management activities associated with invasive species control are often focused on addressing issues related to upland concerns, including creating space for vernal wildflowers or tree seedlings, while management of streams is often focused on issues such as pollution from urban outfalls or agricultural runoff. Our findings provide support for considering riparian management of invasive species as a technique aimed at influencing the aquatic biota. Second, the *L. maackii* removal in this study represented a relatively short distance (150 m) of a much longer stream and the area above the removal was heavily invaded. Many parks in the American Midwest exist as longitudinally elongated stretches along streams with upstream and downstream areas in private ownership. For instance, of the nature parks in the park district where this project took place, there are two larger parks (>60 ha; both with streams) and 11 others that are an average of 4.9 ha in size. Our results indicate that management activities that result in removal of *L. maackii*, even within small reserves in otherwise heavily invaded forests, can have strong influences on the aquatic biota within headwater streams.

The ecology of riparian zones is well understood to play an important role in mediating biodiversity and ecosystem processes in aquatic systems (Baxter et al. 2005; Gregory et al. 1991; Naiman and Decamps 1997). Vegetated riparian zones function as nutrient sinks, prevent bank erosion, and support the transfer of ecosystem subsidies between terrestrial and aquatic habitats (Baxter et al. 2005; Gregory et al. 1991). Alterations in the riparian zone via natural disturbance events (e.g., fire) and anthropogenic activities (e.g., stream channelization) can influence terrestrial–aquatic connections with potential impacts on aquatic biota and how these communities assemble (Dwire and Kauffman 2003; Garssen et al. 2015; Jacobs et al. 2007; Walsh et al. 2005). Headwater streams are more tightly linked with their riparian zones and receive more terrestrial organic matter inputs compared with larger rivers because of the size of the aquatic system in relation to the edge area; this results in aquatic communities within headwater streams being highly responsive to changes in the riparian zone (Richardson et al. 2010). These cross-system interactions are especially important in areas where native vegetation has been highly fragmented by agricultural, suburban, and urban development (Hladyz et al. 2011a), and these conditions are highly conducive to exotic species invasions (Johnson et al. 2006; Yates et al. 2004). Plant invasions along riparian zones often replace native vegetation and contribute large amounts of leaf and woody organic matter

to the aquatic system (Hladyz et al. 2011b). Riparian invasive plant species have strong potential to shift the flow of resources from donor riparian zones to recipient streams and thus can have bottom-up effects on aquatic biota and shift food web structure within and at the interface of terrestrial and aquatic systems (Ehrenfeld 2010; Hladyz et al. 2011b; Keeton et al. 2007; Polis and Strong 1996). Documented shifts in trophic structure associated with plant invasions suggest that impacts may flow up through the food web, impacting fish, birds, and other wildlife (Hladyz et al. 2011b; Levin et al. 2006).

Lonicera maackii (Rupr.) Maxim. (Amur honeysuckle) is considered an invasive shrub in forests throughout much of the contiguous United States and has densely invaded the riparian zones surrounding headwater stream systems in much of the American Midwest (Figures 1a and 1c; McNeish et al. 2015; USDA 1999). This invasive plant is known to suppress the survivorship and reproduction of some native plant species and to alter forest understory recruitment, possibly through resource competition and allelopathic activity (Collier et al. 2002; Gorchov and Trisel 2003; McEwan et al. 2010). *Lonicera maackii* has been reported to also influence arthropod diversity, survivorship, and community dynamics (Buddle et al. 2004; Christopher and Cameron 2012; Cipollini et al. 2008b; Conley et al. 2011; Loomis et al. 2014; McEwan et al. 2009; McNeish et al. 2012; Shewhart et al. 2014). For example, Shewhart et al. (2014) demonstrated that survivorship of the aquatic *Culex pipiens* L. (Dipteran: Culicidae) mosquito larva, a disease vector for West Nile Virus, increased when exposed to *L. maackii* leaf and flower leachate. *Lonicera maackii* leaf litter is high in nitrogen, supports a unique microbial community, and leaf breakdown is up to 5 times faster than native leaves (Arthur et al. 2012; McNeish et al. 2015; Poulette and Arthur 2012; Trammell et al. 2012). *Lonicera maackii* shrubs have been estimated to utilize ~10% of available water resources in wetland forests (Boyce et al. 2012) and reduce throughfall volume available to the forest floor in second-growth forests (McEwan et al. 2012), which suggest this invasive plant influences water resources. Collectively, these studies identify *L. maackii* effects that span multiple ecological scales and suggest this species has similar impacts to those of other invasive plants (e.g., Ballard et al. 2013; Chittka and Schürkens 2001; McNeish and McEwan 2016; Myers and Anderson 2003; Oliver 1996,), making *L. maackii* a good model species to study how riparian invasion influences terrestrial–aquatic linkages.

Our previous work demonstrated that *L. maackii* had effects on headwater streams that may be connected to the in-stream availability of resources that drive the structure of aquatic communities (McNeish et al. 2012, 2015). For instance, in an aquatic leaf pack experiment we found that *L. maackii* leaf breakdown was about four times faster compared with native leaf packs and supported different macroinvertebrate taxonomic and functional feeding group

Figure 1. *Lonicera maackii* riparian invasion (a) compared with a noninvaded primary headwater stream (b). Black Oak riparian forest prior to *L. maackii* removal (c) and post removal (d). Photo credit: R. E. McNeish and R. W. McEwan.

abundances (McNeish et al. 2012). In another study, we reported significantly lower autumnal in-stream leaf litter, lower macroinvertebrate densities, and reduced light available to the aquatic system in *L. maackii*–dominated stream reaches compared with reaches where *L. maackii* had been removed (McNeish et al. 2015). These studies suggest that terrestrial invasion alters basal resources in these streams, potentially resulting in bottom-up effects on the macro-invertebrate community (McNeish and McEwan 2016; McNeish et al. 2015). Past work lends strong support to the notion that riparian invasion alters aquatic habitat and food resources. However, little is known about how aquatic biota respond to removal of riparian invasive species and, to our knowledge, no previous work has addressed this response in terms of functional complexity within the aquatic biota. In this study, we focused on a headwater stream with an intense riparian invasion and our goal was to investigate how removal of *L. maackii* influenced benthic macroinvertebrate density, community composition, and functional diversity. We hypothesized that *L. maackii* removal would result in (H_1) increased macroinvertebrate density and taxonomic and functional diversity compared with *L. maackii*–invaded stream reaches. We further hypothesized that *L. maackii* removal would be accompanied by (H_2) a functional and taxonomic shift in the macroinvertebrate community and,

particularly, that removal would result in a (H_3) divergence and increase in the trait distribution (increased functional diversity) relative to the invaded stream reach.

Materials and Methods

Experimental Design. Black Oak Park stream (BO) is an unnamed tributary within the Little Miami River watershed located in southwestern Ohio (84.12°W, 36.63°N). This is a third-order headwater stream with benthic substrata of sand, clay, and rocks and a streambed 1.5 to 5.0 m wide underlain by limestone geology (Schneider 1957). As part of an ecological restoration project, *L. maackii* was removed from a 160-m stream reach from August to September 2010 as described in McNeish et al. (2015). All woody invasive plants were removed from a 160 by 5–m area directly along each stream bank to create a *L. maackii* removal reach and an upstream *L. maackii* (nonremoval) reach (the honeysuckle reach). The instream buffer between the start of the removal reach and the end of the honeysuckle reach (200-m reach) was an additional 10 m where *L. maackii* had been removed. All native plant species were left intact and all native species coarse organic matter (COM; e.g., leaves, snags) were left in place. AquaNeat® Aquatic Herbicide, an Ohio EPA-approved aquatic herbicide (EPA regulation number: 228-365; Nufarm Manufacturer; active

ingredient Glyphosate N-glycine), was applied to cut stumps of invasive species within 48 h to prevent regrowth in future growing seasons. Maintenance removal took place twice after *L. maackii* removal to prevent regrowth in the removal zone. This included removal of new growth by hand either with hand saws or pulling seedlings from the ground. The experimental stream reach was located within the Centerville–Washington Park district and all aspects of the project were undertaken in cooperation with park district land managers.

Pretreatment measurements indicated there were no preexisting differences in abiotic or biotic conditions along the experimental stream reach. Both stream reaches had similar numbers of riffle habitats and benthic substrata (pebbles, gravel, clay). The pretreatment macroinvertebrate community (McNeish et al. 2012) was similar in composition to the macroinvertebrate community in the honeysuckle-invaded reach in this study. In addition, algal growth measured from another study was found to be similar along the entire reach, including areas which became the "removal" and "honeysuckle" treatments (McNeish et al. 2015). Stream temperature data collected from studies conducted concurrently with this study indicated there were no temperature differences between the honeysuckle (4.4 to 22.2 C) and removal (3.8 to 22.2 C) stream reaches.

Ambient Conditions.   To assess variation in forest canopy conditions following honeysuckle removal, canopy cover and light availability were recorded monthly at random locations within each riffle. Canopy cover was measured with a spherical densiometer in the North, South, East, and West cardinal directions (Lemmon 1959). Light was measured at the surface of the water with a waterproof Milwaukee MW700 standard Portable Lux Meter concurrently with densiometer readings.

Several nutrient parameters were measured monthly from October 2012 to December 2013 in both honeysuckle-invaded and removal stream reaches. One-L water samples were collected at the upstream edge of each riffle ($n = 5$ riffles per reach) along the width of the stream in an acid-washed amber Nalgene container. Samples were stored on ice in the field and then transferred to 4 C in the lab. Samples were processed and analyzed within 24 h for nutrient concentration via colorimetric methods. Total orthophosphate (PO_4-3) was assessed using the malachite green method (D'Angelo et al. 2001). Five-mL samples were acidified with a 1.75% (w/v) ammonium heptamolybdate tetrahydrate solution in 6.3 N sulfuric acid (8.75 g ammonium molybdate and 87.5-mL concentrated sulfuric acid 0.4 L^{-1}) and shaken for 10 min with a benchtop shaker. A 0.035% (w/v) solution of Malachite Green carbinol hydrochloride in 0.53% (w/v) aqueous polyvinyl alcohol solution (0.175 g Malachite Green and 1.75 g polyvinyl alcohol 0.5 L^{-1}) was added to the sample and then shaken for 20 min. The absorbance at 630 nm measured with a spectrophotometer was used to calculate orthophosphate concentrations (P). Nitrogen was represented as the forms of nitrite (NO_2–N), nitrate (NO_3–N), and ammonia (NH_3–N) and analyzed based on available laboratory equipment with the DREL 2800 water quality kit from Hach Company. Nitrite was determined via the diazotization method and read at 507 nm. The cadmium reduction method was used to identify nitrate concentrations colorimetrically at 500 nm after correction for nitrite interference with the addition of bromine water and phenol solution per Hach Company Method 8171. Ammonia was quantified using the Nessler method and absorbance was measured at 524 nm. Total suspended solids (TSS) were measured photometrically at 810 nm after the water sample was homogenized for 2 min with a blender. All colorimetric and photometric measurements were recorded with a DR 2800 Spectrophotometer from Hach Company.

Benthic Macroinvertebrate Sampling.   The benthic macroinvertebrate community was sampled monthly from September 2010 to December 2013 via a Surber sampler ($n = 5$ riffles per reach per month for 28 months; study total $n = 256$) when the stream was flowing and not frozen. The Surber sampler was haphazardly placed in a riffle, and all benthic substrata within a 30 by 30–cm area were scrubbed with a brush to dislodge aquatic macroinvertebrates and COM. All dislodged materials were captured in the sampler net (mesh 280 µm) and preserved in 70% ethanol on site and then transported to a laboratory where macroinvertebrates were identified to genus when possible using Merritt et al. (2008), Peckarsky et al. (1990), and Thorp and Covich (2001). Otherwise, taxa were identified to family or order level as presented in Table S1.

Statistical Analyses.   Macroinvertebrate total density, taxon richness, and taxonomic diversity were evaluated as response variables to riparian honeysuckle removal. Total density represented the number of macroinvertebrate individuals per m^2, taxon richness was the sum of the number of taxa, and diversity was calculated using Hill's numbers (effective taxon numbers) as presented in Jost (2006). Macroinvertebrate density, richness, and diversity failed the Shapiro–Wilk normality test. Thus, these metrics were analyzed with the Wilcoxon matched-pairs test to test for differences between the honeysuckle removal and nonremoval reaches over the sampling period (Sokal and Rohlf 1981; Zar 1999). Macroinvertebrate community taxonomic structure was visualized with nonmetric multidimensional scaling (NMDS). A total of three NMDS tests were conducted using a sample-by-taxon abundance matrix with *metaMDS()* (max try of 100 iterations, Bray-Curtis similarity distance) using the 'vegan' package in R (McCune and Grace 2002; Oksanen et al. 2015). The second and third NMDS ordinations were conducted from the previous best NDMS result. *Procrustes* and *Protest* analyses were conducted between the second and third NMDS

solutions to ensure the final NMDS result was a stable solution. The *Procrustes* test can be used to resize and rotate two ordinations in order to match them for a best-fit solution between the ordinations (Jackson 1995). The difference between each ordination datum and its corresponding partner is then calculated and summed, resulting in the residual sum squared (m^2) that indicates the concordance or similarity between the two ordinations (Jackson 1995). A small m^2 indicates the two ordination solutions are very similar. All m^2 values were <0.0001 (*protest()* using 'vegan'), indicating the final NMDS result was a stable solution relative to previous NMDS solutions. The effect of stream reach (honeysuckle removal and nonremoval) and sampling season (spring, summer, autumn, and winter) and the interaction of these two factors on community dynamics were analyzed using ADONIS (*Adonis()*) in the 'vegan' package.

We took a trait-based approach to evaluate how macroinvertebrate communities responded functionally to *L. maackii* removal. Seven ecological, life history, and morphological functional traits (resulting in 26 trait states; Table 1) were linked with each aquatic macroinvertebrate taxon (Table S1). Traits were identified from those described in Poff et al. (2006) that were considered most likely to be influenced by alterations in terrestrial–aquatic connections. For taxa that were not identified to genus, the most prevalent trait of the broader (e.g., family) taxonomic assignment was chosen or a representative genus trait selected based on most-complete trait information available (Beche et al. 2006). These traits (Table 1) were used to calculate macroinvertebrate functional diversity (FD) indices. Eleven taxa (out of 50) were removed from FD analyses due to insufficient information in the literature to confidently assign a trait state to each trait for these taxa.

Macroinvertebrate FD was calculated via functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) for each sample. Functional richness represents the volume of trait space utilized in *n*-dimensional space, which is the degree of functional convergence or divergence of a community (Mason et al. 2005; Petchey and Gaston 2006; Villéger et al. 2008). Larger FRic values for one treatment indicate more trait space is utilized or filled compared with a treatment with small FRic values (functional divergence; Boersma et al. 2015). Functional evenness represents how even the distribution of traits are in trait space (Mason et al. 2005; Villéger et al. 2008). Functional dispersion detects trait abundance shifts via differences in the relative abundance of traits in each community (Boersma et al. 2015; Laliberté and Legendre 2010). Functional diversity metrics were calculated with a sample-by-trait value presence and absence matrix and a sample-by-species abundance matrix using *dbFD()* from the 'FD' package in R (Laliberté et al. 2015). The cailliez method was used to calculate distance matrices since matrix distance could not be represented in Euclidean space (Laliberté et al. 2015). Functional diversity metrics were checked for normality via the Shapiro–Wilk test and then analyzed with the Wilcoxon matched-pairs test to analyze temporal changes in FD metrics between stream reaches. Overall functional trait community composition was visualized with NMDS using a sample-by-trait value presence and absence matrix (max try of 100 iterations with the Jaccard similarity index) in R using 'vegan'. Functional community trait dynamics were visualized and statistically analyzed as previously explained for taxonomic macroinvertebrate community dynamics. Functional indicator species (functionally relevant taxa compared with other taxa in the same community) were identified as presented by

Table 1. Description of macroinvertebrate functional traits (7) and their trait states (26) used for functional diversity calculations and nonmetric multidimensional scaling community dynamics.

Category	Trait	Trait states
Life history	Voltinism	Semivoltine, univoltine, Bi- or multivoltine
	Development	Slow season Fast seasonal Nonseasonal
Morphology	Respiration	Tegument, gills, aerial
	Size at maturity	Small (<9 mm), medium (9–16 mm), large (>16 mm)
Ecology	Trophic habitat or functional feeding group	Collector–gatherer Collector–filterer Herbivore Detritivore Predator
	Thermal preference	Cold stenothermal/cool Eurythermal, cool/warm Eurythermal, warm Eurythermal
	Habitat	Burrower, climber, sprawler, clinger, swimmer, skater

Ricotta et al. (2015). The functional association was identified for each taxon by measuring the functional distance between the centroids of all samples for each grouping factor and the indicator species (Ricotta et al. 2015). Overall FRic at the community scale was calculated for removal and honeysuckle stream reaches and across seasons by calculating the volume of each community's convex hull (as identified from NMDS results) using *convhulln()* from the 'geometry' package in R (Barber et al. 2015).

Macroinvertebrate functional feeding groups (FFG; trophic habitat trait) within and between stream reaches were calculated as the relative abundance of each FFG per sample. FFG trait states were assigned as presented in Table S1. All FFG data were non-normal; therefore, differences in FFG relative abundances within stream reaches were determined with Friedman's test and between stream reaches (i.e., FFG between stream reaches) were analyzed using Wilcoxon matched-pairs test (Sokal and Rohlf 1981; Zar 1999). FFG pairwise comparisons within each reach were conducted using the *post.hoc.friedman.nemenyi.test()* with the 'PMCMR' package in R (Pohlert 2015).

Differences in ambient conditions were identified between stream reaches for canopy cover, light availability, and nutrient dynamics. All conditions were non-normal and analyzed with the Wilcoxon matched-pairs test within and between stream reaches (Sokal and Rohlf 1981; Zar 1999).

Results and Discussion

Ambient Conditions. Abiotic conditions were strongly influenced by removal of the *L. maackii* riparian invasion. Above-stream canopy cover was significantly greater in the stream reach dominated by *L. maackii* (honeysuckle reach) compared with the experimental reach where *L. maackii* had been removed (removal reach), resulting in a substantial increase in light availability (Figure 2; Figure S1; Table S2). Canopy cover and light availability followed typical seasonal

patterns, with canopy cover peaking during growing seasons and light availability peaking during winter months (Figure 2). All physiochemical parameters were statistically indistinguishable between stream reaches and therefore were not further discussed in this paper (Table S2; Figure S2).

Macroinvertebrate Density and Richness. Macroinvertebrate density and abundance in the honeysuckle reach differed from the removal reach. Over our 28-mo sampling period that was represented by approximately 26,000 macroinvertebrates, the total abundance was two times higher in the removal reach than in the honeysuckle reach (Table S3). The removal reach supported significantly higher macroinvertebrate density and taxonomic richness compared with the honeysuckle reach for most sampling dates (Figure 3; Table S2). Chironomidae (Diptera) and Naididae (Oligochaeta) combined comprised over 80% of the individuals present in both honeysuckle and removal reaches (Table S3). Removal of *L. maackii* resulted in increased Diptera and Trichoptera (true flies and stoneflies) abundance and a 23% reduction in snail (*Pleurocera* and *Physella*) abundance compared with the honeysuckle reach. Macroinvertebrate densities peaked during the spring months, with densities generally greater in the removal reach one year after *L. maackii* removal (Figure 3). A total of 50 taxa were identified in the entire study system, 33 of which were observed in both stream reaches, 7 were unique to the honeysuckle reach, and 10 were unique to the removal reach (Table S3). Taxonomic richness generally increased earlier in the honeysuckle reach but peaks lasted longer in the removal reach (Figure S3a).

Taxonomic and Functional Diversity. Functional and taxonomic characteristics of the macroinvertebrate communities significantly varied between experimental reaches and with time (Table S4). The macroinvertebrate communities were taxonomically distinct between reaches during the spring as
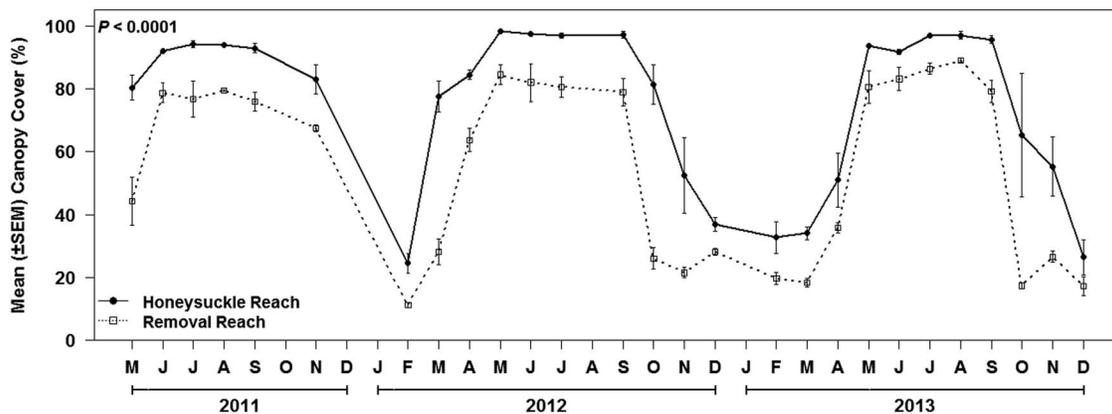

Figure 2. Mean above-stream canopy cover in honeysuckle and removal stream reaches. Letters on the x-axis represent sampling months for years indicated.
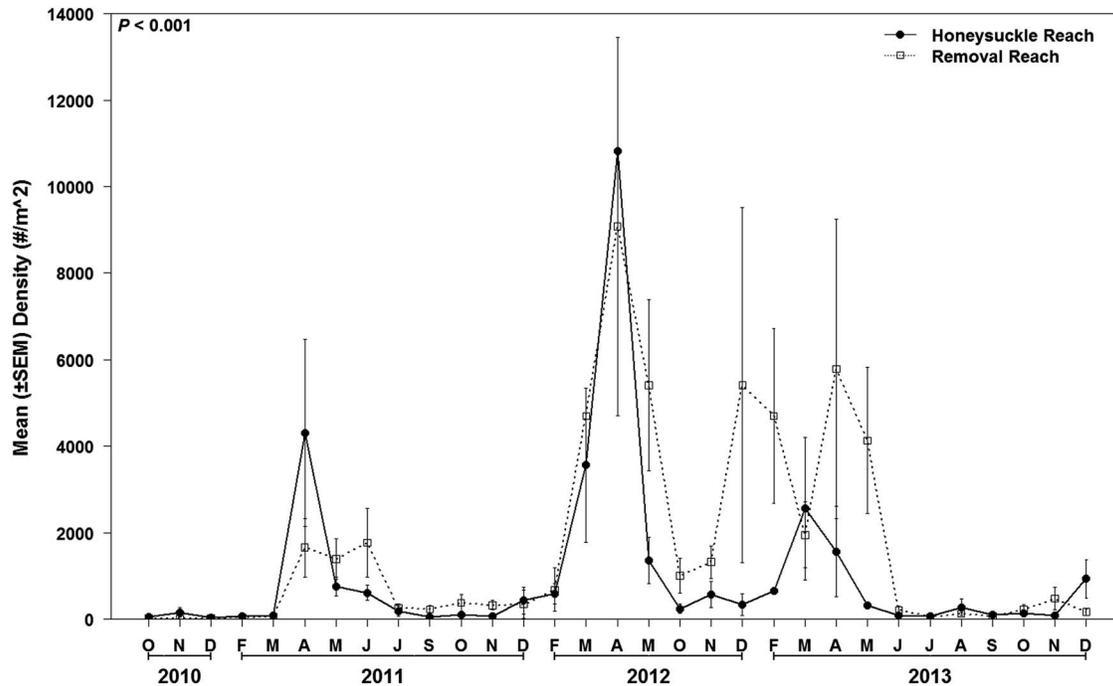
Figure 3. Macroinvertebrate density present within honeysuckle and removal stream reaches. Letters on the x-axis represent sampling months for years indicated.

indicated by separation of community centroids in multidimensional space (Figure 4a; $P = 0.019$; Table S4). Although separation was visually evident in summer, the communities were not statistically different ($P > 0.05$). In the autumn, there was again a significant effect ($P < 0.01$; Table S4); however, in the winter, the centroids largely overlapped and the communities were not statistically distinguishable (Figure 4d). Using a functional trait matrix in the ordination instead of taxonomic values yielded contrasting results (Figure 5). The community functional traits were statistically indistinguishable between reaches during spring, autumn, and winter but differences were detected during summer (Figure 5; $P = 0.0471$). Overall macroinvertebrate community functional richness (as calculated by volume of the convex hull) occupied 86% of trait space in the honeysuckle reach communities whereas the functional richness of removal communities occupied 49% regardless of season (Table 2). Communities in the removal reach during spring and summer seasons had a functional richness that was approximately 1.7 times greater than the honeysuckle reach. Community functional richness in the honeysuckle reach was approximately 1.4 and 2.8 times greater than the removal reach during autumn and winter seasons, respectively (Table 2). Removal of the *L. maackii* riparian forest did not affect the taxonomic diversity, trait space occupied (FRic), trait evenness distribution (FEve), or relative abundance of trait combinations over time (trait shift: FDis; Figures S3b and S4).

A variety of functionally relevant taxa were associated with specific stream reaches and seasons (Tables 3 and 4; Table S5).

Diptera taxa were the most common functionally relevant group in the removal reach, whereas Coleoptera (beetles) and Hirudinea (leeches; i.e., Arhynchobdellida, Rhynchobdellida) were some of the most functionally relevant taxa in the honeysuckle reach (Table 3). Interestingly, many of the indicator taxa in the honeysuckle reach communities were classified as medium to large body sized, whereas taxa indicative of the removal reach were mainly small bodied (Table S1). During spring and winter seasons, most functionally relevant taxa in the removal reach communities were also present in the honeysuckle reach (Table 4). The removal reach had more unique functionally relevant taxa (20 and 85%) compared with the honeysuckle reach (5% and 75%) during summer and autumn seasons, respectively (Table 4). Overall, the *L. maackii*–invaded stream reach supported a macroinvertebrate community that was both taxonomically and functionally distinct from the removal reach and varied over seasons. Macroinvertebrate FFG relative abundance was significantly affected by the removal of the *L. maackii* riparian forest (honeysuckle reach: $X^2 = 25.804$, df = 4, $P < 0.0001$; removal reach: $X^2 = 36.927$, df = 4, $P < 0.0001$). Herbivores were more abundant than predators within the honeysuckle reach (P < 0.05; Figure 6a). Within the removal reach, predator and herbivore relative abundance was less than all other FFG (all $P < 0.05$; Figure 6b). Herbivore relative abundance was significantly greater in the honeysuckle reach compared with the removal reach (Table S2; Figure S5b). Collector–gatherer relative abundance was the dominant

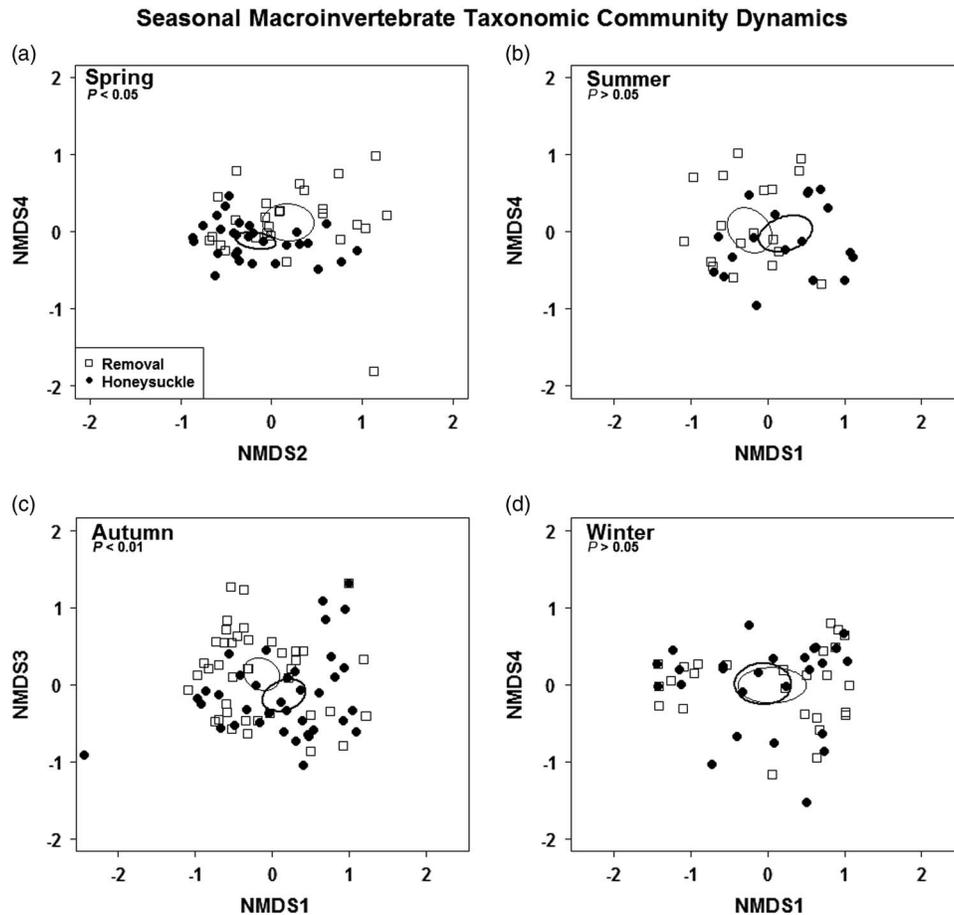## Seasonal Macroinvertebrate Taxonomic Community Dynamics

Figure 4. Taxonomic community relationships between stream reaches within each sampling season. Panels represent 4-D nonmetric multidimensional scaling (NMDS) results on a 2-D axis with standard error 95% confidence ellipses for stream reach and season.

FFG within both stream reaches (all $P < 0.05$; Figure 6). All other FFG relative abundances were similar between reaches (Figure S5).

Aquatic communities are linked to landscape characteristics and ecosystem subsidies including nutrient runoff, leaf litter, and woody debris (Baxter et al. 2005; Townsend et al. 2003). Riparian invasive plants can have substantial impacts on terrestrial–aquatic linkages via alteration of these subsidies (Greene 2014; McNeish et al. 2015). For example, Russian-olive (*Elaeagnus angustifolia* L.) is a riparian invasive tree in the western United States known to increase instream terrestrial organic matter subsidies and organic nitrogen, altering stream ecosystem efficiency and biogeochemistry (Mineau et al. 2011, 2012). Tree-of-heaven [*Ailanthus altissima* (Mill.) Swingle], an invasive tree throughout much of North America and Europe, deposits leaf litter subsidies into aquatic systems that break down faster than native leaf litter species (Swan et al. 2008). In an aquatic leaf litter colonization experiment, the invasive tree Norway maple (*Acer platanoides* L.) supported 70% greater Nemouridae (Spring stoneflies; detritivores/shredders)

abundance compared with native black cottonwood (*Populus trichocarpa* T. & G.; Reinhart and VandeVoort 2006). These studies suggest that replacement of native trees by invasive plant species can alter terrestrial subsidies available in aquatic systems that serve as critical habitat and food resources for aquatic biota. The impact of riparian invasion on aquatic biota could be particularly important in headwater streams in deciduous forests where subsidies from the terrestrial environment are a vital resource for aquatic communities (Vannote et al. 1980). *Lonicera maackii* is a highly successful invasive species in the American Midwest and is an aggressive colonizer of riparian areas. Our previous work demonstrated *L. maackii* riparian invasion has the potential to substantially influence headwater streams (McNeish et al. 2012, 2015). Due to the ubiquity of *L. maackii* invasion in regional forests, removal of this species has become a key priority for many land management agencies and is seen as a form of ecological restoration; however, little is known about the implications of this activity for benthic functional communities.

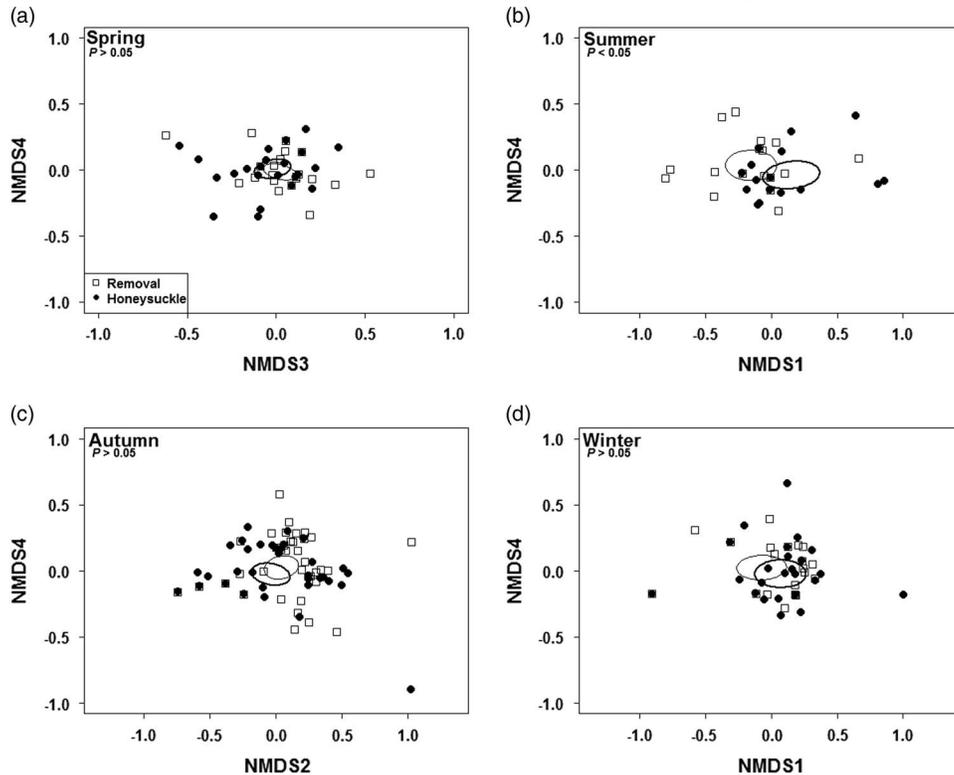**Seasonal Macroinvertebrate Functional Community Dynamics**

Figure 5. Functional community relationships between stream reaches within each sampling season. Panels represent 4-D nonmetric multidimensional scaling (NMDS) results on a 2-D axis with standard error 95% confidence ellipses for stream reach and season.

The removal of *L. maackii* in the riparian forest had substantial effects on the structure and functional traits of the macroinvertebrate community. Removal of *L. maackii* resulted in marked increase in macroinvertebrate density (H_1) and a macroinvertebrate community composition that was both taxonomically and functionally distinct compared with the honeysuckle reach (H_2). Prior research in the site using experimental leaf packs of native species suggests the aquatic biota were similar along the reach prior to restoration activities (McNeish et al. 2012), lending support to the idea that the changes we found in this study (H_1 and H_2) were directly linked to *L. maackii* removal. Our data also indicated that macroinvertebrate communities were functionally indistinguishable between stream reaches during spring and autumn seasons even though these communities were taxonomically different, indicating that functional traits and not taxa associations of these communities were maintained across experimental reaches during these seasons. Communities were taxonomically similar during the summer but functionally different between reaches, which may be attributed to the loss of certain functionally relevant Diptera and Trichoptera taxa in the *L. maackii* reach compared with the removal reach during

Table 2. Community functional richness (trait space utilized) for both stream reaches and between stream reaches within each sampling season. Percent functional richness represents the percent of functional space utilized out of the total functional space (convex hull) occupied by the community. Functional richness is represented by the volume of the convex hull calculated by nonmetric multidimensional scaling results.

Factor	Honeysuckle reach	%	Removal reach	%	Total
Stream reach	0.934	86.08	0.533	49.12	1.085
Spring	0.037	24.03	0.064	41.56	0.154
Summer	0.04	15.09	0.062	23.40	0.265
Autumn	0.487	77.06	0.332	52.53	0.632
Winter	0.216	67.08	0.077	23.91	0.322

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Table 3. Functionally relevant indicator macroinvertebrate taxa for honeysuckle and removal stream reaches.

Honeysuckle reach				Removal reach			
Order	Taxa	Observed value	P-value	Order	Trait	Observed value	P-value
Diptera	Empididae	0.168	< 0.001	Diptera	Chironomidae	0.141	0.010
Diptera	Tipulidae	0.214	0.010	Diptera	*Dasyhelea*	0.216	<0.001
Lumbriculida	Lumbriculidae	0.291	<0.001	Diptera	*Forcipomyia*	0.135	0.010
Haplotaxida	Naididae	0.273	0.031	Diptera	*Maruina*	0.180	<0.001
Cerithioidea	*Goniobasis*	0.18	0.010	Tricladida	Planariidae	0.264	0.010
Planorboidea	*Physella*	0.188	<0.001	Ephemeroptera	Baetidae	0.264	0.041
Arhynchobdellida	*Erpobdella punctata*	0.273	<0.001				
Rhynchobdellida	*Helobdella fusca*	0.23	<0.001				
Rhynchobdellida	*Helobdella stagnalis*	0.23	0.010				
Coleoptera	*Ectopria*	0.177	0.010				
Coleoptera	Lampyridae	0.189	0.020				
Coleoptera	*Stenelmis*	0.225	<0.001				
Copepoda	Copepoda	0.249	0.020				
Hemiptera	*Microvelia*	0.258	0.010				
Isopoda	*Caecidotea*	0.205	0.010				
Amphipoda	*Gammarus*	0.224	<0.001				
Amphipoda	*Hyalella*	0.217	0.031				
Zygoptera	*Agria*	0.221	0.010				
Zygoptera	*Calopteryx*	0.245	<0.001				

summer. An interesting result was the relative abundance of herbivores (grazers) in the honeysuckle reach was greater compared with the removal reach. In a previous study, we demonstrated removal of *L. maackii* did not impact algal growth as expected compared with the honeysuckle reach (McNeish et al. 2015). These collective results suggest periphyton communities may have shifted to dominance of heterotrophic microbes in the low light environment created by *L. maackii* presence in the riparian zone, which could have increased periphyton biomass and supported increased herbivore relative abundance in the honeysuckle reach. *Lonicera maackii* is known to support aquatic mosquito larval survivorship when exposed to *L. maackii* leaf and flower extracts (Shewhart et al. 2014) but resists herbivory of terrestrial insects due to the production of secondary metabolites (e.g., Cipollini et al. 2008b; McEwan et al. 2009), suggesting the potential for aquatic invertebrates to be chemically impacted by *L. maackii* plant material and impact aquatic community functional relationships; however, this avenue of research has yet to be explored. We also saw no differences in nutrient availability between stream reaches, suggesting in-stream nutrient resources may be similar between stream reaches. Overall, these data suggest that functional composition is influenced by the removal of *L. maackii* riparian invasion (H_3); however, the direction of this influence is highly dependent upon season.

Strong seasonal effects on the taxonomic and functional composition of the macroinvertebrate communities should be considered in other studies of riparian plant invasive species effects on aquatic ecosystems. Winter and spring seasons were characterized primarily by stenothermic (cold water preference) organisms while summer and autumn seasons were characterized by eurythermic (warm water preference) organisms, which is likely attributable to seasonal changes in stream water temperature (Allan and Castillo 2007; Cummins 1974). In our study, collector–gatherers were predominately present during winter and spring seasons while herbivores and detritivores characterized summer and autumn seasons, potentially reflecting the seasonal availability of food resources (Cummins and Klug 1979; Richardson 1991; Thompson and Townsend 1999; Wallace and Webster 1996). Additionally, these seasonal effects suggest that there could be riparian plant influence on life history and secondary production of aquatic macroinvertebrates, an area that has not been studied within invasive species ecology and is important for restoration practices. The inherent seasonality of streams (i.e., dry season, deposition of autumnal allochthonous materials) has important repercussions on aquatic organism life history strategies and the availability of resources and serves as an environmental filter (Beche et al. 2006; Hawkins and Sedell 1981; Lytle and Poff 2004; Murphy and Giller 2000; Poff et al. 2006; Verberk et al. 2008). Aquatic macroinvertebrate functional and taxonomic diversity has been directly related to stream hydroperiod (Schriever et al. 2015), which influences the evolutionary strategies of macroinvertebrates (Lytle and Poff 2004). Riparian removal of *L. maackii* did result in increased solar energy available to

Table 4. Functionally relevant indicator macroinvertebrate taxa for each stream reach within each season. An asterisk indicates taxa that were unique to that stream reach within a season.

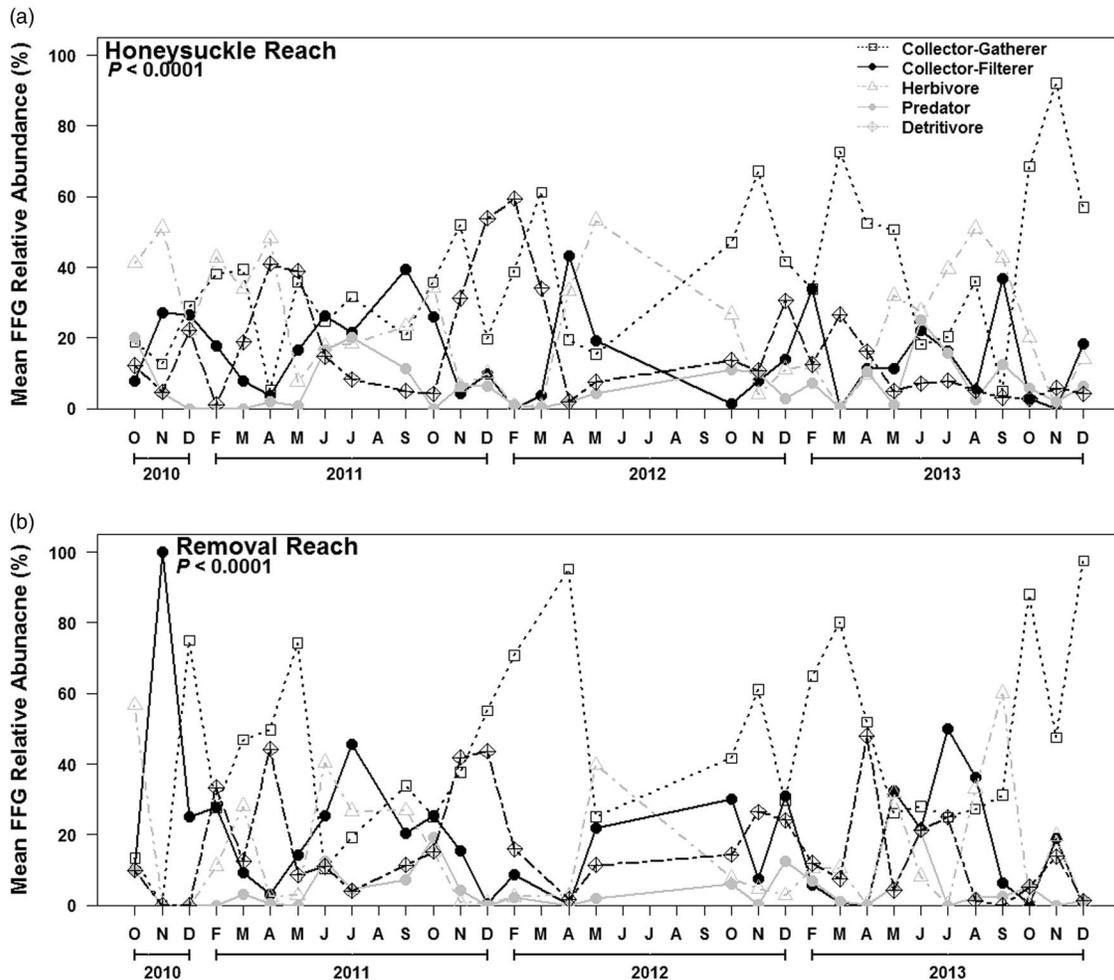|	Honeysuckle reach				Removal reach			
Season	Order	Taxa	Observed value	P-value	Order	Trait	Observed value	P-value
Spring	Diptera	Atrichopogon*	0.221	<0.001	Diptera	Culicoides	0.215	<0.001
	Diptera	Tipulidae*	0.196	0.041	Tricladida	Planariidae*	0.245	0.021
	Diptera	Ceratopogon*	0.177	<0.001	Ephemeroptera	Baetidae	0.249	<0.001
	Diptera	Culicoides	0.219	<0.001				
	Amphipoda	Hyalella*	0.199	0.020				
	Acari	Hydrachnidia*	0.185	0.010				
	Coleoptera	Lampyridae*	0.172	0.041				
	Ephemeroptera	Baetidae	0.258	<0.001				
Summer	Diptera	Empididae	0.128	<0.001	Diptera	Empididae	0.136	<0.001
	Trichoptera	Ceratopsyche	0.104	<0.001	Diptera	Psychoda*	0.175	0.020
	Trichoptera	Hydroptila	0.122	<0.001	Diptera	Tipulidae*	0.2082	0.031
	Coleoptera	Ectopria	0.128	<0.001	Trichoptera	Ceratopsyche	0.084	<0.001
	Coleoptera	Lampyridae	0.154	<0.001	Trichoptera	Cheumatopsyche*	0.094	<0.001
	Coleoptera	Stenelmis	0.19	<0.001	Trichoptera	Hydropsyche*	0.114	<0.001
	Copepoda	Copepoda*	0.226	0.031	Trichoptera	Hydroptila	0.114	<0.001
	Basommatophora	Ferrissia	0.16	<0.001	Cerithioidea	Goniobasis	0.156	<0.001
	Planorboidea	Menetus dilatatus	0.185	0.041	Planorboidea	Physella	0.16	<0.001
	Planorboidea	Physella	0.156	<0.001	Planorboidea	Menetus dilatatus	0.182	0.010
	Rhynchobdellida	Helobdella fusca	0.192	0.010	Basommatophora	Ferrissia	0.165	<0.001
	Rhynchobdellida	Helobdella stagnalis	0.192	<0.001	Coleoptera	Ectopria	0.129	<0.001
	Zygoptera	Agria	0.173	<0.001	Coleoptera	Haliplidae*	0.143	0.031
	Zygoptera	Calopteryx	0.21	<0.001	Coleoptera	Lampyridae	0.164	<0.001
	Decapoda	Orconectes rusticus	0.21	<0.001	Coleoptera	Stenelmis	0.204	<0.001
	Amphipoda	Gammarus	0.189	<0.001	Rhynchobdellida	Helobdella fusca	0.228	0.031
	Arhynchobdellida	Erpobdella punctata	0.223	<0.001	Rhynchobdellida	Helobdella stagnalis	0.228	0.020
	Cerithioidea	Goniobasis	0.127	<0.001	Decapoda	Orconectes rusticus	0.244	<0.001
	Hemiptera	Microvelia	0.248	0.031	Hemiptera	Microvelia	0.249	0.01
	Isopoda	Caecidotea	0.171	<0.001	Isopoda	Caecidotea	0.192	0.010
					Arhynchobdellida	Erpobdella punctata	0.25	<0.001
					Amphipoda	Gammarus	0.201	<0.001
					Zygoptera	Agria	0.178	<0.001
					Zygoptera	Calopteryx	0.224	<0.001
Autumn	Trichoptera	Ceratopsyche	0.121	<0.001	Diptera	Psychoda*	0.179	<0.001
	Trichoptera	Cheumatopsyche*	0.122	0.010	Trichoptera	Ceratopsyche	0.134	0.031
	Trichoptera	Hydropsyche*	0.142	<0.001	Planorboidea	Menetus dilatatus*	0.191	0.031
	Amphipoda	Gammarus*	0.217	0.020	Planorboidea	Physella*	0.188	<0.001
					Coleoptera	Ectopria*	0.181	0.041
					Coleoptera	Haliplidae*	0.149	0.010
					Cerithioidea	Goniobasis*	0.189	0.010
Winter	Diptera	Culicoides	0.226	0.041	Diptera	Culicoides	0.218	0.031
	Diptera	Dasyhelea*	0.207	<0.001	Tricladida	Planariidae	0.242	<0.001
	Tricladida	Planariidae	0.252	<0.001	Ephemeroptera	Baetidae	0.252	0.031
	Emphemeroptera	Baetidae	0.251	<0.001				

Figure 6. Mean macroinvertebrate functional feeding group (FFG) relative abundance within honeysuckle and removal stream reaches. Letters on the x-axis represent sampling months for years indicated.

the stream; however, in a previous study we demonstrated there was no effect on algal growth (McNeish et al. 2015) and stream temperature was still within 1 C of the honeysuckle reach (data not shown), suggesting macroinvertebrate thermal guilds (i.e., stenotherms and eurytherms) were influenced by seasonal patterns. Riparian removal of near-monocultures of *L. maackii* was also shown to substantially increase the overall availability of in-stream leaf litter (McNeish et al. 2015), which may explain why macroinvertebrate density was greater in the removal reach; however, more work linking riparian presence of *L. maackii* and stream abiotic conditions and resources is needed to address this hypothesis.

To our knowledge, this study is the first to show that restoration that involves the removal of a riparian plant invader is linked to the entire taxonomic and functional trait community composition (i.e., not only FFG composition) of aquatic macroinvertebrate communities and identifies seasonal patterns that are important for detecting riparian

forest community effects on stream communities. In summary, our data suggest riparian invasive species affect aquatic macroinvertebrate taxonomic community composition, functional trait diversity, and abundance, likely through changes in allochthonous organic matter quality and timing and changes in light availability. These results further support the concept that riparian invasive plants can have a bottom-up effect on aquatic ecosystems, impacting aquatic food web dynamics and ecosystem function and processes (McNeish and McEwan 2016; McNeish et al. 2015). We hypothesize that macroinvertebrate abundance and functional composition is linked to increased solar energy and temporal availability of leaf litter subsidies in headwater streams when riparian *L. maackii* is removed, resulting in a resource and habitat filter effect. Finally, this study highlights that riparian restoration efforts to remove plant invaders can have major impacts on small stream reaches, resulting in increased aquatic macroinvertebrate abundance and shifts in community dynamics linked to

resource availability. Future work is necessary to understand how riparian restoration practices not only influence resources that support aquatic biota but also the functional aspect of these communities.

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.1017/inp.2017.22

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