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Assessing the influence of riparian invasion by the shrub *Lonicera maackii* on terrestrial subsidies to headwater streams

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ABSTRACT (300 words)

Invasion of Amur honeysuckle (*Lonicera maackii*) into riparian areas of headwater streams creates strong potential for alterations of terrestrial subsidies that may drive bottom-up effects on aquatic biota. In this study, we analyzed effects of *L. maackii* on terrestrial subsidies in stream sites that represented a gradient of invasion intensity in temperate deciduous forests of southwestern Ohio (USA). Leaf litter biomass, terrestrial and aquatic fine woody debris (0.5-9.9 cm diameter) volume and count, and terrestrial and aquatic coarse woody debris (>9.9 cm diameter) volume were analyzed. Based on previous research, we hypothesized that sites with a higher density of *L. maackii* would have decreased native species subsidies due to the dense overarching structure of the invasive shrub preventing materials from entering the stream. Over the course of the study, we found no evidence of differences in native leaf biomass across the invasion gradient. There were marginally significant effects of invasion level on fine woody debris, and regression analysis revealed a significant (R-squared 0.11; P = 0.043) negative relationship between *L. maackii* stem density and fine woody debris volume. Coarse woody debris volume was lower in sites with heavier invasion although no statistically discernable effects were detected. Regression analysis indicated a statistically significant negative relationship between *L. maackii* basal area and coarse woody debris volume (R-squared 0.14; P = 0.026). These results indicate linkage between invasion intensity and terrestrial subsidies mediated through the unique physiognomy of the invasive shrub. Riparian invasion of *L. maackii* may alter the fundamental biology of streams through alterations to deposition of terrestrial organic matter that serves as a structuring component of smaller waterways.

1. Introduction

The biology of small streams is connected to the surrounding landscape through organic matter subsidies. Riparian vegetation is a particularly important contributor of subsidies to aquatic habitats and the amount and quality of organic matter input is critical to aquatic biota as these materials are a source of food and habitat (Vannote et al. 1980, Sweeney et al. 2004). In fact, much of the energy accessible to in-stream biota comes from terrestrial organic inputs (Fisher and Likens 1973). Leaf material is an essential resource for aquatic biota and, in temperate climates, autumnal deposition from deciduous trees is particularly important to the ecology of headwater streams (Vannote et al. 1980, Wallace et al. 1997). Fine and coarse woody debris are subsidies that are fundamental to stream biology as these materials provide a variety of ecological functions including creating habitat complexity and providing substrata for biofilm formation (Benke et al. 1985, Ward and Aumen 1986). Woody debris has been shown to strongly influence the diversity, abundance, and biomass of aquatic species (Benke et al. 1985, Wallace et al. 1997). Alterations to subsidies that influence macroinvertebrate communities can have bottom-up effects influencing higher trophic levels (Baxter et al. 2005). Riparian zones are subject to myriad disturbance processes of both natural and anthropogenic origin and these alterations have strong potential to shift the quality and quantity of terrestrial subsidies (Nilsson and Svedmark 2002).

Riparian invasion by exotic plants has strong potential to alter riparian ecosystem function and shift the composition and quality of cross-system material subsidies. Indirect effects of invasive species may occur when pests or pathogens cause transformation of the riparian vegetation by inducing mortality among important species. For example, invasion of the exotic fungal pathogen *Cryphonectria parasitica* caused loss of American chestnut (*Castanea dentata*) and replacement by oaks (*Quercus* spp.) which have leaves with lower nutritional quality, thus leading to effects on macroinvertebrate shredders (Smock and Macgregor 1988). Direct effects of invasive species are also possible and are particularly likely when the exotic species has traits that are unique to the invaded habitat. For instance, invasive species may have higher foliar nitrogen content (Leishman et al. 2007) which may influence nutrient cycling through increased decomposition rates (Ashton et al. 2005). Deposition of leaf material from the terrestrial environment into streams by riparian Russian olive (*Elaeagnus angustifolia*) was shown to increase the amount of dissolved organic nitrogen in streams thus altering nutrient cycling (Mineau et al. 2011). In addition to foliage, alterations to riparian vegetation have strong potential to influence in-stream fine woody debris (FWD) and coarse woody debris (CWD) which are key components of habitat structure especially in smaller streams (Vannote et al. 1980). Effects on CWD have been linked to changes in riparian vegetation associated with invasion by exotic species (e.g., Tabacchi and Planty-Tabacchi 2003). Invasive species are known to thrive in disrupted habitats (Mack and Antonio 1998, Huston 2004), making riparian forests particularly vulnerable to ecological invasion.

The terrestrial shrub *Lonicera maackii* was introduced to the United States from Asia for horticulture reasons and has become a significant invasive species in many parts of eastern North America (Luken and Thieret 1996). *Lonicera maackii* can create dense stands which have wide-ranging impacts on the biology of the invaded systems (Peebles-Spencer et al. 2017, McNeish and McEwan 2016, Woods et al. 2019). McNeish and McEwan (2016) present a broad framework for *L. maackii* effects on both terrestrial and aquatic habitats including a hypothetical link between terrestrial invasion and stream macroinvertebrate communities mediated through alterations in organic matter deposition. Foliage from *L. maackii* has a unique chemical composition in relationship to native species (Arthur et al. 2012) and previous work has indicated negative effects on terrestrial insect herbivores (McEwan et al. 2009b, Lieurance and Cipollini 2012, 2013). Evidence suggests that submerged leaf litter, fruits and flowers from *L. maackii* can create toxic conditions for aquatic macroinvertebrates (Custer et al. 2017, Borth et al. 2018). The invasion of *L. maackii* into forests surrounding headwater streams has potential for alterations of the riparian physiognomy generating a dense canopy above the stream (bottom panel, Supplemental Figure 1). In a restoration experiment, the removal of *L. maackii* was associated with increased leaf organic matter deposition into a headwater stream (McNeish et al. 2015). This effect was hypothesized to be linked to the physical structure of the invasive shrub and McNeish et al. (2015) posit that the canopy of *L. maackii* represents a physical barrier that traps or deflects falling leaves, altering autumnal deposition. The McNeish et al. (2015) postulate regarding native leaf litter remains untested and, if the dense physiognomy creates a filter effect on native leaves, there is strong possibility for effects on other organic matter subsidies such as FWD and CWD.

In this study, we sought to test the hypothesis that terrestrial-to-aquatic subsidies are altered by the invasion of *L. maackii* into riparian areas surrounding headwater streams in temperate deciduous forests. This study took place on a set of headwater streams that represent a gradient of *L. maackii* invasion intensity that ranged from heavy (HVY) to moderate (MOD) invasion and sites without invasion which we considered reference conditions (REF) (Supplemental Figure 1). Assessment of cross-habitat subsidies included measuring leaf litter and both fine and coarse woody debris. Following the McNeish et al. (2015) observation of lower foliar biomass in areas with *L. macckii* present, we hypothesized that (H_1) sites with a higher invasion density would have decreased total leaf litter biomass deposition. Based on the intentionally established gradient of sites, we also expected *L. maackii* leaf biomass would increase as invasion intensity increased, and due to its extended leaf phenology (McEwan et al. 2009a), we anticipated a pulse of *L. maackii* litter later in the season than native species. We also sought to test the hypothesis that woody biomass in the form of both fine woody debris (H_2) and coarse woody debris (H_3) would decrease along the invasion gradient.

2. Methods

2.1. Establishing the experimental Lonicera maackii *gradient*

This study was focused on a set of five headwater streams and the surrounding riparian zones in the Miami Valley of southwestern Ohio, USA. These were 1st or 2nd order streams that were similar in terms of sinuosity, discharge, size and surrounding land-use. They had no apparent anthropogenic influence from adjacent activities including agriculture or suburban land development and were surrounded by a buffer of forest. The riparian forests were relatively similar across the sites and were representative of secondary forests in the region. Prominent canopy trees included *Acer negundo*, *Celtis occidentalis*, *Gleditsia triacanthos*, *Platanus occidentalis*, *Populus deltoides* and *Tilia americana*, among others. Sites were selected through visual inspection and field scouting after assessing many dozens of streams with the key criteria being that the streams and surrounding habitat be similar in other aspects but vary in the invasion intensity of *L. maackii*. At two of the sites, *L. maackii* was absent as a shrub (reference sites: REF.A and REF.E), at two site there was a moderate invasion of *L. maackii* (MOD.C and

MOD.E) and the final site had a heavy invasion (HVY.B) (Supplemental Figure 1). At each site, five stream plots and six riparian plots were established (Figure 1). Stream plots were established every 6 meters in the thalweg for a 30 meter reach, resulting in a total of five stream plots per site. These plots were used for the survey of aquatic coarse and fine woody debris. Three 6 × 12 m plots were established along each side of the stream encompassing the same total area at each site (Figure 1). These plots were used for measurement of *L. maackii* stems, leaf litter, FWD and CWD (Figure1).

2.1. Measuring *Lonicera maackii* presence in the riparian zone.

Our first goal was to assess the *L. maackii* stems in our research sites to assess the level of invasion along the gradient. All *L. maackii* stems were measured within each of the 6 × 12 m terrestrial plots (data available from Rowekamp et al. 2018c). *Lonicera maackii* has a unique non-linear or "plastic" morphology with a large meristematic burl from which many shoots emerge. To fully measure the importance of this species, diameter measurements were taken of every live and dead *L. maackii* shoot in the plot ≥ 1 cm at a linear distance of 1.4 m from the base of the meristematic burl. Using a linear measurement from the burl, instead of a standard height (such as diameter at breast height: DBH), aided in correcting for the often tilted nature of the *L. maackii* plant.

2.2. Leaf litter

Twenty leaf litter collection baskets were deployed in August of 2015 across all five sites (Figure 1). These baskets were large plastic circular tubs with openings of 1288.25cm^2 and a depth of 36 cm. Holes were drilled into the bottom of the tub to allow for drainage and fine mesh window screen was affixed to the bottom of the tub to prevent very fine litter material from being lost. At each site, one litter collection basket was randomly allocated to four of the previously established vegetation survey plots (Figure 1). The placement of the litter baskets was in the center of the 6m stream edge of the vegetation plots. The bottom of each litter collection basket was elevated a minimum of 0.45m off the ground. Leaf litter was collected on 5 dates during the period ranging from mid-August 2015 to late-February 2016. At the start of the collection period, fine mesh bags were secured to and used to line the previously established litter collection baskets. Dates of collection were determined by naturally occurring autumnal leaf fall. At each collection date, the mesh bag with litter samples was removed and immediately replaced with a new mesh bag, allowing for continuous sampling during the collection period. The litter baskets were never more than ½ full of material so there was always ample space for senesced leaves to be deposited into the basket. The mesh bags containing the organic litter were transported back to the lab for processing. Leaf material was placed in a drying oven at 50˚C for a minimum of 24 hours and was weighed to the ten thousandths of a gram, as an estimate of biomass, using a closed digital balance (Rowekamp et al. 2018d).

2.3. Coarse and fine woody debris sampling

Woody debris sampling took place in the summer and fall of 2016. Both coarse (>9.9cm diameter) and fine (0.5-9.9 cm diameter) woody debris were assessed in both the stream and riparian habitats. In the aquatic habitat, a transect spanning the length of the plot was established in each of the 5 stream plots (Figure 1). During the aquatic FWD sampling, digital calipers were used to take diameter measurements of all fine woody debris that was touching the established transect, at the point of intersection, within the wetted width of the stream (Rowekamp et al. 2018b). In the terrestrial FWD sampling, the 6 previously established *L. maackii* plots were used as the location for a corner-to-corner transect (Figure 1). Along the transect, diameter measurements of FWD were taken at the point of intersection (Rowekamp et al. 2018f). An adaptation (Wallace and Benke 1984, O'Connor 1992, Baillie et al. 1999) of the Van Wagner line intersect method (Van Wagner 1968) was used for the determination of aquatic and terrestrial fine woody debris volume per plot. For CWD, in the aquatic habitat, the entire plot area was sampled stream (Rowekamp et al. 2018a). In the terrestrial habitat the entire area of all six vegetation plots was surveyed (Figure 1; Rowekamp et al. 2018e). Measurements for the coarse woody debris encountered included the large end diameter, small end diameter, and the length of the debris. The formula for a truncated cone was used to determine volume of the coarse woody debris per piece and scaled up per plot.

2.4. Data analysis

Statistical analysis generally focused on two techniques. First, analysis of variance was used to assess differences among the five sites using plots as replicates. Data were first screened for normality and parametric (ANOVA) or non-parametric (Kruskal-Wallis) techniques were pursued with post-hoc comparisons employed if a significant overall model effect was detected. Terrestrial and aquatic coarse and fine woody debris and final, total, leaf biomass were all compared in this way. Leaf litter biomass across the duration of the study was analyzed using two-way ANOVA with both site and time as effects. The second technique we used was regression analysis where each plot was treated as an independent point. This technique is biologically reasonable because *L. maackii* density varied at the plot scale across all sites. We used regression to assess how response variables including total, final, leaf biomass, and woody debris varied at the scale of the terrestrial plot in relationship to *L. maackii* density and basal area. Differences $P \leq 0.05$ were considered statistically significant and those where $P \geq 0.05$ and ≤ 0.1 were considered “marginally” significant. All analyses and data visualizations were completed using R *v* 3.5.0 (R Core Team 2018).

3. Results

Analysis of *L. maackii* stems indicated that the study gradient represented a wide range of stem density. *Lonicera maackii* was effectively absent from the reference sites (REF.A and REF.E) and the number of both live and dead stems present was significantly lower than the other sites in the study ($P < 0.01$ for all; Figure 2). The moderate invasion sites (MOD.E and MOD.C) had significantly higher density than the reference sites, but were indistinguishable from the heavy invasion site (HVY.B; Figure 2). Although the HVY.B site was not statistically separated from the moderate sites, the median density of live stems (4,305 stems/ha) was considerably higher than either MOD.C (3,611 st/ha) or MOD.E (2,708 st/ha) (Figure 2). Approximately one-third of all *L. maackii* measurements were between 1 cm and 2.5 cm (data not shown). Dead, attached, shoots made a large contribution to the overarching structure found over the stream and, strikingly, in the HBY.B site the estimated median number of standing dead shoots per hectare (5,000) was higher than the estimated number of live shoots (4,305) (Figure 2).

Leaf biomass data indicated that *L. maackii* deposition was heaviest where the species was more prevalent and that invasion status did not affect deposition from native canopy trees. Site was not a significant predictor of total non- *L. maackii* leaf material and there was no discernable pattern in biomass related to *L. maackii* invasion intensity (Figure 3, top panel). Regression analysis comparing *L. maackii* density and basal area to non-*L.maackii* leaf biomass indicated no significant relationships (all $P > 0.3$; data not shown). Time was a significant predictor of non-*L. maackii* leaf biomass ($P < 0.001$; Figure 3) which is indicative of the seasonal timing of autumnal leaf drop in this ecosystem. Maximum deposition of *Lonicera maackii* leaves was a month later than native leaves and some deposition occurred between late November and February which is well after the senescence of native trees in the region (Fig.3, bottom panel). Mean biomass of *L. maackii* leaf litter across sites was significantly influenced by time ($P < 0.001$) and there was also a significant treatment effect ($P < 0.001$) (Fig 3, bottom panel). This result was supported by regression analysis which yielded a significant positive relationship between *L. maackii* leaf biomass and both *L. maackii* stem density ($P = 0.026$; R-squared 0.24) and basal area ($P < 0.01$; R-squared 0.41) (data not show). The biomass of *L. maackii* leaf material was much less than the total incoming non-*L. maackii* biomass (Figure 3; note different axis scales).

Terrestrial fine woody debris volume exhibited a marginally significant site effect ($P = 0.086$) and a trend of decreasing volume with increasing invasion intensity (Supplemental Figure 2). This pattern was also present in the in-stream sampling where site was marginally significant for FWD volume (0.093) and a significant effect of site was detected in total piece count ($P =$

0.04) (Supplemental Figure 2) although no significant pairwise differences were detected. Regression analysis indicated a statistically significant (*P* = 0.043), although relatively weak (R-squared: 0.11), negative relationship between *L. maackii* density and fine woody debris volume (Figure 4).

Increasing density of *L. maackii* in the riparian zone was associated with a reduction in coarse woody debris.. There was a pattern of decreasing volume of coarse woody debris associated with increasing *L. maackii* invasion level in the terrestrial habitat although this pattern was not statistically significant (P = 0.11; Figure 5). Analysis of the volume of in-stream "aquatic" coarse woody debris yielded marginally significant site effect (P = 0.07; Figure 5) indicating a reduction across the invasion intensity gradient. Regression analysis indicated a significant negative relationship between both *L. maackii* density (P = 0.031; R-squared = 0.13) and a slightly stronger negative relationship with *L. maackii* basal area (P = 0.026; R-squared = 0.14) (Figure 6). Plots where *L. maackii* was absent had a wide variance in CWD volume and plots where *L. maackii* basal area was highest had very low CWD with relatively lower variance (Figure 6).

4. Discussion

4.1. Influence of L. maackii *invasion on leaf litter in headwater streams*

Invasion by *L. maackii* into forests has significant implications for the biology of forests (Collier et al. 2002, Miller and Gorchov 2004, Peebles-Spencer et al. 2017, Woods et al. 2019) and the headwater streams that meander through those forests (McNeish et al. 2012, , Custer et al. 2017). McNeish et al. (2015) found that riparian forest removal of *L. maackii* was associated with increasing leaf biomass from the native overstory canopy leading to the hypothesis that the physiognomy of the shrub reduces inputs of native organic material. Here we sought to test their hypothesis by assessing leaf biomass across a gradient of *L. maackii* invasion. We found no support for the idea of reduced native leaf biomass with increasing *L. maackii* invasion (refuting H_1). In a litter basket study, Arthur et al. (2012) did not find any differences in total leaf biomass input "under" *vs*. "away" from *L. maackii* within an upland forest, which is consistent with our finding of no difference across a range of *L. maackii* invasion intensity. Notably, both our study and the Arthur et al. (2012) project were litter basket studies, while McNeish et al. (2015) sampled from in-stream plots. This methodological difference may partly explain the different findings; however, the particular ecological reason why results from in-stream plots should vary as compared to stream-adjacent litter baskets remains unclear. Further work will be needed to assess the hypothesis of effects on overstory leaf deposition associated with the dense growth form of *L. maackii* and other species.

Seasonal timing of deposition, and the chemical and physical characteristics of *L. maackii* foliage, may effect stream biota. *Lonicera maackii* leaf litter deposition was significantly higher in sites with more of the shrub present in the riparian zone, an obvious result, and we found a late season pulse of litter from the invasive shrub. McEwan et al. (2009a) found that *L. maackii* leaves appeared to have freeze tolerance that allowed them to have later leaf senescence in relation to their native shrub counterparts. An extended phenology, including late leaf abscission, is a common trait found in invasive shrub species in deciduous forests in the eastern United States (Fridley 2012) and hypothesized benefits include a longer photosynthetic period (McEwan et al. 2009a, Fridley 2012, Smith 2013) and increased production of allelochemicals (Smith

2013). A shift in deposition timing in headwater streams where *L. maackii* is an important riparian species may interact with the life-history timing of aquatic macroinvertebrates, although this ecological relationship is presently unexplored and beyond the scope of the present study. Beyond the late timing of deposition, incoming leaf litter from *L. maackii* may alter in-stream function in numerous ways. Leaves of this species have been found to decompose much faster than leaves from some common native tree species in eastern North America in both aquatic (McNeish et al. 2012) and terrestrial experiments (Arthur et al. 2012; Trammell et al. 2012). This increased rate of decomposition has a wide range of implications as macroinvertebrates rely on leaf litter subsidies as a source of food and habitat (Vannote et al. 1980). In addition to an increased decomposition rate, *L. maackii* foliage has been found to create toxic conditions for aquatic macroinvertebrates (Borth et al. 2018). In fact, Custer et al. (2017) noted toxic effects from flowers and fruits of *L. maackii* and propose that these materials represent a "novel subsidy." Future work is needed to test the effects of aquatic deposition of *L. maackii* leaf materials, especially given its relatively small biomass in comparison to other species (Figure 2), and the fact that we provide evidence refuting the hypothesis that the shrub architecture limits input from native leaves.

4.2. Influence of L. maackii *invasion on fine woody debris- the ecology of labile woody detritus.*

Our data provide evidence of a negative relationship between *L. maackii* invasion and fine woody debris (FWD) (supporting H_2). The biological implication for this relationship could be significant. For instance, an increase in FWD was shown to be associated with an increase in rainbow trout (*Oncorhynchus mykiss*) abundance, possibly due an increase in habitat complexity

(Culp et al. 1996). Links between FWD and habitat complexity in our study system remain unexplored; however, our data indicate that the growth pattern and twig biology of *L. maackii* may be unique. We noted extremely dense stem morphology where the *L. maackii* shrubs hold many dead twigs (Supplemental Figure 4). Luken (1988) found that in dense areas, *L. maackii* growth allocation shifted to new shoot production higher on the plant. This plasticity in allocating growth to new shoots results in an exceedingly high number of standing dead stems. Working with the shrub *Alnus incana*, Huenneke (1987) noted that serial production of new shoots was a critical factor in the persistence of genetic individuals. Similarly, serial production of new shoots is seemingly fundamental to the invasion biology of *L. maackii* and the physical structure created by prolific ramet production may represent a fundamental shift in carbon allocation in forests where the typical dominant physiognomy is tall, single-stemmed, trees with large boles. Native shrubs were sparse in our study sites, which is typical for regional secondary forests, and none of the shrub species that may be present in regional forests exhibit a growth form similar to *L. maackii* (e.g., *Asimina triloba*, *Lindera benzoin*, *Viburnum prunifolium*, *Hamamelis virginiana*). *Lonicera maackii* twigs are “cheap” from an energetics perspective because they are hollow (Supplemental Figure 3). These twigs may represent a more labile source of carbon in ecosystems than is found with native tree species that have stems that are not hollow, and this may interact with other *L. maackii* traits to accelerate carbon cycling in regional forests. For example, Woods et al. (2019) found that the presence of *L. maackii* in forests was associated with higher levels of the enzymes phenol oxidase and peroxidase indicating the potential for accelerated carbon cycling. Future work is needed to assess the ecological implications of the unique *L. maackii* growth habit of holding dead twigs along with the hollow twig morphology.

4.3. Coarse woody debris deposition may be influenced by the physical structure of L. maackii.

Our data suggest a reduction in coarse woody debris along a *L. maackii* gradient (supporting H_3), an effect that could result in significant alterations to the biology of headwater streams. The mechanism of this potential effect deserves further study; however, the dense physiognomy clearly has potential to capture branches and falling trees (Supplemental Figure 4). We have observed coarse woody debris suspended in the tangled branches of *L. maackii*, and although this wood would eventually reach the forest floor, it could be substantially delayed. Shifts in coarse woody debris morphology and density may also be associated with invasion as is the case with *Acer negundo* invasion in Europe (Tabacchi and Planty-Tabacchi 2003). The hollow stem morphology and potentially more rapid decay of coarse woody materials from *L. maackii* may influence stream energetics and habitat characteristics, although this effect is presently untested. Coarse woody debris influences sediment dynamics and accumulation of other organic matter, including leaves and fine woody debris (Speaker et al. 1984) indicating strong potential for effects on stream ecosystem function. Research has connected alterations of terrestrial vegetation such as timber harvesting with changes in CWD in streams (e.g., Bilby and Ward 1991); however, to our knowledge, this project is the first to identify a link between extreme physiognomy changes associated with riparian invasion and a reduction in CWD inputs to streams.

4.4. Summary.

In summary, invasion of riparian habitats by *L. maackii* has strong potential to influence subsidy transfer from terrestrial habitats into headwater streams. We found no evidence of reduced leaf litter from native trees entering streams in areas with heavy *L. maackii* invasion, (refuting H_1); however, the late senescence and unique chemistry of the *L. maackii* leaf input may be a novel subsidy impacting aquatic biota. We found evidence to suggest that fine woody debris was reduced by *L. maackii* invasion (supporting H_2). This may be due to the unique morphology of the *L. maackii* shrubs which hold an exceedingly large number of dead shoots. The ecological ramifications of this physiognomy could provide a fruitful avenue for future research. Finally, we found evidence of reduced coarse woody debris in areas of heavy *L. maackii* invasion, potentially associated with pieces being snarled in the dense growth form. If validated in future research, this outcome of riparian invasion could be a mechanism of alteration in the fundamental biology of streams as woody debris is a crucial structuring component of smaller waterways.

Authors' contributions

Erin Rowekamp and Ryan McEwan designed the study. Erin Rowekamp led and executed field sampling, lab sample processing and other data collection and entry processes. Erin Rowekamp, Julia Chapman and Ryan McEwan conducted data analysis. Erin Rowekamp and Ryan McEwan wrote the manuscript.

Supplemental Figures

Supplemental Figures 1-4.

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FIGURE LEGENDS

Figure 1: Plot schematic employed in this study of Amur honeysuckle (*Lonicera maackii*) invasion in temperate deciduous forests in southwestern Ohio, USA.

Figure 2: Density (stems ha^{-1}) of live and standing dead Amur honeysuckle *(Lonicera maackii*) stems along a gradient of sites that includes heavy invasion (HVY), moderate invasion (MOD) and reference sites where very little *L. maackii* was present (REF). The initial categorizations of *L. maackii* intensity were made after multiple site visits and visual observations. Middle line in the box is the median and letters represent statistically significant differences indicated by post-hoc tests ($P < 0.01$ for all).

Figure 3. Mean biomass (g) of all leaf litter except Amur honeysuckle (*Lonicera* maackii) and mean biomass of leaf material (g) from *L. maackii* across time along a gradient of *L. maackii* invasion in temperate deciduous forests in southwestern Ohio, USA. Gradient includes heavy invasion (HVY), moderate invasion (MOD) and reference sites where very little *L. maackii* was present (REF). Note difference in the scale of y axes.

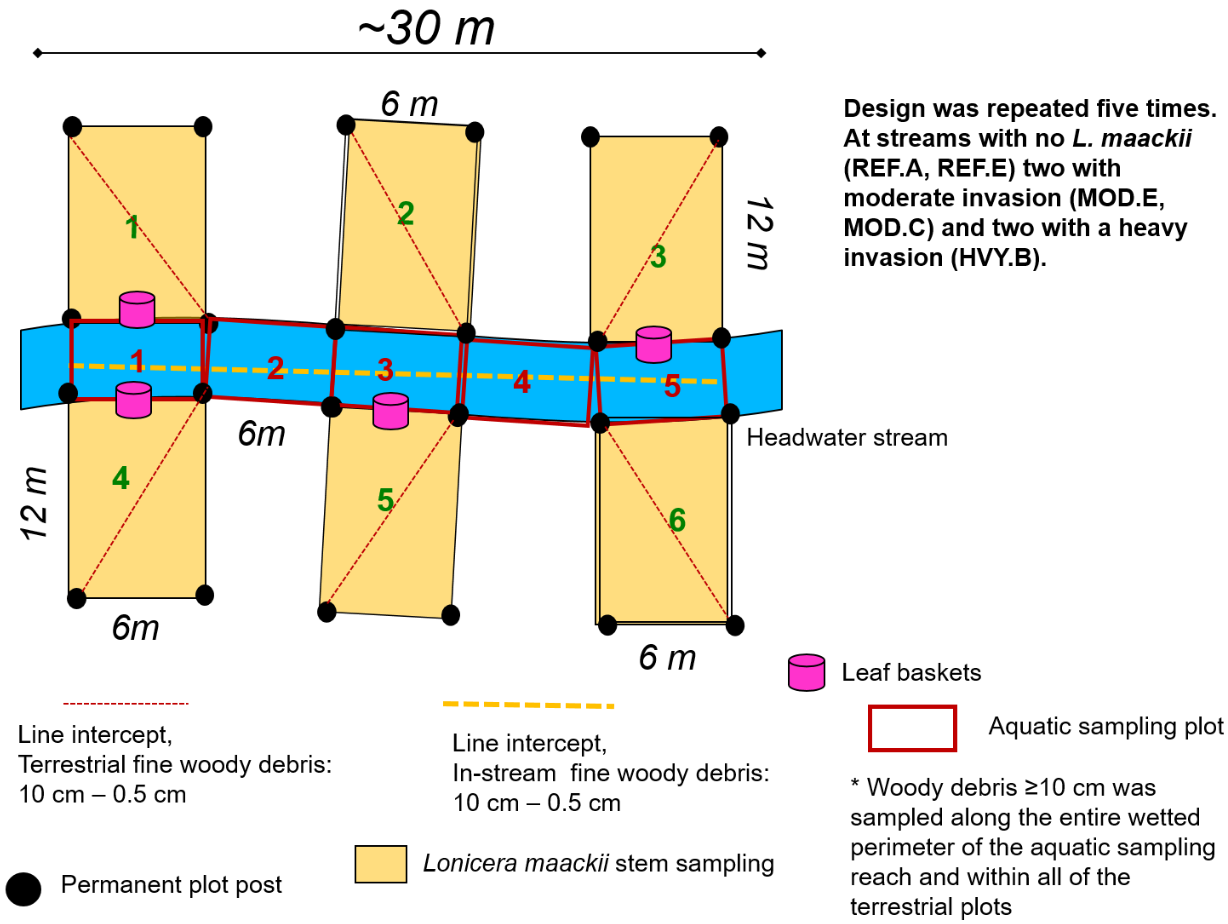
Figure 4. Relationship between *Lonicera maackii* stem density and find woody debris volume in in headwater streams in temperate deciduous forests in southwestern Ohio, USA. Each point is a plot and the line represents a statistically significant relationship ($P = 0.043$; R-squared: 0.11).

Figure 5. Volume (m^3 ha^{-1}) of both terrestrial and aquatic coarse woody debris (diameter >9.9 cm) along a gradient of Amur honeysuckle (*Lonicera maackii*) invasion in temperate deciduous

forests in southwester, Ohio, USA. Gradient includes heavy invasion (HVY), moderate invasion (MOD) and reference sites where very little *L. maackii* was present (REF). Middle line in the box is the median results.

Figure 6. Relationship between *Lonicera maackii* basal area and coarse woody debris (CWD) volume in headwater streams in temperate deciduous forests in southwestern Ohio, USA. Each point is a plot and the line represents a statistically significant relationship (*P* = 0.026; R-squared = 0.14).

Figure 1.



Design was repeated five times. At streams with no *L. maackii* (REF.A, REF.E) two with moderate invasion (MOD.E, MOD.C) and two with a heavy invasion (HVY.B).

* Woody debris ≥10 cm was sampled along the entire wetted perimeter of the aquatic sampling reach and within all of the terrestrial plots

Figure 2.

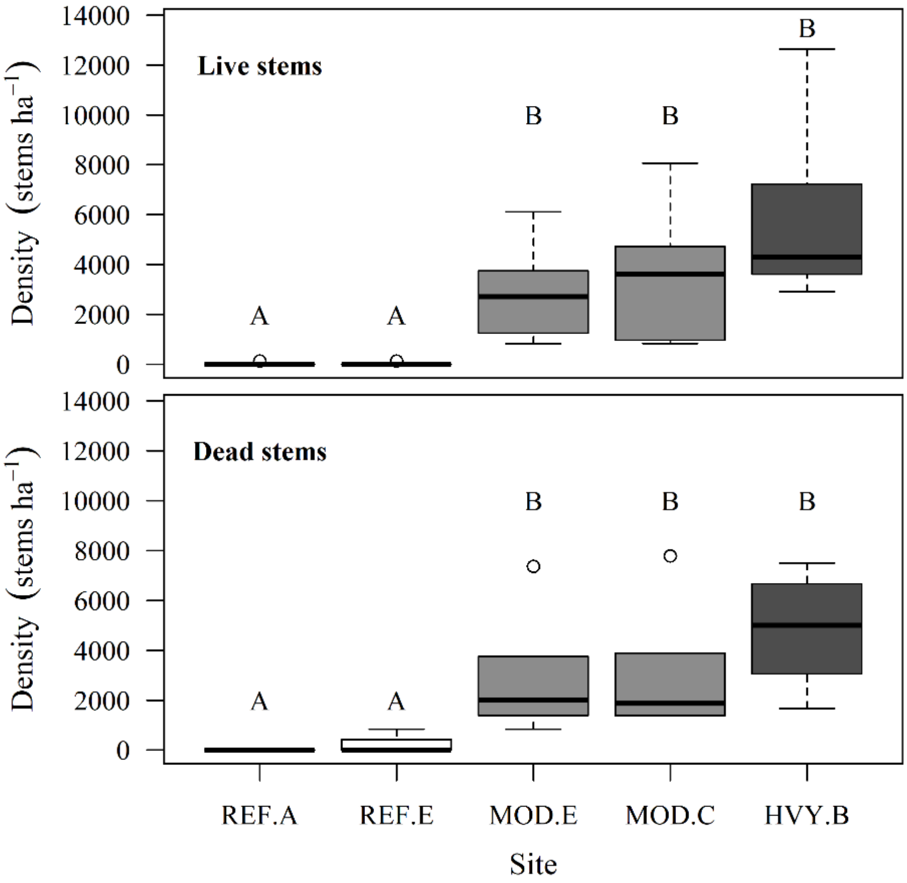

14000
12000
10000
8000
6000
4000
2000
0
Live stems
Density (stems ha^{-1})
A
A
B
B
B
Dead stems
A
A
B
B
B
REF.A
REF.E
MOD.E
MOD.C
HVY.B
Site

Figure 3

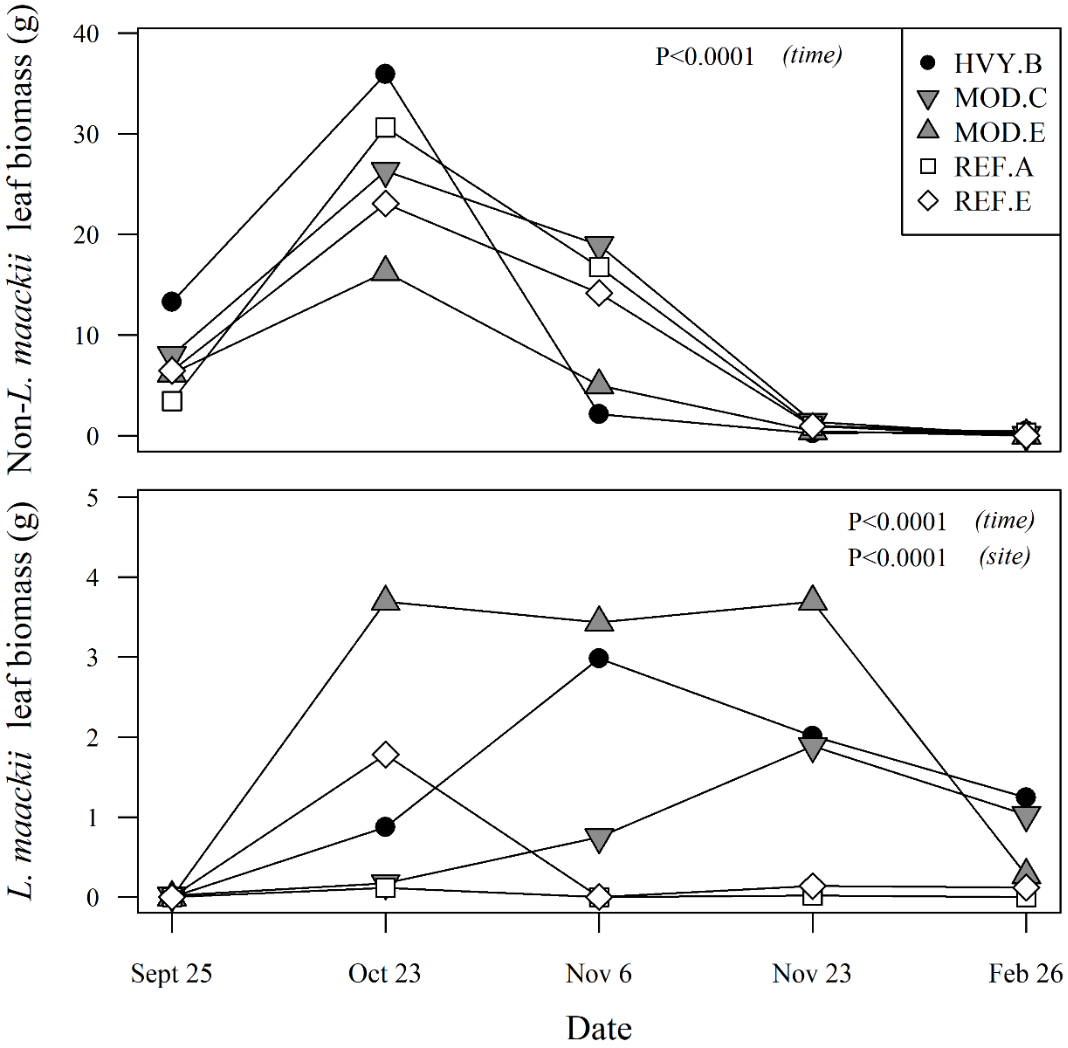

Non-*L. maackii* leaf biomass (g)
40
30
20
10
0
P<0.0001 *(time)*
● HVY.B
▼ MOD.C
▲ MOD.E
□ REF.A
◇ REF.E
L. maackii leaf biomass (g)
5
4
3
2
1
0
P<0.0001 *(time)*
P<0.0001 *(site)*
Sept 25
Oct 23
Nov 6
Nov 23
Feb 26
Date

Figure 4.

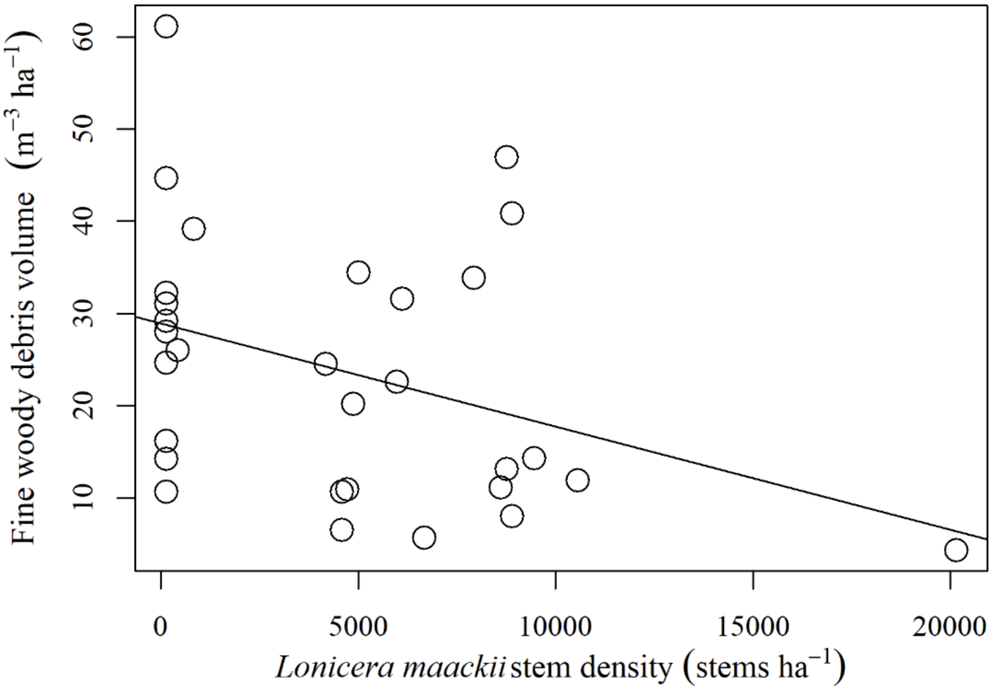
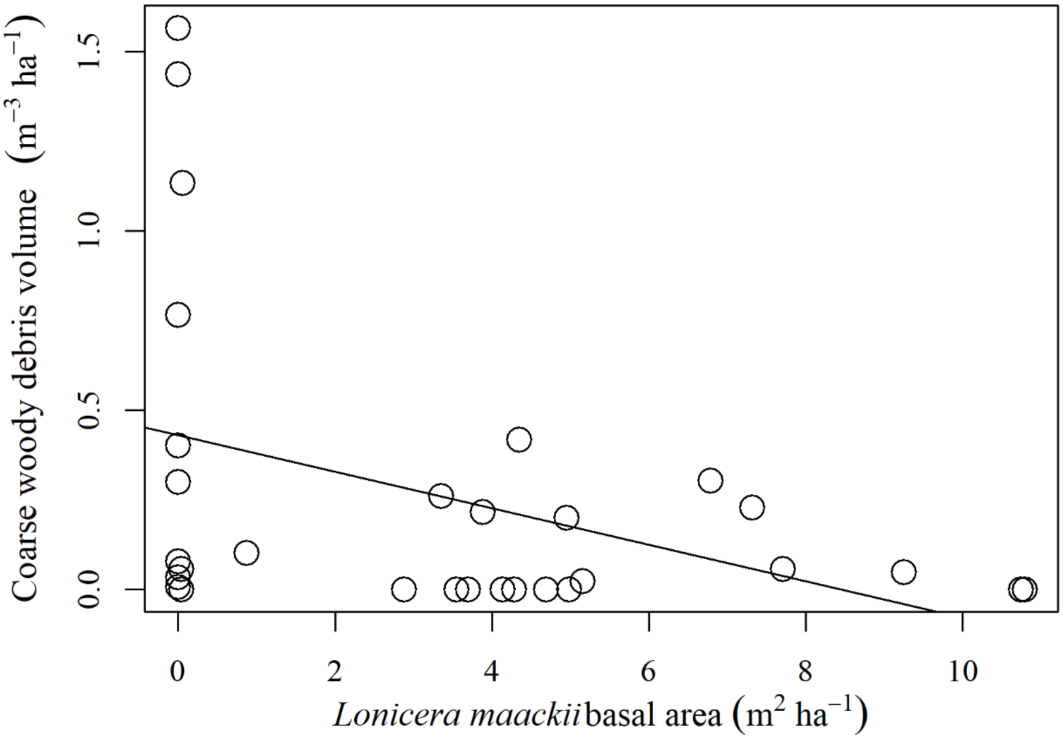

Fine woody debris volume $(m^{-3}\ ha^{-1})$
10
20
30
40
50
60
0
5000
10000
15000
20000
Lonicera maackii stem density $(stems\ ha^{-1})$

Figure 5.

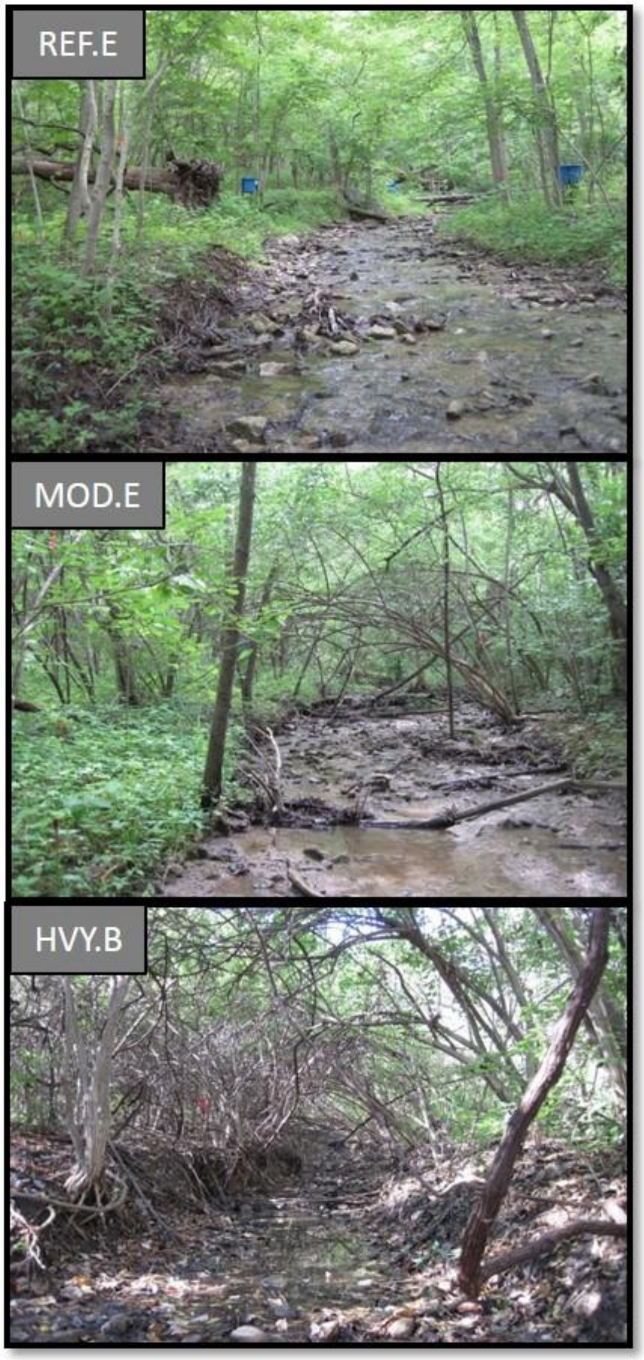
The picture can't be displayed.

Figure 6.

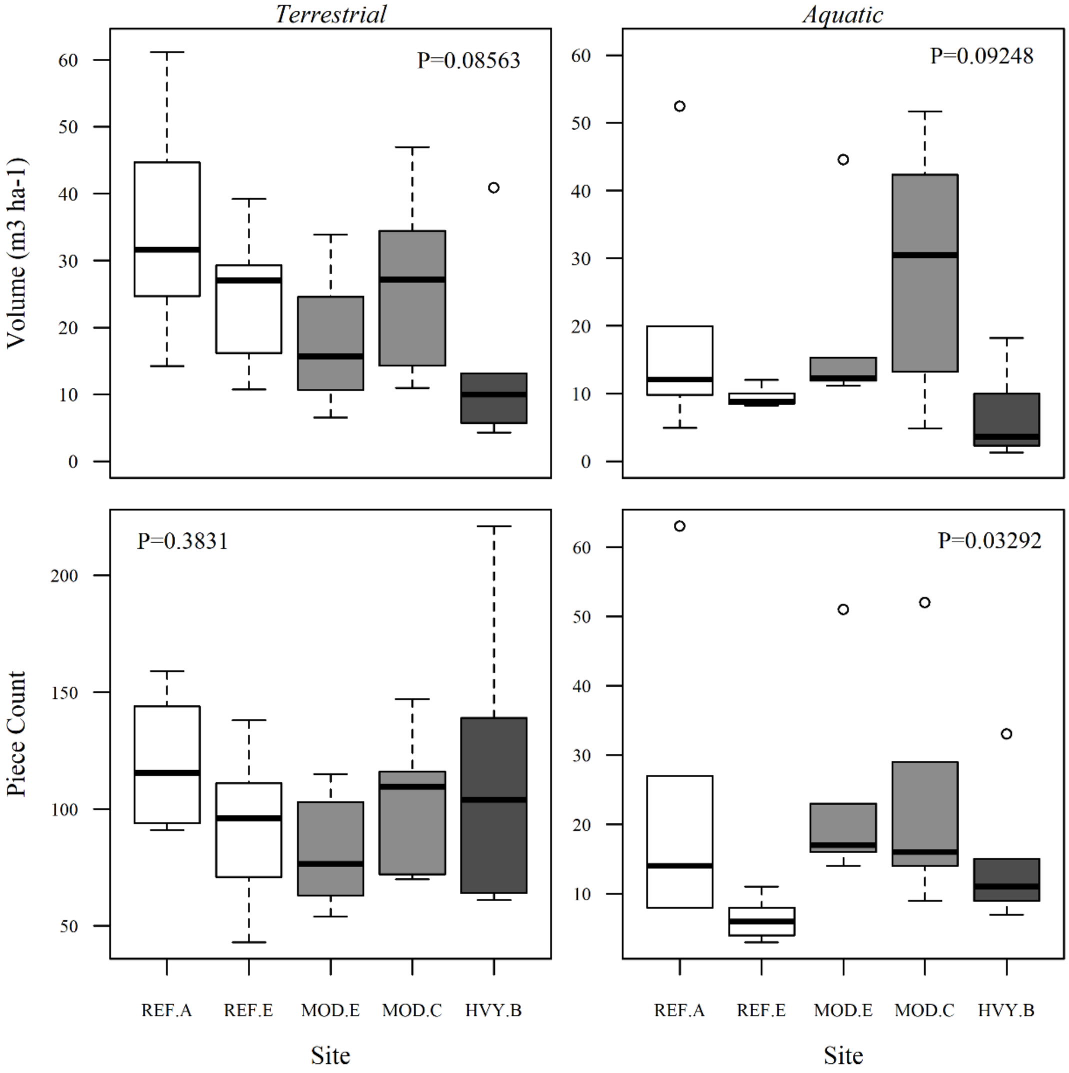


Coarse woody debris volume (m^{-3} ha^{-1})
0.0
0.5
1.0
1.5
0
2
4
6
8
10
Lonicera maackii basal area (m^{2} ha^{-1})

Supplemental Figures



Supplemental Figure 1. View of headwater streams that are (a) not invaded (REF.E) (b) moderately invaded (MOD. E) and heavily invaded (HVY.B) by Amur honeysuckle (*Lonicera maackii*) in headwater stream riparian forest in southwestern Ohio, USA.



Supplemental Figure 2. Terrestrial and aquatic fine woody debris (diameter 0.5 – 9.9 cm) volume (m^3 ha^{-1}) and count along a gradient of Amur honeysuckle (*Lonicera maackii*) invasion in temperate deciduous forests in southwestern Ohio, USA. Gradient includes heavy invasion (HVY), moderate invasion (MOD) and reference sites where very little *L. maackii* was present (REF). Note the difference in scale of the y axis for count between terrestrial and aquatic habitats.

Supplemental Figure 3. Hollow stems are a characteristic of twigs and smaller stems of *Lonicera maackii*. Photo by Ryan McEwan.

Supplemental Figure 4. Snowy scene at the heavy invasion site (Buckeye Trail: HVY.B) gives a visual sense of the density of *L. maackii* stems. Photo by Kevin W. Custer.