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Riparian invasion of *Lonicera maackii* influences throughfall chemistry and rainwater availability

Abstract Riparian forests are a functionally important interface between terrestrial and aquatic communities, facilitating the transfer of subsidies that support aquatic biota and ecosystem processes. Invasion of the non-native shrub Amur honeysuckle (*Lonicera maackii*) in forests of the Midwestern United States has resulted in the formation of a dense monospecific shrub-layer along many headwater streams, substantially altering both the composition and structure of riparian plant communities. We investigated the effects of *L. maackii* on the chemistry of throughfall (rain that has passed through a plant canopy) in a riparian forest. During the growing season of 2015, throughfall collections were made in areas with no plant canopy (Open), a native forest canopy (Upper canopy), and within the forest but immediately under *L. maackii* shrubs (Honeysuckle). The Honeysuckle treatment intercepted 28–64% more throughfall compared to the Upper canopy treatment, resulting in lowered throughfall volume under the shrubs. The Honeysuckle treatment had substantially greater total carbon and total organic carbon concentration in throughfall compared to other throughfall treatments ($P < 0.01$). Total nitrogen and dissolved nitrogen deposition was up to 66% reduced under Honeysuckle treatments compared to a 45% reduction from Upper Canopy collections. In summary, these findings contribute to the growing scientific literature demonstrating that invasion by the exotic shrub *L. maackii* can capture incoming rainwater and alter the chemistry of throughfall, impacting cross-system nutrient subsidies and riparian function.

Keywords Amur honeysuckle · Carbon · Nutrient dynamics · Phosphorus · Riparian forest

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Introduction

Riparian zones act as an interface between terrestrial and aquatic ecosystems, supporting the transfer of subsidies, mediating stormwater runoff, and reducing nutrient loading entering aquatic systems (Vannote et al. 1980; Lowrance et al. 1984; Barling and Moore 1994; Baxter et al. 2005). The biology of riparian zones has taken on increased relevance due to anthropogenic nutrient loading to aquatic systems, which is a global phenomenon often leading to eutrophication of water systems with impacts on aquatic biota and broader ecosystem processes (Anderson et al. 2002; Smith 2003). For example, the Laurentian Great Lakes, USA and the coastal oceans of China have experienced massive algal blooms, resulting in public health concerns due to the threat of algal toxins associated with eutrophication (Zhang 1994; Anderson et al. 2002; Hudnell 2010; Johnson et al. 2010). Point and non-point sources of pollution have been the primary contributors to greater nutrient levels in aquatic ecosystems (Dolan 1993; Carpenter et al. 1998; Heisler et al. 2008). Regulation of point sources (e.g., wastewater facilities) have reduced nutrient loading into aquatic waterbodies; however,

non-point sources (e.g., agricultural runoff) remain a significant problem (Conroy et al. 2005). Riparian zones are natural buffers along aquatic habitats that help mediate non-point pollution sources entering aquatic systems (Lowrance et al. 1984; Barling and Moore 1994), but can also contribute nutrient subsidies to nearby aquatic systems. Riparian function is tightly linked with plant community composition in the riparian zone (Gregory et al. 1991); however, in many regions, riparian zones have become degraded due to forest fragmentation, urbanization, and the introduction of invasive plants (Richardson et al. 2007; Chamier et al. 2012).

Plant invasion of riparian zones has strong potential to alter the structure and function of both the forest and the adjacent aquatic system. The frequent disturbances and high resource availability that characterize riparian forests may facilitate invasion by exotic plants which can alter ecosystem function and potentially disrupt riparian zone function (Richardson et al. 2007, Chamier et al. 2012; Greene 2014). Invasion of exotic plants can substantially alter the quality and quantity of terrestrial subsides entering the aquatic system (Richardson et al. 2007; Chamier et al. 2012; Greene 2014). For example, invasive plants can suppress the growth of potential competitors and reduce herbaceous ground cover, which can result in increased stormwater runoff and nutrient pollution entering the stream (Walsh et al. 2005). Invasion-related alterations of terrestrial-aquatic community dynamics may influence food-web interactions, nutrient cycling, and ecosystem processing (e.g., decomposition) that connect terrestrial and aquatic habitats (Baxter et al. 2005; Davis et al. 2011; Greig et al. 2012). These studies, among others (e.g., Mineau et al. 2011; Claeson et al. 2014), have demonstrated riparian invasive plants can impact aquatic ecosystems and communities through terrestrial-aquatic linkages.

Lonicera maackii (Amur honeysuckle (Rupr.) Maxim.) is a dominant invasive shrub in the Midwestern United States known to change plant composition and species richness in forests (Gould and Gorchov 2000; Musson and Mitsch 2003; White et al. 2014) and is a significant invader in edge habitats and riparian zones (McNeish et al. 2012, 2015). Previous work indicated significant potential for connections between the terrestrial invasion of *L. maackii* and the biology of streams, including reduced macroinvertebrate density and alterations in the leaf subsidies to the stream system (McNeish et al. 2012, 2015). Evidence also suggests low insect herbivory on *L. maackii* leaves both in the field and in ex situ experiments (McEwan et al. 2009b; Lieurance and Cipollini 2012). *L. maackii* leaves have a wider temporal range of photosynthetic activity than many native species (McEwan et al. 2009a) and leaf extracts have been shown to suppress seed germination of other plant species (Cipollini et al. 2008; McEwan

et al. 2010). These collective studies, among others (e.g., Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2004), indicate that *L. maackii* invasion has the potential to reduce native plant survivorship and influence plant community dynamics linked with adjacent aquatic habitats.

The invasion of *L. maackii* into deciduous forests of eastern North America may also influence nutrient cycling and ecosystem function. Arthur et al. (2012) demonstrated that *L. maackii* leaves had significantly higher N and lower lignin than native co-occurring species. Along headwater streams in regional forests, *L. maackii* invasion often results in a dense shrub layer, quasi-monoculture canopy that reaches completely across the stream; thus, throughfall from this species has strong potential for influencing in-stream nutrient cycling (McNeish et al. 2012, 2015). For instance, *L. maackii* was shown to contribute a significant volume of in-stream leaf litter which exhibited 4 times faster breakdown rates than native leaf litter in headwater streams (McNeish et al. 2012, 2015, 2017, McNeish and McEwan 2016). Further, Boyce et al. (2012) found that *L. maackii* impacted forest stand transpiration, resulting in loss of approximately 10% of total stream flow in a forested area. The total volume of rainwater deposition was shown to be reduced under this invasive species (McEwan et al. 2012). The canopy of *L. maackii* has been shown to increase cation deposition in throughfall (rain water that passes through leafy canopies; McEwan et al. 2012); however, this previous research did not address phosphorus, which is a key nutrient in aquatic systems. Previous research indicated no statistically detectable differences in NO_3–N under and away from *L. maackii* while there were consistent reductions in NH_4–N in throughfall under its canopy (McEwan et al. 2012). The authors proposed that the reduction in NH_4–N may be associated with assimilation in microbial communities.

In this study, we sought to understand how riparian *L. maackii* alters the quantity and chemistry of throughfall. We measured throughfall chemistry above and under *L. maackii* in a forest and, simultaneously, in an adjacent open, prairie area that served as a control (Fig. 1). We predicted (P_1) that the presence of *L. maackii* would lead to a reduction in throughfall volume due to interception associated with this plant's leafy canopy. Because concentration of some cations is increased in throughfall under *L. maackii* (McEwan et al. 2012), we predicted (P_2) samples collected under the canopy of this species would exhibit higher concentrations of phosphorous. We were also interested in deposition of carbon under the canopy of *L. maackii* and predicted (P_3) that the presence of this invasive shrub would increase carbon deposition in throughfall. Lastly, following evidence from prior research (McEwan et al.

Fig. 1 Taylorsville MetroPark throughfall field site with invaded *Lonicera maackii* riparian forest in the background and a prairie in the foreground during autumn 2015

2012), we predicted (P₄) there would be a reduction of nitrogen in *L. maackii* throughfall.

Methods

The throughfall study took place at Taylorsville MetroPark located in southwestern Ohio, USA (39.52°N, 84.10°W). A riparian forest site with a native upper canopy and dense shrub layer of *L. maackii*, and an adjacent prairie were selected based on close proximity to each other within 360 m of the Great Miami River (Fig. 1). The upper canopy was composed of a mix of deciduous forest trees commonly found in local riparian forests including *Platanus occidentalis* L. (American sycamore), *Ulmus* spp. L. (em), and *Acer* spp. including *Acer negundo* L. (box elder). The prairie flora consisted of *Dipsacus* L. (teasel), *Asclepias* L. (milkweed), *Schizachyrium scoparium* (Michx.) Naxh (little bluestem) and *Andropogon gerardii* Vitman (big bluestem); however, the funnel installations (see below) were above the influence of these species. Canopy cover during the study was on average 0% for the prairie, 97% under the honeysuckle shrub layer, and 83% under the upper forest canopy but above the honeysuckle canopy. Taylorsville Metropark is part of the Five Rivers Metroparks (https://www.metroparks.org; Accessed 1 April 2018) system and all aspects of the throughfall study took place in cooperation with land managers.

Throughfall sampling devices were set up within the forested and open prairie sites and represented three conditions "Upper canopy," "Open", and "Honeysuckle." The sampling devices were made using a piece of PVC that held 1 L amber Nalgene collection bottles, with 9.3 cm diameter funnels. These funnels were established just prior to each rain event and removed within 10 h after the rain had stopped. Collection bottles were capped during dry periods to prevent atmospheric deposition. Just prior to rain events, bottle caps were replaced with funnels that had a 250 μm mesh insert to prevent debris from entering the bottles and contaminating rain water samples. "Upper canopy" and "Honeysuckle" throughfall sampling devices were haphazardly installed along a transect in the *L. maackii* invaded riparian forest (within 50–120 m from river bank). The throughfall sampling devices were at least 5 m apart under a *L. maackii* crown of at least 2 m in width. In cases where the branching architecture of *L. maackii* was not conducive to sampling (i.e., technician could not physically get through the thicket), the sampling device was placed at the next 5 m distance. The "Upper canopy" collection funnel was established at a height that placed the collection bottle above the *L. maackii* shrub layer (> 1 m in many instances). An additional bottle was attached approximately 70 cm above the ground to capture "Honeysuckle" throughfall that passed through both the forest canopy and the leafy canopy of the *L. maackii* shrub layer. The sampling devices were stabilized with 1 m rebar and a 122 cm fence post.

Samples were collected immediately after rain events on 7 June, 27 July, 31 August, and 5 November of 2015. Samples were processed immediately upon return to the laboratory for carbon, nitrogen, and phosphorus content. Carbon analyses included total carbon (TC), total organic carbon (TOC), dissolved inorganic carbon (DIC), and dissolved organic carbon (DOC). All organic carbon measurements were acidified with 2 N HCl to 2.0 pH. The DOC was measured post acidification and filtered with a 0.45 μm filter, and DIC was calculated as the difference between total dissolved carbon and DOC. All carbon measurements were conducted with a Shi-

madzu TOC-V$_{CSN}$ analyzer (Kyoto, Japan). Total nitrogen (TN) was measured with 10 mL samples that were ampulated with potassium persulfate added as an oxidizer and autoclaved at 121 °C for 4 h, which converted all forms of nitrogen to NO$_3$–N (nitrate). To determine dissolved nitrogen (DN) concentration, 10 mL samples were first filtered through a 0.45 μm filter and then processed as explained for TN. Nitrite (NO$_2$–N), nitrate (NO$_3$–N), and ammonia (NH$_3$–N) were determined via standard colorimetric methods using the DREL 2800 water quality kit from Hach Company (Loveland, Colorado, USA). Nitrate was identified with the cadmium reduction method, which created a pink colored reaction if NO$_3$–N was present and colorimetrically determined with a spectrophotometer at 500 nm. The Nessler method was used to characterize NH$_3$–N concentration, which created a yellow–orange colored reaction that was read at 524 nm. Nitrite concentrations were measured via the diazotization method and resulted in an amber color reaction that was measured at 507 nm. Total orthophosphate (PO$_4^{-3}$; hereafter referred to as P or phosphorus) was measured using the malachite green method (D'Angelo et al. 2001). An additional 5 mL water sample was filtered through a 0.45 μm filter and then processed for soluble reactive P (SRP: also known as dissolved reactive P) using the D'Angelo et al. (2001) method. Deposition estimates were calculated for each nutrient by correcting for the total volume of the sample and circular area of the collection funnel (concentration × sample volume/area based on radius; McEwan et al. 2012).

Statistical analyses

Throughfall volume, pH, and both nutrient concentration and deposition during rain events were compared among the following three conditions: Open (prairie), Upper canopy (native forest canopy only), and Honeysuckle (native forest canopy and *L. maackii*) treatments. Outliers were identified for all parameters and removed if they were greater than 3 times the interquartile range for each treatment within each time point (Quinn and Keough 2004). Data were then screened for normality and homogeneity of variance. Normal data were analyzed with one-way ANOVA due to non-homogeneity of variance (i.e., rmANOVA assumptions not met) within each sampling month while non-normal data were analyzed with Kruskal–Wallis test (Sokal and Rohlf 1981; Zar 1999). In some cases both parametric and non-parametric statistical results were presented due to mixed normality (i.e., at least one treatment failed normality tests within a time point) in order to balance statistical interpretation. Bonferroni pairwise post-tests were only conducted if the treatment main effect was significant using 'pairwise.t.test' in the R base package. The 'post.hoc.kruskal.nemenyi.test' was used to conduct pairwise post-tests among treatments only when the Kruskal–Wallis test was significant with the 'PMCMR'

package in R (Pohlert 2015). Mean percent change in nutrient concentration and deposition relative to Open conditions (prairie controls) was calculated for both Upper Canopy and Honeysuckle conditions ([(treatment value − control value)/control value) × 100)]; see Tables S1 and S2 for original data). All statistical analyses were conducted in R version 3.2.2.

Results

In all 4 months, throughfall volume under *L. maackii* (Honeysuckle) was less than Open conditions (Fig. 2a). The volume of throughfall in the Upper Canopy samples was also significantly lower than the Open treatment except for June (Fig. 2a). Throughfall volume from the Honeysuckle collection was significantly lower than the Upper Canopy treatment in June (Fig. 2a; Table S3) and trended lower in all other collections (Fig. 2a). The Honeysuckle throughfall collection exhibited higher pH (7) than either of the other treatments in June (6.2–6.4, Fig. 2b). For all other sampling events, the pH of Upper Canopy and Honeysuckle collections was statistically indistinguishable (6.7–7) and higher than Open collections (4.6–5.3, Fig. 2b; Table S3).
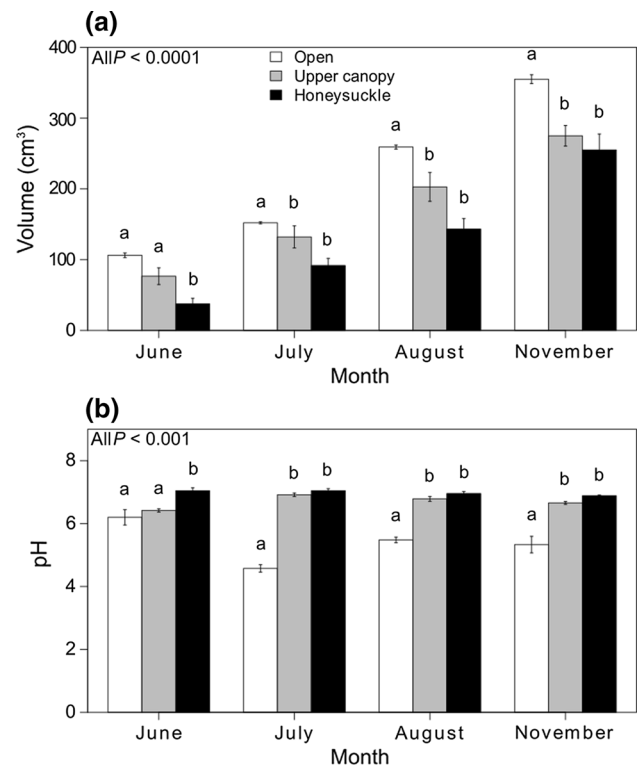

Fig. 2 Mean (± SE, $n = 8$–10) throughfall and rain water **a** volume and **b** pH collected from open prairie (Open), under native forest canopy (Upper canopy) and under *Lonicera maackii* shrubs (Honeysuckle). Letter differences refer to Bonferroni post hoc statistical analyses among treatments within each sampling month. Statistical significance was determined at $P < 0.05$
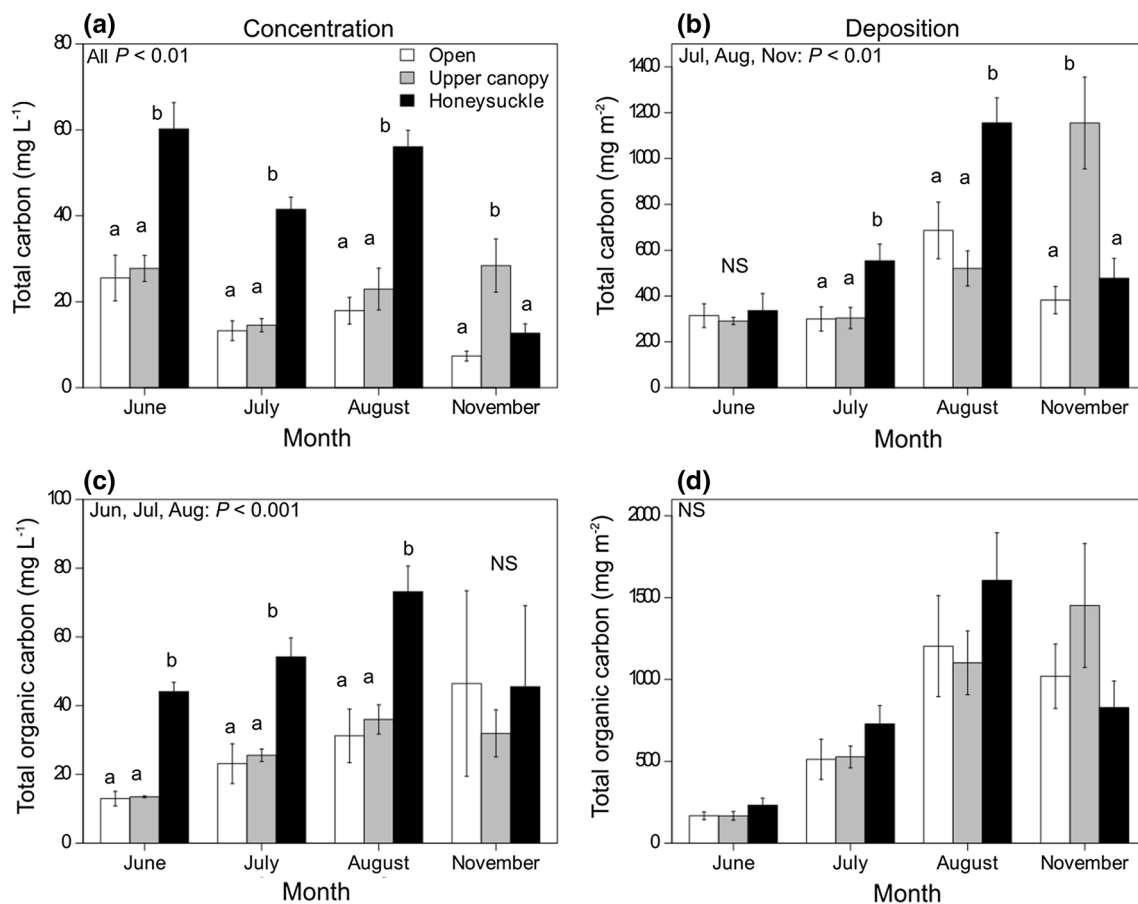
Fig. 3 Mean (± SE, n = 8–10) total carbon and total organic carbon **a**, **c** concentration and **b**, **d** deposition from throughfall and rain water collected from open prairie (Open), under native forest canopy (Upper canopy) and under *Lonicera maackii* shrubs (Honeysuckle). Letter differences refer to Bonferroni post hoc statistical analyses among treatments within each sampling month. Statistical significance was determined at $P < 0.05$

Carbon in throughfall varied among treatments and across seasons (Figs. 3, 4). Total carbon and total organic carbon (TOC) concentration was significantly higher in throughfall from the Honeysuckle collection than the other two treatments in June, July, and August (Table S4; Fig. 3a, c). There was no statistically discernable pattern in TOC concentration in November, nor for deposition during any of the sampling dates (Fig. 3c, d). Both concentration and deposition of total carbon was higher in the Upper Canopy treatment than either Open or Honeysuckle conditions in November (Fig. 3a, b). Overall, *L. maackii* canopy subsidized throughfall with 72–213% more TC relative to the Open treatment, whereas the Upper canopy subsidized throughfall with carbon from 9–285% as compared to the Open treatment (Table 1). Dissolved organic carbon concentration varied among treatments with significantly higher concentration in the Honeysuckle collection when compared to the Open treatment in June, and significantly lower deposition in both July and August (Tables S4 and S5; Fig. 4a, b). Deposition and concentration of DIC was higher in Honeysuckle samples than

either Open or Upper canopy samples in June, July, and August (Fig. 4c, d).

Nitrogen concentration and deposition was differentially influenced by the presence of the *L. maackii* shrub canopy (Tables S4 and S5). Concentration of TN was significantly greater in the Honeysuckle treatment than Open conditions during July and August (Table S4; Fig. S1a). Total N deposition was significantly reduced in throughfall collected under the *L. maackii* canopy compared to Open collections in June and August, with Upper canopy intermediate and statistically indistinguishable from the Honeysuckle and Open conditions (Table S5; Fig. S1b). The Honeysuckle collections exhibited up to 59 and 66% reduction of TN and DN deposition (respectively) while there was up to 34 and 45% reduction in TN and DN deposition under the Upper Canopy (Table 1). Inorganic nitrogen species concentration and depositional patterns were dynamic throughout the sampling period (Tables S4 and S5; Fig. S2). One striking pattern was exhibited by the nitrate values where nitrate concentration in the Honeysuckle collection was significantly higher than Upper
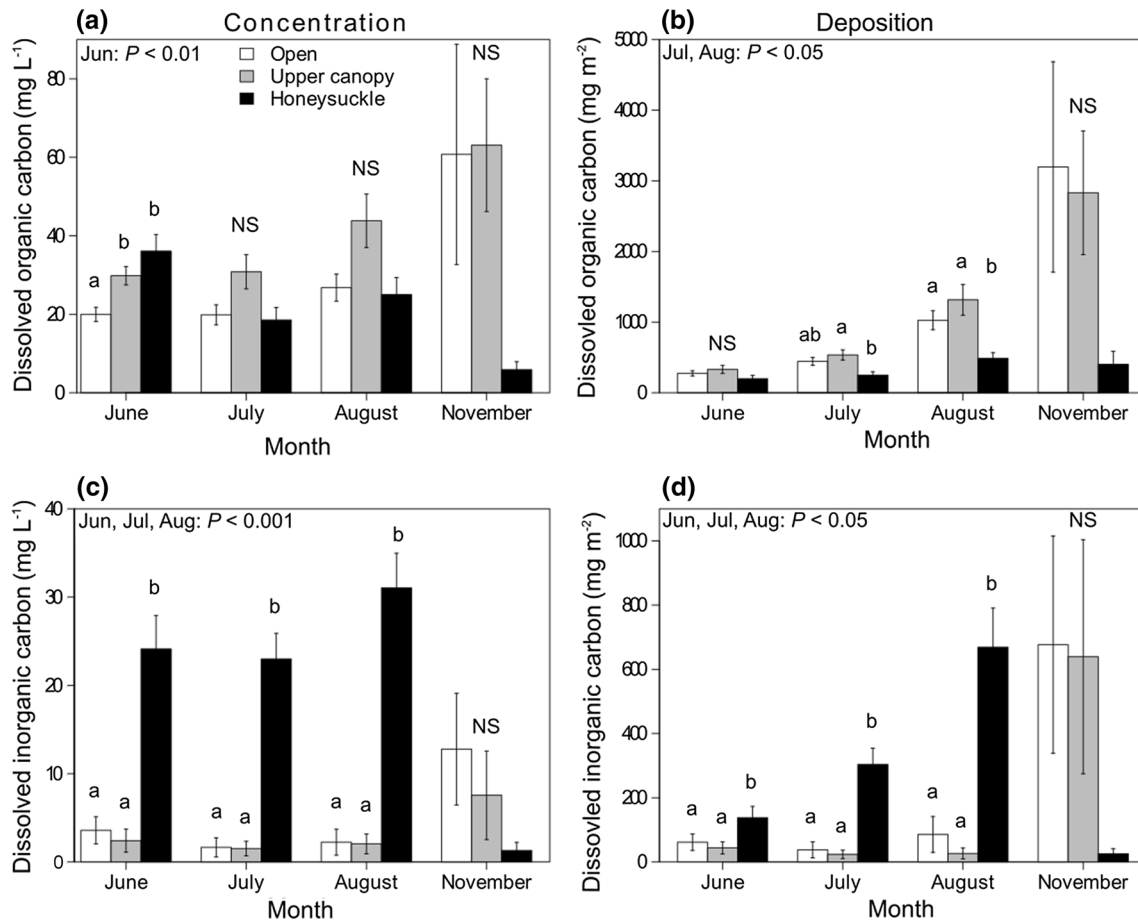
Fig. 4 Mean ($\pm$ SE, $n = 8$–10) dissolved organic carbon and dissolved inorganic carbon **a**, **c** concentration and **b**, **d** deposition from throughfall and rain water collected from open prairie (Open), under native forest canopy (Upper canopy) and under *Lonicera maackii* shrubs (Honeysuckle). Letter differences refer to Bonferroni post hoc statistical analyses among treatments within each sampling month. Statistical significance was determined at $P < 0.05$

Canopy treatment in July and significantly lower than both of the other treatments in August (Fig. S2c). Deposition of nitrate was also significantly lower in the Honeysuckle treatment in August. Ammonia deposition under Honeysuckle and Upper canopies was significantly greater compared to Open collections during August with the opposite pattern observed during November (Table S5; Fig. S2f).

The influence of *L. maackii* on P and SRP was dependent on sampling month (Tables S4 and S5; Fig. S3). Phosphorous and SRP levels during July were found to be nearly 4 times greater compared to all other sampling months (Fig. S3). During July, Upper Canopy P and SRP concentrations were either greater than, or statistically similar to, the other throughfall collections (Fig. S3a, c); however, P deposition in the Honeysuckle collections was significantly reduced compared to Open and Upper Canopy collections (Fig. S3b) and SRP deposition was significantly lower in comparison to Open conditions (Fig. S3d). Honeysuckle collections were typically 5–50% greater in P and SRP concentrations whereas the Upper Canopy treatment increased

concentrations by 2–10% but intercepted up to 91% of the phosphorus available from Open collections (Table 1).

Discussion

The presence of a dense *L. maackii* canopy may lead to a reduction in throughfall volume arriving at the forest floor with potential implications for plant competition and nutrient cycling. Pfeiffer and Gorchov (2015) found that *L. maackii* was responsible for throughfall interception in August but not in June of 2012, while McEwan et al. (2012) reported significant effects of *L. maackii* on throughfall in June, August, and November. In our study, throughfall volume was significantly lower in the Honeysuckle collection than either the Open or Upper Canopy collections in June, and lower than the Open treatment in all other collections, similar to our prediction (P_1). Volume of throughfall under *L. maackii* was numerically lower, though statistically indistin-

Table 1 Mean percent difference of nutrient concentration and deposition for Honeysuckle and Upper canopy throughfall relative to the open treatment

Month	Treatment	TC	TOC	DOC	DIC	TN	DN	NO$_2$	NO$_3$	NH$_3$	P	SRP
Concentration (mg L^{-1})												
June	Honeysuckle	136	240	81	574	− 5	− 7	283	0	29	50	50
	Upper canopy	9	4	49	− 33	− 5	− 15	330	138	− 35	− 91	− 85
July	Honeysuckle	213	134	− 7	1289	38	0	70	37	61	5	− 1
	Upper canopy	10	11	55	− 8	− 2	− 29	14	− 42	− 21	10	2
August	Honeysuckle	213	134	− 7	1289	32	13	14	− 49	1756	231,710	–
	Upper canopy	28	15	64	− 8	6	0	30	− 9	1257	63,600	–
November	Honeysuckle	72	− 2	− 90	− 90	15	34	25	38	− 88	− 36	31
	Upper canopy	285	− 31	4	− 41	4	23	− 14	9	− 94	− 15	− 3
Deposition (mg m^{-2})												
June	Honeysuckle	7	38	− 28	124	− 59	− 66	− 46	57	− 33	− 22	− 27
	Upper canopy	− 7	− 1	20	− 29	− 34	− 30	102	561	− 31	− 92	− 76
July	Honeysuckle	85	42	− 44	702	− 12	− 35	1	− 19	− 10	− 38	− 32
	Upper canopy	1	3	21	− 37	− 24	− 45	− 5	− 43	− 37	− 5	− 11
August	Honeysuckle	68	33	− 53	680	− 43	− 38	− 37	− 71	888	–	–
	Upper canopy	− 24	− 8	28	− 69	− 15	− 17	− 1	− 28	1077	–	–
November	Honeysuckle	25	− 19	− 87	− 96	− 24	− 6	− 13	− 3	− 91	2	35
	Upper canopy	202	42	− 11	− 6	− 17	− 6	− 28	− 9	− 96	− 7	− 20

TC total carbon, *TOC* total organic carbon, *DOC* dissolved organic carbon, *DIC* dissolved inorganic carbon, *TN* total nitrogen, *DN* dissolved nitrogen, *NO$_2$ (NO$_2$–N)* nitrite, *NO$_3$* nitrate (NO$_3$–N), *NH$_3$* ammonia (NH$_3$–N), *P* orthophosphate, *SRP* soluble reactive phosphorus

guishable, from the Upper canopy in July, August, and November.

Fluctuations in volume related to nutrient content are important for understanding the potential influences of *L. maackii* on throughfall chemistry. In some instances, there were discordant patterns between mass inputs and concentrations within the throughfall. Increased concentration of a substance in the throughfall may not translate into increased deposition if the total volume of inputs is reduced. From a whole ecosystem perspective, total deposition is the key measure; however, the concentration of a substance within throughfall may also be important. For instance, in regional headwater streams, flow is highly variable and during dry periods these streams may be reduced to a series of stagnant pools where most flow is sluggish or subterranean. During low flow conditions, rainfall that passes through a *L. maackii* canopy and arrives at the stream surface with high nutrient concentration may influence stream organisms even though the total deposition is reduced by canopy interception. During high flow periods, the larger volume of water in the stream will dilute the incoming throughfall and the influence of *L. maackii* on stream chemistry is likely to be reflected by deposition and to be highly dependent upon total leaf area along the stream. Scaling up to model effects of *L. maackii* at the watershed scale was beyond the scope of this project but is an interesting area for future research.

We predicted an increase in phosphorous (P$_2$) in *L. maackii* throughfall when compared to both the existing Upper canopy and Open conditions. The phosphorus prediction was supported by some measurements and refuted by others. For example, the Honeysuckle collection had higher phosphorus deposition than the Upper canopy in June and lower deposition in July. A similarly contradictory pattern was demonstrated in SRP, where the Honeysuckle collection was lower in SRP than the Open treatment in July but higher in August, and in other instances the Upper Canopy collection was intermediate.

An important component of throughfall is dissolved organic carbon (DOC; Qualls and Haines 1992; Liu and Sheu 2003), which is a key source of energy in stream systems that could be influenced by changes in plant communities (Webster and Meyer 1997; Gergel et al. 1999). For DOC in this study, throughfall deposition in the Honeysuckle collection was significantly lower than the Upper canopy in both July and August. Total carbon, TOC, and DIC were significantly greater in the Honeysuckle collection compared to the Upper canopy and Open collections supporting our prediction (P$_3$).

Nitrogen varied among sample location and TN and DN deposition was generally reduced under *L. maackii* canopies compared to the Upper canopy and Open treatments, supporting our prediction (P$_4$). We found an overall increase in NH$_3$–N concentration under Honeysuckle canopies compared to Open collections, but no significant differences when compared to Upper canopy collections. In comparison, McEwan et al. (2012) reported significantly lower NH$_4$–N under *L. maackii* canopies in comparison to forest only samples.

Variation in throughfall chemistry may be linked to the role of *L. maackii* as a receiving surface for atmospheric deposition of particulates that "wash off" during rain events or through leaching from the plant itself. Atmospheric deposition of nitrogen on plant canopies has been linked to an increase in nitrogen in forest and aquatic systems (Lindberg et al. 1986; Lovett 1994; Anderson et al. 2002), acidification of freshwater ecosystems (Lepori and Keck 2012), and organic matter

processing in streams (Chadwick and Huryn 2003). Plant location within the forest can also influence atmospheric deposition onto leaves, with forest edge habitats known to have higher atmospheric deposition of nitrogen compared to interior locations (Weathers et al. 2001). Our forest throughfall sampling devices were not set up in an edge habitat, but rather under an intact riparian forest (within 50–100 m of stream bank), which may have reduced atmospheric deposition even though *L. maackii* shrubs have a large leaf crown. In this study we did not attempt to tease apart the relative role of deposition and leaching with respect to alterations of throughfall chemistry. Two of our results suggest a role for atmospheric deposition on the canopy of *L. maackii* may be an important driver of variation in throughfall chemistry. First, we found much higher concentrations of phosphorus in July across all three locations than in other seasons. We hypothesize this may be related to regional deposition of particulate phosphorus associated with agricultural activities. Second, both concentration and deposition of DIC was much higher in the Honeysuckle collection than those from the Upper canopy or Open collections in June, July, and August. It is likely the case that this increase is associated with atmospheric deposition potentially as carbonate in dust; however, it was beyond the scope of this study to assess the particular source of this increase in DIC. These results indicate that particle deposition on the morphological surfaces created by the *L. maackii* leafy canopy may be a key source of changes to throughfall chemistry under this invasive species.

Nutrient fluxes during rain events can be driven in part by canopy exchange from leaves and stems (Liu and Sheu 2003; Hafner et al. 2005) and the influence of *L. maackii* on throughfall chemistry may be linked to plant traits including leaf morphology and microbial colonization on the phyllosphere. *Lonicera maackii* does not have a thick waxy cuticle and tends to be structurally flimsy (lignin content 7.15% Trammell et al. 2012; personal observation) and these physical characteristics may be linked with greater nutrient concentrations in throughfall (Tukey 1966; Potter et al. 1991). The availability of nitrogen has been linked to the external and internal concentration of the leaf and microbial activities (Schjoerring et al. 2000; Jetten 2008), with phyllospheric microbes on leaf surfaces known to facilitate nitrification from throughfall (e.g. Watanabe et al. 2016). The microbial community known to colonize *L. maackii* leaves can be unique compared to native leaves (Arthur et al. 2012; McNeish and McEwan 2016), which may partially explain this species influence on throughfall chemistry.

The deposition of "novel subsides" (sensu Custer et al. 2017) from *L. maackii* may result in toxic effects on aquatic organisms and our data add to a growing body of evidence that suggests *L. maackii* may be fundamentally altering nutrient cycling in forests where it has invaded. The strongest evidence comes from greatly accelerated leaf decomposition (Arthur et al. 2012;

McNeish et al. 2012), which likely impacts the detrital basal resource in streams and accelerates nutrient cycling (McNeish et al. 2012, 2015). Strong evidence exists now which suggests that *L. maackii* intercepts rainwater and alters the chemistry of throughfall. Modelling these empirical results to estimate nutrient budgets at the watershed scale would shed significant light on the potential effects of *L. maackii* invasion and help move toward more general predictions of how aquatic nutrient dynamics are linked to terrestrial environments.

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