

# Increasing donor ecosystem productivity decreases terrestrial consumer reliance on a stream resource subsidy

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**Abstract** Because nutrient enrichment can increase ecosystem productivity, it may enhance resource flows to adjacent ecosystems as organisms cross ecosystem boundaries and subsidize predators in recipient ecosystems. Here, we quantified the biomass and abundance of aquatic emergence and terrestrial spiders in a reference and treatment stream that had been continuously enriched with nitrogen and phosphorus for 5 years. Because we previously showed that enrichment increased secondary production of stream consumers, we predicted that aquatic emergence flux would be higher in the treatment stream, subsequently increasing the biomass and abundance of terrestrial spiders. Those increases were predicted to be greatest for spiders specializing on aquatic emergence subsidies (e.g., Tetragnathidae). By adding a  $^{15}\text{N}$  stable isotope tracer to both streams, we also

quantified nitrogen flow from the stream into the riparian community. Emergence biomass, but not abundance, was higher in the treatment stream. The average body size of emerging adult insects and the relative dominance of Trichoptera adults were also greater in the treatment stream. However, spider biomass did not differ between streams. Spiders also exhibited substantially lower reliance on aquatic emergence nitrogen in the treatment stream. This reduced reliance likely resulted from shifts in the body size distributions and community composition of insect emergence that may have altered predator consumption efficiency in the treatment stream. Despite nutrient enrichment approximately doubling stream productivity and associated cross-ecosystem resource flows, the response of terrestrial predators depended more on the resource subsidy's characteristics that affected the predator's ability to capitalize on such increases.

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J.M. Davis conceived the experiment, designed and conducted data collection, and analyzed the data. A.D. Rosemond contributed to experimental design. G.E. Small developed the dynamic mixing model. All authors contributed to the writing of the manuscript.

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## Introduction

Resource and energy flows across ecosystem boundaries can alter the structure and function of recipient ecosystems; however, the exact forms of these flows vary (Polis et al. 1997; Baxter et al. 2005). Marine resource subsidies, such as seaweed detritus and seabird guano, can help maintain desert island productivity (Polis and Hurd 1995). Consumers in freshwater ecosystems can also depend on subsidies of terrestrial detritus and invertebrates, which alter their community structure and increase productivity (Wallace et al. 1997; Pace et al. 2004; Baxter et al. 2005). Furthermore, algal detritus, which becomes stranded along

river banks after floods, can be important for terrestrial herbivores, while terrestrial predators can depend on freshwater invertebrate production when it is exported as adult insect emergence (Sanzone et al. 2003; Baxter et al. 2005; Marczak and Richardson 2007; Gratton et al. 2008).

The importance of aquatic–terrestrial linkages for stream ecosystems has long been recognized (Hynes 1975), but more recent research has assessed how changes in these linkages alter recipient ecosystems (Polis et al. 1997; Marczak et al. 2007b). Specifically, populations of consumers that specialize on subsidies can increase when subsidy flows increase, even when in situ resource availability does not change (Marczak et al. 2007b). As many terrestrial predators rely on aquatic resource subsidies, such as adult insect emergence (Baxter et al. 2004), this suggests that when environmental change alters stream ecosystems and aquatic emergence it may similarly affect terrestrial predators. Accordingly, the introduction of rainbow trout (*Oncorhynchus mykiss*) to a forested stream reduced biomass of benthic invertebrate larvae and adult insect emergence, with subsequent declines in terrestrial spider abundance (Baxter et al. 2004). In the South Fork Eel River, California, damming may reduce adult emergence and spider abundance because it can decrease the prevalence of algal mats, which are important aquatic emergence hotspots (Power et al. 2004). Conversely, because nutrient enrichment can increase aquatic productivity (Slavik et al. 2004; Cross et al. 2006), it may increase aquatic emergence and terrestrial predator populations. However, because studies have not quantified the effects of nutrient enrichment on coupled aquatic–terrestrial ecosystems, we have limited ability to predict these bottom-up effects on resource subsidies and the terrestrial organisms that depend on them.

To assess whether nutrient enrichment would increase cross-ecosystem resource flows and terrestrial predator populations, we sampled aquatic adult emergence and terrestrial spiders in a reference and nutrient-enriched headwater stream that exhibited greater secondary production. Five years of nutrient enrichment more than doubled the rate of secondary production for benthic invertebrate larvae (Davis et al. 2010a), a metric that integrates several measures of consumer response (i.e., abundance, biomass, growth rate, and survivorship) (Benke 1993). Because aquatic emergence production can be ca. 25% of benthic larval production (e.g., Jackson and Fisher 1986 and references cited therein), greater secondary production due to enrichment may have increased adult emergence production. Enrichment also disproportionately increased the secondary production and biomass of large-bodied benthic larvae and the maximum larval body size of a dominant stream consumer (Davis et al. 2010a, b). These larger sized larvae were relatively predator-resistant; thus,

their greater dominance decreased the proportion of benthic production that was eaten by instream predators (Davis et al. 2010a). As enrichment increased overall productivity of stream consumers and a larger proportion of this productivity bypassed instream predator pathways (Davis et al. 2010a), we predicted that the export of aquatic insect emergence to terrestrial ecosystems would increase.

Increased resource subsidies can have positive effects on subsidized consumers (Marczak et al. 2007b); thus, we predicted that greater aquatic emergence flux would increase terrestrial spider populations. Aquatic emergence can be important for both arboreal and ground spiders (Sanzone et al. 2003; Paetzold and Tockner 2005). However, we predicted that population increases would be greater for arboreal spiders because several of these spider families rely more heavily on aquatic emergence, allowing their populations to more closely track aquatic emergence availability in other ecosystems (e.g., Tetragnathidae) (Sanzone et al. 2003; Marczak et al. 2007b). We also tested whether these disparate responses would alter spider community composition in the nutrient-enriched stream. By using a whole-stream stable isotope tracer ( $^{15}\text{N}$ ) addition, we quantified spiders' reliance on aquatic-derived nitrogen (N). Because nutrient enrichment stimulated nutrient flow within the stream food web (Cross et al. 2007), we predicted that enrichment would increase the proportion of spider N originating from aquatic emergence.

## Materials and methods

We conducted this study at the USDA Forest Service Coweeta Hydrologic Laboratory, a long-term Ecological Research site in the southern Appalachian Mountains (Macon County, North Carolina). Coweeta is a heavily-forested experimental watershed (2,185 ha) composed of mixed hardwoods (oak, maple, tulip poplar) with a dense understory of *Rhododendron maximum* that limits light availability. This light limitation reduces autotrophic production and increases stream consumer reliance on heterotrophic microbes that colonize terrestrial leaf inputs (Wallace et al. 1997; Cross et al. 2007).

We used a paired-watershed approach that combined a whole-stream  $^{15}\text{N}$  tracer addition with sampling of aquatic emergence flux and terrestrial spiders (April–June 2005) in a reference (C53) and a treatment stream (C54). The study was conducted at the end of a 5-year ecosystem-level manipulation that examined the effects of nutrient enrichment on stream-dwelling organisms and consequent effects on nutrient and carbon dynamics (see Cross et al. 2006; Davis et al. 2010a). The pairing of the  $^{15}\text{N}$  tracer addition with assessments of spider and aquatic emergence population responses allowed us to determine the effects of

nutrient enrichment on cross-ecosystem resource and nutrient fluxes in a diverse stream ecosystem.

The reference and treatment streams did not differ in nutrient concentrations prior to the experimental manipulation (mean  $\pm$  SE, Reference: DIN:  $23.2 \pm 8.5 \mu\text{g L}^{-1}$ , SRP:  $6.8 \pm 3.0 \mu\text{g L}^{-1}$ ; Treatment: DIN:  $29.3 \pm 4.9 \mu\text{g L}^{-1}$ , SRP:  $9.5 \pm 2.3 \mu\text{g L}^{-1}$ ). From July 2000 to August 2005, we enriched a 150-m reach of the treatment stream with nitrogen ( $\text{NH}_4\text{NO}_3$ ) and phosphorus ( $\text{K}_2\text{HPO}_4$  and  $\text{KH}_2\text{PO}_4$ ). We added nutrients continuously along the entire 150-m experimental reach using an irrigation line running down the center of the stream. The delivery system increased nutrient concentrations in the treatment stream to a moderate-level enrichment (DIN:  $506.2 \pm 36.3 \mu\text{g L}^{-1}$ , SRP:  $80.0 \pm 5.6 \mu\text{g L}^{-1}$ ), which was comparable to watersheds experiencing agricultural and urban land use (Alexander and Smith 2006). Reference stream concentrations during this same period were similar to the pretreatment period (DIN:  $31.0 \pm 3.4 \mu\text{g L}^{-1}$ , SRP:  $8.0 \pm 1.3 \mu\text{g L}^{-1}$ ). Nutrient concentrations were measured every 2 weeks at three points along the 150-m reach of the treatment stream and at the weir of the reference stream (APHA 1998). Stream discharge was monitored at 5-min intervals with an Isco data logger (Teledyne Isco).

#### Isotopic enrichment

To quantify the effect of enrichment on resource subsidies and N flow from the treatment stream, we applied an isotopic tracer to both streams from 24 April 2005 to 06 June 2005. We continuously added 99%  $^{15}\text{N}$ -labeled  $\text{NH}_4\text{Cl}$  in both streams to achieve 2,500‰ enrichment without additionally affecting nutrient concentrations. We used a battery-powered fluid metering pump (Fluid Metering) to add the solution for 44 days at a location that provided adequate stream mixing. Because the amount of solute released was adjusted daily according to stream discharge, the release was proportional to flow and nutrient concentrations (Reference: 0.39 g  $^{15}\text{N}$  was added as  $^{15}\text{NH}_4\text{Cl}$ ; Treatment: 5.53 g  $^{15}\text{N}$  was added as  $^{15}\text{NH}_4\text{Cl}$ ).

#### Emergence sampling

Our study period coincided with the typical timing of peak emergence from these ecosystems (J.B. Wallace, personal communication). From 19 April to 6 June 2005, we affixed 0.25-m<sup>2</sup> emergence traps (0.5-mm mesh) to the stream substrate to collect emerging adult insects that were analyzed for isotopic composition, total biomass flux, and total abundance flux (hereafter referred to as ‘biomass’ and ‘abundance’). By dividing total biomass by total abundance for each trap on each date, we also calculated a community-level average body size for emerging adults. To

quantify background isotopic concentrations, we collected emergence 1 week prior to the initiation of the isotopic drip. On a weekly basis during the study period, traps were deployed at sunrise for 48 h at ca. 10-m intervals downstream of the isotopic enrichment (10, 20, 30, 40, and 48 m). Emerging insects were collected every 24 h and frozen. Most adults were identified to family level; Diptera were identified to order level. Samples were dried at 60°C and weighed. Because of low spatial and temporal sampling resolution at the family level, we combined individuals at the order level for isotopic analysis. For each sampling date and location, multiple individuals from the same order were ground and analyzed for isotopic composition using a mass spectrophotometer (Finnigan Delta Plus).

#### Spider sampling

We used separate methods to sample ground and arboreal spiders. To collect ground spiders, five transects of pitfall traps were deployed weekly at ca. 10-m intervals downstream of the point of isotopic addition. At each of these transects, a pitfall trap (diameter: 11 cm) was deployed at 0 (streamside), 10, and 25 m from the stream margin. This distribution determined the lateral extent that the effects of aquatic emergence reached into upland habitat. Traps were filled with tap water and a small amount of soap. Traps were deployed for 48 h beginning at sunrise. Spiders were removed, rinsed to eliminate any soap residue that might affect isotopic analysis, and frozen prior to analysis. To calculate background isotopic signatures, we sampled spiders 1 week prior to the initiation of the isotopic drip.

We sampled arboreal spiders via timed-beat sampling at each of the pitfall trap locations. Arboreal spiders are less mobile than ground spiders and may experience localized population depression from excessive sampling (F. Coyle, personal communication); thus, we restricted our sampling to every 2 weeks (weeks 2, 4, and 6). During these weeks, beat sampling coincided with the second day that pitfall traps were open. To calculate background isotopic signatures, we also sampled arboreal spiders 1 week prior to the initiation of the isotopic drip. Shortly after sunrise, we selected a random direction at each sampling point and spread a 1-m<sup>2</sup> white canvas below the vegetation. We then beat the vegetation for 5 min and collected all individuals on the canvas. Individuals were frozen for later analysis. To increase our sample size for isotopic analysis, we also systematically collected spiders at each sampling location on the final day of isotopic enrichment (day 44). Spiders collected during the pretreatment period and on day 44 were not used to estimate spider abundance or biomass, but were used for isotopic analyses.

Using a dissecting microscope, spiders were identified to family level based on Ubick et al. (2005). Spiders were dried at 60°C and weighed. Isotopic analyses were limited to taxa that possessed sufficient temporal sampling resolution to calculate isotopic enrichment curves at a given sampling location. For arboreal spiders, we analyzed Tetragnathidae, Araneidae, Anyphaenidae, and Linyphiidae. For ground spiders, we analyzed Amaurobiidae, Gnaphosidae, and Lycosidae. Other taxa, such as Pisauridae (fishing spiders), were not sufficiently sampled to calculate isotopic curves. However, the seven families represented ca. 70% of spider biomass collected (Davis 2009). We composited multiple individuals from the same family that were collected at the same location and date (range 1–14 individuals; ca. 40% of the samples had >1 individual). Composite samples were ground and analyzed using a mass spectrophotometer.

#### Estimation of trophic transfer of $^{15}\text{N}$

Isotopic equilibria were not achieved in either stream, whereby spider  $^{15}\text{N}$  signatures were still increasing after 44 days of isotopic enrichment. Thus, we could not use a two-source mixing model because it assumes that the isotopic signature is at steady state (e.g., Phillips and Gregg 2003). We used the following dynamic mixing model adapted from Hall et al. (1998) to quantify the mass of spider N derived from emergence N.

$$\delta_{t+1,i,j} = \frac{(\delta_{\text{SP},i,j} * M_{\text{SP}}) + (Ing_{\text{SP}} * \delta_{\text{AQ},i} * \% \text{Aq}) + (Ing_{\text{SP}} * \delta_{\text{TERR}} * (1 - \% \text{Aq}))}{(M_{\text{SP}} + Ing_{\text{SP}})} \quad (1)$$

where

$\delta_{t+1,i,j}$  = the background corrected isotopic signature of spiders for time period  $t + 1$  (in days) at sampling location  $i$  meters downstream of isotopic enrichment (10, 20, 30, 40, or 48 m) and  $j$  meters laterally from streamside (0, 10, or 25 m).

$\delta_{\text{SP},i,j}$  = the background corrected isotopic signature of spiders for time period  $t$  (in days) at sampling location  $i$  meters downstream of isotopic enrichment and  $j$  meters from streamside.

$M_{\text{SP}}$  = the mass of spider N

$Ing_{\text{SP}}$  = the mass-specific N ingestion rate of spiders

$\delta_{\text{AQ},i}$  = the background corrected isotopic signature of aquatic emergence at sampling location  $i$ , which was a biomass-weighted average  $\delta^{15}\text{N}$  of emerging adults

$\% \text{Aq}$  = the proportion of spider N originating from aquatic emergence, and

$\delta_{\text{TERR}}$  = the background corrected isotopic signature of terrestrial prey.

Isotope values used in the model were background corrected; thus, the calculations represent only changes in the  $^{15}\text{N}$  tracer. The mass-specific N ingestion rate of spiders was calculated by multiplying the mass-specific prey ingestion rate by known spider and prey body N content (this study) and spider assimilation efficiency. We used a literature value of 0.03 mg prey mg spider $^{-1}$  day $^{-1}$  for mass-specific spider ingestion rates (Moulder and Reichle 1972; Tanaka 1991). Based on Moulder and Reichle (1972), assimilation efficiency was set at 0.90.

Because we sampled the isotopic signature of aquatic emergence weekly, but we fit the model on a daily basis, we interpolated isotopic signatures on a 1-day time step. We used these interpolated data in our dynamic mixing model (see Eq. 1). We fit the mixing model to the actual isotopic signature of ground and arboreal spiders. To find the best model approximation ( $\delta_{t+1,i,j}$ ) of the actual isotopic signature, we varied the proportion of spider N originating from aquatic emergence (%Aq). To assess which %Aq value best approximated the actual spider isotopic signature, we used sum of squares to compare the actual and modeled isotopic signature ( $\delta_{t+1,i,j}$ ). The model with the lowest sum of squares was considered the best estimate of the spiders' reliance on aquatic emergence. This process was repeated for each spider family at each sampling location where we had sufficient data to fit the model.

We did not directly measure several model parameters; therefore, the model was based on several assumptions that may have affected our results. We did not measure spider ingestion rates or assimilation efficiencies. However, any change in these assumptions would have been applied to both streams and led to similar interstream trends. The mixing model also assumed that a spider at a specific sampling location consumed emergence originating from that same location. We attempted to validate the isotopic signature of the aquatic emergence available at a sampling location through additional sampling (e.g., light traps, sticky traps, and sweep netting), but these methods were ineffective at quantifying aquatic emergence and their isotopic signatures. If emerging adults move upstream during oviposition (MacNeale et al. 2005), spiders may have consumed emergence that originated downstream. This would have overestimated the isotopic signature of the consumed aquatic emergence and potentially underestimated spiders' reliance on emergence. However, because these watersheds did not differ in their physical attributes (e.g., discharge, slope, watershed area, or elevation) (see Lugthart and Wallace 1992), upstream flight was likely similar between streams. Any correction would have been applied to both streams and led to similar interstream differences in aquatic emergence reliance.

Statistical analyses

To test whether aquatic emergence abundance, biomass, and average individual body size differed between streams, we used separate one-way repeated measures ANOVAs with nutrients (reference vs. treatment stream) as the main effect (SAS v.9.2; SAS Institute, Cary, NC). Subsequent ANOVAs were conducted for individual insect orders. Biomass and abundance responses of arboreal and ground spiders were analyzed with separate two-way repeated measures ANOVAs. Additional ANOVAs were applied to the seven spider families that were used in the isotope model. For the two-way ANOVAs, the main effects were nutrients and lateral distance from the stream (0, 10, and 20 m). When necessary, we transformed the data to meet statistical assumptions. We also implemented a false discovery rate correction, which is a less conservative alternative to a Bonferroni correction and controls both type I and II errors (Verhoeven et al. 2005). When the multiple comparison correction was applied, we report adjusted *P* values (*P*<sub>adj</sub>) that were calculated using PROC MULT-TEST (SAS v.9.2).

We did not statistically analyze the results from the dynamic mixing model because of small sample sizes. However, we fit separate models for each downstream

sampling location (10, 20, 30, 40, or 48 m) and lateral distance (0, 10, or 25 m). Using this spatial replication, we calculated the mean aquatic emergence reliance for a specific lateral distance. We graphically compared means to evaluate whether spiders differed in their aquatic emergence reliance.

To assess differences in spider community composition based on abundance and biomass, we applied a Bray–Curtis similarity index and non-metric multidimensional scaling ordination (NMDS) to log<sub>10</sub>-transformed data. Analysis was at the family level and limited to streamside spiders (i.e., 0 m) because differences would be greatest at the stream margin. To reduce outlier influence, we excluded rare families (i.e., occurred in <5% of the samples) and used an analysis of similarity (ANOSIM) to test for significant differences between the streams (PRIMER v.6.1; Clarke and Gorley 2006). Small sample sizes at the family level precluded a multivariate analysis of aquatic emergence (see “Results”); thus, differences in community composition were assessed by comparing the relative contribution of each order to the total community.

Because this ecosystem-level manipulation used one reference and one treatment stream, use of nutrients in our model violates assumptions of sample independence in ANOVA, as our nutrient treatment was pseudoreplicated

**Table 1** Statistical results (*F* statistics, degrees of freedom, and *P* values) from the repeated measures one-way ANOVA testing the main effects of nutrient enrichment on emergence biomass, abundance, and average body size of emerging adults

	Biomass		Abundance	
Combined emergence				
Nutrients	<i>F</i> <sub>1,8</sub> = <b>16.55</b>	<b>0.018</b>	<i>F</i> <sub>1,8</sub> = 0.76	0.59
Time	<i>F</i> <sub>6,48</sub> = <b>2.58</b>	<b>0.050</b>	<i>F</i> <sub>6,48</sub> = <b>3.34</b>	<b>0.013</b>
Nutrients × time	<i>F</i> <sub>6,48</sub> = 2.03	0.19	<i>F</i> <sub>6,48</sub> = 1.68	0.18
Trichoptera				
Nutrients	<i>F</i> <sub>1,8</sub> = <b>8.95</b>	<b>0.043</b>	<i>F</i> <sub>1,8</sub> = 6.37	0.18
Time	<i>F</i> <sub>6,48</sub> = <b>2.71</b>	<b>0.050</b>	<i>F</i> <sub>6,48</sub> = 1.11	0.37
Nutrients × time	<i>F</i> <sub>6,48</sub> = 1.81	0.19	<i>F</i> <sub>6,48</sub> = 3.01	0.056
Diptera				
Nutrients	<i>F</i> <sub>1,8</sub> = 0.66	0.62	<i>F</i> <sub>1,8</sub> = 0.36	0.59
Time	<i>F</i> <sub>6,48</sub> = <b>2.77</b>	<b>0.050</b>	<i>F</i> <sub>6,48</sub> = <b>4.40</b>	<b>0.0065</b>
Nutrients × time	<i>F</i> <sub>6,48</sub> = 0.62	0.71	<i>F</i> <sub>6,48</sub> = 1.95	0.15
Ephemeroptera				
Nutrients	<i>F</i> <sub>1,8</sub> = 0.50	0.62	<i>F</i> <sub>1,8</sub> = 2.63	0.36
Time	<i>F</i> <sub>6,48</sub> = 1.74	0.13	<i>F</i> <sub>6,48</sub> = 1.30	0.34
Nutrients × time	<i>F</i> <sub>6,48</sub> = 0.62	0.71	<i>F</i> <sub>6,48</sub> = 0.44	0.85
Plecoptera				
Nutrients	<i>F</i> <sub>1,8</sub> = 0.01	0.94	<i>F</i> <sub>1,8</sub> = 0.32	0.59
Time	<i>F</i> <sub>6,48</sub> = 2.04	0.10	<i>F</i> <sub>6,48</sub> = <b>3.92</b>	<b>0.0073</b>
Nutrients × time	<i>F</i> <sub>6,48</sub> = 2.11	0.19	<i>F</i> <sub>6,48</sub> = 2.75	0.056
Average adult body size				
Nutrients	<i>F</i> <sub>1,8</sub> = <b>5.35</b>	<b>0.050</b>		
Time	<i>F</i> <sub>6,48</sub> = 2.07	0.075		
Nutrients × time	<i>F</i> <sub>6,48</sub> = 4.90	0.35		

Odonata were not analyzed because of insufficient sample sizes. The average body size comparison reports uncorrected *P* values because it was based on a single comparison. All other comparisons report *P* values that were adjusted (*P*<sub>adj</sub>) using a false discovery rate correction. Significant comparisons are in bold

(sensu Hurlbert 1984). However, it would not have been possible to conduct the combined nutrient enrichment and stable isotope study on a greater number of streams, as it would have precluded the simultaneous assessment of spider population responses and their reliance on aquatic emergence N. Therefore, we suggest caution in interpreting the nutrient effect and we provide additional substantiating data where possible.

## Results

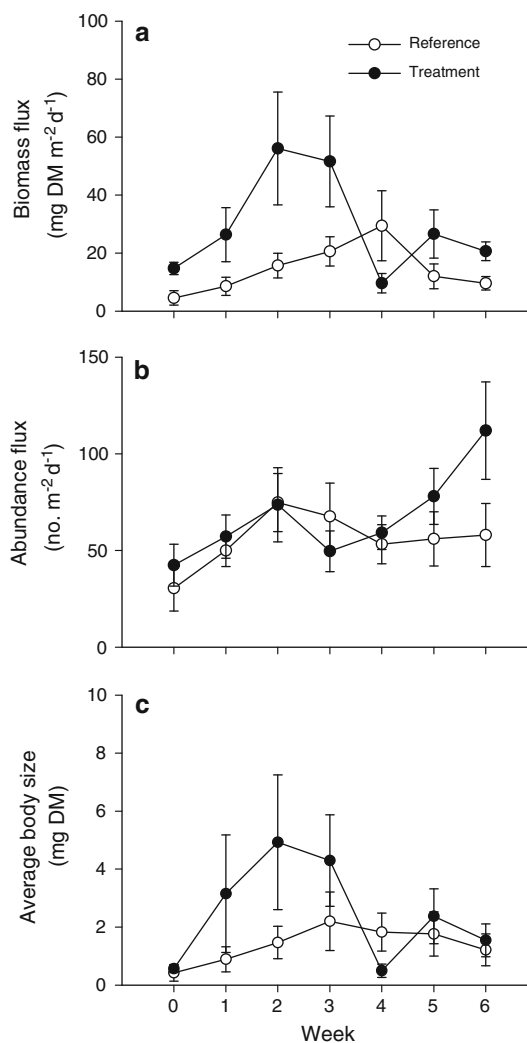
### Aquatic insect emergence response

Total aquatic emergence biomass, but not abundance, was significantly higher in the treatment versus the reference stream (Table 1; Fig. 1a, b). The average body size of emerging adults was marginally greater in the treatment stream (Table 1; Fig. 1c). When averaged over the entire sampling period, adults were 71% bigger in the treatment versus reference stream (mean  $\pm$  SE,  $2.61 \pm 0.59$  vs.  $1.52 \pm 0.28$  mg dry mass).

Total biomass was higher in the treatment stream, but responses varied at the order level (Table 1; Fig. 2a–d). Because of small sample sizes at the family level, we analyzed aquatic emergence at the order level. Trichoptera biomass, but not abundance, was higher in the treatment versus the reference stream (Table 1; Fig. 2a). The biomass and abundance of Diptera, Ephemeroptera, and Plecoptera were similar in both streams (Table 1; Fig. 2b–d). The sample size of Odonata was insufficient for analysis. The contribution of Trichoptera was ca.  $3\times$  greater in the treatment versus reference stream (Fig. 2a). Diptera contribution was lower in the treatment stream, but Ephemeroptera and Plecoptera were similar in each stream (Fig. 2b–d).

### Biomass and abundance response of spiders

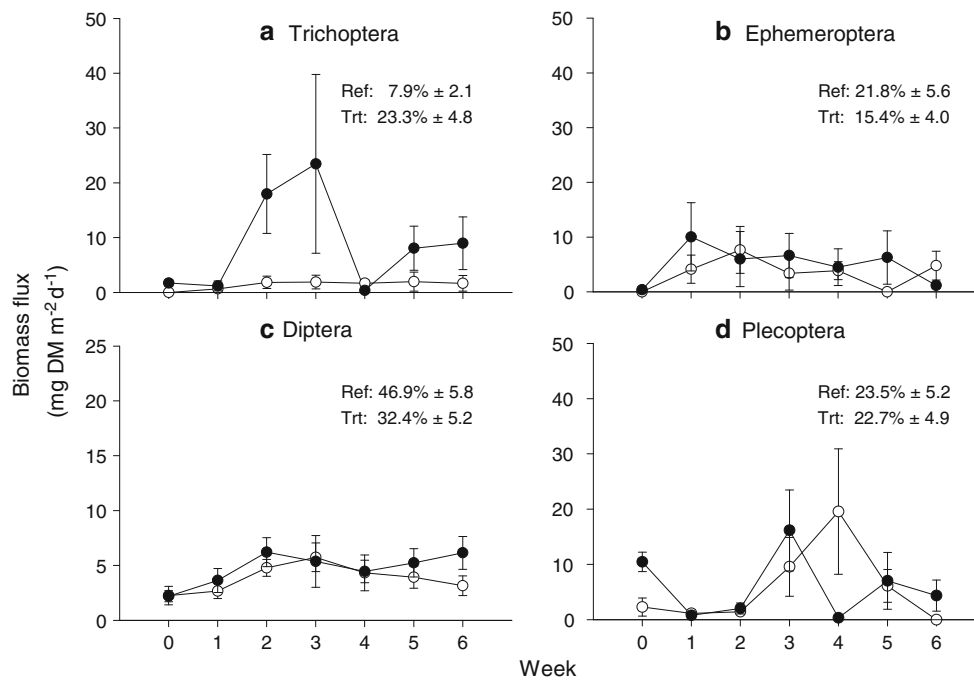
Combined arboreal spider abundance was lower in the treatment stream, but biomass did not differ between streams (Table 2; Fig. 3a, b). Combined arboreal spider biomass and abundance did not vary with distance from the stream (Table 2; Fig. 3a, b). When analyzed at the family level, the biomass and abundance of most arboreal spider families did not differ based on stream or distance. In fact, the biomass and abundance of known aquatic emergence specialists (e.g., Tetragnathidae) did not differ between streams (Table 2). However, Linyphiidae abundance was lower in the treatment stream (Table 2). Community composition based on abundance or biomass did not differ between streams (ANOSIM: Abundance Global  $R = 0.061$ ,  $P = 0.10$ ; Biomass Global  $R = 0.040$ ,  $P = 0.17$ ). The NMDS analysis of biomass and abundance community



**Fig. 1** Aquatic insect emergence: **a** biomass flux, **b** abundance flux, and **c** average body size from the reference and treatment (i.e., nutrient-enriched) streams (mean  $\pm$  SE). Emergence traps were deployed weekly for 48 h. Average adult body size was calculated for each sampling date by dividing total biomass flux by total abundance flux per emergence trap. Repeated measures one-way ANOVA results are listed in Table 1. *DM* Dry mass

composition generated two dimensional solutions for the 12 dominant arboreal spider families (stress for both solutions = 0.12).

The biomass and abundance of ground spiders, either combined or at the family-level, did not differ between streams (Table 3; Fig. 3c, d). However, the biomass and abundance of all ground spiders were dramatically lower at the stream margin relative to upland habitat (Table 3; Fig. 3c, d). The low occurrence of ground spiders at the stream margin precluded a multivariate analysis of community similarity because such methods are inappropriate for small data sets.



**Fig. 2** Aquatic emergence biomass flux (mean ± SE) categorized by insect order for the reference (*open circles*) and treatment streams (*closed circles*): **a** Trichoptera, **b** Ephemeroptera, **c** Diptera, **d** Plecoptera. The average contribution of each order to total biomass flux for reference (*Ref*) and treatment (*Trt*) streams during the entire

7-week sampling period is listed (mean percentage ± SE). Odonata are not shown due to small sample sizes. Note the different scale used for Diptera. Repeated measures one-way ANOVA results are listed in Table 1. *DM* Dry mass

### Contribution of stream-derived N to arboreal spiders

Arboreal spiders relied heavily on aquatic emergence, but this reliance decreased in the treatment versus reference stream. Based on the mixing model (see Eq. 1), three of the four arboreal spider families relied less on aquatic emergence N in the treatment stream relative to the reference (Fig. 4a–d). Tetragnathidae on the margin of the reference stream obtained ca. 100% of their N from aquatic emergence (range: all five models returned values of 100%) (Fig. 4a), but individuals in the treatment stream only obtained ca. 50% of their N from emergence (range: 15–95%) (Fig. 4a). Similar patterns for Araneidae were observed (Fig. 4b). Araneidae on the margin of the reference stream obtained ca. 75% of their N from aquatic emergence (range: 50–100%), but this reliance declined in the treatment stream (ca. 52%, range: 5–100%). However, Linyphiidae increased their emergence reliance in the treatment stream (Fig. 4c). Under reference conditions, streamside Linyphiidae obtained ca. 12% of their N from emergence (range: 0–35%), but reliance increased to 79% (range: 35–100%) in the treatment stream. Streamside Anyphaenidae relied heavily on aquatic emergence in the reference stream (ca. 90%, range: 80–100%), but less so in the treatment stream [50%, range not determined (ND)] because only a single sampling location had a sufficient

sample size to calculate aquatic emergence reliance (Fig. 4d). Reliance on aquatic emergence generally declined in upland habitats relative to the stream margin for three of the four arboreal spider families (Fig. 4a–d). In 16 of the 84 mixing models, the model returned values greater than 100% (i.e., they were more enriched than could be explained by the measured isotopic values of emergence). We interpreted these results as the spiders obtaining 100% of their N from aquatic sources (average of those exceeding 100%: 180%, max: 500%). Thus, arboreal spiders relied heavily on aquatic-derived N, but this reliance decreased in the treatment versus reference stream.

### Contribution of stream-derived N to ground spiders

Ground spiders largely did not rely on aquatic emergence in either stream, averaging between 0 and 20% (Fig. 5a–c). Amaurobiidae at the reference stream margin obtained ca. 10% of their N from emergence (range: ND), but in the treatment stream they obtained no N from emergence (range: both models returned values of 0%). Because of small sample sizes at the stream margin, we could not assess the emergence reliance of streamside Lycosidae in the reference stream (Fig. 5b). However, individuals 10 m from the reference stream obtained 15% of their N from emergence (range: 0–45%). Lycosidae in the treatment

**Table 2** Adjusted *P* values from the repeated measures two-way ANOVAs testing the effects of nutrients and distance from the stream on arboreal spider biomass and abundance

	Biomass		Abundance	
<b>Combined arboreal spiders</b>				
Nutrients	$F_{1,24} = 2.15$	0.26	$F_{1,24} = \mathbf{8.06}$	<b>0.023</b>
Distance	$F_{2,24} = 0.62$	0.82	$F_{2,24} = 0.14$	0.91
Nutrients $\times$ distance	$F_{2,24} = 1.69$	0.76	$F_{2,24} = 2.49$	0.26
Time	$F_{2,48} = 2.35$	0.27	$F_{2,48} = 0.25$	0.97
Time $\times$ nutrients	$F_{2,48} = 0.41$	0.83	$F_{2,48} = 2.33$	0.35
Time $\times$ distance	$F_{4,48} = 0.73$	0.69	$F_{4,48} = 2.51$	0.13
Time $\times$ nutrients $\times$ distance	$F_{4,48} = 0.29$	0.93	$F_{4,48} = 0.20$	0.96
<b>Tetragnathidae</b>				
Nutrients	$F_{1,24} = 0.31$	0.73	$F_{1,24} = 0.01$	0.94
Distance	$F_{2,24} = 0.38$	0.82	$F_{2,24} = 0.09$	0.91
Nutrients $\times$ distance	$F_{2,24} = 0.39$	0.81	$F_{2,24} = 0.11$	0.42
Time	$F_{2,48} = 4.96$	0.055	$F_{2,48} = 4.61$	0.074
Time $\times$ nutrients	$F_{2,48} = 0.55$	0.83	$F_{2,48} = 1.31$	0.35
Time $\times$ distance	$F_{4,48} = 1.31$	0.69	$F_{4,48} = 1.08$	0.63
Time $\times$ nutrients $\times$ distance	$F_{4,48} = 0.21$	0.93	$F_{4,48} = 0.20$	0.96
<b>Araneidae</b>				
Nutrients	$F_{1,24} = 0.03$	0.87	$F_{1,24} = 3.00$	0.16
Distance	$F_{2,24} = 1.43$	0.65	$F_{2,24} = 4.53$	0.11
Nutrients $\times$ distance	$F_{2,24} = 1.25$	0.76	$F_{2,24} = 3.16$	0.26
Time	$F_{2,48} = 0.33$	0.72	$F_{2,48} = 0.03$	0.97
Time $\times$ nutrients	$F_{2,48} = 0.64$	0.83	$F_{2,48} = 1.55$	0.35
Time $\times$ distance	$F_{4,48} = 0.56$	0.69	$F_{4,48} = 0.06$	0.99
Time $\times$ nutrients $\times$ distance	$F_{4,48} = 0.25$	0.93	$F_{4,48} = 0.75$	0.96
<b>Linyphiidae</b>				
Nutrients	$F_{1,24} = 4.64$	0.21	$F_{1,24} = \mathbf{15.42}$	<b>0.0030</b>
Distance	$F_{2,24} = 0.20$	0.82	$F_{2,24} = 0.50$	0.91
Nutrients $\times$ distance	$F_{2,24} = 0.48$	0.81	$F_{2,24} = 0.23$	0.80
Time	$F_{2,48} = 0.98$	0.64	$F_{2,48} = 2.35$	0.18
Time $\times$ nutrients	$F_{2,48} = 1.28$	0.83	$F_{2,48} = 1.60$	0.35
Time $\times$ distance	$F_{4,48} = 0.67$	0.69	$F_{4,48} = 0.40$	0.99
Time $\times$ nutrients $\times$ distance	$F_{4,48} = 0.79$	0.93	$F_{4,48} = 0.50$	0.96
<b>Anyphaenidae</b>				
Nutrients	$F_{1,24} = 3.23$	0.21	$F_{1,24} = 2.22$	0.19
Distance	$F_{2,24} = 2.39$	0.56	$F_{2,24} = 2.58$	0.24
Nutrients $\times$ distance	$F_{2,24} = 0.21$	0.81	$F_{2,24} = 0.25$	0.80
Time	$F_{2,48} = 0.40$	0.72	$F_{2,48} = 3.03$	0.14
Time $\times$ nutrients	$F_{2,48} = 0.00$	1.00	$F_{2,48} = 0.08$	0.92
Time $\times$ distance	$F_{4,48} = \mathbf{6.65}$	<b>0.0010</b>	$F_{4,48} = \mathbf{8.20}$	<b>0.00050</b>
Time $\times$ nutrients $\times$ distance	$F_{4,48} = 0.25$	0.93	$F_{4,48} = 0.15$	0.96

Significant comparisons are in bold. When significant, nutrient effects were negative in this particular test

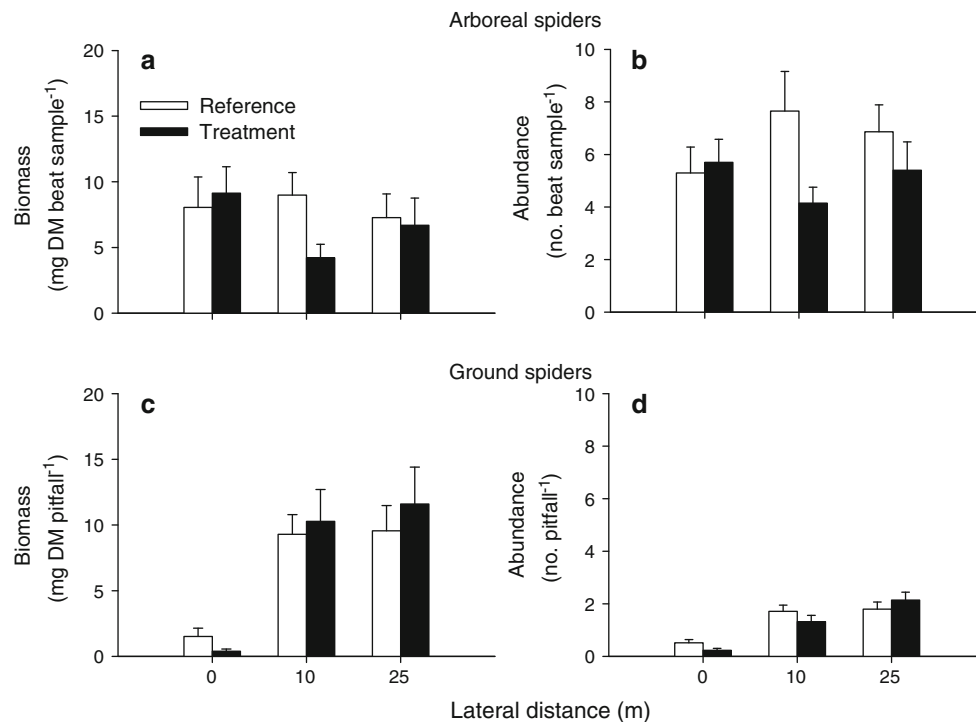
stream margin and at 10 m relied less on emergence; these spiders derived only 0.1% (range: ND) and 0.05% (range: 0–0.1%) of their N from emergence, respectively (Fig. 5b). Gnaphosidae at the margins of both streams did not rely on aquatic emergence (0%, range:ND) (Fig. 5c). The emergence reliance of ground spiders was less consistent based on lateral distance, but on average, did not reach above 20% (e.g., Amaurobiidae; Fig. 5a). Thus, ground spiders in both streams relied little on aquatic emergence N (Fig. 5a–c).

## Discussion

Taxon-specific traits alter the effects of resource subsidies on consumers

Our results provide evidence that greater donor-ecosystem productivity and associated cross-ecosystem resource flows do not always increase populations of subsidized consumers. Specifically, aquatic emergence biomass was





**Fig. 3** **a, c** Biomass and **b, d** abundance of combined arboreal spiders (*top row*) and combined ground spiders (*bottom row*) sampled 0, 10, and 25 m from the stream margin in the reference and treatment streams, mean + SE. Spiders were sampled along transects placed at 10-m intervals downstream of the isotopic enrichment. Arboreal spiders were sampled via 5-min beat sampling, while ground spiders

were sampled with 48-h deployments of pitfall traps. Data are presented as averages over the entire sampling period and do not explicitly incorporate temporal changes. However, actual statistical analyses incorporated time (i.e., repeated measures two-way ANOVA) and are presented in Tables 2 and 3. *DM* Dry mass

more than doubled in the treatment versus reference stream, exhibited increased average body size, and had a relatively greater dominance of Trichoptera. Despite increased emergence biomass, spider biomass did not differ between streams and arboreal spider abundance was lower in the treatment stream. The lack of a spider biomass response was unexpected because 5 years of nutrient enrichment increased the overall productivity of this headwater stream, whereby the secondary production of benthic insect larvae was approximately double compared to the reference stream (Davis et al. 2010a). It also decreased the proportion of stream prey production that was consumed by instream predators, allowing a larger amount of prey production to bypass instream predator populations (Davis et al. 2010a). Thus, we predicted a priori that more stream insect production would be exported as aquatic emergence to terrestrial habitats, where it would be eaten by terrestrial predators. Emergence biomass was higher in the treatment stream, which corroborates our previous findings of increased production of benthic larvae, but this greater stream productivity and emergence biomass did not benefit terrestrial predators that are known emergence specialists.

The lack of a spider response suggests that predicting consumer responses to increases in resource subsidies requires an understanding of the subsidy's taxonomic identity and how environmental changes may alter this identity. Our results add to the growing body of literature indicating that multiple factors determine the relationship between resource subsidies and consumers (Marczak et al. 2007b). Predator identity and the physical nature of ecosystem boundaries can alter predator response to subsidies (Witman et al. 2004; Marczak et al. 2007b). For example, subsidies have larger effects on predators with traits that allow them to specialize and capitalize on greater availability of resource subsidies (e.g., Tetragnathidae vs. other spiders; Marczak et al. 2007b). Thus, greater resource subsidies should increase predator populations when ecosystems are dominated by subsidy specialists. However, even for predators that specialized on aquatic subsidies from our study system (i.e., Tetragnathidae), greater stream productivity and insect emergence biomass did not increase their population sizes, despite similar predator assemblages in both streams. This suggests that prey identity and taxon-specific traits also may alter subsidy effects. This possibility is supported by our previous finding that increased

**Table 3** Statistical results from the repeated measures two-way ANOVA testing the main effects of nutrient enrichment and distance from the stream margin on ground spider biomass and abundance

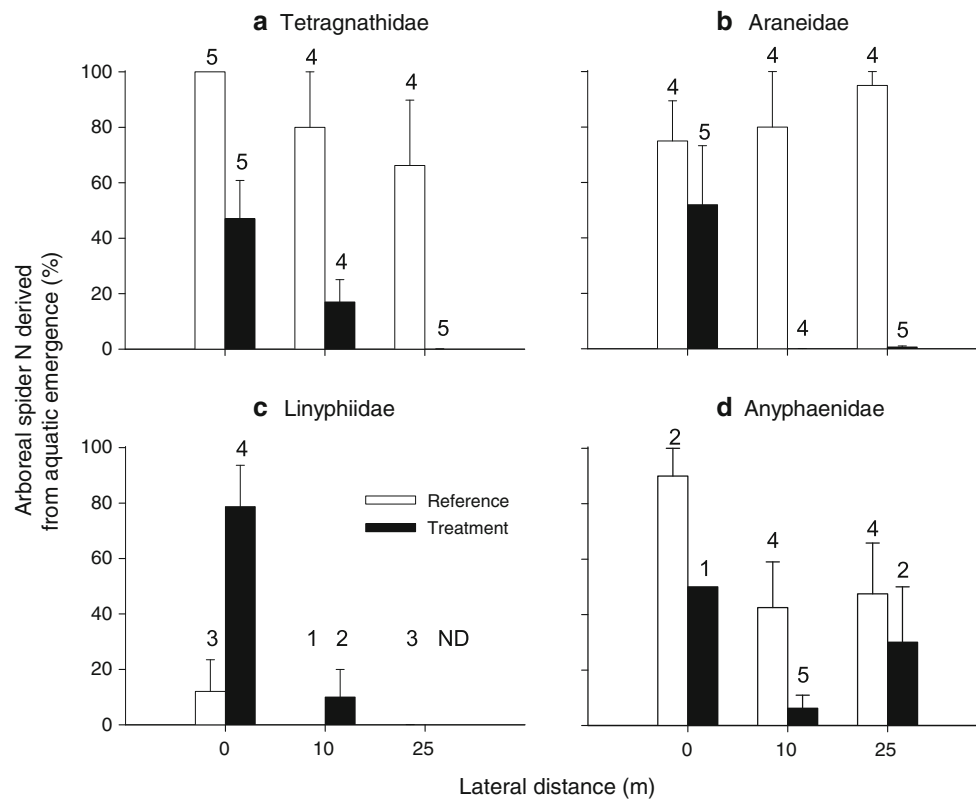
	Biomass		Abundance	
<b>Combined ground spiders</b>				
Nutrients	$F_{1,24} = 0.33$	0.66	$F_{1,24} = 2.27$	0.19
Distance	$F_{2,24} = 45.21$	<b>&lt;0.0001</b>	$F_{2,24} = 60.00$	<b>&lt;0.0001</b>
Nutrients $\times$ distance	$F_{2,24} = 1.09$	0.47	$F_{2,24} = 3.39$	0.12
Time	$F_{6,144} = 9.02$	<b>&lt;0.0001</b>	$F_{6,144} = 8.69$	<b>&lt;0.0001</b>
Time $\times$ nutrients	$F_{6,144} = 1.34$	0.32	$F_{6,144} = 0.77$	0.60
Time $\times$ distance	$F_{12,144} = 3.18$	<b>0.0010</b>	$F_{12,144} = 2.11$	<b>0.039</b>
Time $\times$ nutrients $\times$ distance	$F_{12,144} = 1.91$	0.076	$F_{12,144} = 1.17$	0.62
<b>Amaurobiidae</b>				
Nutrients	$F_{1,24} = 4.89$	0.074	$F_{1,24} = 3.91$	0.12
Distance	$F_{2,24} = 9.74$	<b>0.0012</b>	$F_{2,24} = 4.48$	<b>0.020</b>
Nutrients $\times$ distance	$F_{2,24} = 3.90$	0.14	$F_{2,24} = 0.78$	0.63
Time	$F_{6,144} = 4.59$	<b>0.00030</b>	$F_{6,144} = 2.26$	<b>0.040</b>
Time $\times$ nutrients	$F_{6,144} = 0.68$	0.67	$F_{6,144} = 1.55$	0.23
Time $\times$ distance	$F_{12,144} = 3.70$	<b>0.00040</b>	$F_{12,144} = 1.96$	<b>0.040</b>
Time $\times$ nutrients $\times$ distance	$F_{12,144} = 1.01$	0.58	$F_{12,144} = 0.65$	0.79
<b>Lycosidae</b>				
Nutrients	$F_{1,24} = 0.20$	0.66	$F_{1,24} = 2.50$	0.22
Distance	$F_{2,24} = 9.08$	<b>0.0012</b>	$F_{2,24} = 11.94$	<b>0.00060</b>
Nutrients $\times$ distance	$F_{2,24} = 1.37$	0.47	$F_{2,24} = 3.28$	0.12
Time	$F_{6,144} = 7.21$	<b>0.00013</b>	$F_{6,144} = 8.14$	<b>&lt;0.0001</b>
Time $\times$ nutrients	$F_{6,144} = 2.00$	0.26	$F_{6,144} = 3.31$	<b>0.018</b>
Time $\times$ distance	$F_{12,144} = 2.73$	<b>0.0032</b>	$F_{12,144} = 3.30$	<b>0.0012</b>
Time $\times$ nutrients $\times$ distance	$F_{12,144} = 2.53$	<b>0.019</b>	$F_{12,144} = 3.72$	<b>0.00040</b>
<b>Gnaphosidae</b>				
Nutrients	$F_{1,24} = 5.79$	0.074	$F_{1,24} = 4.80$	0.12
Distance	$F_{2,24} = 9.07$	<b>0.0012</b>	$F_{2,24} = 8.94$	<b>0.0017</b>
Nutrients $\times$ distance	$F_{2,24} = 0.50$	0.61	$F_{2,24} = 0.43$	0.65
Time	$F_{6,144} = 10.92$	<b>0.00013</b>	$F_{6,144} = 11.58$	<b>&lt;0.0001</b>
Time $\times$ nutrients	$F_{6,144} = 1.68$	0.26	$F_{6,144} = 1.93$	0.16
Time $\times$ distance	$F_{12,144} = 1.98$	<b>0.030</b>	$F_{12,144} = 1.84$	<b>0.047</b>
Time $\times$ nutrients $\times$ distance	$F_{12,144} = 0.80$	0.65	$F_{12,144} = 0.87$	0.77

Reported  $P$  values were adjusted ( $P_{\text{adj}}$ ) using a false discovery rate correction  
Significant comparisons are in bold

dominance of predator-resistant prey (i.e., large-bodied larval prey) led to enrichment increasing the secondary production of benthic invertebrate prey without a concomitant increase of instream predator production (Davis et al. 2010a, b). Thus, if environmental change increases donor-ecosystem productivity and cross-ecosystem resource flows, but the majority of these increases are in a form that is unavailable to consumers, formerly subsidized consumers may not benefit.

It has long been recognized that organisms differ in their susceptibility to consumption by higher trophic levels (i.e., grazer- or predator-resistance) and that such heterogeneity can help predict the bottom-up effects of increased ecosystem productivity on in situ predator populations (Abrams 1993). This conceptual framework has not been applied to studies describing the effects of subsidies on consumers, but

it has the potential to add to our understanding of these relationships. For example, shifts in body size distributions may have increased the predator resistance of aquatic emergence and reduced prey availability for spiders in the treatment stream. The average body size of emerging adults was larger in the treatment stream, which agrees with previous results from our study streams showing that enrichment increased the maximum body size of a dominant stream consumer and dominance of large-bodied benthic larvae (Davis et al. 2010b). Spiders can eat large-bodied prey (Kato et al. 2003, 2004), but spider diets are frequently dominated by small-bodied prey such as Chironomidae and other small Diptera (Tanaka 1991; Williams et al. 1995; Henschel et al. 2001). Despite larger prey being captured by spider webs, the difficulties associated with handling them can increase prey handling time (Olive 1980) or increase the



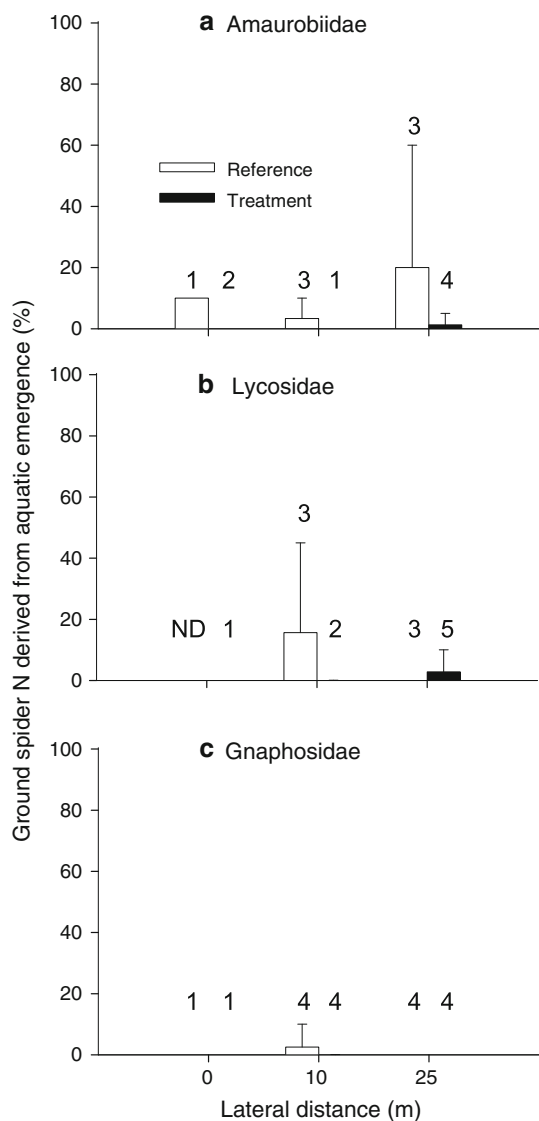
**Fig. 4** Percentage of arboreal spider N derived from aquatic insect emergence in reference and treatment populations 0, 10, and 25 m lateral distance from the stream margin. Percentages (mean + SE) were based on the dynamic mixing model (Eq. 1) and calculated for **a** Tetragnathidae, **b** Araneidae, **c** Linyphiidae, **d** Anyphaenidae. Numbers above each bar represent the number of sampling locations

that had sufficient sample sizes for the calculations. To apply Eq. 1, we required 2–4 composite samples at each location over the 44-day enrichment period. Due to small sample sizes, some percentages were not determined (*ND*). Averages excluded an *error bar* when all models returned the same value or the calculation was based on a single value

rate at which that spiders reject these prey (Nentwig and Wissel 1986). Spiders more readily eat prey that are ca. 50–80% of their size, although some larger spiders will consume larger prey (Nentwig and Wissel 1986). Thus, if spiders prefer small prey, the greater dominance of large-bodied adult emergence may have reduced the benefits for spider populations by decreasing spider capture efficiency. This possibility is supported by our isotopic tracer results showing that a known aquatic emergence specialist (i.e., Tetragnathidae) relied heavily on emergence in the reference stream, but this reliance declined in the treatment stream. Other riparian predators exhibit size-specific predation (e.g., Marczak et al. 2007a); thus, our results may be particularly applicable to such predators.

Because spiders frequently eat Diptera, which did not increase with enrichment, reduced spider emergence reliance may have been related to the increased dominance of large-bodied Trichoptera, which was 3× greater in the treatment versus the reference stream. This shift was similar to previous findings that Trichoptera contribution to benthic larval secondary production was ca. 2.8× greater in the treatment versus the reference stream during the fifth year

of enrichment when we quantified aquatic emergence (ca. 25 vs. 71%) (Davis 2009). Spiders can eat Trichoptera (Kato et al. 2004), but evidence suggests that this order may not comprise a large proportion of their diet. Because of wing scales and increased mobility, Lepidoptera, a close relative of Trichoptera, can readily escape from spider webs (Olive 1980). Trichoptera have wing hairs that may function like wing scales; thus, spider webs may be less able to retain these prey. In fact, Tetragnathidae along another stream disproportionately captured Chironomidae and Ephemeroptera, despite high availability of Trichoptera and Plecoptera (Williams et al. 1995). Trichoptera and Plecoptera can also disperse farther than Ephemeroptera (Francis et al. 2006), which may minimize their time spent at stream margins and reduce their availability to streamside predators. However, the overall importance of flight ability may be small because aquatic emergence availability declines exponentially with distance from the stream (Griffith et al. 1998; Power et al. 2004), whereby the majority of Trichoptera and Plecoptera adults can be captured within ca. 15 m of the stream margin (up to 90 and 50% of adults, respectively) (Peterson et al. 1999). The combination of this



**Fig. 5** Percentage of ground spider N derived from aquatic insect emergence in reference and treatment populations 0, 10, and 25 m lateral distance from the stream margin. Percentages (mean + SE) were based on the dynamic mixing model (Eq. 1) and calculated for **a** Amaurobiidae, **b** Lycosidae, **c** Gnaphosidae. Numbers above each bar represent the number of sampling locations that had sufficient temporal sampling resolution for the calculations. To apply Eq. 1, we required 2–5 composite samples at each location over the 44-day enrichment period. Due to small sample sizes, some percentages were not determined (ND). Averages excluded an error bar when all models returned the same value or the calculation was based on a single value

evidence and our isotopic tracer results suggest that prey identity may not only decouple instream predator and prey relationships (Davis et al. 2010a), but may also alter the effects of aquatic subsidies on terrestrial predators.

Previous studies have shown a positive relationship between aquatic emergence and spider abundances (Kato et al. 2003; Marczak and Richardson 2007). Moreover,

aquatic emergence and spider biomass were positively related in Sycamore Creek (Sanzone et al. 2003). These studies contrast with our spider responses, likely due to differences in the subsidy's predator resistance. Emergence in Sycamore Creek is dominated by Chironomidae and Ephemeroptera (primarily *Baetis* spp.) (Jackson and Fisher 1986; Sanzone et al. 2003), which are typically smaller-bodied than most of the Trichoptera dominating our stream's emergence. Thus, the smaller-bodied adult emergence from Sycamore Creek may have been more readily eaten by spiders and maintained the positive relationship between emergence and spider biomass.

We cannot completely eliminate the possibility that 5 years of enrichment may have increased the growth of riparian vegetation, increased the productivity and relative availability of terrestrial arthropods, and allowed spiders to shift their reliance from aquatic to terrestrial prey. However, we think this alternate hypothesis is unlikely for several reasons. First, if enrichment reduced spider reliance on aquatic emergence due to increases in terrestrial prey populations, greater terrestrial prey availability should have still increased spider populations in the treatment stream. Second, the riparian zones along our study streams were dominated by a dense understory of *Rhododendron maximum*, which contains defensive secondary compounds and is not readily consumed by terrestrial arthropods (Smith 2011). These factors suggest that terrestrial arthropods were unlikely to benefit from stream nutrient enrichment or exhibit larger populations that allowed spiders to switch to terrestrial prey in the treatment stream.

#### Fate of aquatic emergence

Enrichment increased emergence biomass and decreased its importance for spiders, which suggests that a substantial proportion of aquatic emergence may have been consumed by other organisms. Although assessing the ultimate fate of aquatic emergence was outside the scope of this study, greater emergence may have benefited bats and avian insectivores because aquatic insect production can represent a significant subsidy for such aerial predators (Nakano and Murakami 2001; Fukui et al. 2006). Unconsumed adult emergence also likely returned to the stream ecosystem during oviposition (e.g., Werneke and Zwick 1992); thus, returning adults may have stimulated instream food web pathways as ovipositing adults died and were consumed by instream detritivores and predators.

#### Conclusions

Our results suggest that the effects of increased donor-ecosystem productivity and resource subsidies on consumers

may be nullified by shifts in the size structure or taxonomic composition of the subsidy, which reduce the ability of subsidized consumers to utilize it. Although the abundance of emerging insects did not differ, aquatic emergence biomass was two times greater in the treatment versus the reference stream, reflecting the size structure shift. However, greater emergence biomass did not increase the biomass or abundance of spiders known to rely on aquatic emergence (e.g., Tetragnathidae). In fact, their reliance on aquatic emergence was lower in the treatment stream, potentially due to the increased dominance of larger-bodied adult emergence and Trichoptera that may not have been eaten by spiders.

Given the ubiquity of anthropogenic nutrient enrichment of stream ecosystems (Alexander and Smith 2006), our results have broad applicability in understanding how enrichment may alter coupled aquatic–terrestrial food webs. This study also agrees with previous results from our streams showing that increased dominance of predator-resistant prey can attenuate instream predator responses, despite enrichment doubling benthic prey production (Davis et al. 2010a). Thus, taxon-specific traits, which increase the predator resistance of prey, may not only decouple in situ predator–prey relationships (Abrams 1993; Davis et al. 2010a) but may also alter these dynamics across ecosystem boundaries. Because many organisms reduce their consumption risk via herbivore- and predator-resistant traits (Abrams 1993), we provide empirical support for incorporating the broader concept of consumption resistance into food web models that predict subsidy effects on higher trophic levels.

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