Food Webs 36 (2023) e00302

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.elsevier.com/locate/fooweb

Small stream predators rely heavily on terrestrial matter energy input in the fall, regardless of riparian buffer size

Jeffery Marker [a,*], Eva Bergman [a], Rachel E. Bowes [a,b], Denis Lafage [a]

[a] *Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden*
[b] *Department of Biological Sciences, Emporia State University, Emporia, Kansas, USA*

ARTICLE INFO

Keywords:
Allochthonous resources
Aquatic subsidies
Forested buffers
Riparian
Stable isotopes
Terrestrial subsidies

ABSTRACT

Stream ecosystems are reliant on the reciprocal exchange of terrestrial and aquatic energy subsides to maintain a productive and stable food web. Land use around streams can have strong effects on the size and availability of resource subsidies for stream and riparian predators such as fish and spiders. A common forestry technique around streams is the establishment of forested buffers to protect aquatic and riparian ecosystems from upland disturbances. Buffer size may determine prey abundance, richness, and spatial extent of prey reach into both the aquatic and terrestrial systems. To test the effects of forested buffers subsidy direction, we explored the carbon and nitrogen stable isotope signatures of brown trout (*Salmo trutta*), Tetragnathidae and Lycosidae spiders, and their aquatic and terrestrial prey sources around twelve streams in southern Sweden. For both predator groups, buffer presence showed no effect on resource subsidy source. We found that both brown trout and spiders are significantly reliant on terrestrial sources of prey for their diets in the fall. To support the terrestrial subsidy into small streams it is vital to maintain ecologically functional riparian zones by conserving complex surrounding habitats that optimize habitat and both terrestrial and aquatic prey diversity.

1. Introduction

Energy subsidy fluctuation between aquatic and terrestrial ecosystems, and the reciprocal dependence between the aquatic and terrestrial habitat, is critical to maintain ecosystem productivity and food web stability (Wallace et al., 1997; Bartels et al., 2012; Nakano and Murakami, 2001). Stream ecosystems are dependent on terrestrial subsidies providing a strong bottom-up trophic effect throughout an aquatic food web (Baxter et al., 2005; Wallace et al., 1999). Detritus and terrestrial invertebrates are the sources for most of the terrestrial subsidies entering into an aquatic system (Richardson et al., 2010). Conversely, terrestrial ecosystems bordering streams are dependent on aquatic subsidies, such as emerging aquatic invertebrates, providing a nearly equal amount of carbon resource to the terrestrial systems as it provides back to a stream (Bartels et al., 2012). These cross-ecosystem subsides are especially important to the function of the riparian zones that separate the aquatic environment from the upland terrestrial system (Baxter et al., 2005) and it is crucial to understand how the surrounding land use affects riparian species that rely on these subsidies.

Resource subsidies from both aquatic and terrestrial systems greatly benefit riparian predators such as mammals (Fukui et al., 2006), birds (Philpott et al., 2009), and reptiles (Sabo and Power, 2002). Brown trout (*Salmo trutta*) is a common drift-feeding salmonid predator found in Swedish streams relying on both in-stream prey and falling terrestrial invertebrates drifting on the water surface and in the water column for their diet (Nakano et al., 1999; Wipfli, 1997). Spiders in riparian systems consume a significant number of aquatic invertebrates, in some cases constituting up to 100% of their diet during certain times of the year (Akamatsu et al., 2004; Krell et al., 2015). Riparian systems provide a diverse vegetation structure that support complex spider assemblages (Lafage et al., 2019). Species of the Lycosidae family are active ground hunters often found in high numbers in riparian systems exploiting the aquatic subsidy to supplement a mostly terrestrial invertebrate diet (Briers et al., 2005; Paetzold et al., 2005). Similarly, many species of web-building spiders, especially those in the family Tetragnathidae, are riparian specialists utilizing systems with high aquatic insect production (Collier et al., 2002; Goedeker et al., 2021). Stream use and the spatial extent and availability of aquatic and terrestrial prey determine how beneficial one diet subsidy is compared to the other (Baxter et al., 2005; Muehlbauer et al., 2014).

---

[*] Corresponding author at: Karlstad University, Faculty for Health, Science, and Technology, Department of Environmental and Life Sciences, 65188 Karlstad, Sweden.

E-mail address: jeffery.marker@kau.se (J. Marker).

https://doi.org/10.1016/j.fooweb.2023.e00302
Received 17 March 2023; Received in revised form 19 June 2023; Accepted 20 July 2023

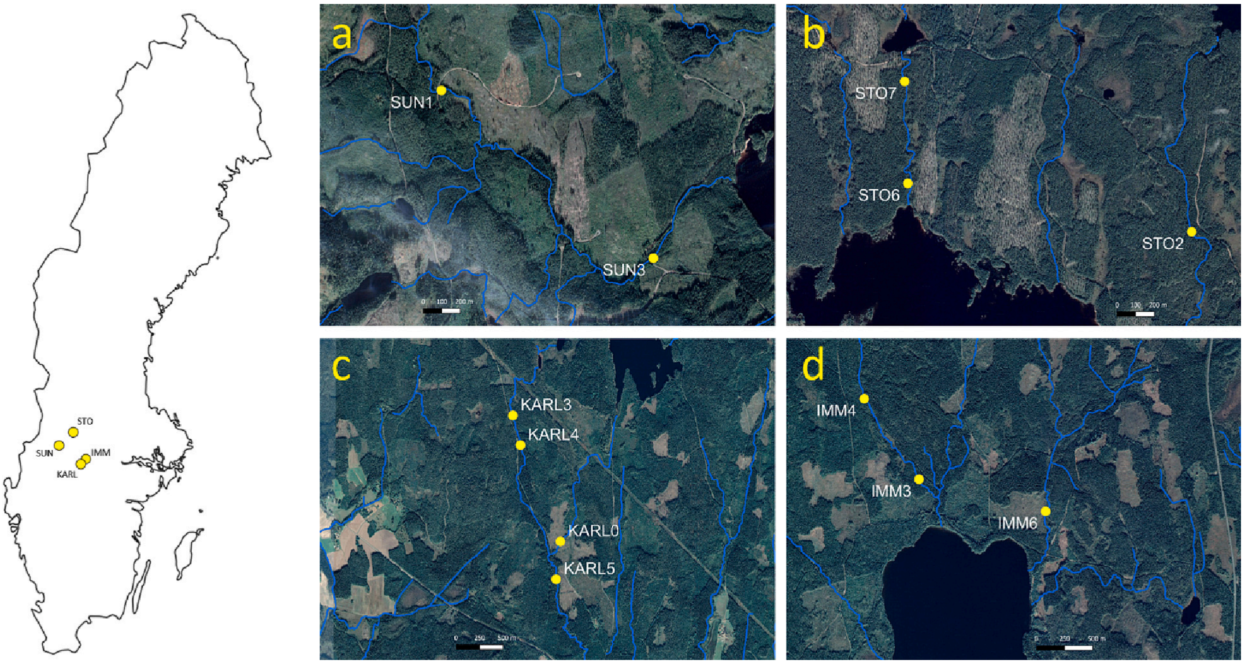

Fig. 1. Site locations in southern Sweden. a) Two sites ~10 km east of the town of Sunne (SUN); b) three sites just north of Lake Storsjön (STO); c) four sites ~18 km northwest of the town of Karlskoga (KARL); and d) 3 sites just north of Lake Immen (IMM).

Table 1

Site names and stream and buffer characteristics. Study area refers to nearest major landmark. Buffer widths (m) is the smallest buffer measured on either side of the streams at each site. Buffer name is the referenced name used through the manuscript. Stream width (m) and Stream depth (m) are the average wetted width and depth at the time of sampling. Bottom substrate is the dominate bottom substance of each streambed described as Fine (<0.02 cm), Sand (0.02–0.2 cm), Gravel (0.2–2 cm), or Large stone (10–20 cm). We removed sites IMM4, KARL3, and STO6 from the analysis.

Study area	Site name	Buffer width	Buffer name	Stream width	Stream depth	Bottom substrate
Lake Immen	IMM3	120	Buffered-1	3.0	0.5	Gravel
	IMM4	Forested	–	3.5	0.3	Large stone
	IMM6	0	Unbuffered-2	1.8	1.0	Sand
	KARL0	0	Unbuffered-1	1.8	0.25	Gravel
	KARL3	Forested	–	1.3	0.25	Sand
	KARL4	60	Buffered-2	2.0	0.3	Gravel
Karlskoga	KARL5	25	Buffered-3	2.5	0.5	Sand
	STO2	Forested	Forested-1	4.5	0.3	Gravel
	STO7	Forested	Forested-2	1.5	0.6	Sand
Lake Storsjön	STO6	37	–	2.5	0.5	Sand
	SUN1	0	Unbuffered-3	1.3	0.3	Fine
Sunne	SUN3	17	Buffered-4	2.5	0.2	Sand

Fish and riparian spider communities, as well as their potential prey, respond to surrounding land use and environmental variables such as canopy cover and forested buffer conditions as they affect the subsidy direction and quantity (Gustafsson et al., 2014; Krell et al., 2015). Land use influences the reciprocal exchange of energy subsidies, through riparian zones, between aquatic and terrestrial ecosystems at local, catchment, and global scales (Lafage et al., 2019; Larsen et al., 2016). Local land use involving agriculture and forestry is an especially important factor that can determine resource subsidy and magnitude for riparian spiders (Krell et al., 2015; Stenroth et al., 2015). Previous studies have suggested that riparian Tetragnathidae and Lycosidae spiders are more reliant on aquatic prey subsides in anthropogenically altered upland environments (Krell et al., 2015). Further, riparian spider density may be negatively impacted by reduced riparian vegetation and canopy density (Tagwireyi and Sullivan, 2015). Forestry action is known to impact food availability for trout and other insectivorous fish through the decline in organic matter into the streams and the regulation of aquatic and terrestrial prey abundance as a result of reductions in plant and tree coverage (Albertson et al., 2018; England and Rosemond, 2004). The effects of terrestrial land use on riparian systems and the adjacent streams can have direct and indirect effects on the predators that rely on those systems.

A common forestry technique to separate streams from upland land use is the establishment of forested buffers (Broadmeadow and Nisbet, 2004; Cole et al., 2020). Some studies consider the effects of riparian buffers on taxonomic diversity measures of riparian fauna (Forio et al., 2020; Marczak et al., 2010; Popescu et al., 2021), and fewer consider buffer effects on functional diversity (Baldissera et al., 2020; Marker et al., 2022). However, the exploration of the effects of forested buffers on food webs are few with most focusing on streams surrounded by agricultural production rather than forestry (Ramberg et al., 2020). Predator and prey diversity drives the functional diversity of an ecosystem, and both are linked to the overall food web. For example, riparian buffers can reduce the in-stream density of aquatic invertebrate larvae and the dispersal distance of adult aquatic invertebrates directly affecting the amount of aquatic subsidies available to terrestrial predators (Greenwood, 2014). However, forested sites have also been shown to subsidize terrestrial predators at a great distance from a stream channel when compared to sites with little or no riparian buffer (Carlson et al., 2016). With a basis of understanding the effects of riparian buffers

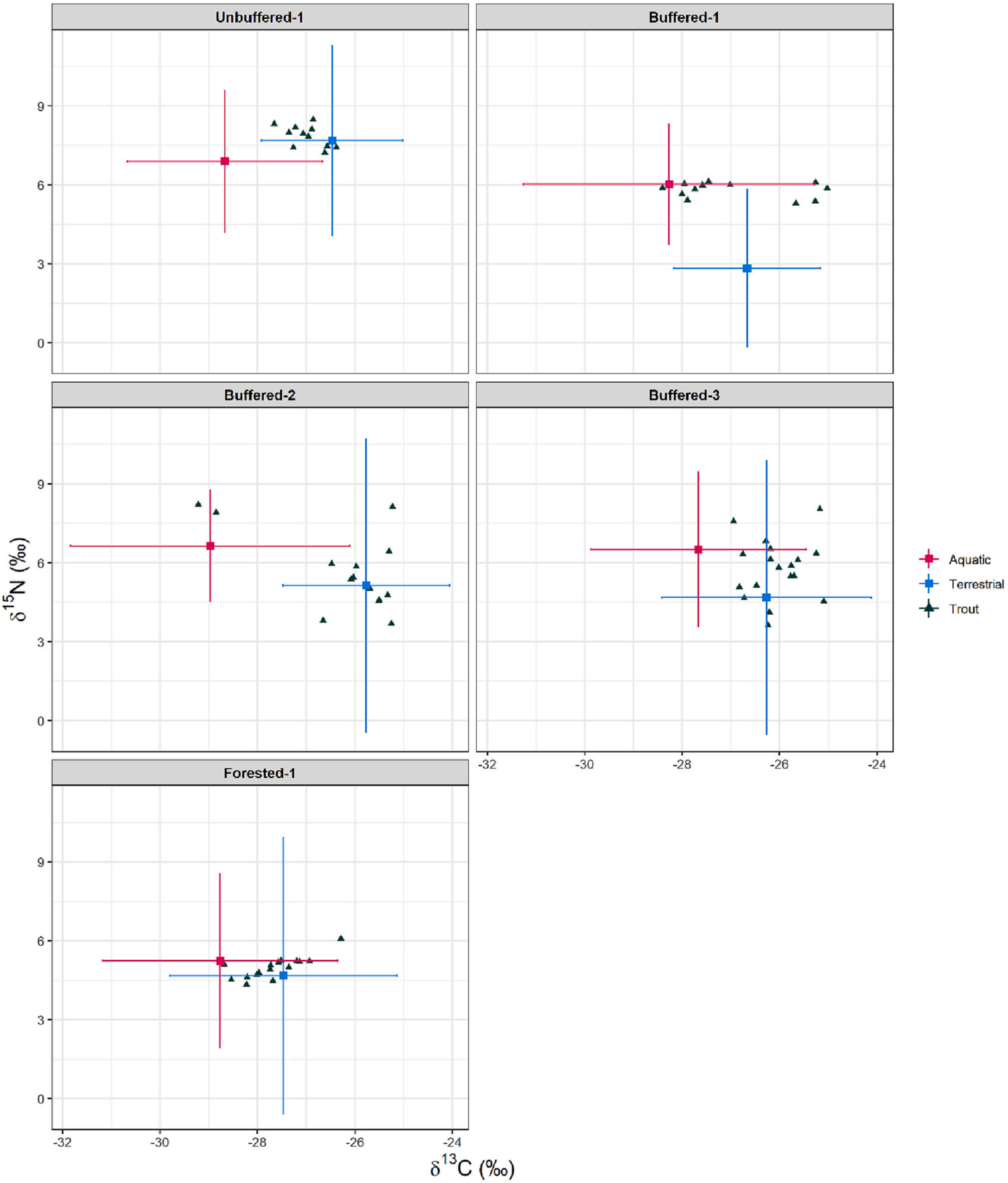

Fig. 2. Biplots presenting the isotopic values (δ^{13}C and δ^{15}N) of brown trout and the mean and standard deviation of their suspected aquatic and terrestrial food sources for each site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on species and functional diversity, it is essential also to understand buffer effects on resource subsides provided to riparian predators.

In this study, we explored the carbon and nitrogen stable isotopic composition of two major predator groups to determine the predominant prey pathway in unbuffered, buffered, and forested riparian systems surrounding small forest streams. We predicted that brown trout, Tetragnathidae, and Lycosidae spiders have a higher proportion of aquatic prey in unbuffered systems, as light availability in these systems affects aquatic invertebrate abundance through increased primary production (Göthe et al., 2009). We also investigated whether brown trout body size had an impact on the diet proportion with and without buffer or site effects. Finally, we tested if spider life stage, genera, or

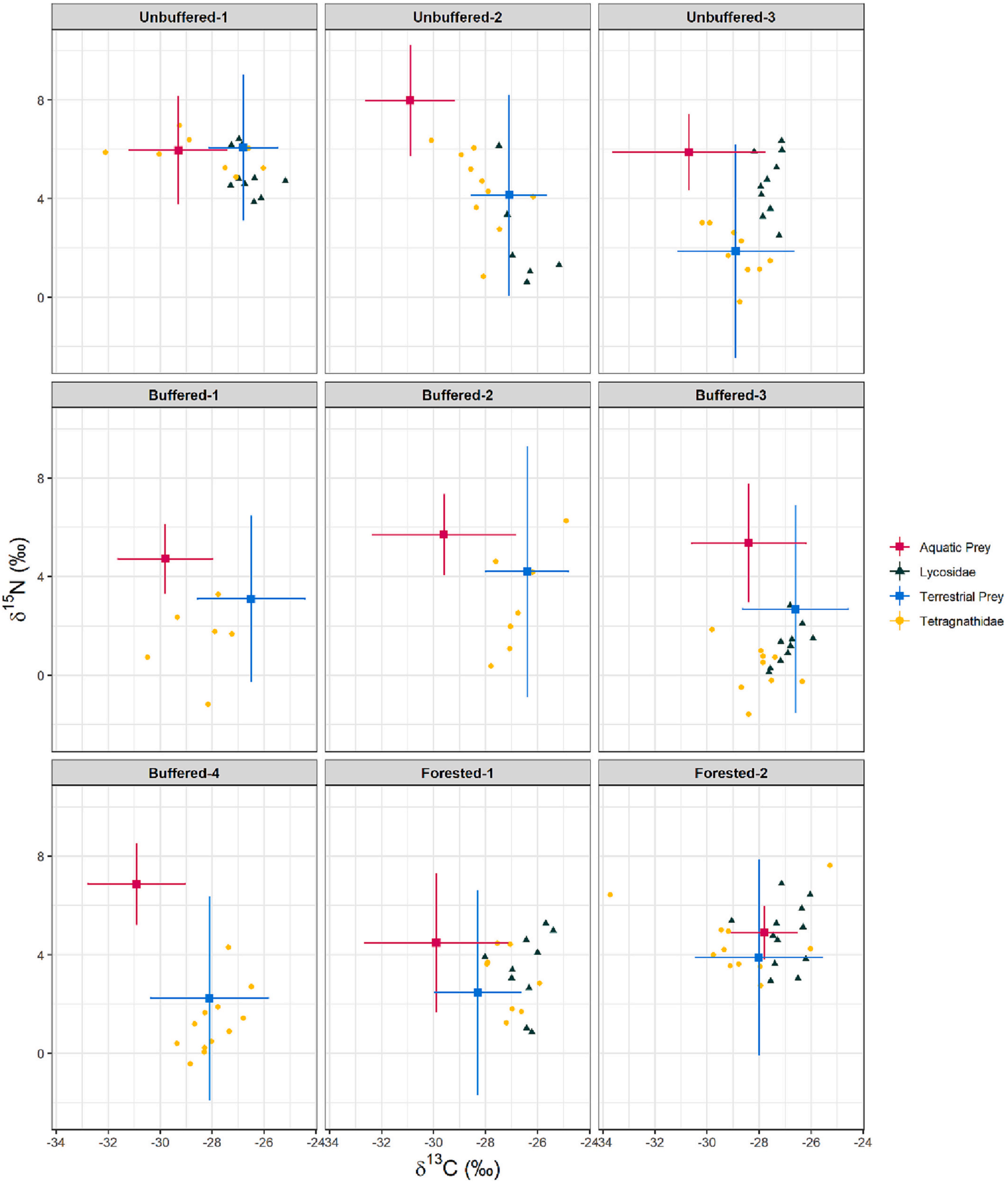

Fig. 3. Biplots presenting the isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of Tetragnathidae and Lycosidae spiders and the mean and standard deviation of their suspected aquatic and terrestrial food sources for each site. Only Tetragnathidae species of spiders were collected at buffered sites 1, 2, and 4.

Table 2
$\delta^{15}N$ and $\delta^{13}C$ isotopic range (‰) and number of samples used for analysis for all aquatic prey at each site. The same prey were used in both the Tetragnathidae and Lycosidae mixing models. Trout were not present at sites IMM6, STO7, SUN1 or SUN3.

Site	Buffer Name	Trout prey				Spider prey			
		$\delta^{15}N$ range	n	$\delta^{13}C$ range	n	$\delta^{15}N$ range	n	$\delta^{13}C$ range	n
IMM3	Forested-3	0.34 to 7.90	33	−33.1 to −23.7	33	0.34 to 4.45	28	−33.1 to −27.8	28
IMM6	Unbuffered-2	–		–		0.40 to 8.10	34	−34.1 to −28.8	34
KARL0	Unbuffered-1	−0.56 to 7.10	26	−34.9 to −27.0	26	−0.56 to 7.10	26	−34.9 to −27.0	26
KARL4	Buffered-2	0.98 to 6.12	26	−36.1 to −27.2	26	0.98 to 6.11	26	−36.1 to −27.2	26
KARL5	Buffered-3	−3.47 to 6.34	36	−32.4 to −23.1	36	−3.47 to 5.44	32	−32.4 to −23.1	32
STO2	Forested-1	−1.11 to 8.43	35	−35.0 to −24.7	35	−1.12 to 8.43	39	−36.9 to −24.7	39
STO7	Forested-2	–		–		0.66 to 4.11	30	−30.7 to −26.4	30
SUN1	Unbuffered-3	–		–		1.71 to 5.57	12	−34.4 to −27.0	12
SUN3	Buffered-4	–		–		0.72 to 6.19	19	−33.6 to −28.3	19

Table 3
$\delta^{15}N$ and $\delta^{13}C$ isotopic range (‰) and number of samples used for analysis for all terrestrial prey at each site. The same prey were used in both the Tetragnathidae and Lycosidae mixing models. Trout were not present at sites IMM6, STO7, SUN1 or SUN3.

Site	Buffer Name	Trout prey				Spider prey			
		$\delta^{15}N$ range	n	$\delta^{13}C$ range	n	$\delta^{15}N$ range	n	$\delta^{13}C$ range	n
IMM3	Forested-3	−4.07 to 2.87	17	−31.5 to −26.3	17	−4.07 to 7.90	22	−31.5 to −23.7	22
IMM6	Unbuffered-2	–		–		−3.95 to 10.7	26	−29.9 to −23.1	26
KARL0	Unbuffered-1	−0.99 to 10.7	35	−29.7 to −24.4	35	−0.99 to 10.7	28	−29.2 to −24.4	28
KARL4	Buffered-2	−4.95 to 13.0	24	−29.0 to −23.9	24	−4.95 to 13.0	24	−29.0 to −23.9	24
KARL5	Buffered-3	−6.34 to 13.8	32	−30.7 to −23.0	32	−6.34 to 6.76	25	−30.7 to −23.0	25
STO2	Forested-1	−4.88 to 11.8	31	−32.9 to −24.8	31	−4.88 to 8.93	21	−31.3 to −25.9	21
STO7	Forested-2	–		–		−3.77 to 12.6	29	−33.1 to −23.5	29
SUN1	Unbuffered-3	–		–		−5.68 to 9.61	21	−32.6 to −24.9	21
SUN3	Buffered-4	–		–		−5.66 to 6.59	25	−32.9 to −23.6	25

Table 4
$\delta^{15}N$ isotopic range (‰) and number used for analysis for all trout and spider predators at each site. Trout were not present at sites IMM6, STO7, SUN1 or SUN3. Lycosidae were not present at sites IMM3, KARL4, or SUN3.

Site	Buffer Name	Trout		Lycosidae		Tetragnathidae	
		$\delta^{15}N$ range (‰)	n	$\delta^{15}N$ range (‰)	n	$\delta^{15}N$ range (‰)	n
IMM3	Forested-3	5.30 to 6.13	12	–		−1.18 to 3.29	6
IMM6	Unbuffered-2	–		0.61 to 6.14	6	0.85 to 6.36	10
KARL0	Unbuffered-1	7.22 to 8.49	11	3.87 to 6.42	10	4.88 to 6.39	5
KARL4	Buffered-2	3.69 to 8.21	14	–		0.37 to 6.27	7
KARL5	Buffered-3	3.62 to 8.04	18	0.13 to 2.83	10	−1.57 to 1.85	9
STO2	Forested-1	4.34 to 6.09	16	0.87 to 5.27	10	1.24 to 4.47	8
STO7	Forested-2	–		2.94 to 6.89	12	2.74 to 7.63	10
SUN1	Unbuffered-3	–		2.50 to 6.36	10	−0.18 to 3.02	9
SUN3	Buffered-4	–		–		−0.42 to 4.30	12

Table 5
$\delta^{13}C$ range (‰) and number used for analysis for all trout and spider predators at each site. Trout were not present at sites IMM6, STO7, SUN1 or SUN3. Lycosidae were not present at sites IMM3, KARL4, or SUN3.

Site	Buffer Name	Trout		Lycosidae		Tetragnathidae	
		$\delta^{13}C$ range (‰)	n	$\delta^{13}C$ range (‰)	n	$\delta^{13}C$ range (‰)	n
IMM3	Forested-3	−28.4 to −25.0	12	–		−30.5 to −27.2	6
IMM6	Unbuffered-2	–		−27.5 to −25.2	6	−30.1 to −26.2	10
KARL0	Unbuffered-1	−27.7 to −26.4	11	−27.3 to −25.2	10	−28.9 to 26.0	5
KARL4	Buffered-2	−29.2 to −25.2	14	–		−27.8 to −24.9	7
KARL5	Buffered-3	−27.0 to −25.1	18	−27.6 to −25.9	10	−29.8 to −26.3	9
STO2	Forested-1	−28.7 to −26.3	16	−28.0 to −25.4	10	−27.9 to −25.9	8
STO7	Forested-2	–		−29.1 to −26.0	12	−29.8 to −25.3	10
SUN1	Unbuffered-3	–		−28.2 to −27.1	10	−30.2 to −27.6	9
SUN3	Buffered-4	–		–		−29.3 to −26.5	12

competition with fish had an impact on the diet proportion of both Tetragnathidae and Lycosidae families with and without buffer or site effects.

2. Materials and methods

2.1. Study area

Our study took place in the central part of the Northern European country of Sweden. We completed sampling at twelve sites in four areas in the Värmland and Örebro counties within the Göta Älv catchment (Fig. 1, Table 1). Sampling sites were located in riparian zones along 100 m sections of small, shallow streams in Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) productions forests. At buffered and forested sites, understory vegetation was dominated by European blueberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idaea*) and *Sphagnum* spp. while non-buffered sites were mostly made up of *Calamagrostis* spp. of grasses. All streams were comparable in size (mean width ± SD: 2.3 ± 0.97 m; mean depth ± SD: 0.42 ± 0.22 m) but were surrounded by variable sizes of forested buffers separating the streams

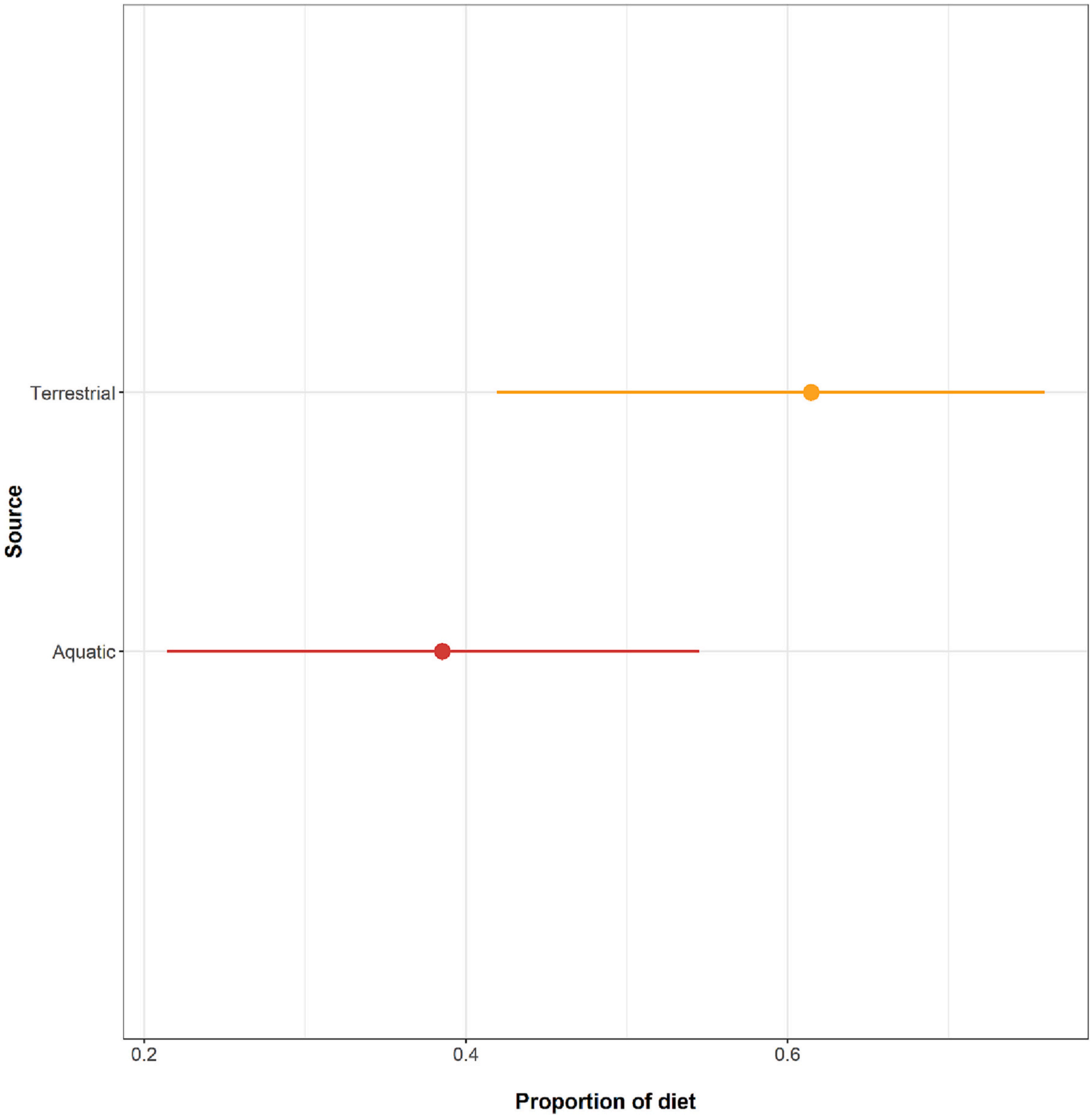

Fig. 4. Diet contributions for brown trout as an average of all sites. X-axis is the percent proportion of diet between terrestrial and aquatic sourced prey. Points are the median diet contribution and horizontal lines are the 95% confidence intervals for each prey contribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and forestry felling operations (Table 1). We categorized each site as unbuffered, buffered (1–120 m of forest buffer) or forested (>120 m).

2.2. Sample collection

We collected samples of Lycosidae and Tetragnathidae spiders, brown trout (*Salmo trutta*), and the potential food sources of each predator group in September of 2021 (Appendix A). Spiders were collected within 1 m of the edge of the stream on both side. We collected spiders on each side of the stream as we assumed the narrow stream widths allowed easy access to both sides by these spider families and as such, collection side was not considered an important factor. Lycosidae were hand collected from the ground level while Tetragnathidae were collected from vegetation and trees using a beat sheet between 0.5 and 2 m above the ground. Spiders were immediately separated into individual vials filled with 80% ethanol. All spiders were identified to species level and life stage was recorded. Trout were collected by electrofishing, and all fish were measured by maximum total length in the field to the nearest 5 mm. Fish less than ~100 mm were euthanized in an overdose of benzocaine (ethyl para-aminobenzoate) anesthesia solution and immediately stored in an 80% ethanol solution. Prior to analysis, the adipose fin and part of the tail fin was removed from the smaller euthanized fish and stored in 80% ethanol. Larger fish were lightly anesthetized in benzocaine in the field, their adipose fin was removed with sterilized micro-dissecting scissors and placed in 80% ethanol, and once recovered the fish was placed back into the stream. Single fin-clips of the adipose fin have a negligible effect on brown trout survival and they are considered an acceptable non-lethal alternative to muscle tissue sampling for SIA (Hammer and Lee Blankenship, 2001; Hanisch et al., 2010). Brown trout and Lycosidae were not present at all sites and those sites were removed from the analysis for each predator.

Potential terrestrial prey was collected simultaneously with spider samples within 1 m of the stream edge at five locations at 10, 25, 50, 75, and 90 m on both sides for a total of ten samples at each site. Ground level invertebrates were collected using a suction sampler, while other terrestrial prey were collected from vegetation and trees using a beat sheet between 0.5 and 2 m above the ground. Potential aquatic invertebrate prey were collected using a kick seine net, hand collection from

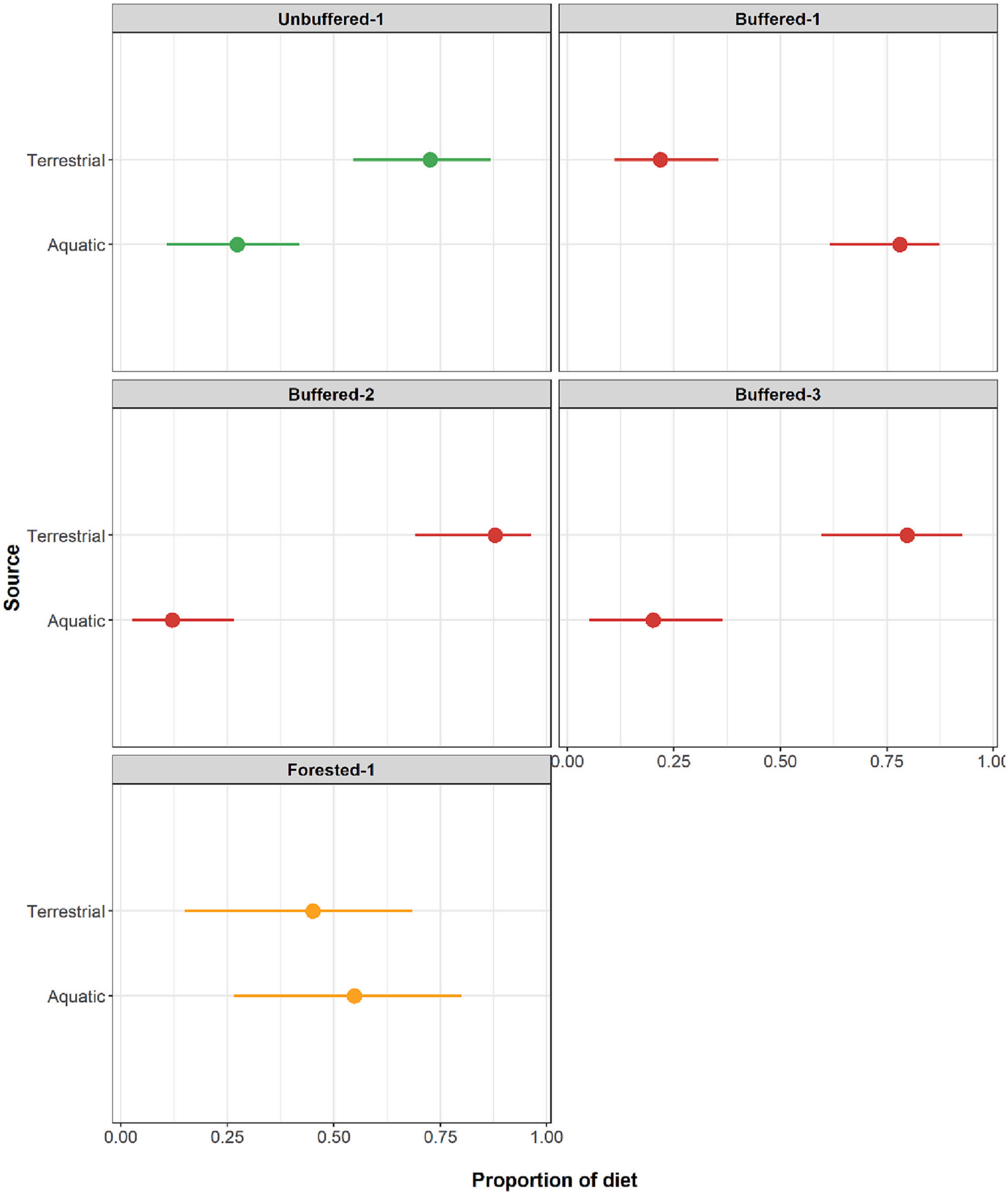

Fig. 5. Diet contributions for brown trout at each site. X-axis is the percent proportion of diet between terrestrial and aquatic sourced prey. Points are the median diet contribution and horizontal lines are the 95% confidence intervals for each prey contribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rocks, or hand collection from aquatic vegetation at representative riffles, runs, and pools along the entire stretch where spider and fish samples were taken. All potential prey were immediately stored in an 80% ethanol solution. We identified all prey to at least family level apart from Collembola, which were identified to order (Appendix A).

2.3. *Stable isotope analysis*

Stable isotope analysis is a method that involves measuring the relative isotopic ratios in a sample. By comparing the isotopic ratios between consumers and their potential prey, we are able to approximate what percentage of prey in a consumer diet is terrestrial or aquatic in origin. All brown trout, spider, and prey samples were placed in clean glass vials and dried at 60 °C for 48 h. Smaller prey items were grouped

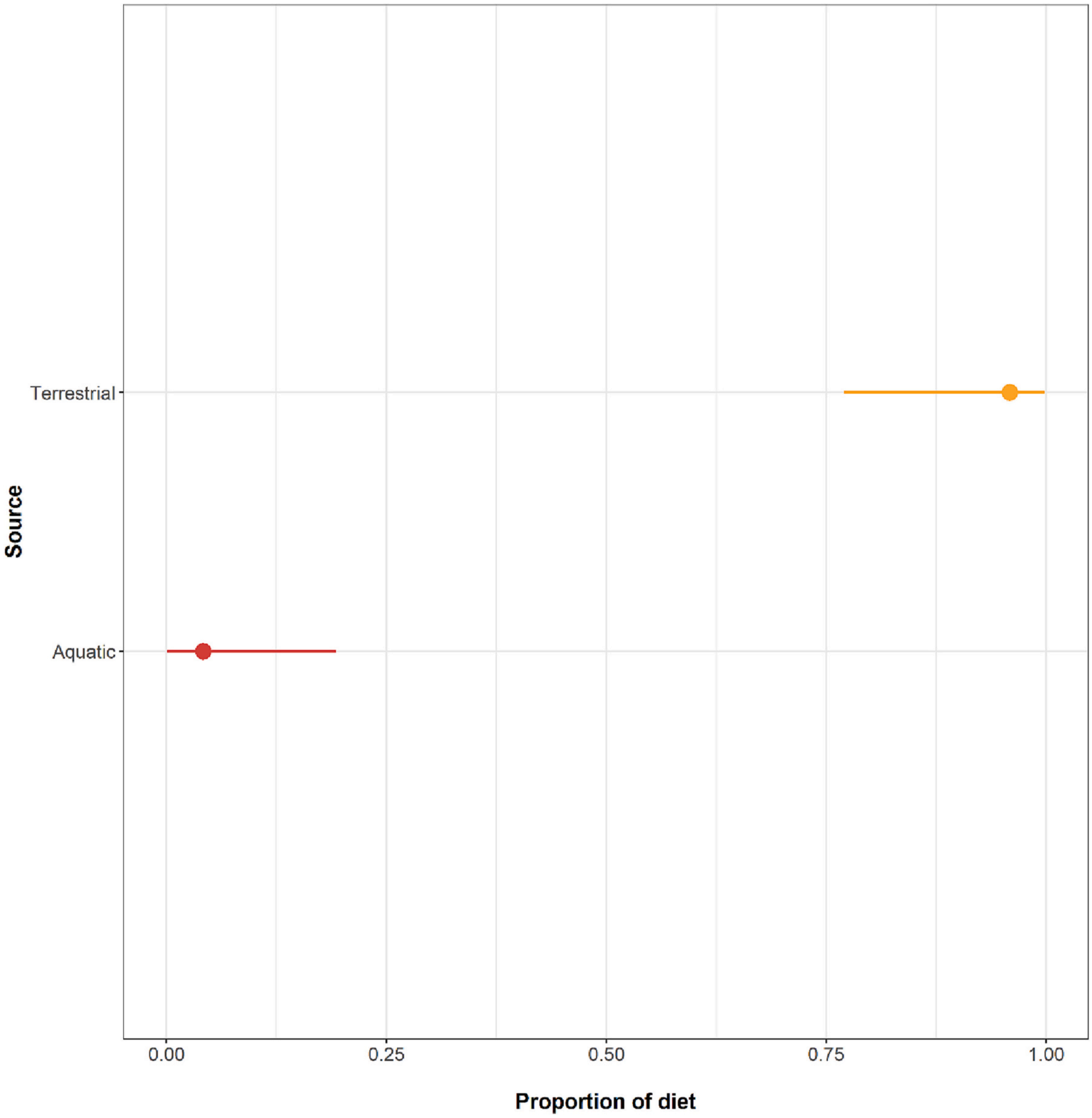

Fig. 6. Diet contributions for Tetragnathidae as an average of all sites. X-axis is the percent proportion of diet between terrestrial and aquatic sourced prey. Points are the median diet contribution and horizontal lines are the 95% confidence intervals for each prey contribution.

to ensure sufficient material for analysis. Each sample was pulverized to a fine homogeneous powder and stored in a desiccator until sent for analysis. SIA was performed by the W. M. Keck Paleoenvironmental and Environmental Stable Isotope Laboratory (Lawrence, Kansas, USA) using a Costech 4010 Elemental Analyzer connected to Thermofinnigan MAT 253.

2.4. Data analysis

To remove overlapping prey groups and identify consumer outliers, we created $\delta^{15}N$ and $\delta^{13}C$ isotopic biplots for each site (Appendix B). All prey items were separated into functional groups based on feeding guild, those that appeared overlapping in the biplots were considered redundant, and one was removed. Consumers outside of the source polygon in the biplots were assumed to be consuming other prey than we collected and were removed as outliers. One site was removed from the analysis, KARL3, as most of the consumers fell outside of the source polygon. With most of consumers outside of the source polygon it is assumed that we did not collect the predominant prey sources for trout and spiders at this site. Prior to statistical analysis, we grouped all prey items as either aquatic or terrestrial in origin based on where larval or nymphal stages occurred according to the literature (Appendix A). $\delta^{13}C$ isotopic signatures for both aquatic and terrestrial prey were tested for differences as this is prerequisite for mixing models to be able to distinguish between food sources (Appendix C). A *t*-test showed two sites, IMM4 and STO6 ($t(52) = -0.94$, $p = 0.35$ and $t(56) = -0.22$, $p = 0.82$, respectively), had overlapping $\delta^{13}C$ signatures in potential prey and both sites were removed from the analysis.

To estimate the proportion of aquatic versus terrestrial diet of brown trout and each spider family, we ran Bayesian mixing models using the R package MixSIAR version 3.1.12 (Stock and Semmens, 2016) in R version 4.2.2 (R Core Team, 2022). $\delta^{15}N$ and $\delta^{13}C$ values of potential diet sources were built into mixing models that included site and buffer category as fixed factors for all predators. Body size ($<$ 8 cm, $>$ 8 cm) was added as a fixed factor for brown trout models as this size is the generally accepted threshold for young-of-the-year trout versus +1 trout. Genera (*Tetragnatha* or *Metellina* [Tetragnathidae]; *Alopecosa*, *Hygrolycosa*, *Pardosa*, *Piratula* [Lycosidae]), life stage (adult, sub-adult, juvenile), and fish presence/absence in the adjacent stream were added as fixed factors for spider models. We tested each fixed effect

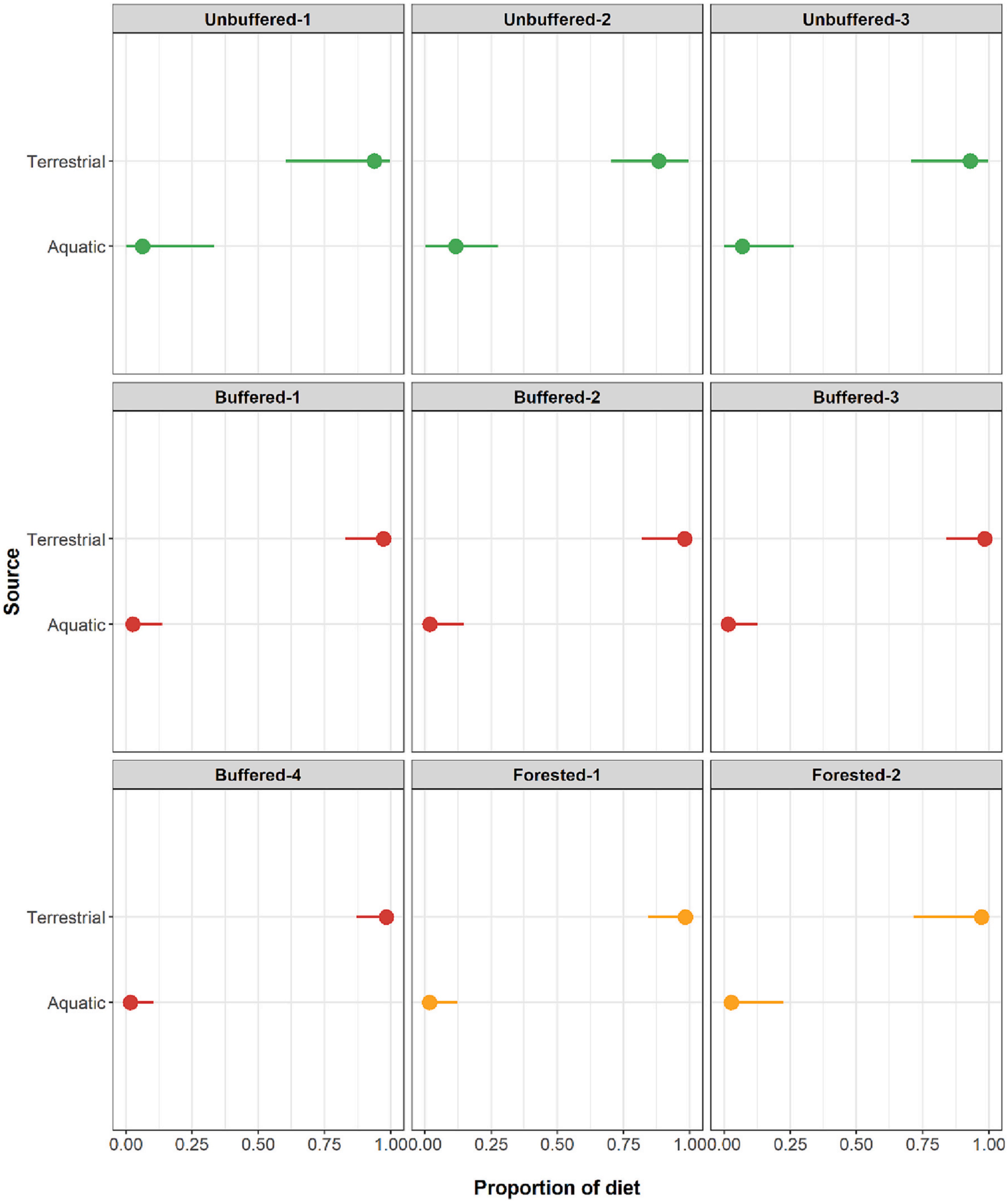

Fig. 7. Diet contributions for Tetragnathidae at each site. X-axis is the percent proportion of diet between terrestrial and aquatic sourced prey. Points are the median diet contribution and horizontal lines are the 95% confidence intervals for each prey contribution.

separately and as a combination of two factors for each model as MixSIAR only allows for a maximum of two fixed effects per model run. Trophic enrichment factors for brown trout (δ^{15}N 3.23 ± 0.79 and δ^{13}C 1.03 ± 0.29; Jensen et al., 2012) and spiders (δ^{15}N 2.3 ± 0.28 and δ^{13}C 0.4 ± 0.17; McCutchan Jr et al., 2003) were incorporated into all biplots and each model. Each model was run using Markov chain Monte Carlo (MCMC) sampling using three replicate chains, each with 100,000 iterations, with a burn-in of 50,000 iterations. Chain convergence was confirmed with Gelmen-Rubin and Geweke diagnostics. We used uninformative priors that assume all combinations of aquatic or terrestrial prey in predator diets is equally likely. We compared MixSIAR model output for each group of predators using the leave-one-out cross-validation (LOO) method and calculating the relative weight of each model (Vehtari et al., 2017). The estimated proportions of diet were reported as the median and associated 95% credible intervals (CI).

3. Results

Isotopic values for brown trout (Fig. 2) and both spider families (Fig. 3) varied by site. The mean δ^{15}N value for brown trout at all sites (5.90 ± 1.3; 95% confidence interval [CI] 5.61–6.20) was more enriched than the potential aquatic (2.98 ± 2.0; CI, 2.58–3.24) and terrestrial prey (2.06 ± 4.2; CI, 1.36–2.75). The mean δ^{15}N value for Lycosidae at all sites (3.70 ± 1.9; CI, 3.21–4.18) was similar to potential aquatic prey (3.37 ± 2.1; CI, 3.14–3.66) but more enriched than terrestrial prey (1.20 ± 3.9; CI, 0.68–1.71). The mean δ^{15}N value for

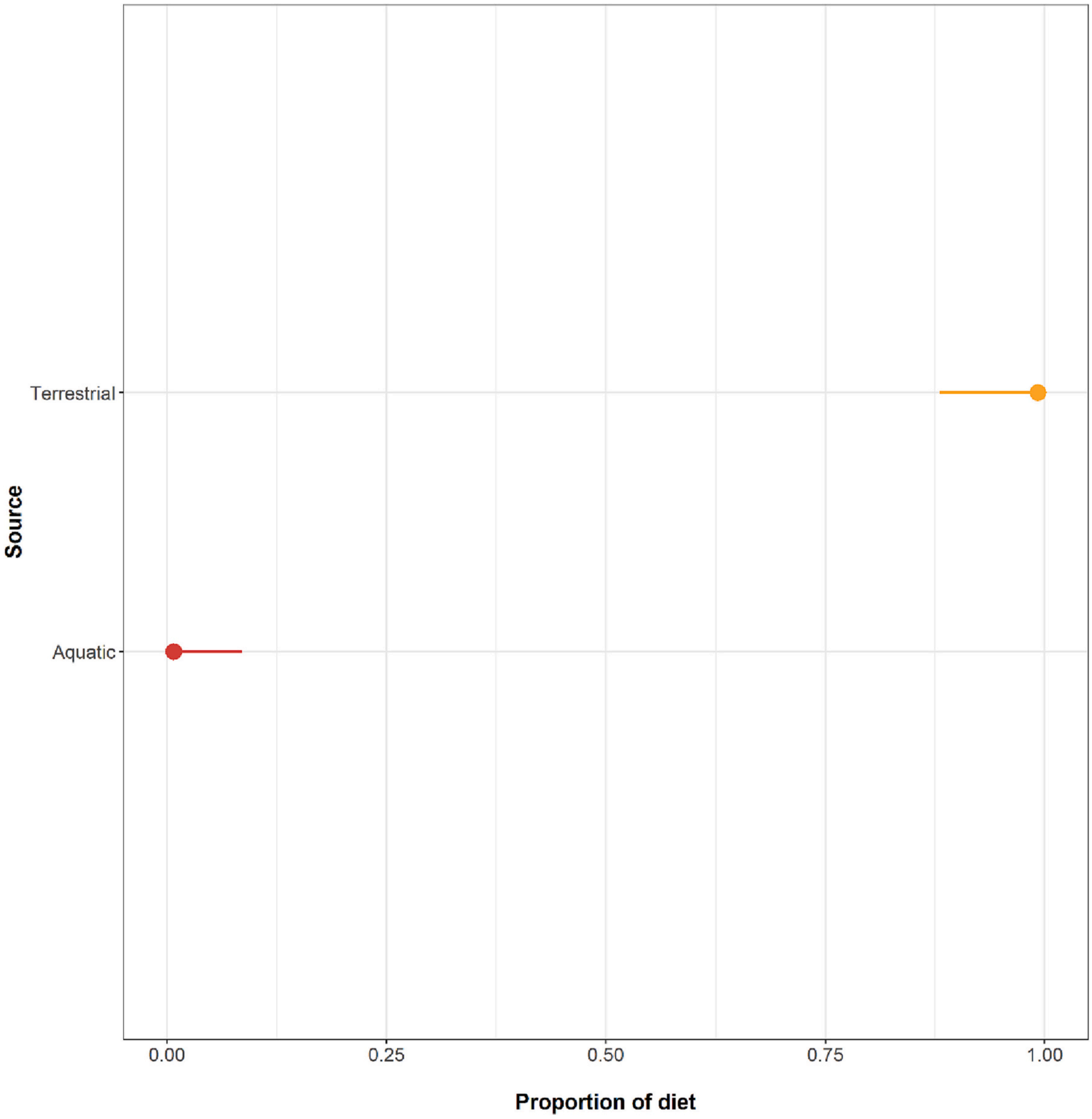

Fig. 8. Diet contributions for Lycosidae as an average of all sites. X-axis is the percent proportion of diet between terrestrial and aquatic sourced prey. Points are the median diet contribution and horizontal lines are the 95% confidence intervals for each prey contribution.

Tetragnathidae at all sites (2.79 ± 2.1; CI, 2.32–3.26) was more depleted than potential aquatic prey (same as Lycosidae)) but more enriched than terrestrial prey (same as Lycosidae) (Fig. 3). All predators fell within the range of the selected aquatic and terrestrial prey for each site (Tables 2 & 3). All predator groups showed a wide range of δ^{15}N values across sites, but brown trout exhibited a much lower variability than the spiders (Table 4). The mean δ^{13}C value for brown trout at all sites (−26.7 ± 1.1; CI, −27.0 to −26.5) was more enriched than the potential aquatic (−29.5 ± 2.3; CI, −29.8 to −29.1) and terrestrial prey (−27.6 ± 1.7; CI, −27.9 to −27.3). The mean δ^{13}C value for Lycosidae at all sites (−26.9 ± 0.75; CI, −27.1 to −26.7) was more enriched than potential aquatic (−30.0 ± 2.2; CI, −30.3 to −29.7) and terrestrial prey (−27.8 ± 1.9; CI, −28.0 to −27.5). The mean δ^{13}C value for Tetragnathidae at all sites (−28.0 ± 1.3; CI, −28.3 to −27.8) was more enriched than potential aquatic prey (same as Lycosidae) but more depleted than potential terrestrial prey (same as Lycosidae). Brown trout showed a moderate range of δ^{13}C across sites, but Lycosidae and Tetragnathidae showed much higher variability (Table 5).

Posterior estimates of diet proportions showed that terrestrial prey were the main food source for spiders and provided a very large portion of the food source for brown trout. For brown trout, the median contribution of aquatic and terrestrial prey across all sites was 39% (CI, 21.6–58.0%) and 61% (CI, 42.0–78.4%), respectively (Figs. 4 & 5). For Tetragnathidae the median contribution of aquatic and terrestrial prey across all sites was 4.3% (CI, 0–23.1%) and 95.7% (CI, 77–100%), respectively (Figs. 6 & 7). Lycosidae exhibited the most extreme proportional contributions between aquatic and terrestrial prey across all sites, 2% (CI, 0–11.8%) and 98% (CI, 88.3–100%), respectively (Figs. 8 & 9). We found that *site* and *buffer* as a covariate combination provided the best model fit for all predators (Table 6). For Tetragnathidae and Lycosidae, *fish presence* also carried some weight when combined with *site* but results were not notably different from the *site* and *buffer* model (Table 6). All other covariates, whether in combination or alone, were not found to affect model fit (Table 6).

4. Discussion

Predators at all sites had ranges of both δ^{15}N and δ^{13}C isotopic signatures that fell within the isotopic signatures of the collected potential prey with the added trophic enrichment factors, suggesting a reliance on

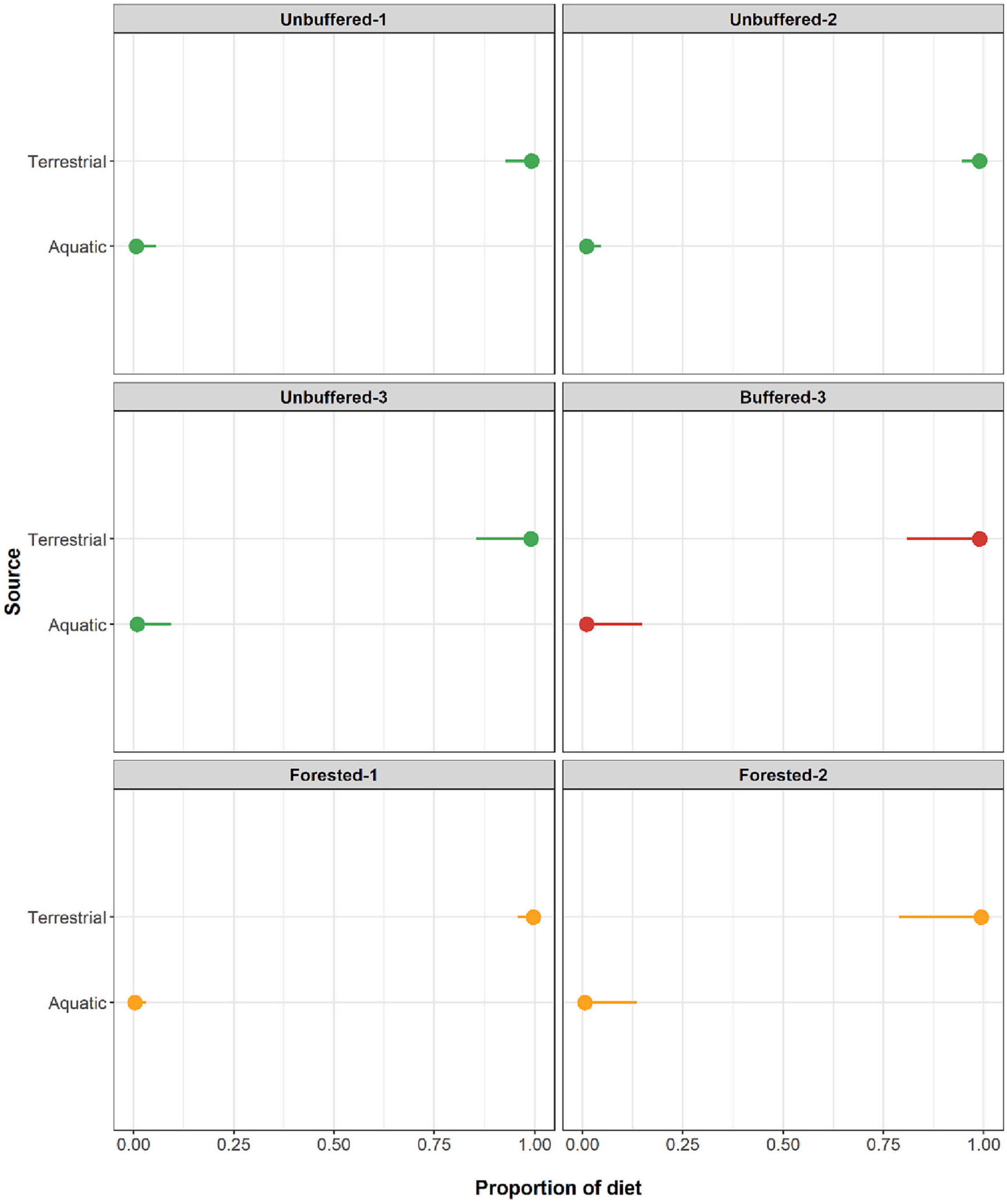

Fig. 9. Diet contributions for Lycosidae at each site. X-axis is the percent proportion of diet between terrestrial and aquatic sourced prey. Points are the median diet contribution and horizontal lines are the 95% confidence intervals for each prey contribution.

multiple trophic levels of prey from both aquatic and terrestrial environments. However, our results present a picture of aquatic and riparian predators with a considerable dependence on terrestrial prey items. Terrestrial prey made up almost 100% of the diets of both Tetragnathidae and Lycosidae at all sites. Brown trout had more mixed diets but showed a higher proportion of terrestrial prey at three out of five sites, and those sites had no riparian buffer or a buffer of 120 m. Thus, our data does not support our hypothesis and predators in unbuffered sites did not appear to consume a higher portion of aquatic prey over terrestrial prey compared to buffered or fully forested sites.

We found trout diets to be mixed between terrestrial and aquatic subsidies, but with an overall more significant reliance on terrestrial subsidies. At only two, out of five, sites brown trout showed a higher proportion of aquatic prey in the diet. Aquatic prey can comprise up to 85% of brown trout diets (Dunlop et al., 2021), but terrestrial prey can also be important to trout diet, especially in late summer coinciding with a peak abundance of terrestrial invertebrates (Milardi et al., 2016). We collected our samples in early fall, and our results show that brown trout diets contained both terrestrial and aquatic prey sources. At the remaining three sites, brown trout had a distinct separation between the diet contributions from both sources and were predominately terrestrial sourced. Terrestrial subsidies to fish are seasonally variant and the findings at these sites agree with other authors who noted an increase in terrestrial invertebrate input in late summer and early fall (Nakano and Murakami, 2001; Saunders and Fausch, 2007). However, there was no apparent pattern pointing to an effect of riparian buffer size on brown

Table 6
Leave-one-out cross-validation information criterion (LOOic) values (Vehtari et al., 2017) of each model tested with the three different predator groups. Weights closer to 1 indicate the strongest model for predicting diet proportions.

Predator group	Model	LOOic	Std error LOOic	Weight
Trout	Site + buffer	59.0	27.9	0.562
	Site	59.5	27.9	0.438
	Site + body size	130.6	18.4	0.0
	Buffer + body size	148.3	14.7	0.0
	Buffer	153.4	14.2	0.0
	Null	173.5	13.1	0.0
	Body size	173.8	13.3	0.0
	Site + buffer	123.5	16.2	0.403
	Site	124.1	16.1	0.299
	Site + fish presence	124.1	16.2	0.299
	Buffer + genera	146.8	14.9	0.0
	Site + genera	147.7	14.7	0.0
	Genera	157.2	13.7	0.0
	Site + life stage	157.4	14.6	0.0
	Buffer + life stage	157.5	14.7	0.0
	Buffer	162.8	14.2	0.0
	Life stage	162.9	14.1	0.0
Tetragnathidae	Null	163.2	14.1	0.0
	Site + buffer	241.6	20.3	0.447
	Site + fish presence	242.2	20.7	0.331
	Site	243.0	20.9	0.222
	Buffer + life stage	312.9	14.7	0.0
	Buffer + genera	313.4	14.7	0.0
	Site + genera	313.7	14.7	0.0
	Buffer	313.9	14.6	0.0
	Site + life stage	313.9	14.9	0.0
	Null	314.4	14.7	0.0
	Genera	314.6	14.7	0.0
Lycosidae	Life stage	314.7	14.6	0.0

trout diet. Although our results did not indicate that fish size was an important factor, it is possible that trout life stage influenced the higher terrestrial diet proportions seen in our study. Brown trout in the Göta Älv catchment are lifetime residents growing to around 80 mm as young-of-the-year (Erős et al., 2012). Sánchez-Hernández and Cobo (2016, 2018) found that brown trout shift from aquatic to falling terrestrial prey closer to the surface after reaching a length of 81 mm and older trout increase reliance on terrestrial prey. Across all sites, 66.2% of our sampled trout were above 80 mm in length suggesting many of our fish were older and may have been feeding more often on the stream surface where they would have a higher chance of encountering falling terrestrial prey. The enrichment of δ^{15}N in brown trout being greater than their potential prey points to these fish as a group that is likely at the top of the food chain in their environment. Brown trout are well known to engage in intraguild piscivory (Sanchez-Hernandez, 2020) and this may have contributed to the enriched δ^{15}N level, but we did not collect fish as potential prey items and this interaction should be further investigated.

Our findings indicate that riparian spiders around small streams are highly dependent on terrestrial subsidies regardless of forested buffer size. Previous studies involving larger rivers have found aquatic prey to be significant parts of riparian spider diets (Akamatsu et al., 2004; Collier et al., 2002; Paetzold et al., 2005). These authors carried out their studies in rivers buffered by upland forests and intact riparian vegetation that contribute more terrestrial organic matter and more habitat for increased aquatic invertebrate abundance. The spider reliance on terrestrial prey in our study could be explained by the fact that unbuffered and small-buffered systems may have reduced abundance of aquatic prey because of low woody debris input. However, for our forested streams, even with likely increased woody debris additions and higher abundances of aquatic prey, spiders relied heavily on terrestrial subsidies and it is possible that stream size per se was an important factor. Working in small streams like those in our study with up to 53% riparian tree cover, Siebers et al. (2021) found that riparian spiders consume very little aquatic prey, a fact that did not change with season or stream flow intermittency. Alp et al. (2013), also working in small, head-water streams, found little evidence that aquatic prey contributed to spider diets. Regardless of stream size it is possible that aquatic-derived prey, because of changing isotopic signals when growing from larvae to adult stages, will become “isotopically cryptic” and therefore indistinguishable from terrestrial-derived prey (Alp et al., 2013). However, our grouped aquatic and terrestrial prey did have significantly different isotopic signatures and we do not believe aquatic prey in our study was mistaken for terrestrial prey. Stream size, and not buffer nor isotopically cryptic prey, is a likely factor in determining what riparian spiders consume.

Although we found no evidence of riparian buffer size affecting the diet of fish or spiders, previous studies have highlighted the impact of forestry and upland land use on aquatic and riparian systems (Albertson et al., 2018; Gustafsson et al., 2014; Krell et al., 2015). If we limit the terrestrial input in the form of woody debris, leaf litter, and diverse terrestrial invertebrates, to small streams, this would likely affect the cascading bottom-up effect through both the aquatic and terrestrial food chains. Several authors have reported that limited amount of terrestrial inputs of falling insects and/or other organic matter have a negative effect on fish growth (Erős et al., 2012; Atlas et al., 2013), but Atlas et al. (2013) showed that predatory fish in streams with limited terrestrial subsidies would not increase feeding on aquatic subsidies to compensate. This suggesting that the use of the forested upland system may have a greater impact on small tributary streams regardless of whether forested buffers are present. However, Albertson et al. (2018) admits that fish populations are sustainable as long as they have just enough food to guarantee a positive growth rate, but they stress that the condition of the riparian habitat is critical to maintain that food source. Maintaining the condition of riparian habitats is crucial for ensuring a sustainable food source for fish populations, regardless of the presence of forested buffers or the limited terrestrial inputs in small streams.

Our study only investigated the effects of buffers where they stood, i.e. ignoring any downstream effects, despite the fact that there are distinct linkages between headwater streams and downstream ecosystems (Wipfli et al., 2007). Thus, the buffer effects at our study sites may have been visible downstream. Further, we did not control for seasonal variation in predator diets, and it is possible that the fish and spiders in our study area were more reliant on aquatic insects at times that coincide with aquatic insect emergence or that isotopic signatures of primary producers vary over time thus affecting prey signatures (Post, 2002). Paetzold et al. (2005) and Kato et al. (2004) showed a significantly higher abundance of aquatic insects earlier in the summer that may have affected predator isotopic signature in our study. However, these studies were performed in larger streams that may support high numbers of emerging aquatic invertebrates that can easily outnumber terrestrial prey even in high production riparian zones. Aquatic prey abundance in the small, low-order streams in our study may still be very low compared to the terrestrial prey abundance, even at different times of the year. Although, we did not explore prey abundance, it is not necessarily an important factor in spider diet (Stenroth et al., 2015) and we chose to sample during a time of the year with the highest productivity with the intent that our predators would have ample prey from terrestrial and aquatic habitats from which to choose. Further, we also did not expect the effect of the buffer size, as our main factor, to change during the year and thus seasonality should not be considered a limiting factor for buffers in our study.

Our study concluded that spiders around small streams are heavily reliant on terrestrial subsidies with no clear connection to riparian buffer size. For trout, the results were less definite, with a more overlapping diet at the forested site, a high reliance on aquatic subsidies at one of the buffered sites, and a clear reliance on terrestrial subsides at the remaining buffered and unbuffered sites. Our data shows no major effects of riparian buffer size for either predator group, but it is likely that other environmental factors within and around the riparian systems are important. Beyond the riparian condition and environment, the fall season is likely a critical factor that drives the influx and dependence of terrestrial prey for both trout and riparian spiders. An important factor in increasing and maintaining aquatic and terrestrial prey diversity around streams and rivers is through establishing and preserving riparian habitat (Albertson et al., 2018; Popescu et al., 2021). Litter exclusion in small streams reduces the flow of carbon subsidies to invertebrate predators (Hall Jr et al., 2000), further evidence that increased and varied leaf litter and detritus is important to maintain stable and complex food webs in smaller streams. Creating ecologically functional riparian zones (Lind et al., 2019) by providing complex biological, functional, and structural diversity, is one possible way to support food chain complexity of riparian systems around small, low-order streams. But riparian functional diversity can still be high in both buffered and unbuffered streams (Marker et al., 2022). Streams that lack forested buffers may still provide ample terrestrial prey and aquatic litter that can also maintain a high level of food web complexity. To support the important influx of terrestrial prey for trout and riparian spider diets, riparian maintenance in late fall should avoid disturbances that may have a direct effect on terrestrial invertebrate habitat. Seasonality of subsidy exchange through the riparian zone is an important factor regardless of the time of the year.

CRediT authorship contribution statement

Jeffery Marker: Methodology, Investigation, Writing – original draft, Formal analysis, Visualization. **Eva Bergman:** Writing – review & editing, Supervision. **Rachel E. Bowes:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Denis Lafage:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing, Supervision.

Declaration of Competing Interest

None.

Acknowledgements

This work was supported by Svenska Forskningsrådet (FORMAS), Grant No. 2018-00412. The authors thank Tina Westlund with the Church of Sweden, Karlstad Diocese for approving forest access and assisting with site selection. The authors also thank Frida Afzelius and Tova Gullstrand for leading the demanding fieldwork and sample collection. We would like to thank the two anonymous reviewers for taking the time to review the manuscript which helped us to improve its quality. Finally, we thank Kalle Filipson, Jaqueline Hoppenreijs, Louis Addo, and Sebastian Rock for assisting with electrofishing and aquatic prey sampling.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2023.e00302.

References

Akamatsu, F., Toda, H., Okino, T., 2004. Food source of riparian spiders analyzed by using stable isotope ratios. Ecol. Res. 19 (6), 655–662.

Albertson, L.K., Ouellet, V., Daniels, M.D., 2018. Impacts of stream riparian buffer land use on water temperature and food availability for fish. J. Freshw. Ecol. 33 (1), 195–210.

Alp, M., Peckarsky, B.L., Bernasconi, S.M., Robinson, C.T., 2013. Shifts in isotopic signatures of animals with complex life-cycles can complicate conclusions on cross-boundary trophic links. Aquat. Sci. 75, 595–606.

Atlas, W.I., Palen, W.J., Courcelles, D.M., Munshaw, R.G., Monteith, Z.L., 2013. Dependence of stream predators on terrestrial prey fluxes: food web responses to subsidized predation. Ecosphere 4 (6), 1–16.

Baldissera, R., de Quadros, S.O., Galeti, G., Rodrigues, E.N.L., Lazzarotto, L.M.V., de Oliveira, A.D., 2020. Spider assemblage structure and functional diversity patterns in clear-cut, logged, and undisturbed areas in a large Atlantic Forest remnant. Can. J. For. Res. 50 (7), 608–614. https://doi.org/10.1139/cjfr-2019-0302.

Bartels, P., Cucherousset, J., Steger, K., Eklöv, P., Tranvik, L.J., Hillebrand, H., 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology 93 (5), 1173–1182. https://doi.org/10.1890/11-1210.1.

Baxter, C.V., Fausch, K.D., Carl Saunders, W., 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshw. Biol. 50 (2), 201–220. https://doi.org/10.1111/j.1365-2427.2004.01328.x.

Briers, R.A., Cariss, H.M., Geoghegan, R., Gee, J.H., 2005. The lateral extent of the subsidy from an upland stream to riparian lycosid spiders. Ecography 28 (2), 165–170.

Broadmeadow, S., Nisbet, T.R., 2004. The effects of riparian forest management on the freshwater environment: a literature review of best management practice. Hydrol. Earth Syst. Sci. 8 (3), 286–305.

Carlson, P.E., McKie, B.G., Sandin, L., Johnson, R.K., 2016. Strong land-use effects on the dispersal patterns of adult stream insects: implications for transfers of aquatic subsidies to terrestrial consumers. Freshw. Biol. 61 (6), 848–861.

Cole, L.J., Stockan, J., Helliwell, R., 2020. Managing riparian buffer strips to optimise ecosystem services: a review. Agric. Ecosyst. Environ. 296, 106891.

Collier, K.J., Bury, S., Gibbs, M., 2002. A stable isotope study of linkages between stream and terrestrial food webs through spider predation. Freshw. Biol. 47 (9), 1651–1659. https://doi.org/10.1046/j.1365-2427.2002.00903.x.

Dunlop, K., Eloranta, A.P., Schoen, E., Wipfli, M., Jensen, J.L., Muladal, R., Christensen, G.N., 2021. Evidence of energy and nutrient transfer from invasive pink salmon (*Oncorhynchus gorbuscha*) spawners to juvenile Atlantic salmon (*Salmo salar*) and brown trout (Salmo trutta) in northern Norway. Ecol. Freshw. Fish 30 (2), 270–283.

England, L.E., Rosemond, A.D., 2004. Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. Freshw. Biol. 49 (6), 721–734.

Erős, T., Gustafsson, P., Greenberg, L.A., Bergman, E., 2012. Forest-stream linkages: effects of terrestrial invertebrate input and light on diet and growth of brown trout (Salmo trutta) in a boreal forest stream. PLoS One 7 (5), e36462.

Forio, M.A.E., De Troyer, N., Lock, K., Witing, F., Baert, L., Saeyer, N.D., Goethals, P., 2020. Small patches of riparian woody vegetation enhance biodiversity of invertebrates. Water 12 (11), 3070.

Fukui, D.A.I., Murakami, M., Nakano, S., Aoi, T., 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. J. Anim. Ecol. 75 (6), 1252–1258.

Goedeker, S.J., Wrynn, T.E., Gall, B.G., 2021. Orientation behavior of riparian long-jawed orb weavers (Tetragnatha elongata) after displacement over water. Ecology and Evolution 11 (6), 2899–2906.

Göthe, E., Lepori, F., Malmqvist, B., 2009. Forestry affects food webs in northern Swedish coastal streams. Fundam. Appl. Limnol. 175 (4), 281.

Greenwood, M.J., 2014. More than a barrier: the complex effects of ecotone vegetation type on terrestrial consumer consumption of an aquatic prey resource. Austral Ecol. 39 (8), 941–951.

Gustafsson, P., Greenberg, L.A., Bergman, E., 2014. Woody debris and terrestrial invertebrates–effects on prey resources for brown trout (*Salmo trutta*) in a boreal stream. Environ. Biol. Fish 97 (5), 529–542.

Hall Jr., R.O., Wallace, J.B., Eggert, S.L., 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology 81 (12), 3445–3463.

Hammer, S.A., Lee Blankenship, H., 2001. Cost comparison of marks, tags, and mark-with-tag combinations used in salmonid research. N. Am. J. Aquac. 63 (2), 171–178.

Hanisch, J.R., Tonn, W.M., Paszkowski, C.A., Scrimgeour, G.J., 2010. δ13C and δ15N signatures in muscle and fin tissues: nonlethal sampling methods for stable isotope analysis of salmonids. N. Am. J. Fish Manag. 30 (1), 1–11. https://doi.org/10.1577/M09-048.1.

Jensen, H., Kiljunen, M., Amundsen, P.A., 2012. Dietary ontogeny and niche shift to piscivory in lacustrine brown trout *Salmo trutta* revealed by stomach content and stable isotope analyses. J. Fish Biol. 80 (7), 2448–2462.

Kato, C., Iwata, T., Wada, E., 2004. Prey use by web-building spiders: stable isotope analyses of trophic flow at a forest-stream ecotone. Ecol. Res. 19 (6), 633–643.

Krell, B., Röder, N., Link, M., Gergs, R., Entling, M.H., Schäfer, R.B., 2015. Aquatic prey subsidies to riparian spiders in a stream with different land use types. Limnologica 51, 1–7.

Lafage, D., Bergman, E., Eckstein, R.L., Österling, E.M., Sadler, J.P., Piccolo, J.J., 2019. Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: a worldwide meta-analysis. Ecosphere 10 (4), e02697. https://doi.org/10.1002/ecs2.2697.

Larsen, S., Muehlbauer, J.D., Marti, E., 2016. Resource subsidies between stream and terrestrial ecosystems under global change. Glob. Chang. Biol. 22 (7), 2489–2504. https://doi.org/10.1111/gcb.13182.

Lind, L., Hasselquist, E.M., Laudon, H., 2019. Towards ecologically functional riparian zones: a meta-analysis to develop guidelines for protecting ecosystem functions and biodiversity in agricultural landscapes. J. Environ. Manag. 249, 109391 https://doi.org/10.1016/j.jenvman.2019.109391.

Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L., Richardson, J.S., 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications 20 (1), 126–134.

Marker, J., Bergman, E., Eckstein, R.L., Lafage, D., 2022. Forested riparian buffer environmental variables are more important than size for species functional diversity in production forests. For. Ecol. Manag. 526, 120599.

McCutchan Jr., J.H., Lewis Jr., W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102 (2), 378–390.

Milardi, M., Thomas, S.M., Kahilainen, K.K., 2016. Reliance of brown trout on terrestrial prey varies with season but not fish density. Freshw. Biol. 61 (7), 1143–1156.

Muehlbauer, J.D., Collins, S.F., Doyle, M.W., Tockner, K., 2014. How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. Ecology 95 (1), 44–55.

Nakano, S., Murakami, M., 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc. Natl. Acad. Sci. 98 (1), 166–170.

Nakano, S., Miyasaka, H., Kuhara, N., 1999. Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80 (7), 2435–2441. https://doi.org/10.1890/0012-9658(1999)080[2435:TALRAI]2.0.CO;2.

Paetzold, A., Schubert, C.J., Tockner, K., 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. Ecosystems 8 (7), 748–759.

Philpott, S.M., Soong, O., Lowenstein, J.H., Pulido, A.L., Lopez, D.T., Flynn, D.F., DeClerck, F., 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecol. Appl. 19 (7), 1858–1867.

Popescu, C., Oprina-Pavelescu, M., Dinu, V., Cazacu, C., Burdon, F.J., Forio, M.A.E., Rîşnoveanu, G., 2021. Riparian vegetation structure influences terrestrial invertebrate communities in an agricultural landscape. Water 13 (2), 188.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83 (3), 703–718.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ramberg, E., Burdon, F.J., Sargac, J., Kupilas, B., Rîşnoveanu, G., Lau, D.C., McKie, B.G., 2020. The structure of riparian vegetation in agricultural landscapes influences spider communities and aquatic-terrestrial linkages. Water 12 (10), 2855.

Richardson, J.S., Zhang, Y., Marczak, L.B., 2010. Resource subsidies across the land–freshwater interface and responses in recipient communities. River Res. Appl. 26 (1), 55–66.

Sabo, J.L., Power, M.E., 2002. River–watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83 (7), 1860–1869.

Sanchez-Hernandez, J., 2020. Drivers of piscivory in a globally distributed aquatic predator (brown trout): a meta-analysis. Sci. Rep. 10 (1), 11258.

Sánchez-Hernández, J., Cobo, F., 2016. Ontogenetic shifts in terrestrial reliance of stream-dwelling brown trout. J. Limnol. 75 (2).

Sánchez-Hernández, J., Cobo, F., 2018. Modelling the factors influencing ontogenetic dietary shifts in stream-dwelling brown trout (Salmo trutta). Can. J. Fish. Aquat. Sci. 75 (4), 590–599.

Saunders, W.C., Fausch, K.D., 2007. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. Trans. Am. Fish. Soc. 136 (5), 1216–1230.

Siebers, A.R., Paillex, A., Robinson, C.T., 2021. Riparian hunting spiders do not rely on aquatic subsidies from intermittent alpine streams. Aquat. Sci. 83, 1–11.

Stenroth, K., Polvi, L.E., Fältström, E., Jonsson, M., 2015. Land-use effects on terrestrial consumers through changed size structure of aquatic insects. Freshw. Biol. 60 (1), 136–149.

Stock, B.C., Semmens, B.X.. MixSIAR GUI User Manual. Version 3.1.12. https://github.com/brianstock/MixSIAR.

Tagwireyi, P., Sullivan, S.M.P., 2015. Distribution and trophic dynamics of riparian tetragnathid spiders in a large river system. Mar. Freshw. Res. 67 (3), 309–318.

Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27 (5), 1413–1432.

Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277 (5322), 102–104.

Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1999. Effects of resource limitation on a detrital-based ecosystem. Ecol. Monogr. 69 (4), 409–442. https://doi.org/10.1890/0012-9615(1999)069[0409:EORLOA]2.0.CO;2.

Wipfli, M.S., 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Can. J. Fish. Aquat. Sci. 54 (6), 1259–1269.

Wipfli, M.S., Richardson, J.S., Naiman, R.J., 2007. Ecological linkages between headwaters and downstream ecosystems: Transport of organic matter, invertebrates, and wood down headwater channels. J. Am. Water Resour. Assoc. 43 (1), 72–85.