Beaver activity increases aquatic subsidies to terrestrial consumers

MAGNUS MCCAFFERY[†] AND LISA EBY

The Wildlife Biology Program, College of Forestry and Conservation, The University of Montana, Missoula, MT 59812, USA

SUMMARY

1. The occurrence and importance of fluxes of nutrients and organic matter between aquatic and terrestrial habitats is well established, but how catchment characteristics influence these fluxes remains unclear. Beaver (*Castor canadensis*) alter freshwater ecosystems and increase aquatic production, but it is unknown how these changes influence the magnitude and lateral dispersal of aquatic nutrients into terrestrial ecosystems.

2. We examined differences in abundances of dominant aquatic invertebrates, wolf spiders (Lycosidae), and deer mice (*Peromyscus maniculatus*), at beaver and non-beaver sites. We used stable isotopes to track aquatic-derived carbon in terrestrial consumers and linear mixed-effects models to examine the importance of beaver presence and distance from stream channel on the percentage of aquatic-derived carbon in terrestrial consumers.

3. Sites with beaver activity had >200% higher aquatic invertebrate emergence rates as well as 60% and 75% higher abundances of spiders and deer mice, respectively, relative to non-beaver sites.

4. The tissues of both spiders and deer mice exhibited a greater percentage of aquatic-derived carbon at sites with beaver activity than at non-beaver sites.

5. Aquatic-derived carbon in deer mice declined linearly with distance from the stream edge at both beaver and non-beaver sites. The contribution of aquatic-derived carbon in mice extended farther from the stream edge in beaver-modified catchments. Aquatic-derived carbon in spiders also declined linearly with distance from the stream at beaver sites but not at non-beaver sites.

6. We documented a novel example of increased aquatic subsidy to riparian areas with beaver activity, leading to changes in the magnitude of the lateral dispersal of aquatic nutrient subsidies to the terrestrial environment in small stream systems. Understanding the effects of natural disturbance regimes, such as beaver modification, will be important for management and, where appropriate, restoration of natural catchment processes.

Keywords: aquatic-derived carbon, deer mouse, resource subsidies, stable isotopes, wolf spider

Aquatic and terrestrial ecosystems are inextricably linked, and the effects of habitat alteration in one habitat can propagate throughout their linked food webs (Reiners & Driese, 2001; Saunders & Fausch, 2007). The input of terrestrial detritus (e.g. leaves, woody debris), sediment and nutrients into lotic systems was a crucial component of early ecological conceptual models describing longitudinal gradients from headwaters to river ecosystems (Vannote *et al.*, 1980). More recently, studies have elucidated the importance of reciprocal fluxes that pro-

vide habitat, nutrients and energy to subsidise food webs. For instance, subsidies can increase individual growth rates (e.g. Wipfli *et al.*, 2003) and population sizes (e.g. Barrett *et al.*, 2005) of organisms in receiving systems, as well as influence community structure and trophic dynamics (e.g. Baxter, Fausch & Carl Saunders, 2005; Burdon & Harding, 2008; Richardson, Zhang & Marczak, 2010). As an understanding of subsidies continues to evolve, ecologists are investigating the influence of factors such as spatial scale (e.g. Stapp & Polis,

---

Correspondence: Magnus McCaffery, The Wildlife Biology Program, College of Forestry and Conservation, The University of Montana, Missoula, MT 59812, USA. E-mail: magnus.mccaffery@tedturner.com

[†]Current address: Turner Endangered Species Fund, 901 Technology Blvd., Bozeman, MT 59718, USA.

2003) and heterogeneity on subsidy effects (e.g. Darimont, Paquet & Reimchen, 2009; Collins & Baxter, 2014). By incorporating the spatial extent of stream subsidies to terrestrial food webs, Muehlbauer *et al.* (2014) delimited 'biological stream width' to describe the distance of influence for aquatic-derived carbon. Even though the proportion of aquatic subsidies in recipient organisms typically declines with increasing distance from a stream, the biological stream width can be hundreds of metres from the stream banks (Muehlbauer *et al.*, 2014). The influence of catchment characteristics on the magnitude and lateral dispersal of aquatic fluxes to terrestrial food webs is just beginning to be explored, but is a crucial element to consider in the conservation and restoration of catchment processes.

Disturbances to stream and riparian habitats can alter fluxes between aquatic and terrestrial habitats. For instance, exotic salmonids can influence insect emergence through selective predation, which can indirectly reduce riparian consumer densities (Baxter *et al.*, 2004). Intense cattle grazing of riparian habitats (Saunders & Fausch, 2007) and deforestation can reduce allochthonous stream inputs, affecting aquatic food webs (England & Rosemond, 2004). Natural forms of ecological disturbance also have measurable effects on cross-habitat subsidies. For example, the magnitude of a flood event can influence subsidies of prey to riparian spiders, where spiders attain peak biomass at intermediate levels of disturbance (Greenwood & McIntosh, 2008). Severe riparian wildfire can increase cross-habitat subsidies, with a higher adult aquatic insect emergence and greater spider abundances at sites exposed to high severity fire versus low severity and unburned sites (Malison & Baxter, 2010).

Beaver (*Castor canadensis*) drive a natural disturbance regime with potentially large effects on reciprocal habitat fluxes. Beaver activity increases catchment heterogeneity (Johnston & Naiman, 1990) by altering channel geomorphology (Butler & Malanson, 2005) and hydrology (Naiman, Melillo & Hobbie, 1986). These lead to changes in sediment characteristics and the processing of organic matter from upstream sources (Rosell *et al.*, 2005), which in turn can enhance algal production (Coleman & Dahm, 1990) and aquatic invertebrate abundances (McDowell & Naiman, 1986). Beaver impoundment of water creates a transition from lotic to lentic macroinvertebrate assemblages (Sprules, 1941; McDowell & Naiman, 1986; Harthun, 1999; Margolis, Raesly & Shumway, 2001), while invertebrate assemblages associated with the dam structure itself can be typical of a more free-flowing environment (Clifford, Wiley & Casey, 1993). Beaver also modify riparian vegetation

structure, composition and dynamics (Huntly, 1995; McKinstry, Caffrey & Anderson, 2001; Wright, Jones & Flecker, 2002). These changes have numerous effects on the broader terrestrial ecosystem (see Rosell *et al.*, 2005). For example, beaver shape the distribution of multiple bird species through the provision of high levels of invertebrate production (McKinstry *et al.*, 2001) and habitat creation (Carr, 1940).

Despite thorough documentation of biological and physical changes that occur in catchments influenced by beavers, there is little information on how beaver-driven alteration of aquatic invertebrate community composition and emergence densities might affect aquatic subsidies to terrestrial environments. Based on the idea that increases in *in situ* macroinvertebrate biomass can correspond to increased emergent adult biomass (Davis, Rosemond & Small, 2011), an increase in aquatic emergence from beaver ponds can be expected, as well as an increase in the spatial extent of influence by aquatic-derived carbon at these sites. Examining the magnitude of aquatic subsidies to terrestrial landscapes across lateral dispersal distances (i.e. spatial extent) in beaver-influenced streams can improve understanding of the ecological influence of beaver modifications on catchment processes.

The goal of this study was to determine whether beaver activity influenced the magnitude and spatial extent of aquatic-derived carbon fluxes into terrestrial food webs. We assessed whether changes in emergence densities of aquatic invertebrate taxa at sites with beaver impoundments were reflected in the terrestrial food web by evaluating the abundance of, and aquatic-derived carbon flow to, two terrestrial consumer taxa: wolf spiders (Lycosidae) and deer mice (*Peromyscus maniculatus*). We addressed the following questions by comparing non-beaver and beaver-influenced sites. (i) Do beaver-influenced sites have higher abundances and emergence of aquatic invertebrate taxa, and, if so, are spider and deer mouse abundances higher at beaver-influenced sites? (ii) Do spiders and deer mice contain more aquatic-derived carbon at beaver-influenced sites than at non-beaver sites? (iii) Is there evidence for greater aquatic-derived carbon at distances further from the stream edge at sites with beaver than at sites without beaver?

Methods

Study system

We studied three beaver (B) sites and three non-beaver (NB) reference sites, in the Ruby River and Big Hole

catchments of the Beaverhead-Deerlodge National Forest of Montana, U.S.A. (Fig. 1a; see Table S1 in Supporting Information). One beaver site with an upstream drainage area of 80 km² was located in the upper Ruby River (elevation = 2124 m), and two beaver sites with upstream drainage areas of 13 km² (elevation = 2158 m) and 17 km² (elevation = 2090 m) were located on Seymour Creek (Fig. 1a). All beaver sites comprised a single beaver dam impounding a discrete pond with no lateral areas of standing water. We chose non-beaver, reference sites that had no current discernible signs of beaver activity in the upper Ruby River (elevation = 2072 m; upstream drainage area = 102 km²), Coal Creek (elevation = 2172 m; upstream drainage area = 30 km²) and Twelvemile Creek (elevation = 1955 m; upstream drainage area = 17 km²; Fig. 1a). We measured the wetted width (m) and middle depths of ponds/streams and deployed two iButton digital temperature loggers (model-DS1920: Maxim Integrated Products, Dallas semi-conductor, Sunnyvale, CA, USA) in the channel
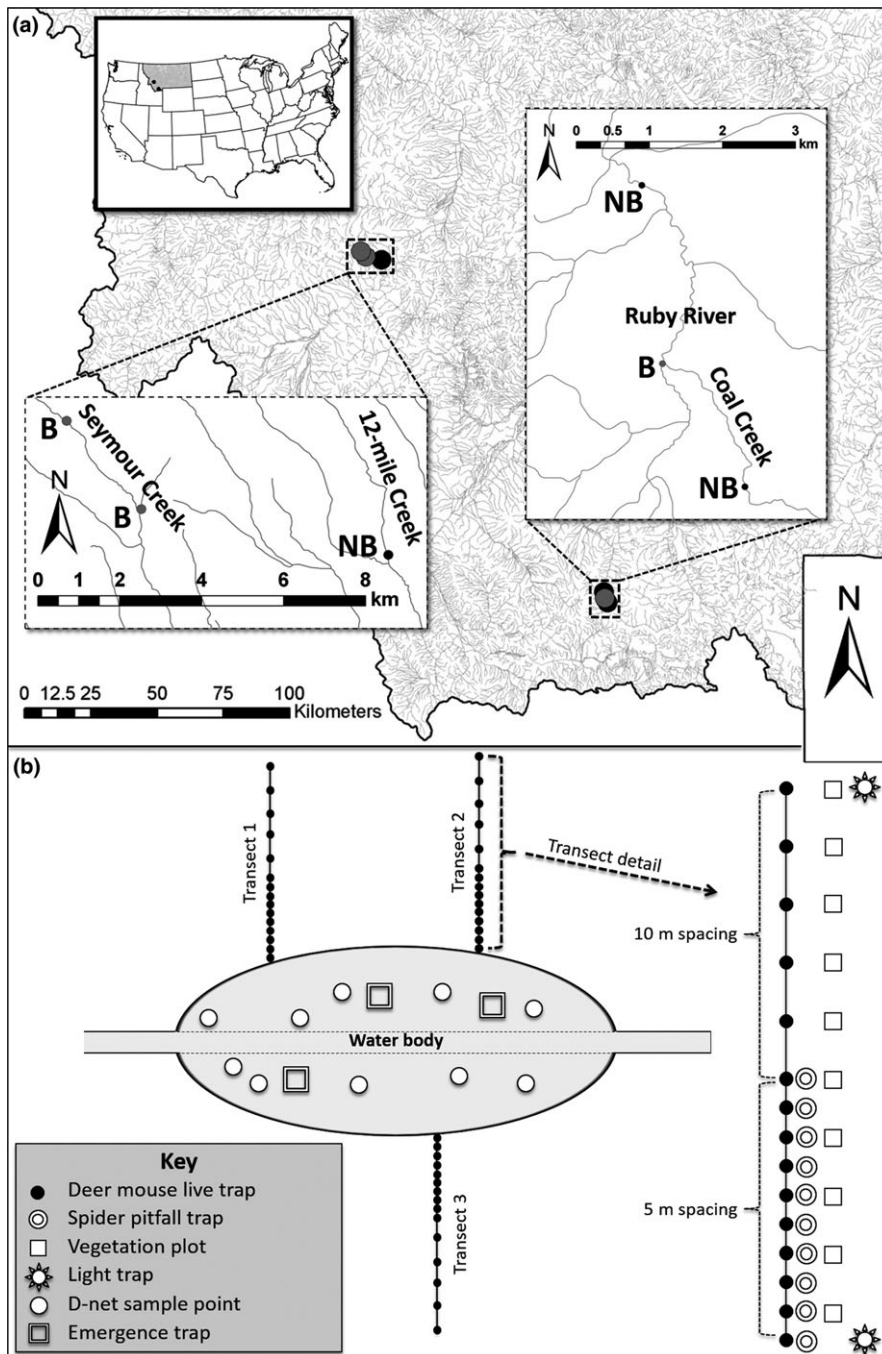

Fig. 1 (a) Map of western Montana showing locations of beaver (B) and non-beaver (NB) study sites. (b) The sampling design and trapping placement used at each beaver and non-beaver site.

thalweg/mid-beaver pond at each study site. Loggers were shielded from direct solar radiation and set to record water temperature (0.5 °C precision; every 30 min) from 1 July 2005 to 31 August 2005 (Table S1). Riparian vegetation structure was similar at all study sites and dominated by willow (*Salix* spp.) with diverse grass/forb communities.

Sites were greater than 2-km apart to ensure independence given home range size and dispersal behaviours of the taxa central to this study: aquatic invertebrates (see Bilton, Freeland & Okamura, 2001), Lycosidae spiders (Kuenzler, 1958) and deer mice (Abramson *et al.*, 2006). The two terrestrial consumer taxa were chosen based on their diets, relatively limited home ranges and availability for capture. Wolf spiders (family Lycosidae) are ground-dwelling arthropod generalists (Nyffeler, 1999; Toft & Wise, 1999) and provide an abundant and easily captured taxon that can be important terrestrial consumers of aquatic macroinvertebrate prey (e.g. Paetzold, Schubert & Tockner, 2005). Similarly, omnivorous deer mice were targeted due to their high reproductive potential and prominent role in terrestrial food webs, making them potentially important vectors for inland aquatic nutrient transport (Stapp & Polis, 2003).

To ensure that non-beaver sites were not strongly physically influenced by beaver impoundments, we monitored hydrological and temperature characteristics using arrays of piezometers and temperature loggers to ensure that sites located within the same drainage area were not influencing each other. Water levels in riparian piezometers in all non-beaver sites followed stream base flows and typical seasonal temperatures; beaver sites had elevated water levels and temperatures. All study sites had similar gradient and salmonid populations [Ruby River and Coal Creek: westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and Arctic grayling (*Thymallus arcticus*); Seymour Creek and Twelvemile Creek: westslope cutthroat trout and brook trout (*Salvelinus fontinalis*)].

Field methods

Vegetation sampling. To establish baseline carbon and nitrogen isotopic signatures of aquatic and terrestrial primary producers at each site, we sampled vegetation at Coal Creek and Ruby River sites from 6-8 July 2005. Seymour Creek and Twelvemile Creek were sampled during the period 2–6 August 2005. We collected aquatic mosses, macrophytes and filamentous algae by hand from five random locations along the waterbody margins (within 1 m of the bank) as well as at five random

locations in the channel. We collected terrestrial vegetation at each site along three transects extending away from the waterbody. We placed 1 m² quadrats every 10 m along each transect up to 100 m (Fig. 1b). Vegetation in quadrats was identified to the genus level (Parish, Coupe & Lloyd, 1996), and representative samples of each were collected.

Capture of aquatic and terrestrial consumers. Beaver and non-beaver sites located within the same drainage systems (i.e. Ruby River and Big Hole River catchments) were paired and sampled concurrently, with aquatic invertebrate surveys occurring during the periods of 6–8 July 2005 in Coal Creek and Ruby River and 5–7 August 2005 in Seymour Creek and 4–6 August 2005 in Twelvemile Creek. We used three sampling techniques (D-net, light trap, emergence trap) at each site to estimate aquatic invertebrate abundances, but only used macroinvertebrates collected in D-net surveys for tissue material in our stable-isotope analysis. Specifically, aquatic macroinvertebrates were sampled using the following protocols. (i) Kick-net sampling (D-net, mesh size: 500 μm) at non-beaver sites and D-net (mesh size: 500 μm) sweeps at beaver sites were used to collect macroinvertebrates in 1 day from 10 random 1 m² points (Fig. 1b); (ii) terrestrial light traps (CDC Miniature Light Trap Model 512) were situated at 0 m and 100 m on each of the three transects at each site (i.e. six total/site; Fig. 1b) and deployed for 3 days; (3) to ensure light traps characterised consistent patterns of aquatic invertebrate emergence, we also deployed three 20 cm × 20 cm floating emergence traps (Fig. 1b) for a 28-day period from 1–29 June 2005 at each site. We used a modified version of Cushman's (1983) emergence trap design to construct bottomless wooden box traps with an effective capture area of 400 cm², provisioned with lateral 0.5 mm stainless steel mesh openings and topped with 0.2 mm clear cellulose acetate film which was lightly coated on the underside with Tree Tanglefoot (Contech, Inc., Victoria, B.C.). Emergence traps were deployed at three random locations of each site for the period 1–29 June 2005. We checked emergence traps weekly over the 28-day capture period, whereby the sticky cellulose acetate film was removed from the trap and replaced with a new piece. The removed acetate film, with the previous weeks' macroinvertebrate captures adhering to it, was submerged in paint thinner to dissolve the acetate, and after 24 h, all insects were collected and preserved in 70% ethanol for identification.

We captured spiders and deer mice at each site for abundance estimation and stable-isotope analysis. Spider

and deer mouse trapping occurred over a 3-day period during the following dates at each site: Coal Creek and Ruby River sites = 6–8 July 2005; Seymour Creek sites = 5–7 August 2005; Twelvemile Creek 4–6 August 2005. We sampled spiders using paired pitfall traps (250 mL cups) deployed at 5-m intervals from 0 to 45 m along each of three stream-to-upland transects at each study location, making a total of 60 traps per site (Fig. 1b). Pitfall traps contained a small amount of water to improve capture efficiency; daily checks allowed us to remove and freeze spiders for later isotope analysis. We captured deer mice using 30 Sherman live-traps arranged along each of the three stream-to-upland transects at each site; with two traps, baited with sunflower seeds, located at each transect point. Trap points were spaced at 5-m intervals along the first 50 m of each transect, then at 10-m intervals up to 100 m from the water's edge (Fig. 1b). Baited traps were set for three consecutive nights but checked and closed each morning to reduce trapping mortality. We collected a 2- to 3-mm piece of tail tissue from each new capture for stable-isotope analysis. All captured individuals were released immediately at their location of capture. Tissue samples were frozen prior to preparation for isotope analysis.

Analyses

Abundance estimation of aquatic and terrestrial organisms. We identified all aquatic invertebrate (Merritt & Cummins, 1996; Voshell, 2002) and spider (Ubick *et al.*, 2005) individuals to the taxonomic level of order. We counted the number of each aquatic invertebrate taxon captured at each of the ten 1 m^2 D-net sample points at each site. Counts of each taxon captured by each of three emergence traps were scaled to the number caught per square metre and expressed as the number caught per day. Invertebrates captured by light traps at 0 and 100 m from the water's edge were expressed in terms of the number of individuals captured per unit trapping effort [CPUE = (# captures/light trap nights) * 100]. Trapping effort was three light trap nights per distance point (0 and 100 m) per transect.

We used CPUE as an index of abundance for spiders within 45 m of the water's edge for each of the three transects. Spider trapping effort was 60 trap nights per transect (based on 20 traps, set for 3 days). We estimated an index of abundance for deer mice within 100 m of the waterbody at each site, using the number of unique captures per unit effort on each transect. To account for a loss of trapping effort through sprung traps, we used a corrected index (CPUE$_{corr}$; Cunningham & Moors,

1996), with half a night subtracted for each sprung trap (whether it had captured an animal or not) based on the assumption that it had been sprung for at least half a night (eqn 1). Total deer mouse trapping effort on each transect was 90 trap nights (based on 30 traps, set for three nights). A single index of deer mouse abundance was calculated for each transect at each site.

$$\text{CPUE}_{\text{corr.}} = \frac{\text{captures}}{\text{trapnights} - \frac{\text{sprungtraps}}{2}} \times 100 \qquad (1)$$

To evaluate how beaver presence influenced total and order-level abundances of aquatic invertebrates, and the CPUE of spiders and mice, we used generalised linear mixed-effects regression models in R 3.0.2 (lmer function, lme4 package; Bates, Maechler & Bolker, 2012) to analyse untransformed data. Models incorporated the categorical variable of beaver presence as a fixed-effect and site as a random effect, which allowed us to use our within-site, abundance measurements (i.e. D-net = 10 measurements/site; emergence trap = 3 measurements/site; light trap 0 m = 3 measurements/site; light trap 100 m = 3 measurements/site; spider pitfall trap = 3 measurements/site, deer mouse = 3 measurements/site) in this analysis to better account for within-site variance (Pinheiro & Bates, 2000; Crawley, 2007). We used likelihood ratio tests to compare the statistical significance of model factors (Pinheiro & Bates, 2000; Bolker *et al.*, 2009). We compared the full model that included the fixed effect (beaver presence) against a reduced model that did not include the fixed effect and determined the fixed effect to be significant if the difference between the likelihood of the two-model comparison was significant ($\alpha = 0.05$) as indicated by a chi-square metric. We considered the full model to be supported if it had the lowest AIC value, a chi-square metric with a *P*-value <0.05, and 95% confidence intervals of fixed-effects parameters that did not overlap zero.

Stable-isotope preparation and analysis. We collected stable-isotope samples from all study sites, but due to cost constraints, we analysed samples from only four sites: two beaver [Ruby River (B) and Seymour Creek (B)] and two non-beaver sites [Ruby River (NB) and Coal Creek (NB)]. In the laboratory, we identified spiders and D-net-captured aquatic invertebrates to the taxonomic level of order, and dried all samples (vegetation, aquatic invertebrates, spiders, deer mice tail tissue) at 50°C for 48 h. We made a composite sample from multiple individuals of the same taxon, collected at the same sampling location, and homogenised the sample using a

96-well bead mill homogenizer (2000 Geno/Grinder, SPEX CertiPrep, NJ, USA). We then measured a minimum of 2–3 mg of powdered vegetation and 1 mg of powdered animal tissue (macroinvertebrates, spiders, deer mouse) into tin capsules (Costech Analytical Technologies, Inc.) for analysis. Three to six replicates of each taxon at each sampling point were prepared and sent to the UC Davis Stable Isotope Facility for analysis of natural abundances of ^{13}C and ^{15}N using a PDZ Europa ANCA-GSL elemental analyser interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd. Cheshire, UK). Stable carbon and nitrogen isotope compositions were expressed as δ values (‰) relative to international standards of PeeDee Belemnite for carbon and atmospheric nitrogen for N. The $\delta^{13}C$ and $\delta^{15}N$ values for vegetation, invertebrates, spiders and deer mice were averaged and associated variances calculated.

We determined the proportion of carbon derived from aquatic sources (henceforth the aquatic-derived carbon value) in spider and deer mice samples, within 45 m and 100 m of the water's edge, respectively, using a two source mass balance mixing model for carbon isotopes (Phillips & Koch, 2002):

$$\delta^{13}C_M = f_X(\delta^{13}C_X + \Delta^{13}C_{tissue-X}) + f_Y(\delta^{13}C_Y + \Delta^{13}C_{tissue-Y});$$
$$1 = f_X + f_Y$$

where X = aquatic vegetation signature; Y = terrestrial vegetation signature; M = mixture of aquatic/terrestrial carbon in the consumer; f = proportion of carbon mass from a food source; $\Delta^{13}C_{tissue-X}$ = trophic fractionation (assumed negligible fractionation with trophic transfer of carbon in food webs; Peterson & Fry, 1987).

To assess the relative importance of beaver presence and the distance from the waterbody on spider and deer mouse aquatic carbon values, we developed a suite of generalised linear mixed-effects regression models in R 3.0.2 (lmer function, lme4 package; Bates *et al.*, 2012) to analyse our untransformed proportion data (as suggested in Warton & Hui, 2011). Model fixed-effects included distance from the water's edge in metres and the presence of beaver as a categorical variable. Site was included as the random effect to account for the spatial pseudoreplication inherent in our nested study design (Pinheiro & Bates, 2000; Crawley, 2007). Similarly, we used likelihood ratio tests to compare the statistical significance of model factors (Pinheiro & Bates, 2000; Bolker *et al.*, 2009). We used the same model evaluation criteria as described above to compare full models (that included the fixed effects of interest) against reduced models (without the fixed effect of interest).

To examine the magnitude of aquatic-derived spider and deer mouse carbon values with increasing distance from the water's edge and compare it with existing studies, we calculated the aquatic signal as the aquatic-derived carbon value of a given sample, divided by the maximum aquatic-derived carbon value recorded at that site (see Muehlbauer *et al.*, 2014). We plotted the aquatic signal of spider and deer mouse samples within distances of 45 m and 100 m, respectively, for each of the four sites and fitted linear regression trend lines in R 3.0.2 to each data set. We then used the regression equation to identify the distance at which the aquatic signal of spiders and deer mice was 50% of the maximum value, thereby providing an indication of the spatial extent of the aquatic subsidy (see Muehlbauer *et al.*, 2014).

Results

Abundance estimates of aquatic and terrestrial organisms

Total abundances of macroinvertebrates were significantly larger at beaver versus non-beaver sites for all sampling methods, with D-net sampling yielding 82% more macroinvertebrates [$\chi^2(1) = 14.07$, $P < 0.001$; Table S2], emergence traps yielding 235% more [$\chi^2(1) = 25.14$, $P < 0.001$; Table S3], and light traps yielding 200% and 105% higher total abundances at 0 m [$\chi^2(1) = 17.01$, $P < 0.001$; Table S4] and 100 m [$\chi^2(1) = 7.09$, $P = 0.008$; Table S4] from the waterbodies, respectively. Ephemeroptera, Plecoptera, Trichoptera, Diptera and Odonata were the dominant aquatic macroinvertebrates, representing over 95% of the total aquatic insect abundance found at each site.

Of the five taxa captured in their immature form using D-net sampling, all exhibited significant differences in abundance between beaver and non-beaver sites (Fig. 2a; Table S2). Ephemeroptera comprised 47% of the macroinvertebrate community at non-beaver sites, with a CPUE five times higher than at beaver sites [$\chi^2(1) = 13.55$, $P < 0.001$; Table S2] where they comprised only 5% of the community. The CPUE of Plecoptera was significantly higher at non-beaver sites [$\chi^2(1) = 10.28$, $P = 0.001$; Table S2], where they comprised 17% of the community compared with 4% at beaver sites. In contrast, we found three-fold higher abundances of larval Diptera [$\chi^2(1) = 22.48$, $P < 0.001$; Table S2] and seven-fold higher abundances of larval Trichoptera [$\chi^2(1) = 13.86$, $P < 0.001$; Table S2] at beaver sites relative to non-beaver sites. Diptera comprised 43% of the macroinvertebrate community at beaver sites compared
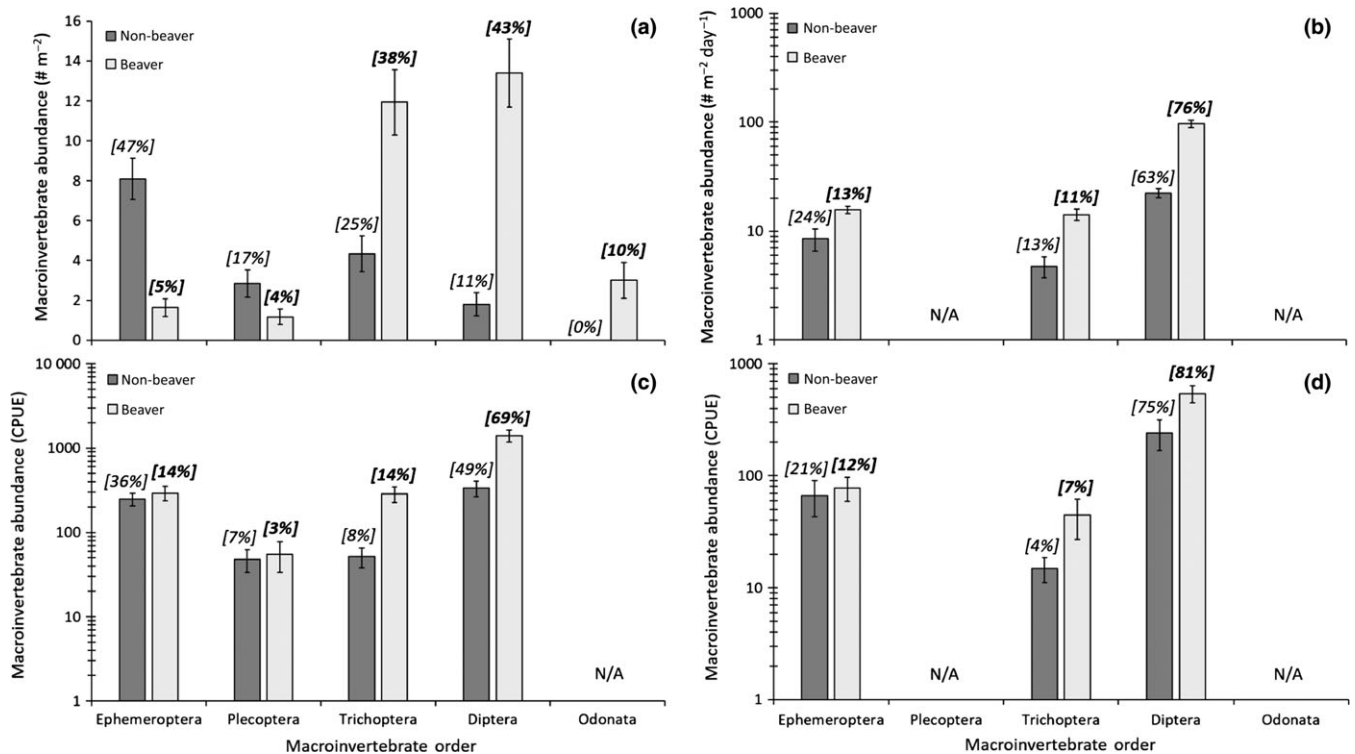
Fig. 2 Abundances (means ± 1 SE) of aquatic macroinvertebrates at beaver and non-beaver sites, estimated using various sampling methods: (a) D-net kick sampling, (b) emergence traps, (c) light trap located at 0 m from water's edge, (d) light trap at 100 m from the water's edge. CPUE = Catch Per Unit Effort. Percent values within squared brackets indicate percent composition of each taxonomic group at non-beaver (italics) and beaver sites (bold italics). N/A indicates where taxa were not detected at a given site. Note log scale except for panel (a).

with 11% at non-beaver sites. Similarly, Trichoptera comprised 38% of the macroinvertebrate community at beaver ponds versus 25% at non-beaver. Odonata comprised 10% of individuals captured at beaver sites, but were entirely absent from the non-beaver sites.

We found that overall daily emergence rates from emergence traps in beaver sites were over twice those at non-beaver sites (Fig. 2b; Table S3). Although the percent community composition of Ephemeroptera was lower at beaver sites (13%) than at non-beaver sites (24%), we found that approximately twice as many emerged per day at beaver sites [$\chi^2(1) = 11.41$, $P < 0.001$; Table S3]. Similarly, Trichoptera at beaver sites comprised 11% of the community and 13% at non-beaver sites, but emergence rates at beaver sites were three times higher than at non-beaver sites [$\chi^2(1) = 11.67$, $P < 0.001$; Table S3]. Diptera contribution to community composition was higher at beaver sites (76%) than at non-beaver sites (63%), and emergence was almost 4.5 times [$\chi^2(1) = 27.71$, $P < 0.001$; Table S3] that at non-beaver sites.

In the case of aerial, adult aquatic invertebrates that were captured in light traps, we found no statistical differences in Ephemeroptera or Plecoptera abundances

between beaver and non-beaver sites (Table S4), although these taxa were twice as numerous in the non-beaver macroinvertebrate fauna (Fig. 2c,d). Diptera were considerably more numerous at beaver sites and made a higher percent contribution to community composition, with numbers immediately adjacent to the beaver pond around four times higher than next to the stream channel at non-beaver sites [$\chi^2(1) = 17.79$, $P < 0.001$; Table S4] and twice as many at 100 m [$\chi^2(1) = 6.96$, $P = 0.008$; Table S4]. Diptera in the light traps could represent a mix of aquatic and terrestrial species, but the increased catches in the light traps are consistent with the increases in aquatic emergence of Diptera. Trichoptera also had higher percent community composition at beaver sites than at non-beaver sites and exhibited large differences in abundance immediately adjacent to the waterbody at beaver sites, with approximately 5.5 times the number captured at non-beaver areas [$\chi^2(1) = 6.93$, $P = 0.008$; Table S4]. While more Trichoptera individuals were captured 100 m from the water's edge at beaver sites (Fig. 2d), these were not statistically different from non-beaver sites [$\chi^2(1) = 1.11$, $P = 0.29$; Table S4].

Spider and deer mouse abundances were positively related to beaver presence {spider: [$\chi^2(1) = 7.48$, $P = 0.006$]; deer mouse: [$\chi^2(1) = 9.09$, $P = 0.002$]}, with approximately 60% and 75% higher abundances, respectively, at beaver sites (Fig. 3; Table S5).

Stable-isotope analysis

Macrophytes and algae constituted the aquatic resource base, and we assumed that their $\delta^{13}C$ values represented 100% autochthonous organic carbon. Aquatic primary producers at each site had higher $\delta^{13}C$ than terrestrial primary producers (Fig. 4), which were predominantly *Salix* spp., Poaceae spp., *Artemisia tridentata*, *Lupinus* spp., *Achillea millefolium*, *Fragaria virginiana* and *Potentilla* spp.

We examined stable-isotope signatures of Ephemeroptera, Plecoptera, Trichoptera, Diptera and Odonata captured in our aquatic D-net surveys. Overall, $\delta^{13}C$ values of Ephemeroptera reflected the values of aquatic primary producers, while Plecoptera and Trichoptera had strong terrestrial-derived $\delta^{13}C$ values. Aquatic Diptera captured in D-net surveys had $\delta^{13}C$ values intermediate between aquatic and terrestrial basal resource values. However, dipterans at beaver sites had $\delta^{13}C$ values approximately 4‰ higher than at non-beaver sites, implying a larger contribution of aquatic-derived carbon to dipteran production at beaver pond sites. Odonata, which were found only at beaver sites, also exhibited intermediate $\delta^{13}C$ signatures (Fig. 4).

To examine whether spiders and/or mice exhibited higher percent aquatic-derived carbon values at beaver-influenced sites, we analysed spider and deer mouse isotope signatures by distance with each study site and by site type (i.e. beaver and non-beaver sites). We found a statistically significant effect of beaver presence on the aquatic-derived carbon values of both spiders [$\chi^2(1) = 7.72$, $P = 0.005$; Table S6] and deer mice [$\chi^2(1) = 5.00$, $P = 0.02$; Table S7], with around 8% and 9% higher aquatic-derived carbon values, respectively, associated with these taxa at beaver sites (Fig. 5).

We then examined isotope signatures along the lateral transects to determine if there was a higher magnitude of aquatic-derived carbon at greater distances from the stream edge at beaver sites. Contrary to our expectation that every site would demonstrate some decline in the aquatic signal with distance, we found no relationship between aquatic signal and distance from waterbody for spiders at non-beaver sites (Coal NB: $y = 0.0005x + 0.5393$, $P = 0.823$, Ruby NB: $y = -0.0019x + 0.781$, $P = 0.325$; Fig. 6a), with spiders exhibiting similar aquatic signals with distance from the stream banks. However, deer mice did show a negative relationship between aquatic signal and distance at non-beaver sites (Coal NB: $y = -0.0041x + 0.7733$, $R^2 = 0.41$, $P < 0.001$, 50% signature = 66 m; Ruby NB: $y = -0.0034x + 0.7926$, $R^2 = 0.36$, $P = 0.002$, 50% signature = 86 m; Fig. 6c). At beaver sites, we measured a linear decline in the aquatic signal with increasing distance from the waterbody for both spiders (Ruby B: $y = -0.0091x + 0.9193$, $R^2 = 0.57$, $P < 0.001$, 50% signature = 49 m; Seymour B: $y = -0.0097x + 0.8559$, $R^2 = 0.60$, $P < 0.001$, 50% signature = 37 m; Fig. 6b) and deer mice (Ruby B: $y = -0.0033x + 1.0033$, $R^2 = 0.25$, $P = 0.01$, 50% signature = 152 m; Seymour B: $y = -0.0025x + 0.9117$, $R^2 = 0.52$, $P < 0.001$, 50% signature = 165 m; Fig. 6d).

With increased distance from waterbody, we found a significant negative effect on the aquatic-derived carbon values of terrestrial consumers [spiders: $\chi^2(1) = 46.46$, $P < 0.001$, Table S6, Fig. S1a,b; deer mice: $\chi^2(1) = 32.96$, $P < 0.001$, Table S7, Fig. S1c,d], manifested by a 0.2% per metre reduction in aquatic-derived carbon of spiders and a 0.1% per metre decline in deer mice. In addition, there was an interactive effect between beaver presence and distance from waterbody for spiders [$\chi^2(1) = 39.00$, $P < 0.001$], though not for deer mice [$\chi^2(1) = 0.17$, $P = 0.68$].

Discussion

We demonstrated that beaver-mediated disturbance can increase the magnitude of aquatic subsidies by increasing macroinvertebrate emergence rates, resulting in a higher aquatic signal in terrestrial consumers. Our key
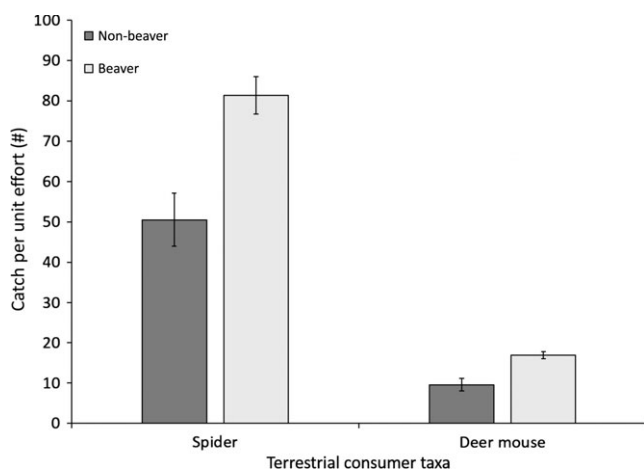

Fig. 3 Catch per Unit Effort (CPUE, means ± 1 SE) of spiders and deer mice at beaver and non-beaver study sites. Deer mouse abundance estimates reflect a Corrected Catch per Unit Effort value (see Field Methods: Analyses section).
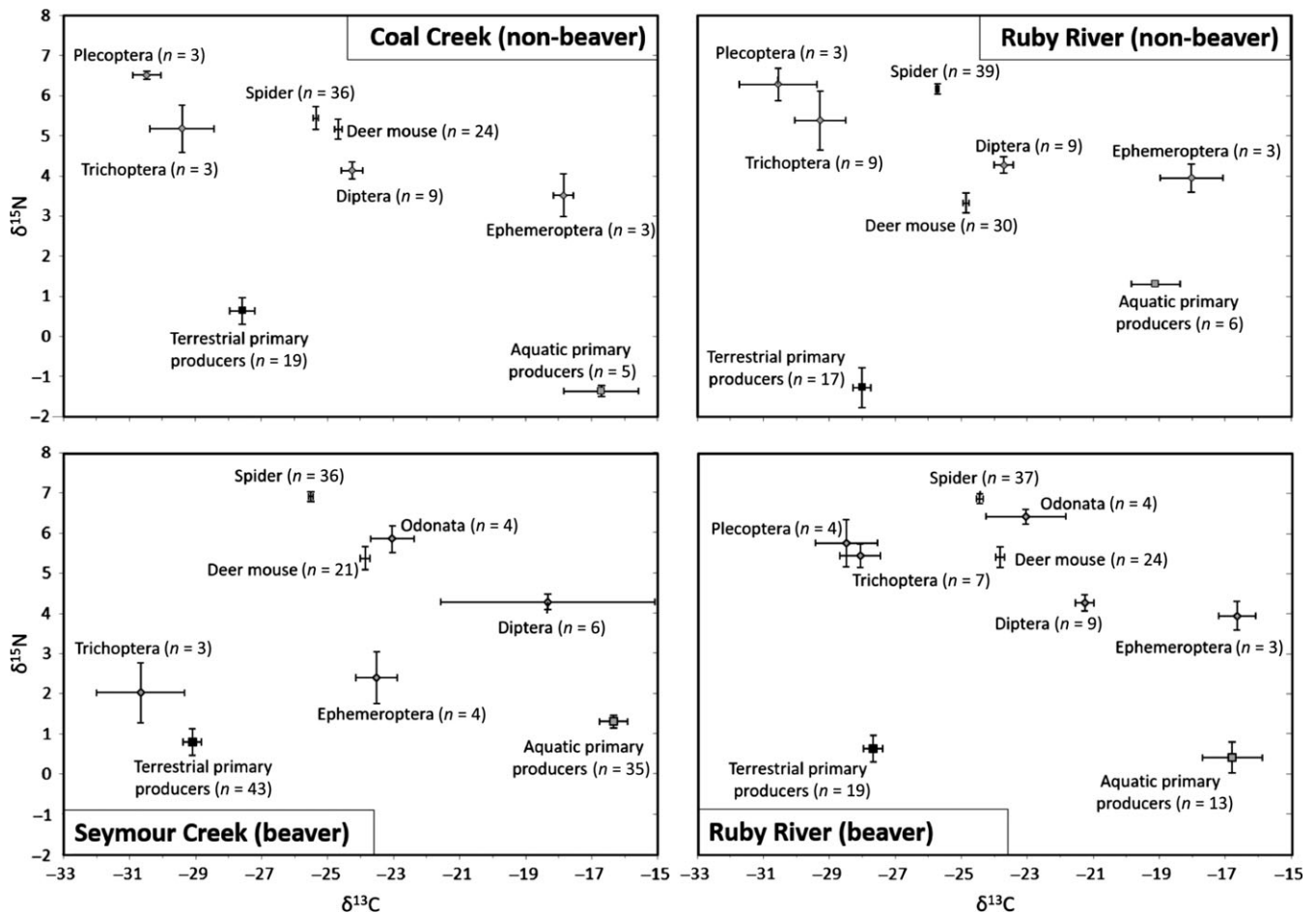
Fig. 4 Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable-isotope signatures (means ± 1 SE, with associated sample sizes for each taxon) of aquatic and terrestrial primary producers, aquatic macroinvertebrates, wolf spiders (Lycosidae) and deer mice for each site where isotopic analysis was conducted.

results show significantly larger aquatic subsidies at beaver sites than at free-flowing stream sites, with beaver-influenced sites having: (i) higher abundances of some aquatic invertebrate taxa; (ii) higher local spider and deer mouse abundances and (iii) higher aquatic-derived carbon values in spiders and deer mice. While other studies have documented effects of beaver activity on other species, our study documents a greater potential influence of aquatic-derived carbon at beaver sites than at non-beaver sites. Enhanced carbon subsidy from beaver-influenced streams to terrestrial upland habitats demonstrates another mechanism through which beaver-modified catchments can enhance local terrestrial consumer populations.

Aquatic and terrestrial consumer abundances

Beaver-influenced sites in our study exhibited more abundant aquatic invertebrate communities that also dif-fered in composition relative to unmodified stream channels. This particular result is supported by a wealth of previous research (e.g. McDowell & Naiman, 1986; Clifford *et al.*, 1993; Harthun, 1999; Margolis *et al.*, 2001; Rolauffs, Hering & Lohse, 2001). However, we also addressed a previously unstudied facet of beaver modi-fication to small streams; specifically how the changes at sites with beaver impoundments also promote higher abundances of emergent aquatic invertebrates (driven by increases in Trichoptera and Diptera) whose relative abundances remained higher into the upland environ-ment, thereby presumably increasing their availability as prey for terrestrial consumers.

Beaver are known to have widespread effects on other catchment biota. Amphibians in beaver systems can exhibit increased occupancy correlated with pond area (Popescu & Gibbs, 2009), enhanced survival and production (Karraker & Gibbs, 2009) and higher juve-nile recruitment (Stevens, Paszkowski & Foote, 2007).
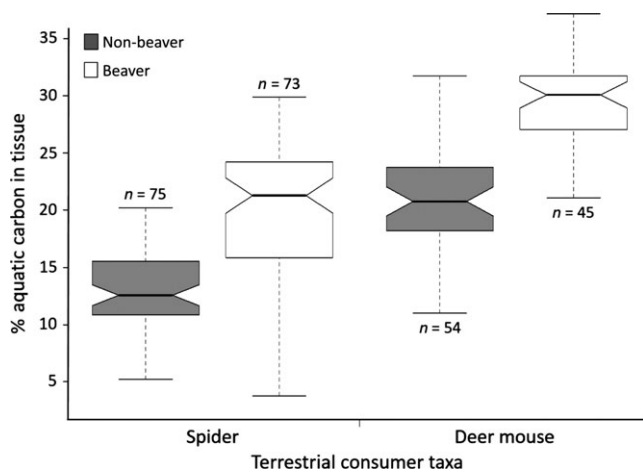
Fig. 5 Notched boxplots showing % aquatic carbon values of all wolf spider and deer mouse isotope samples collected from non-beaver and beaver sites within 45 m (for spiders) and 100 m (for deer mice) from the waterbody. Boxplots for each taxon show the minimum, first quartile, median, third quartile and maximum of the aquatic values found for each site type. The notch indicates the 95% confidence interval around the median, and the sample size is indicated above or below each boxplot.

Small mammals have been documented at 200–300% higher abundances in beaver-influenced willow (*Salix* spp.) shrub land habitats compared with adjacent riparian habitat (Medin & Clary, 1991). Our results of 60% and 75% higher spider and deer mouse abundances, respectively, in the vicinity of beaver ponds illustrate the substantial role that beaver can play as catchment engineers, with tangible impacts on physical and biological processes which lead to altered population dynamics of consumer organisms in terrestrial habitats.

While our results provide evidence for higher aquatic invertebrate prey emergence as a driver of increased terrestrial consumer abundance, we acknowledge that there may be other pathways by which beaver activity could influence terrestrial consumers. For instance, the ability of beaver to alter structural aspects of stream ecosystems raises the possibility of modified nutrient dynamics through increased availability of discrete lateral standing waterbodies (Shaw, 2009) and/or direct consumption of aquatic emergent vegetation by terrestrial consumers (Johnston & Naiman, 1987). Such factors have ecosystem-structuring roles in beaver systems, although we suggest that the increased aquatic invertebrate emergence that we detected was the dominant vector of aquatic-derived carbon transport to the terrestrial system due to the simple structure of beaver ponds chosen for our study.

Stable-isotope analysis

High aquatic invertebrate abundances at beaver ponds are likely to have formed a large carbon reservoir at these sites relative to our non-beaver study sites. Isotopic analysis of aquatic taxa allowed us to examine which components of these beaver-system macroinvertebrates were the most important exporters of aquatic-derived carbon. Dipterans extended farthest into the terrestrial environment, consistent with observations by Muehlbauer *et al.* (2014). Even though dipterans can be aquatic or terrestrial, our high emergence rates indicated this taxon was probably a major vector for the transfer of aquatic-derived carbon to terrestrial consumers. Detritivorous trichopterans at all sites exhibited terrestrial isotopic signatures and are likely to benefit in beaver systems through enhanced accumulation of terrestrial detritus. Therefore, since Trichoptera achieve higher abundances in beaver systems but ultimately derive carbon from primarily terrestrial sources, the subsidies from beaver ponds via aquatic invertebrates was likely to have been underestimated in our study. Even though we found significantly higher aquatic-derived carbon fluxes to terrestrial consumers in beaver-influenced catchments, this is still likely to be an underestimate of the food-web effect. In free-flowing lotic systems, the importance of emerging aquatic invertebrates to riparian predators is well established (Lynch, Bunn & Catterall, 2002) and can contribute up to 90% of the diet of a terrestrial predator (Kato, Iwata & Wada, 2004). Our study demonstrates that beaver engineering of stream sections had measurable effects on the aquatic to terrestrial flux of aquatic-derived carbon subsidies.

We found that deer mice at beaver sites exhibited higher aquatic signatures across distances farther from the stream's edge in beaver versus non-beaver systems, with a 50% stream signature (see Muehlbauer *et al.*, 2014) of deer mouse tissue found at 152 m (Ruby River) and 165 m (Seymour Creek) from beaver ponds compared with 66 m (Coal Creek) and 86 m (Ruby River) at lotic sites. This difference between sites with and without beaver could be due to several factors associated with the increased number of emergent insects, an increase in invertebrate growth rates or shifts in aquatic insect community composition to those that disperse farther. A recent meta-analysis that examined lateral distance penetration of stream-to-land aquatic subsidies indicated that aquatic subsidies decay more gradually with distance from the stream as in-stream productivity increases (Muehlbauer *et al.*, 2014). This could be because of more abundant emergent macroinvertebrates
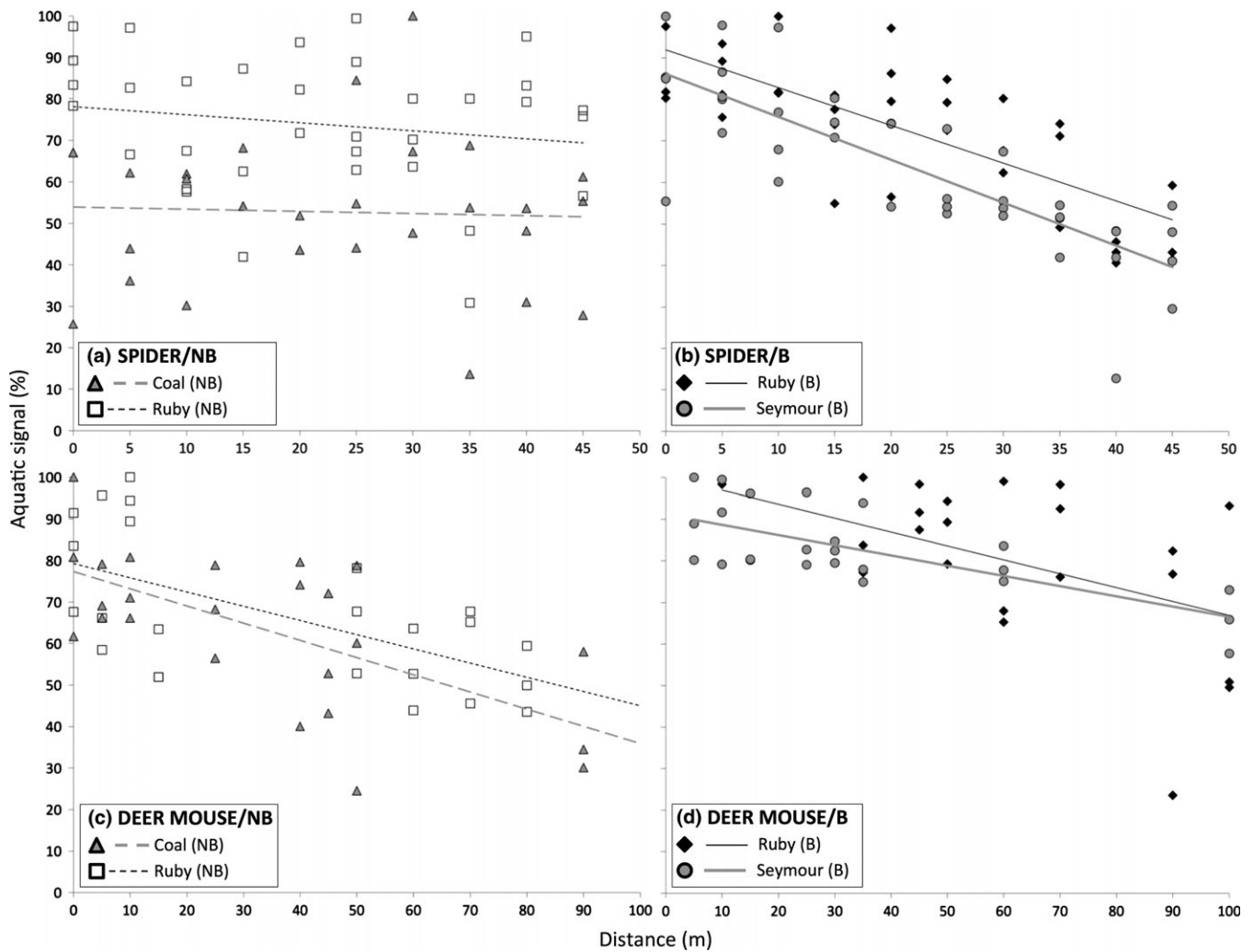
Fig. 6 Scatterplots of the percentage aquatic signal as a function of distance from waterbody at beaver (B) and non-beaver (NB) study sites for (a) wolf spiders and (b) deer mice. Linear regression fit lines are shown for each site. Missing data points at some sampling distances are due to low capture success and/or insufficient sample collected for that taxon at that sampling location.

oversaturating the consumption ability of near-stream predators (Muehlbauer *et al.*, 2014) or because higher productivity allows aquatic invertebrates to grow larger, or shifts their population structure to larger-bodied taxa, making them less vulnerable to near-bank predation (Davis *et al.*, 2011).

We are aware of only one other stable-isotope study of deer mice as terrestrial recipients of aquatic subsidies. In that case, Stapp & Polis (2003) found deer mice on a small island with roosting seabirds (area = 0.1 km²) in the Gulf of California to exhibit high marine-derived carbon signatures as far as 200 m from the shore, whereas those of mice on a larger island without seabirds (area = 1.41 km²) declined sharply at 50 m from the shore. The authors speculated that more readily available marine resources on the smaller

(seabird-influenced) island allowed deer mice to reach high densities and persist in an environment with unpredictable terrestrial productivity. Stapp & Polis (2003) suggested that spatial trophic subsidies might help explain the inverse relationship between small mammal population densities and habitat area (Telleria, Santos & Alcantara, 1991; Adler & Levins, 1994; Nupp & Swihart, 1996). Thus, we posit that more readily available freshwater resources could lead to deer mice attaining higher densities at beaver sites. Even though we did not measure movements of mice in our study, we might expect foraging movements similar to those seen by Stapp & Polis (2003), who found mean movement distances of deer mice to be 23.8 m and 15.9 m on their small and large study islands. This is supported by our isotopic pattern, but is smaller than one previous mea-

sure of the diameter of deer mouse home range at 100 ± 25 m (Abramson *et al.*, 2006) which would entirely encompass our sampling transects.

We observed an overall trend of lower aquatic carbon values at non-beaver sites than at beaver sites in spiders as well, but we did not detect the anticipated decay in aquatic signal with distance from the stream edge at sites without beaver. This unexpected absence of a trend in spider aquatic signal with increased lateral distance at non-beaver sites may be due to one or more limiting factors that were not accounted for in our study design, such as (i) differences in the habitat availability; (ii) variability in spider home range sizes, with home ranges for Lycosidae spiders reported to vary by two orders of magnitude from 0.6 to 41.8 m^2 (Kuenzler, 1958) and/or (iii) different species of spider at the sites. Specifically, Krell *et al.* (2015) highlighted that Lycosidae include both riparian specialist and generalist species whose reliance on aquatic subsidies can differ. We did, however, detect a linear decline in the aquatic signal of spiders at sites with beaver activity, with spiders at the Ruby River and Seymour Creek beaver sites exhibiting 50% stream signatures at 49 m and 37 m from the pond edge, respectively. Our average aquatic carbon values (ranging from 11% to 26%) were lower than most other reported Lycosidae aquatic nutrient values of 55% (Collier, Bury & Gibbs, 2002), 20% (Sanzone *et al.*, 2003) and 43% (Briers *et al.*, 2005) immediately adjacent to a stream. However, our values of aquatic carbon (12–23%) at 20 m from the stream channel were higher than other studies of <1% (Briers *et al.* (2005) and 3% aquatic-derived nitrogen (Sanzone *et al.*, 2003). Thus, while aquatic nutrient values found in our study were lower than have been reported by other studies of spiders adjacent to the channel, the magnitude of aquatic-derived carbon was higher at 20–25 m than previously reported for Lycosidae.

In conclusion, incorporating cross-habitat nutrient and organic matter fluxes into the field of food-web ecology and recognising the modifying role of disturbance presents a more complete picture of how natural communities operate. Viewing food webs in a broader scope is already elucidating how spatially discrete populations can receive subsidies from distant sources. Factoring into this, the influence of species such as beaver, that are capable of altering structural aspects of stream habitats, provides insight into an important aspect of heterogeneity in cross-habitat subsidies. Through the creation and maintenance of impoundments, beaver may play a pivotal role in structuring wetland ecosystems (see Hood & Bayley, 2008). Therefore, understanding the effects of natural disturbance regimes, such as beaver modification, will be critical to efforts to manage and, where appropriate, restore natural catchment processes.

Acknowledgments

References

Abramson G., Giuggioli L., Kenkre V.M., Dragoo J.W., Parmenter R.R., Parmenterm C. et al. (2006) Diffusion and home range parameters for rodents: *Peromyscus maniculatus* in New Mexico. *Ecological Complexity*, **3**, 64–70.

Adler G.H. & Levins R. (1994) The island syndrome in rodent populations. *The Quarterly Review of Biology*, **69**, 473–490.

Barrett K., Anderson W.B., Wait D.A., Grismer L.L., Polis G.A. & Rose M.D. (2005) Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos*, **109**, 145–153.

Bates D., Maechler M. & Bolker B. (2012) *lme4: Linear mixed-effects models using S4 classes (R package version 0.999375-39)*. http://lme4.r-forge.r-project.org/.

Baxter C.V., Fausch K.D. & Carl Saunders W. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, **50**, 201–220.

Baxter C.V., Fausch K.D., Murakami M. & Chapman P.L. (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, **85**, 2656–2663.

Bilton D.T., Freeland J.R. & Okamura B. (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, **32**, 159–181.

Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. et al. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

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

Burdon F.J. & Harding J.S. (2008) The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshwater Biology*, **53**, 330–346.

Butler D.R. & Malanson G.P. (2005) The geomorphic influences of beaver dams and failures of beaver dams. *Geomorphology*, **71**, 48–60.

Carr W.H. (1940) Beaver and birds. *Bird Lore*, **42**, 141–146.

Clifford H.F., Wiley G.M. & Casey R.J. (1993) Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology*, **71**, 1439–1447.

Coleman R.L. & Dahm C.N. (1990) Stream geomorphology: effects on periphyton standing crop and primary production. *Journal of the North American Benthological Society*, **9**, 293–302.

Collier K.J., Bury S. & Gibbs M. (2002) A stable isotope study of linkages between stream and terrestrial food webs through spider predation. *Freshwater Biology*, **47**, 1651–1659.

Collins S.F. & Baxter C.V. (2014) Heterogeneity of riparian habitats mediates responses of terrestrial arthropods to a subsidy of Pacific salmon carcasses. *Ecosphere*, **5**, 1–14.

Crawley M.J. (2007) *The R Book*. John Wiley & Sons Ltd, Chichester.

Cunningham D.M. & Moors P.J. (1996) *Guide to the Identification and Collection of New Zealand Rodents*. Department of Conservation, Wellington.

Cushman R.M. (1983) An inexpensive, floating, insect-emergence trap. *Bulletin of Environmental Contamination and Toxicology*, **31**, 547.

Darimont C.T., Paquet P.C. & Reimchen T.E. (2009) Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology*, **78**, 126–133.

Davis J.M., Rosemond A.D. & Small G.E. (2011) Increasing donor ecosystem productivity decreases terrestrial consumer reliance on a stream resource subsidy. *Oecologia*, **167**, 821–834.

England L.E. & Rosemond A.D. (2004) Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. *Freshwater Biology*, **49**, 721–734.

Greenwood M.J. & McIntosh A.R. (2008) Flooding impacts on responses of a riparian consumer to cross-ecosystem subsidies. *Ecology*, **89**, 1489–1496.

Harthun M. (1999) The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) of brooks in Hesse (Germany). *Limnologica*, **29**, 449–464.

Hood G.A. & Bayley S.E. (2008) Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, **141**, 556–567.

Huntly N. (1995) How important are consumer species to ecosystem functioning? In: *Linking Species and Ecosystems* (Eds C.G. Jones & J.H. Lawton), pp. 72–83. Chapman & Hall, New York.

Johnston C.A. & Naiman R.J. (1987) Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology*, **1**, 47–57.

Johnston C.A. & Naiman R.J. (1990) Aquatic patch creation in relation to beaver population trends. *Ecology*, **71**, 1617–1621.

Karraker N.E. & Gibbs J.P. (2009) Amphibian production in forested landscapes in relation to wetland hydroperiod: a case study of vernal pools and beaver ponds. *Biological Conservation*, **142**, 2293–2302.

Kato C., Iwata T. & Wada E. (2004) Prey use by web-building spiders: stable isotope analyses of trophic flow at a forest-stream ecotone. *Ecological Research*, **19**, 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 - Ecology and Management of Inland Waters*, **51**, 1–7.

Kuenzler E.J. (1958) Niche relations of three species of Lycosid spiders. *Ecology*, **39**, 494–500.

Lynch R.J., Bunn S.E. & Catterall C.P. (2002) Adult aquatic insects: potential contributors to riparian food webs in Australia's wet-dry tropics. *Austral Ecology*, **27**, 515–526.

Malison R.L. & Baxter C.V. (2010) The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 570–579.

Margolis B.E., Raesly R.L. & Shumway D.L. (2001) The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands*, **21**, 554–563.

McDowell D.M. & Naiman R.J. (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, **68**, 481–489.

McKinstry M.C., Caffrey P. & Anderson S.H. (2001) The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association*, **37**, 1571–1577.

Medin D.E. & Clary W.P. (1991) *Small mammals of a beaver pond ecosystem and adjacent riparian habitat in Idaho*. Research Paper INT-445. USDA Forest Service, Intermountain Research Station, Ogden.

(Merritt R.W. & Cummins K.W. eds). (1996) *An Introduction to the Aquatic Insects of North America*, Third Edit. Kendall/Hunt Publishing Company, Dubuque.

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**, 44–55.

Naiman R.J., Melillo J.M. & Hobbie J.E. (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, **67**, 1254–1269.

Nupp T.E. & Swihart R.K. (1996) Effect of forest patch area on population attributes of white-footed mice (*Peromyscus leucopus*) in fragmented landscapes. *Canadian Journal of Zoology*, **74**, 467–472.

Nyffeler M. (1999) Prey selection of spiders in the field. *Journal of Arachnology*, **27**, 317–324.

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

Parish R., Coupe R. & Lloyd D. (1996) *Plants of the Southern Interior British Columbia and the Inland Northwest*. Lone Pine Publishing, Vancouver.

Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.

Phillips D.L. & Koch P.L. (2002) Incorporating concentration dependence in stable isotope mixing models. *Oecologia*, **130**, 114–125.

Pinheiro J.C. & Bates D.M. (2000) *Mixed-Effects Models in S and S-Plus*. Springer-Verlag, New York.

Popescu V.D. & Gibbs J.P. (2009) Interactions between climate, beaver activity, and pond occupancy by the cold-adapted mink frog in New York State, USA. *Biological Conservation*, **142**, 2059–2068.

Reiners W.A. & Driese K.L. (2001) The propagation of ecological influences through heterogeneous environmental space. *BioScience*, **51**, 939.

Richardson J.S., Zhang Y. & Marczak L.B. (2010) Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications*, **26**, 55–66.

Rolauffs P., Hering D. & Lohse S. (2001) Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia*, **459**, 201–212.

Rosell F., Bozser O., Collen P. & Parker H. (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, **35**, 248–276.

Sanzone D.M., Meyer J.L., Marti E., Gardiner E.P., Tank J.L. & Grimm N.B. (2003) Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia*, **134**, 238–250.

Saunders W.C. & Fausch K.D. (2007) Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. *Transactions of the American Fisheries Society*, **136**, 1216–1230.

Shaw E.L. (2009) *Lateral exchange of water and nitrogen along a beaver-dammed stream draining a Rocky Mountain valley*. M.S. Thesis, Department of Geography and Planning, University of Saskatchewan.

Sprules W.M. (1941) The effect of a beaver dam on the insect fauna of a trout stream. *Transactions of the American Fisheries Society*, **70**, 236–248.

Stapp P. & Polis G.A. (2003) Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia*, **134**, 496–504.

Stevens C.E., Paszkowski C.A. & Foote A.L. (2007) Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. *Biological Conservation*, **134**, 1–13.

Telleria J.L., Santos T. & Alcantara M. (1991) Abundance and food-searching intensity of wood mice (*Apodemus sylvaticus*) in fragmented forests. *Journal of Mammalogy*, **72**, 183–187.

Toft S. & Wise D.H. (1999) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different qualities. *Oecologia*, **119**, 191–197.

(Ubick D., Paquin P., Cushing P.E. & Roth V. eds). (2005) *Spiders of North America: An Identification Manual*. American Arachnological Society, Keene, NH.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Science*, **37**, 130–137.

Voshell J.R. (2002) *A Guide to Common Freshwater Invertebrates of North America*. The McDonald & Woodward Publishing Company, Blacksburg.

Warton D.I. & Hui K.K.C. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, **92**, 3–10.

Wipfli M.S., Hudson J.P., Caouette J.P. & Chaloner D.T. (2003) Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society*, **132**, 371–381.

Wright J.P., Jones C.G. & Flecker A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Scatterplots showing mean (±SE) aquatic carbon values with distance from waterbody of spiders at (a) non-beaver-NB sites and (b) beaver-B sites; and deer mice at (c) non-beaver-NB sites and (d) beaver-B sites.

Table S1. Habitat characteristics and locations of study sites.

Table S2. Fixed-effects estimates from mixed-effects models that examined the presence of beaver (beaver) on the catch per unit effort (CPUE) of aquatic invertebrate taxa captured using D-net sampling.

Table S3. Fixed-effects estimates from mixed-effects models that examined the presence of beaver (beaver) on the catch per unit effort (CPUE) of aquatic invertebrate taxa captured using emergence traps.

Table S4. Fixed-effects estimates from mixed-effects models that examined the presence of beaver (beaver) on the catch per unit effort (CPUE) of aquatic invertebrate taxa captured using light traps positioned at 0 m and 100 m from waterbody.

Table S5. Estimates from mixed-effects models that examined the impact of beaver presence (fixed effect) on spider and deer mouse abundances.

Table S6. Fixed-effects estimates from mixed-effects models that examined the presence of beaver (beaver) and the lateral distance from water (distance) on the percent aquatic-derived carbon value of spiders (%C_S).

Table S7. Fixed-effects estimates from mixed-effects models that examined the effects of the presence of beaver (beaver) and the lateral distance from water (distance) on the percent aquatic-derived carbon value of deer mice (%C_M).

(Manuscript accepted 5 January 2016)