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Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage

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SUMMARY

1. Aquatic resource fluxes from streams can provide significant subsidies for riparian consumers. Because aquatic resource fluxes can be highly variable in space and time, the subsidy efficiency (i.e. transfer to the recipient food web) is controlled by the short-term aggregative response of riparian consumers.
2. Field manipulations of stream-derived invertebrate prey subsidies were used to examine specific aggregative responses of ground-dwelling arthropods to riverine subsidy pulses in a braided-river (Tagliamento River, NE Italy). Subsidy manipulation comprised short-term reductions of natural stream-derived subsidies and increased subsidies of stream-derived invertebrate prey during four seasons.
3. We hypothesised that specific aggregative responses of riparian arthropods depend on their specialisation on aquatic insects which was inferred from stable isotope analysis. Natural riverine subsidy sources including aquatic insect emergence and surface-drifting organisms were quantified.
4. Arthropods responded significantly with a reduction in abundance by 51%, at reduced subsidies and an increase by 110% at increased subsidies, when averaged over all seasons. Different arthropod taxa responded differently to subsidy manipulations in relation to their specialisation on aquatic subsidies: ground beetles with a diet consisting predominantly of aquatic insects responded only to subsidy reductions, indicating that their local abundance was not limited by natural stream-derived subsidies; lycosid spiders with a partly aquatic diet showed no significant response; and ants, although relying on a terrestrial diet, responded positively to added stream-derived invertebrate prey, indicating that stranding of surface-drifting terrestrial invertebrates represented an important subsidy pathway.
5. Ground beetles and lycosid spiders were seasonally separated in their use of aquatic subsidies. Results indicate that the life-history characteristics of riparian consumers can control the subsidy efficiency for the recipient community. By the effective uptake of pulsed riverine-derived subsidies, riparian arthropods can enhance the transfer of riverine food sources to the riparian food web.

Keywords: allochthonous input, aquatic–terrestrial linkages, braided river, insect emergence, surface drift

Introduction

The movement of resources across habitats (i.e. spatial subsidies) can alter the dynamics and structure of recipient consumer populations and communities (Polis, Anderson & Holt, 1997; Zhang *et al.*, 2003; Baxter, Fausch & Saunders, 2005). Productivity gradients and the physical features of habitat boundaries are assumed to be primary factors controlling the efficiency (i.e. transfer to the recipient food web) of spatial subsidies (Polis & Hurd, 1996; Cadenasso, Pickett & Weathers, 2004; Witman, Ellis & Anderson,

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2004). However, the complexity of feeding linkages among a diversity of consumers and resources, an important factor in general food web dynamics (Hunter & Price, 1992; Polis & Strong, 1996; Woodward & Hildrew, 2002), has received little attention in subsidy studies (Baxter *et al.*, 2005). Much of the complexity results from the fact that communities comprise various species with different life-history traits (Polis *et al.*, 1996). Further complexity in the dynamics of spatial subsidies might be added by the heterogeneity in allochthonous inputs (Polis *et al.*, 1997). To understand the interrelationship of spatial subsidies and food web complexity, we need to examine how heterogeneity in the allochthonous resources and the composition of the consumer community affect subsidy efficiency (i.e. uptake into the riparian food web).

A major productivity difference between contiguous habitats exists along the banks of braided rivers that flow through unproductive areas of exposed gravel (Tockner *et al.*, 2006). These gravel banks are inhabited by a diverse riparian arthropod fauna including spiders, rove beetles, ground beetles and ants (Hering & Plachter, 1997; Sadler, Bell & Fowles, 2004; Paetzold, Schubert & Tockner, 2005). Large differences in productivity, together with a diverse assemblage of predators, make gravel banks model systems to study taxon-specific responses to spatial subsidies. Recent studies have demonstrated that riparian arthropods can be substantially subsidised by emerging aquatic insect (Collier, Bury & Gibbs, 2002; Paetzold *et al.*, 2005). Another potentially important, yet overlooked, subsidy for riparian arthropods can be derived from stranding of surface-drifting organisms (Hering & Plachter, 1997). Both of these subsidy types can be temporally and spatially very heterogeneous. Mass emergence during a short period of the year is common among aquatic insects (Hershey & Lamberti, 2001; Kato *et al.*, 2003), and peaks in surface-drifting organisms occur during storms through input of terrestrial invertebrates to the stream (Mason & Macdonald, 1982). The availability of these subsidies can vary considerably within a few metres along riverbanks, e.g. floating organic matter accumulates at certain retention structures and algal mats are hotspots of aquatic insect emergence (Power, 1990; Thorp & Delong, 1994). As a consequence, the subsidy efficiency of riverine inputs will largely depend on the short-term aggregative response of riparian consumers. However, little is known regarding the efficiency of riparian arthropod response to pulsed and local subsidies.

To examine whether riparian arthropods respond rapidly to aquatic subsidy pulses, we experimentally reduced and increased aquatic subsidies on small-scale plots along a braided riverbank. To test the hypothesis that taxon-specific life-history traits affect the efficiency of aquatic subsidies, we analysed specific responses of distantly related riparian arthropod taxa (lycosid spiders, ground beetles and ants). We hypothesised that specific aggregative responses of riparian arthropods depend on their specialisation on aquatic insects which was inferred from stable isotope analysis. Isotope data are based on a comprehensive stable isotope study by Paetzold *et al.* (2005). We selected isotope data that are specifically useful in the context of the subsidy manipulation experiment. We conducted the experiment in different seasons because natural subsidies of stream-derived invertebrate prey as well as community composition of riparian arthropods can strongly vary among seasons (Nakano & Murakami, 2001; Paetzold & Tockner, 2005). We collected aquatic insect emergence and surface drift to relate numerical responses of riparian arthropods to the natural availability of aquatic subsidies. Finally, we determined the origin of surface-drifting organisms (aquatic versus terrestrial) as a natural source of stranded organisms to understand the dominant pathway (water to land versus land to water to land) of this subsidy source.

Methods

Study site

The study was conducted along the gravel bank in the braided section of the 7th order Tagliamento River, NE Italy (46°N, 12°30′E). The river is characterised by a flashy flow regime, with highest average discharge in spring (snowmelt runoff) and autumn (rainy period) (detailed description in Tockner *et al.*, 2003).

Exposed alluvial sediments along the channel formed an up to 60-m wide gravel bar bordered by upslope riparian forest. Ground cover was predominantly bare gravel along the stream edge with sand and patches of grass (*Calamagrostis* spp.) in higher, less frequently flooded habitats. The 500-m gravel bank section represented the dominant type of river–

riparian interface along the entire braided-river corridor (Petts *et al.*, 2000). The channel had an average width of 20 m at low water level and comprised pool, run, riffle and backwater sections.

The riparian fauna along the stream edge was dominated by carnivorous ground-dwelling arthropods: lycosid spiders (Lycosidae), ground beetles (Carabidae), rove beetles (Staphylinidae) and ants (Formicidae) (Paetzold *et al.*, 2005).

Subsidy manipulation experiment

To study the aggregative response of riparian arthropods to pulsed aquatic subsidies, we experimentally manipulated subsidies of stream-derived invertebrate prey. The experimental design included the exclusion of aquatic subsidies (aquatic insect emergence and surface-drifting organisms), an elevated supply of aquatic invertebrates, and control plots (ambient inputs of aquatic insect emergence and surface-drifting organisms) in a replicated block design (Fig. 1). Manipulation treatments were randomised within each block. Three experimental blocks were positioned randomly along a 500-m stretch of gravel shore, directly at the stream edge. The different habitat types (pools, riffles and backwaters) included in the river stretch could potentially affect the quantities and qualities of stream-derived subsidies to adjacent riverbanks (Power *et al.*, 2004; Baxter *et al.*, 2005). However, we applied a randomised design to reflect an average subsidy situation of the gravel bank because we know very little how different geomorphic features of the channel and the riverbank affect the type and level of stream-derived subsidies (Baxter *et al.*, 2005). Experiments were conducted in April, June, August and October 2002. Arthropods were counted in individual 1-m^2 plots (07:00–09:00 hours) before and four times (in 2-day intervals) after the start of each experiment. Arthropods were collected from the ground using aspirator and forceps and were captured in containers. After identification and counting in the field, all arthropods were released in the same plot from which they were captured. Dominant taxa were identified to species or genus, less frequent taxa to genus or family. The dominant lycosid spiders, *Pardosa wagleri* (Hahn) and *Arctosa cinerea* (Fabricius), were classified as juveniles and adults. Following each experiment, at least 10 specimens of each dominant taxon, and age class for lycosid spiders, were collected for determination of average dry mass.

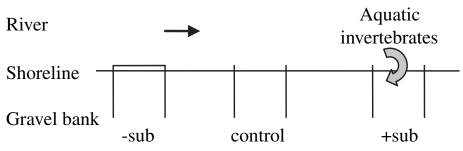

Fig. 1 Design of a subsidy manipulation experimental block involving a reduced-subsidy plot (−sub), a control plot with ambient subsidies of stream-derived invertebrate prey, and an increased-subsidy plot (+) with experimental additions of aquatic invertebrates to simulate stranding. All plots encompassed 1 m^2 gravel bank and were randomised within each of three blocks.

To control the natural input of aquatic invertebrates yet allow normal water level fluctuations, each experimental plot was delineated with a metal frame (1.0 × 1.0 × 0.5 m) covered with 1 mm mesh screening on each of the three sides. One side of the frame faced the water and the upslope side was left open to allow unhindered movements of ground-dwelling riparian arthropods. Inside each frame, we buried a net (mesh-size: 1 mm) about 10 cm deep into the sediment to control for aquatic invertebrates that move ashore or emerge from the interstitial. In control and added-subsidy plots we used the same frame construction except that the front side (facing the water) was open and no bottom screens were installed, to control for possible cage effects, such as lateral movements of riparian arthropods. To increase aquatic subsidies (i.e. imitating stranding of invertebrates), we collected benthic invertebrates from the adjacent river channel using a Kick net (250 μm). Benthic invertebrates were placed abundantly (50–100 mg dry weight) in the additional subsidy plots each evening (18:00–18:30 hours). The biomass of the subsidy addition was approximately 2–10 times the average biomass of aquatic insect emergence on the gravel bank (Paetzold & Tockner, 2005). The added subsidy treatment mimicked aquatic insect larvae that crawl on land prior to emergence and also the natural process of stranding of organisms, as exposed aquatic invertebrates were less mobile on dry gravel and died quickly. We sampled aquatic invertebrates concurrently with the experiments to mimic the seasonal composition of aquatic invertebrates that could potentially strand on the riverbank. Terrestrial invertebrates that accidentally fall into the stream may provide an additional natural source of stranded organisms. However, for practical reasons we only used aquatic invertebrates in the subsidy addition treatment because extreme daily and seasonal variation in the amount of surface drifting organisms impeded a constant supply of fresh invertebrate prey from the surface drift.

Emergence traps

Concurrently with each subsidy experiment, we installed emergence traps along the stream edge to estimate the natural availability of aquatic insect emergence during the experiments. Emergence traps were placed in pairs ($n = 4$ pairs) perpendicular to the stream edge: one trap was placed over shallow water (depth: 1–10 cm, aquatic trap) and the other trap was placed over dry substrate (terrestrial trap) immediately adjacent to the stream edge to collect aquatic insects that crawl on land to emerge. We used pyramidal emergence traps with a square base that covered a surface area of 0.25 m^2. Traps were covered with a white mesh (500 μm) and had a collecting head (ecoTech GmbH, Bonn, Germany) at the top, filled with water and some drops of surfactant. We fixed emergence traps 2–3 cm above the ground or water surface to allow unimpeded movements of aquatic insects larvae under the terrestrial traps prior to emergence and to avoid settlement of aquatic insect larvae on the ground frame of aquatic traps. All traps were fixed at their position with metal bars. Traps were emptied twice per day (07:00–08:00 and 19:00–20:00 hours). We identified emerging insects to family and classified them as 'morphospecies' (Derraik *et al.*, 2002) for estimates of total biomass. We dried (60 °C) and weighed 10 individuals of each 'morphospecies' to estimate average dry weight.

Surface drift

To estimate the origin of surface-drifting organisms as potential food sources for riparian arthropods, we sampled surface drift continuously over 4 days and four nights in June, August and October 2002 concurrently with the subsidy experiments. We collected drift samples in shallow water (depth: 5–10 cm) directly along the steam edge because, there, surface-drifting organisms are most likely to get washed ashore or can get directly consumed from the water surface by riparian arthropods. We used a 500-μm net attached to a 50 × 25 cm frame, which was fixed with metal rods in the stream in such a way that only the upper 2 cm of the water column were sampled. Flow rate through the net was measured with a Pocket MiniAir2 velocitymeter (Schiltknecht AG, Gossau, Switzerland) to calculate the area of water surface filtered through each net. Organisms were hand-picked from drift samples and identified to order or family to establish their origin as aquatic or terrestrial. Composite dry weights were determined for terrestrial arthropods, aquatic insect larvae, and adults of aquatic insects. We calculated the average daily surface drift in 1 m^2 of water surface directly along the steam edge using the average velocity along the water's edge (0.2 m s^{-1}) to provide an estimate of allochthonous prey supply for riparian arthropods.

Sampling for isotope analysis

Arthropod samples for isotope analysis were collected in April, June, August and October 2002 (Paetzold *et al.*, 2005). Common ground-dwelling riparian arthropods were collected from the ground at randomly selected locations within 1 m from the stream edge along the 500-m study stretch. Riparian ground beetles (Carabidae) comprised specimens of *Bembidion* spp. and *Nebria picicornis* (Fabricius). We sampled only specimens of *P. wagleri* for riparian lycosid spiders, and *Manica rubida* (Latreille) for riparian ants.

We inferred possible terrestrial food sources of riparian arthropods indirectly from predaceous ground-dwelling arthropods sampled at distance of more than 50 m from the stream edge (terrestrial arthropods) because we assumed that they integrated isotope signals from a wide variety of terrestrial food sources. To test our assumption that the terrestrial arthropods reflected the isotopic signal of terrestrial prey, we checked for similarity in carbon isotopic signatures with a primary terrestrial consumer on the gravel bar (the grasshopper *Sphingonotus caerulans* (Linnaeus), Caelifera, Acrididae). We sampled predaceous terrestrial arthropods from the ground at randomly selected locations directly adjacent to the riparian forest concurrently with riparian arthropods. To infer potential terrestrial prey for riparian arthropods more specifically, we collected similar terrestrial arthropod taxa further away from the stream edge, including ground beetles [*Cicindela* spp., *Carabus cancellatus* Illiger, *Broscus cephalotes* (Linnaeus), *Bembidion* spp., *Asaphidion flavipes* (Linnaeus), *Calathus* spp., *Lionychus quadrillum* (Duftschmid)], lycosid spiders of the genus *Pardosa* and ants (Myrmicinae and Formicinae) because taxon-specific foraging behaviours mostly determine the potential prey.

We sampled late-instar larvae of the most abundant aquatic insect taxa as potential aquatic food sources for the riparian arthropods, using a 500-μm kick net. Aquatic insect larvae were sampled at 10 randomly selected locations in the river channel and identified to family. The mayflies (Ephemeroptera) consisted of Heptageniidae and Baetidae, the caddisflies (Trichoptera) of Polycentropidae, Hydrospychidae and Rhyacophilidae, the stoneflies (Plecoptera) included Chloroperlidae, and the true flies (Diptera) consisted of Chironomidae and Limoniidae. We assumed a trophic fractionation of 3.4‰ for δ^{15}N (Minagawa & Wada, 1984; Post, 2002).

Aquatic insect samples were frozen shortly after sampling and riparian arthropods were held in containers for at least 1 day for gut clearance. Specimens were identified in the laboratory, rinsed and then freeze-dried. Several individuals (5–10) of each taxon were ground into fine powder to obtain a homogenised composite sample, except for the large ground beetle *N. picicornis* which were analysed individually. Carbon and nitrogen isotopic composition was measured using a ThermoQuest NC 2500 elemental analyser (Carlo Erba Instruments, Milan, Italy) connected via an open split to a Micromass mass spectrometer (Isoprime, GV Instruments, Manchester, U.K.). International standards used for calibration were NBS 19, IAEA-CO-8, IAEA-N-1, IAEA-N-2, and IAEA-NO-3; laboratory standards were EA-NAC1 ($NaHCO_3$), EA-UREA-1, and a coastal sediment. The results are reported in the δ notation:

$$\delta^{13}\mathrm{C}\ (‰) = \left\{{}^{13}\mathrm{C}/{}^{12}\mathrm{C}_{\mathrm{sample}}/{}^{13}\mathrm{C}/{}^{12}\mathrm{C}_{\mathrm{standard}} - 1\right\} \times 1000$$

for carbon and

$$\delta^{15}\mathrm{N}\ (‰) = \left\{{}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{sample}}/{}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{standard}} - 1\right\} \times 1000$$

for nitrogen, and expressed relative to Vienna PeeDee Belemnite (VPDB) and air respectively.

Data analysis

All statistical tests were performed in SYSTAT 10.0 (SPSS, Chicago, IL, U.S.A., 2000) using square-root transformed data for abundance measures and (ln + 1) transformed data for biomass to standardise variances and improve normality. We analysed differences in the numerical response of arthropods using repeated measures ANOVA with site as the blocking factor, and subsidy and season as main effects. We report Huyn–Feldt corrected *P* values that are robust against deviation from the repeated measures ANOVA assumption of compound symmetry (Potvin, Lechowicz & Tardif, 1990; von Ende, 2001). For multiple comparisons, we adjust significance levels to Bonferroni corrections. Unless indicated otherwise, values presented are mean ± standard error of the mean.

Results

Numerical response of riparian arthropods to subsidy manipulation

Subsidy manipulations resulted in significant response in riparian arthropod abundance (Fig. 2). Arthropod abundance significantly increased during the experiments across all seasons at the subsidy addition (+sub, stranding) treatment and significantly decreased at the reduced subsidy (−sub) treatment, indicated by significant time × treatment interactions between −sub and control and between control and +sub treatments (Table 1). Relative average abundance of riparian arthropods decreased by 51% (16.9 individuals m^{-2}) in the reduced subsidy treatment (−sub) and increased by 110% (15.9 individuals m^{-2}) in the added-subsidy treatment (+sub) between the start (day 0) and the end of the experiment (day 8) when averaged over all seasons. In control plots, arthropod abundance decreased by 7% (6.5 individuals m^{-2}). Subsidy addition resulted in the greatest increase in relative abundance in June (165%) and in the lowest increase in April by 52% (Fig. 2). Total biomass of riparian arthropods showed no significant response to the subsidy treatments (Fig. 2, Table 1).

Numerical response by different taxa

Common riparian arthropods responded differently to the subsidy treatments (Table 2). Changes in the abundance of ground beetles during the experiments were significantly different between −sub and control across all seasons. The average abundance of ground

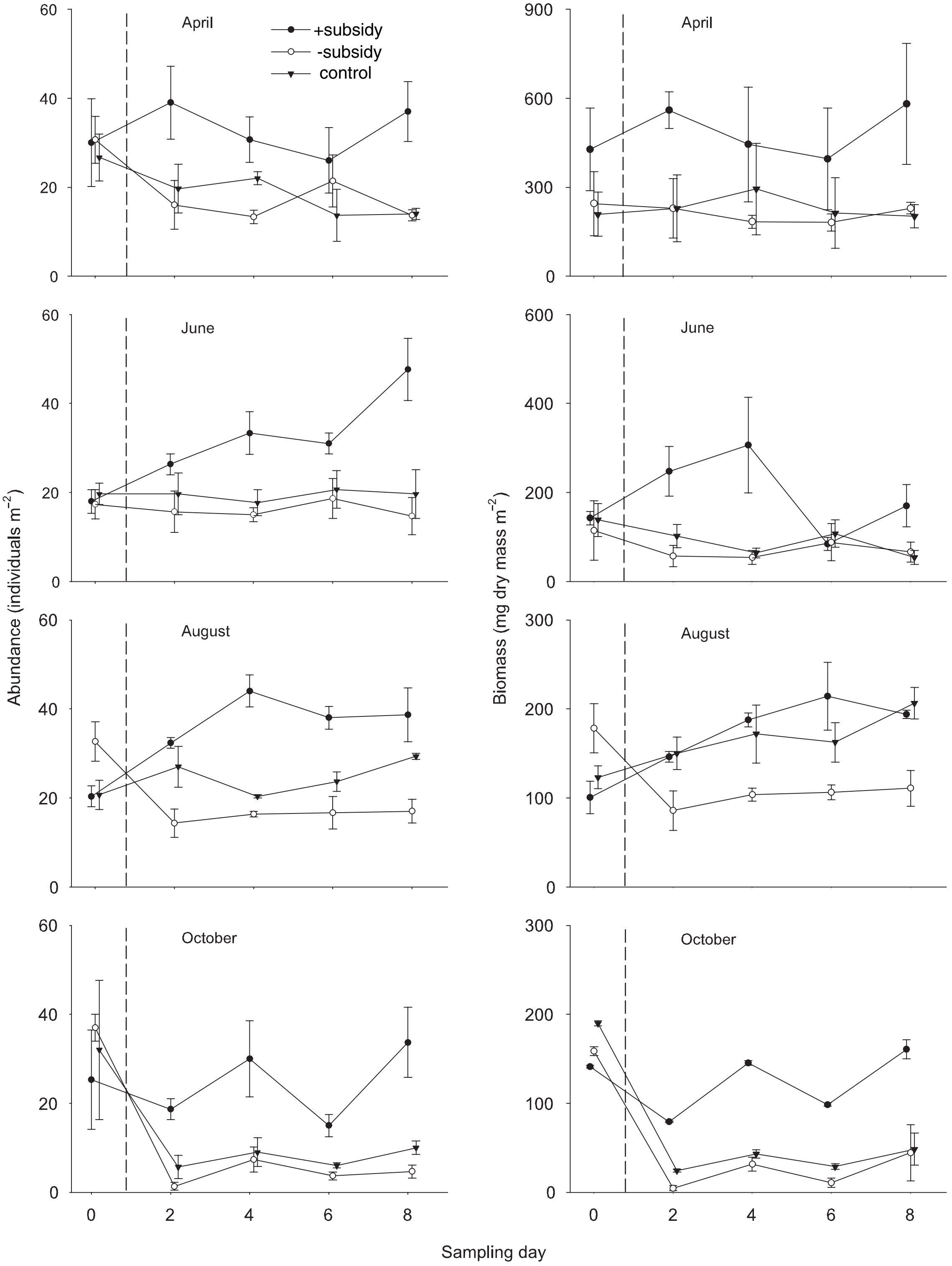

Fig. 2 Response of riparian arthropod abundance (left panels) and biomass (right panels) to subsidy treatments in different seasons (note the different scales for the biomass). Subsidy treatments included reduction of subsidies of stream-derived invertebrate prey (−subsidy), ambient subsidies of stream-derived invertebrate prey (control), and addition of aquatic invertebrates (+subsidy). Mean (±1 SE) on each sampling date for the different treatments. Dashed vertical lines indicate the beginning of each treatment.

Table 1 Within-subject results of repeated-measures ANOVA on abundance and biomass of riparian arthropods with treatment and season as main factors

		Abundance		Biomass	
	d.f.	*F*	*P*	*F*	*P*
Contrast of −subsidy and control					
Time	4	1.43	0.005*	7.06	<0.001*
Time × treatment	4	3.02	0.025*	0.68	0.612
Time × season	12	3.95	<0.001*	3.31	0.001*
Time × block	8	1.60	0.145	1.43	0.204
Time × treatment × season	12	1.22	0.296	0.58	0.853
Error	56				
Contrast of control and +subsidy					
Time	4	7.94	<0.001*	0.97	0.423
Time × treatment	4	4.24	0.005*	1.62	0.206
Time × season	12	2.51	0.010*	1.61	0.159
Time × block	8	0.77	0.627	0.74	0.656
Time × treatment × season	12	0.93	0.526	0.79	0.662
Error	56				

*Significant values with Bonferroni critical α level = 0.025.

beetles decreased by 46% (12.3 individuals m^{-2}) in the −sub, and increased in the control and +sub by 10% (−7.2 individuals m^{-2}) and 45% (0.5 individuals m^{-2}) respectively, between the start and the end of the experiment across all seasons.

Changes in the abundance of ants were significantly different between +sub and control, whereas −sub had no significant effect compared with the control. The average abundance of ants increased by 614% (9.6 individuals m^{-2}) in the +sub and decreased in the control and −sub by 13% (0.4 individuals m^{-2}) and 0.4% (0.7 individuals m^{-2}) respectively, between the start and the end of the experiment when averaged over all seasons. Lycosid spiders showed no significant change in abundance during the experiments when averaged across seasons.

Isotopic composition

Isotopic signatures of terrestrial arthropods and aquatic insects showed a clear separation (Fig. 3). Mayflies (Ephemeroptera) differed in their isotopic signal from other aquatic insect orders. Riparian ground beetles were similar in their isotopic signal to aquatic insects (except for Ephemeroptera) considering fractionation, and significantly different from terrestrial ground beetles (δ^{13}C: $t = -10.5$, $P < 0.001$, δ^{15}N: $t = 12.3$, $P < 0.001$). This result indicates that riparian ground beetles predominantly fed on aquatic insects. The isotopic signal of riparian lycosid spiders was more separate from that of the aquatic insects but significantly different from terrestrial lycosid spiders (δ^{13}C: $t = -4.07$, $P < 0.001$, δ^{15}N: $t = 7.84$, $P < 0.001$), indicating a mixed diet with a significant proportion of aquatic insects. Riparian ants were similar in their isotopic signal to terrestrial ants, reflecting a mainly terrestrial diet.

Seasonal patterns in emergence, arthropod biomass and surface drift

Aquatic insect emergence showed strong seasonal fluctuations (Fig. 4). Biomass of aquatic insect emergence from both aquatic and terrestrial shoreline plots

Table 2 Within-subject results of repeated measures ANOVA on abundance of lycosid spiders, ground beetles, and ants with treatment and season as main factors

		Lycosid spiders		Ground beetles		Ants	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Contrast of −subsidy and control							
Time	4	1.05	0.390	19.49	<0.001*	0.92	0.458
Time × treatment	4	0.49	0.747	3.21	0.019*	0.87	0.488
Time × season	12	1.09	0.385	3.69	0.001*	1.88	0.058
Time × block	8	0.97	0.471	0.96	0.479	0.96	0.479
Time × treatment × season	12	0.66	0.780	0.34	0.978	0.52	0.817
Error	56						
Contrast of control and +subsidy							
Time	4	1.10	0.367	4.28	0.004*	5.76	0.001*
Time × treatment	4	0.42	0.796	0.71	0.587	5.75	0.001*
Time × season	12	0.93	0.525	1.48	0.162	0.98	0.482
Time × block	8	1.18	0.326	0.61	0.766	0.57	0.802
Time × treatment × season	12	0.94	0.518	0.83	0.624	0.69	0.754
Error	56						

*Significant values with Bonferroni critical α level = 0.025.

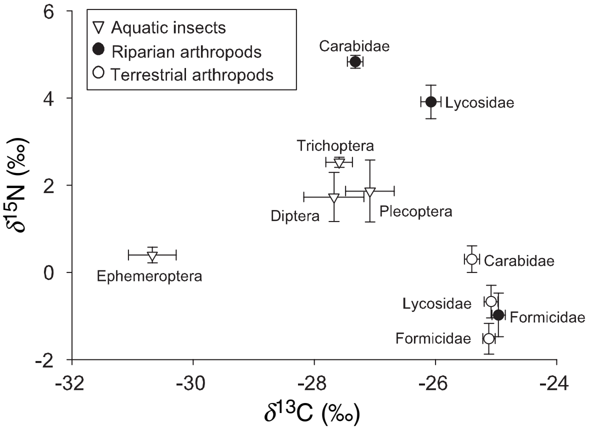

Fig. 3 Natural δ^{13}C and δ^{15}N values (mean ± SE) of common riparian arthropods, comparable terrestrial arthropods, and aquatic insects, based on data by Paetzold *et al.* (2005). Aquatic insects were grouped as Ephemeroptera (mayflies, $n = 15$), Trichoptera (caddisflies, $n = 12$), Plecoptera (stoneflies, $n = 5$), and Diptera (true flies, $n = 6$). Riparian and terrestrial arthropods were grouped as riparian Carabidae (ground beetles, $n = 74$), riparian Lycosidae (lycosid spiders, $n = 20$), riparian Formicidae (ants, $n = 10$), terrestrial Carabidae ($n = 19$), terrestrial Lycosidae ($n = 10$), and terrestrial Formicidae ($n = 18$). Replicates are composite samples of 5–10 individuals (except for the riparian ground beetle *Nebria picicornis* ($n = 32$) which were analysed individually).

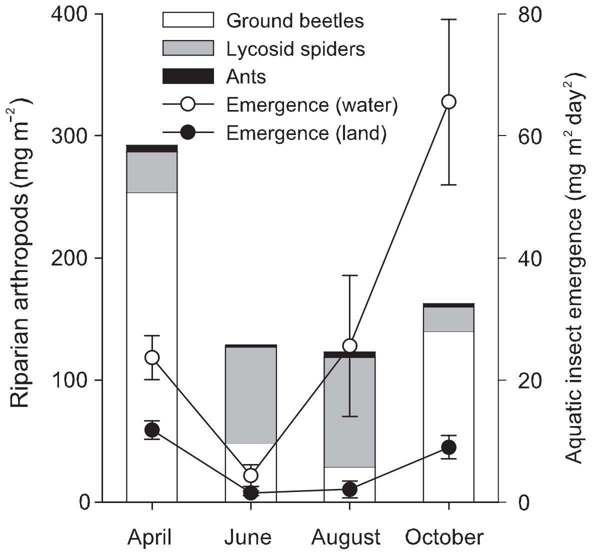

Fig. 4 Average daily biomass of aquatic insect emergence (mean ± 1 SE) in aquatic ($n = 4$ each season) and terrestrial ($n = 4$ each season) steam edge plots in different seasons. Bars show respective biomass of common riparian arthropods (mean, $n = 12$ each season) along the stream edge.

was lowest in June. Emergence from the terrestrial shoreline plots was highest in spring and autumn.

The composition in riparian arthropod biomass changed seasonally (Fig. 4). Ground beetles dominated the riparian arthropod biomass in April and October (85% and 81% respectively), but contributed only 34% and 16% to the riparian arthropod biomass in June and August respectively. The dominant ground beetle was *N. picicornis* in April and *Bembidion* spp. in October. The seasonal variation of average ground beetle biomass was similar to the variation of aquatic insect emergence from the terrestrial part of the shore (Pearson's correlation, $r = 0.97$, d.f. $= 2$, $P = 0.033$). Lycosid spiders dominated the riparian arthropod biomass in June and August (60% and 74% respectively). Biomass of lycosid spiders was dominated by large *Arctosa cinerea* in June and by smaller *P. wagleri* during the rest of the year. *Pardosa wagleri* was the most abundant lycosid spider in all seasons.

The biomass of surface-drifting organisms was highest in October and lowest in June (Fig. 5). Excluding aquatic insect larvae, which could actively enter the drift net, terrestrial arthropods contributed a major proportion to total drift biomass in all seasons (58–67%), with the lowest proportion in October.

Discussion

Response of riparian arthropods to aquatic subsidy manipulations

Studies along different rivers have demonstrated that aquatic insect emergence can provide significant energy subsidies for riparian spiders and ground beetles (Hering & Plachter, 1997; Collier *et al.*, 2002; Sanzone *et al.*, 2003; Briers *et al.*, 2005; Paetzold *et al.*, 2005). We demonstrated that ground-dwelling riparian arthropods can efficiently respond to spatially heterogeneous riverine subsidy pulses via rapid redistributions according to the subsidy level. However, individual riparian arthropod taxa exhibited different short-term numerical responses to the subsidy treatments, being related to their degree of specialisation on aquatic food sources. The degree of specialisation on aquatic insect emergence also appears to influence the distribution pattern of different web-building spiders (Kato *et al.*, 2003). Another factor that can potentially contribute to consumers' ability to track subsidies over space and time is their mobility (Power *et al.*, 2004). However, we can expect a similar resource-tracking

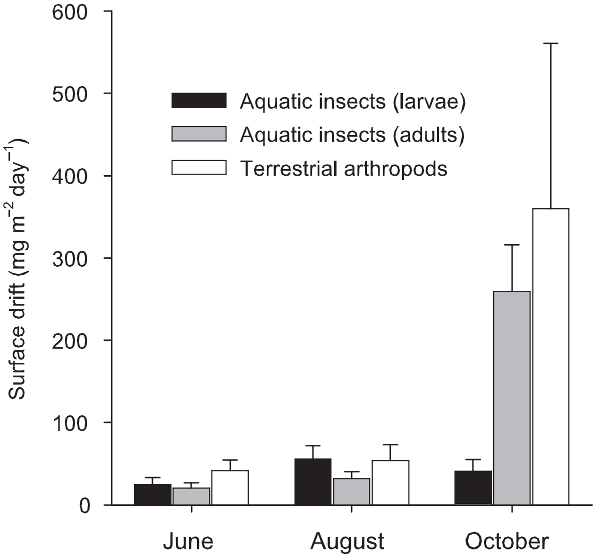

Fig. 5 Daily biomass (mean ± SE) of surface-drifting organisms per m^2 of water surface close to the steam edge in different seasons ($n = 8$ each season), standardised by an average velocity along the water's edge (0.2 m s^{-1}). Organisms were grouped by their origin as terrestrial arthropods, aquatic insect larvae and adults.

ability among the different arthropod taxa because the ground-dwelling arthropods of braided riverbanks are generally highly mobile organisms (Plachter & Reich, 1998).

The strong response of riparian ground beetles to subsidy reduction, together with their stable isotope signal, showed that ground beetles mainly fed on emerging aquatic insects. Ground beetles showed no significant aggregative response to the aquatic invertebrate addition when averaged across seasons. Numerical responses may be limited by interspecific competition, behavioural limitation, or intraguild predation. The stable isotope data indicate that interguild predation was not an important food web linkage within the riparian arthropod community. If strong intraguild predation had occurred the intraguild predator would be significantly enriched in the nitrogen stable isotope signal. Direct interference could have occurred with ants that strongly aggregated in the added subsidy plots. Ground beetles, however, can apply behavioural tactics to partly avoid interference competition with ants, and ground beetles are generally active during the night, whereas ants are mainly active during daytime (Sabo & Power, 2002b; Reznikova & Dorosheva, 2004). A more likely explanation appears to be that ground beetles were saturated by natural aquatic subsidy levels. Ground beetles exhibited highest seasonal abundances along the stream edge at the same time when emergence of aquatic insects from terrestrial shoreline plots was high. Ground beetles predominantly feed on aquatic insects that crawl on land for emergence, such as many stoneflies (Hering & Plachter, 1997; Paetzold & Tockner, 2005). The relatively high proportion of terrestrial arthropods in the surface drift together with the high proportion of aquatic insects in ground beetle diets, as indicated from stable isotope results, suggests that stranding of floating organisms were not an important food source for ground beetles.

Ants showed no significant reduction in abundance at the reduced subsidy plots compared with controls because aquatic insects were not an important dietary component, as clearly shown in their isotopic signal. However, ants strongly responded to the subsidy addition treatment. The experimental addition of aquatic invertebrates was comparable with the natural process of stranding of organisms, as exposed aquatic invertebrates were less mobile on dry gravel and died quickly. Major stranding of organisms naturally occurs after flow pulses associated with storms, predominantly by terrestrial organisms that accidentally fall into the water from riparian vegetation (Mason & Macdonald, 1982). Our results also show a high contribution of terrestrial invertebrates to the surface drift. Ants, as typical scavengers, seemed to opportunistically use this riverine-derived subsidy (stranded terrestrial organisms). Shortly after a flood, we observed ants removing stranded terrestrial organisms from floating organic matter that had become deposited along the shoreline (A. Paetzold, unpublished data). The ability of ants to form attractive trails between the nest and the food source allows them to exploit pulsed resources very effectively (Hölldobler & Wilson, 1990). This subsidy pathway (terrestrial organisms transported by the river) cannot be detected by stable isotope studies alone because of its predominant terrestrial origin.

Lycosid spiders did not respond to subsidy additions even though their stable isotope signal indicated that aquatic insects contributed significantly to their diet. However, in our experiment we only increased the abundance of less mobile prey in stream edge plots. Lycosid spiders generally detect only moving prey and feed on aquatic insects that directly emerge from the water surface (Foelix, 1996; Paetzold &

Tockner, 2005). Low amounts of subsidies of stream-derived invertebrate prey in June (emergence and surface floating organisms) and low abundances of lycosid spiders along the steam edge in April and October might have limited the aggregative responses of lycosid spiders to subsidy reductions.

Our results suggest that individual riparian arthropod taxa used different types of riverine derived subsidies to different extents: ground beetles predominantly fed on aquatic insects that emerged along the stream edge; lycosid spiders fed partly on aquatic insect emergence; and riparian ants were probably collectors of stranded terrestrial organisms. The consumption of surface-floating terrestrial organisms that strand along the riverbank by riparian arthropods represents a feedback mechanism of terrestrial derived energy back into the terrestrial food web. For this subsidy type, the river functions as a conveyer that transports terrestrial invertebrate biomass produced further upstream to consumers inhabiting downstream gravel banks. The high shoreline length and extensive gravel areas in braided rivers (van der Nat *et al*., 2002) are likely to result in a high retention of surface-drifting organisms. Thus, stranding of surface-drifting organisms appears to be an important subsidy for riparian arthropods along braided rivers.

Riparian arthropods were temporally separated in their use of riverine-derived subsidies. Diel separation can be expected among ants, ground beetles and lycosid spiders. Ants are predominantly diurnal, lycosid spiders are crepuscular and nocturnal, and ground beetles are largely nocturnal (Foelix, 1996; Sabo & Power, 2002b). Ground beetles and lycosid spiders were also seasonally separated. Resource partitioning (Schoener, 1974) by riverine subsidy type (aquatic insect emergence versus stranded organisms) and temporal separation of riparian arthropods reduced interspecific competition among riparian arthropod taxa. Therefore, the diversity of life-history traits of riparian consumers may enhance the efficient use of riverine subsidies by riparian food webs.

Potential effects of subsidised riparian arthropods on in situ *prey*

The aggregative response of riparian arthropods to aquatic subsidies together with their degree of specialisation on riverine inputs can be used to predict their potential effects on alternative terrestrial prey (see Holt & Kotler, 1987). Alternative terrestrial prey organisms exhibited only low densities along the river's edge and were mainly abundant at larger distances from the river (A. Paetzold, unpublished data). Therefore, lycosid spider predation on aquatic prey in summer should lead to a seasonal decrease in predation pressure on alternative terrestrial prey as a result of prey switching. However, subsidised lycosid spiders that seasonally migrate to habitat patches at greater distance from the stream may exhibit strong predation pressure on terrestrial prey during other seasons. For instance, the riparian lycosid *Arctosa cinerea* tends to retreat from the water in autumn prior to winter diapause (Framenau *et al*., 1996). The potential of riparian spiders subsidised by aquatic insect emergence to depress riparian herbivores has been demonstrated along a lowland river in Germany (Henschel, Mahsberg & Stumpf, 2001). Pulsed subsidies of stranded organisms may result in an increase in ant population density, with potential negative long-term effects on alternative terrestrial prey. Ground beetles should have little effect on terrestrial prey because ground beetles were specialised on or satiated by aquatic insect emergence. These predictions suggest that taxon-specific responses to allochthonous inputs need to be considered to understand indirect effects of spatial subsidies on *in-situ* prey.

Conclusions

Riparian arthropods can provide an important food source for other riparian consumers, such as birds and lizards (Jackson & Fisher, 1986; Sabo & Power, 2002a,b). Physiological abilities allow riparian arthropods to maintain high densities by pulsed resources, e.g. spiders can withstand long periods of starvation by depressing metabolic rates and ingest large amounts of food when prey is abundant (Foelix, 1996). With the effective uptake of pulsed riverine-derived subsidies, riparian arthropods can transform pulsed resource inputs into a more stable food source for higher trophic levels in the riparian food web. This effect might be particularly important for consumers in higher trophic levels that are seasonally subsidised by riverine food sources. For instance, Iwata, Nakano & Murakami (2003) showed that riparian birds feeding on emerging aquatic insects also consumed riparian arachnids to a substantial degree. Therefore, pulsed resource inputs can cause long-term responses on recipient consumer communities and may affect overall subsidy efficiency. Nakano & Murakami (2001) proposed that the seasonal asynchrony between aquatic prey inputs and secondary productivity in the riparian habitat controls the efficiency of aquatic subsidies for riparian predators. Our results suggest that we need to add irregular pulses of riverine inputs to this concept. The integration of aquatic subsidy pulses appears to be particularly important along rivers with a flashy flow regime where irregular flow pulses (*sensu* Tockner, Malard & Ward, 2000) can cause resource pulses of stranded organisms and where emergence is synchronised with long-term flood dynamics rather than being seasonal (Lytle & Poff, 2004).

In conclusion, riparian arthropods can effectively use pulsed aquatic subsidies by rapid redistribution. Stranding of surface-drifting organisms represents an important subsidy for riparian arthropods, predominantly for ants. Life-history characteristics of riparian consumers can control the subsidy efficiency for the recipient community. Our results suggest that the diversity of riparian consumers enhanced the resource flux from the river to the riparian zone due to resource partitioning by aquatic subsidy type and temporal separation among riparian arthropod taxa. By the effective uptake of pulsed riverine derived subsidies, riparian arthropods can enhance the transfer of riverine food sources to the riparian food web.

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