

FLOODING IMPACTS ON RESPONSES OF A RIPARIAN CONSUMER TO CROSS-ECOSYSTEM SUBSIDIES

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Abstract. Landscape-driven processes impact the magnitude and direction of cross-ecosystem resource subsidies, but they may also control consumers' numerical and functional responses by altering habitat availability. We investigated effects of the interaction between habitat availability and subsidy level on populations of a riparian fishing spider, *Dolomedes aquaticus*, using a flood disturbance gradient in the Waimakariri River catchment, New Zealand. *D. aquaticus* predominantly eat aquatic prey as they hunt from the water surface. However, *D. aquaticus* biomass peaked at rivers with intermediate flood disturbance, rather than at less flood-prone rivers where the biomass of aquatic insect prey was markedly higher. Flooding positively influenced spider habitat quality, and an experimental manipulation at stable rivers indicated that unembedded cobbles, preferred *D. aquaticus* habitat, were a limiting factor, preventing response to the increased prey resource at stable sites. Potential terrestrial prey abundance was low, did not vary across the disturbance gradient, and is likely to have been a much smaller component of the fishing spiders' diet than aquatic insect prey. Thus landscape-driven factors not only controlled the magnitude of resource subsidies, but also influenced the ability of consumers to respond to them by altering the physical nature of the ecosystem boundary.

Key words: disturbance; *Dolomedes aquaticus*; fishing spider; flood disturbance gradient; predator-prey interactions; river; Waimakariri River catchment, New Zealand.

INTRODUCTION

Energy flows across ecosystem boundaries are integral to both recipient and donor ecosystems as they alter the stability of food webs (Huxel and McCann 1998, Takimoto et al. 2002) and the likelihood that trophic cascades will occur across the boundary (Sabo and Power 2002, Knight et al. 2005). Recent research, stimulated by Polis and colleagues' (1997) review of spatially subsidized food webs, has highlighted the role of landscape-scale factors in influencing the importance, direction, and magnitude of energy flows. These factors include differential permeability of boundaries to energy flux and organism movement (Laurance et al. 2001, Power and Dietrich 2002), boundary shape (Iwata et al. 2003) and boundary length relative to the area of the recipient system (Anderson and Polis 1999), and seasonal differences in productivity between adjacent habitats (Nakano and Murakami 2000). In addition to controlling food-web subsidies, landscape-scale factors such as habitat fragmentation, disturbances, or geographic barriers may also limit the ability of consumer organisms to respond numerically or functionally to spatiotemporal changes in allochthonous prey availability by changing the availability of other important resources. Here, we used a flood disturbance gradient to investigate interactions between these two processes on

populations of a riparian fishing spider *Dolomedes aquaticus* (Pisauridae) (Goyen 1887).

River size and the nature of the riparian boundary within a riverscape often alter the direction, magnitude, and population- and community-level consequences of energy flow between aquatic and terrestrial ecosystems (Power and Rainey 2000, Iwata et al. 2003, Baxter et al. 2005, Ballinger and Lake 2006). Flood disturbances are likely to have pervasive influences on the extent and consequences of aquatic insect subsidies to riparian consumers because they have the potential to reduce the size of aquatic insect populations in addition to altering the suitability of the riparian zone as a habitat (Bell et al. 1999, Ballinger et al. 2005) and foraging ground (e.g., Power and Rainey 2000).

Dolomedes aquaticus is a riparian cursorial spider that lives among cobbles and boulders on riverbanks throughout New Zealand (Forster and Forster 1999; see Plate 1). It is an open-riverbank specialist and is largely nocturnal (Williams 1979). Although an opportunistic feeder, it lives within several meters of the river edge and feeds from the water surface, anchored to the bank by its back legs, meaning that emerging adult aquatic prey form a large percentage of its diet (Williams 1979). Many aquatic insects, e.g., stoneflies and caddisflies, that remain in the riverbank habitat after emerging as adults are likely prey. In nighttime surveys of *Dolomedes* feeding in river beds, 99% of prey removed from the spiders' chelicerae were aquatic in origin ($n = 76$ prey organisms [Williams 1979]).

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PLATE 1. A typical hunting pose of the juvenile fishing spider (*Dolomedes aquaticus*) beside a New Zealand high-country river. Photo credit: M. Greenwood.

We expected that, in rivers with unconstrained channels, the flood regime would control the supply of aquatic insect prey as well as influence habitat availability, and potentially restrict the ability of spiders to benefit from the aquatic resource subsidy. We hypothesized that at more flood-disturbed rivers the availability of aquatic prey would decline due to the scouring action of spates (rapid rise and fall of rivers after rainfall). However, we expected that habitat availability would be high at these sites where cobbles are abundant. At more stable rivers we expected to find high aquatic prey availability but limited spider habitat resources as river banks are more vegetated and exposed cobbles are limited. Thus we predicted that the interaction of habitat and aquatic prey availability at rivers across a flooding disturbance gradient was likely to drive *D. aquaticus* population abundances.

METHODS

The Waimakariri River, South Island, New Zealand, where the study was conducted, is a large braided river subject to frequent and unpredictable flood events at any time of the year, yet within its catchment there is a diverse range of rivers from stable, alluvial floodplain springs to frequently disturbed braided rivers. The area covered by this study has a mean annual rainfall ranging from 2000 mm/yr in the west to 800 mm/yr in the east,

and the catchment geology is largely greywacke and argillite with localized areas of limestone (Cowie et al. 1986). Generally the riverbanks of all study rivers were largely unvegetated and cobble or boulder dominated. The vegetation that did occur was an occasional shrub in a mainly tussock/grassland matrix. Thirteen rivers spanning the disturbance gradient of this catchment were studied (Appendix).

Measuring flood disturbance

To measure the timing and intensity of floods we used the painted rock method of Townsend et al. (1997), modified to include grids of rocks on the riverbank within 3 m of the river edge as well as in the water, with 30 rocks at each river. Rock movement was checked monthly between November 2004 and December 2005 and the average proportion of rocks that had moved was calculated as a measure of disturbance. In addition, channel and bank stability were assessed using the river disturbance index (abbreviated here to RDI) (Pfankuch 1975) for the 100-m study reach on each river. This index incorporates 15 categories of visually estimated flood-related factors and covers the upper banks, lower banks, and the river bottom. The ratings for each category are summed to give an overall index score (32–152), with a higher score indicating a more physically unstable river. Death and Winterbourn (1994) found

that Pfankuch river disturbance scores correlated strongly ($r^2 = 0.83$) with a multivariate stability index that included measures of substrate movement, tractive force, variability of depth, and current velocity when evaluated on rivers in the same catchment as the present study, including four of the same rivers.

Field survey

Surveys of *D. aquaticus* populations, their habitat, and potential aquatic and terrestrial prey were conducted between 26 January and 6 February 2005. A 100-m reach was defined at each river, extending 3 m back from the water's edge on both banks (total 600 m²). A reach this large reduced the effects of small-scale variations in spider abundance associated with habitat patchiness.

D. aquaticus lives under unembedded riverbank rocks within 3 m of the wetted channel edge. To measure the quantity and quality of habitat available to *D. aquaticus* at each river we defined three habitat quality categories based on survey data obtained over the previous year (M. Greenwood, unpublished data). Areas that were too vegetated (>50% coverage) or had few unembedded rocks (<50% of rocks unembedded) provided little habitat for spiders and were classified as "poor." Banks with less than 50% of the rocks (>50 mm longest axis, LA) embedded in fine sediments provide usable habitat and if vegetation coverage was 5–50% they were classified as "good." The presence of riparian vegetation, generally grasses and emergent macrophytes, indicated a less flood-prone area that could retain more prey or be important for nest sites. Areas with less than 50% of the rocks (>50 mm LA) embedded in fine sediment and with <5% vegetation coverage were defined as "intermediate." Each square meter of the 100-m reach was defined visually as "good," "intermediate," or "poor" and the area of each habitat type was calculated to the nearest square meter for all rivers.

To check our visual differentiation of habitat types we also measured the size (LA) and degree of embeddedness of 50 random particles in each of the three habitat types at each river. Depth of embeddedness was calculated by measuring the total height of the rock perpendicular to the ground and how much was buried in fine sediment (<3–4 mm).

At each river, 20 1-m² quadrats within each of the three habitat types were searched for *D. aquaticus*. Quadrats per habitat type were stratified with distance from the river edge. All spiders were digitally photographed on a 2-mm grid and sexed. The wet mass of spiders was calculated from a regression of cephalothorax (ct) width (mm) to wet mass (mg), $y = 0.024x^{2.69}$ ($r^2 = 0.90$, $n = 151$, $P < 0.001$). *D. aquaticus* abundance and biomass in each habitat type were multiplied by the extent of that habitat type in the 300-m² strip along each river bank and summed.

Biomass of aquatic invertebrates was calculated to estimate availability of aquatic prey resources. At each river, four Surber samples (0.09 m², 500- μ m mesh) were

taken in riffles within 3 m of the river edge and later frozen. Invertebrates with a winged adult stage (and therefore likely to be available to spiders as prey) were later counted, identified to genus where possible using standard keys (Winterbourn et al. 2000), oven-dried at 60°C for 48 hours, and weighed in taxonomic groups, generally order. The biomass of potential aquatic prey per 100-m reach was estimated by multiplying mean river width to a maximum of 5 m by the mean dry mass of aquatic insects per square meter. Because fishing spiders hunt from the river edge they are unlikely to have access to prey over the entire width of the river; hence the restriction to a 5 m width maximum.

To measure terrestrial food availability within the riparian zone, five randomly located quadrats (0.25 m²) within 3 m of the river channel were sampled and the area vacuumed with a portable vacuum cleaner (modified auto vacuum, 12 V, 60 W) in each of the three habitat types. Samples were frozen prior to all invertebrates being counted and identified to order. Subsequently, terrestrial invertebrates were oven-dried at 60°C for 48 hours and weighed to the nearest 0.1 mg.

Habitat manipulation experiment

To determine the influence of habitat availability on the abundance and biomass of *D. aquaticus* we manipulated the bank habitat alongside five stable rivers (≤ 60 on river disturbance index) between 29 December 2004 and 3 January 2005. The purpose of the experiment was to test whether the availability of habitat limited spider numbers at locations where resource subsidies were high. At each river, three treatments were established: (1) substrate removed to reduce available habitat, (2) substrate added to increase available habitat, and (3) no change in habitat availability (unmanipulated control). Treatment units were 10 m long and 2 m wide and were at least 3 m apart, with the control treatment in the center and the other two treatments assigned randomly upstream or downstream. Because insufficient adjacent habitat was present at Cave Stream the control site was sited 30 m upstream of the removal and addition treatments.

To assess habitat availability we measured the size of 50 randomly selected substratum particles in each treatment area as well as their degree of embeddedness (as described previously) prior to the experimental manipulation. In the habitat reduction treatment all unembedded rocks > 50 mm LA were removed and placed loosely on top of the rocks already present in the habitat addition treatment. In this way, available interstitial spaces were effectively doubled in the habitat addition area, bringing the proportion of usable habitat up to a level similar to that found in more disturbed rivers (>90 on the Pfankuch river disturbance index). In the control treatment, all unembedded rocks over 50 mm were picked up and replaced to control for substrate movement effects. All sites were searched for *D. aquaticus* before the habitat manipulation and individ-

uals were digitally photographed on a 2-mm grid and sexed before being replaced where they were found. Presence of egg sacs was also recorded. Subsequently spider abundance was measured monthly for three months and again after 14 months using the same method. Substrate size and embeddedness were recorded on all dates except in the second month after the manipulation.

Analyses

Linear and nonlinear regressions were performed to evaluate relationships between the river disturbance index and tracer rock movement as well as aquatic food availability, respectively. Relationships between spider biomass and abundance and the river stability index were tested with quadratic regressions. For all analyses, rivers were treated as replicates ($n = 13$) and post hoc Tukey tests were performed where necessary. To test for between-treatment differences before the experimental habitat manipulation was applied, one-way ANOVAs were used with substrate size, substrate embeddedness, spider abundance, spider biomass, and the proportion of large females as the responses. To evaluate the influence of the habitat manipulation, post-manipulation spider abundance, biomass, and habitat characteristics were tested using a repeated-measures design with treatment and time as main effects and rivers ($n = 5$) as replicates. Analyses of habitat characteristics used all three treatments, whereas analyses of spider biomass, number, and the proportion of collected spiders that were large females used the change in numbers relative to the control at each time to account for seasonal changes in abundances at the different rivers.

Analyses of physical characteristics and the habitat manipulation experiment were performed in Statistica (Statsoft, Tulsa, Oklahoma, USA), whereas those for the spider populations were conducted using R (R Development Core Team 2005). All data were $\log_e(y + 1)$ -transformed when necessary to meet assumptions of normality and heteroscedasticity.

RESULTS

The visually assessed categories of habitat type showed good concordance with measured substrate size and embeddedness as shown by substrate size being significantly larger in good habitat than in intermediate or poor habitat (one-way ANOVA, $F_{2,12} = 6.21$, $P < 0.01$, Tukey post hoc test). In addition, the proportion of usable *D. aquaticus* habitat (i.e., unembedded rocks > 50 mm) was higher in the good and intermediate habitat categories than in the poor habitat (one-way ANOVA, $F_{2,12} = 75.46$, $P < 0.001$, Tukey post hoc test). We found a significant positive linear relationship ($r^2 = 0.85$) between movement of painted tracer rocks over 12 months and the river disturbance index (RDI; Fig. 1a) indicating that the two methods used to define flood disturbance gave similar results. As the RDI integrates the effects of floods over a longer time period than our

rock tracer study, the index was used as a measure of flooding disturbance in all subsequent analyses.

The biomass of benthic insects with a winged adult stage in each river was significantly and positively related to the number of adult aquatic insects caught in the riparian vacuum samples ($F_{1,12} = 8.99$, $P = 0.012$, $r^2 = 0.45$), indicating that biomass of aquatic larvae in these rivers is a good surrogate for the abundance of adult aquatic insects available as potential prey for *D. aquaticus*. However, the biomass of aquatic invertebrates, i.e., potential prey for *D. aquaticus*, was highest, although variable, in the least disturbed rivers (RDI < 60) and lower in more disturbed rivers (RDI > 60 ; Fig. 1b). Although, we are likely to have overestimated the biomass of aquatic prey available to *D. aquaticus* as they mainly catch prey emerging on the water surface (Williams 1979), the relative pattern across the disturbance gradient should remain the same. Potential terrestrial prey for *D. aquaticus* changed little across the disturbance gradient (Fig. 1c).

The proportion of usable spider habitat ("good" and "intermediate" categories summed) showed the opposite pattern (Fig. 1d), with a higher proportion of habitat present in the more disturbed rivers. Stable rivers therefore contained more potential prey than disturbed rivers but less habitat for the spiders. Despite the high abundance of aquatic prey at stable rivers, spider biomass peaked at intermediate levels of stability (Fig. 1e, f). *D. aquaticus* were present in very low numbers in stable rivers and were two to three times more abundant in rivers with intermediate levels of disturbance. Numbers and biomass declined almost linearly after this point with increasing flood disturbance.

Habitat manipulation experiment

The habitat manipulation experiment directly tested whether habitat availability limited spider abundance, despite the high amount of food in the stable rivers. Neither substrate size (Fig. 2a; $F_{2,4} = 0.37$, $P = 0.70$) nor the proportion of usable habitat (Fig. 2b; $F_{2,4} = 1.77$, $P = 0.22$) was significantly different across treatments before the habitat manipulation. However, after the manipulation, both substrate size and the proportion of usable habitat increased in the habitat-addition treatments (Fig. 2a, b; substrate size, $F_{2,9} = 6.74$, $P = 0.02$; usable habitat, $F_{2,9} = 17.56$, $P = 0.001$). In contrast, we observed significant decreases after the manipulation in substrate size ($F_{2,18} = 3.57$, $P = 0.05$) and the proportion of usable habitat ($F_{2,18} = 4.42$, $P = 0.03$).

Numbers of spiders did not differ among treatments before the manipulations (treatment, $F_{1,4} = 0.86$, $P = 0.39$); however, after the manipulation numbers of spiders tended to increase in the addition treatment and tended to decrease or remain similar in the removal treatment compared to the control (Fig. 2c; treatment, $F_{1,8} = 3.8$, $P = 0.07$). Spider biomass did not vary between treatments before the manipulation ($F_{1,4} = 0.07$,

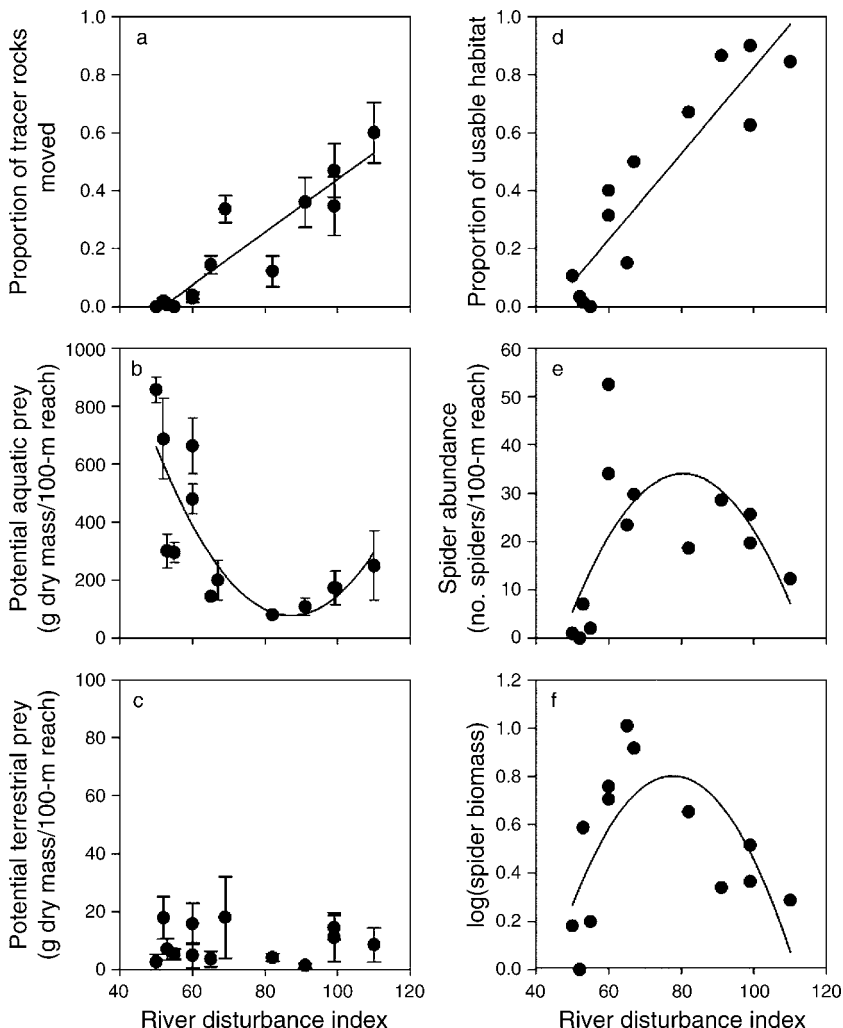


FIG. 1. (a) Mean proportion of instream and riverbank tracer rock movement over 12 months ($r^2 = 0.85$, $P < 0.001$); (b) mean dry mass of potential aquatic prey per 100-m reach of river ($r^2 = 0.66$, $P < 0.001$, $y = 84.4x/[-44.8 + x]$); and (c) mean dry mass of potential terrestrial prey per 100-m reach of river across a flood disturbance gradient measured by the river disturbance index. For panels a–c, error bars indicate \pm SE of river means. (d) Proportion of usable habitat (i.e., loose, unembedded rocks) available within 3 m of the river edge over a 100-m reach ($r^2 = 0.83$, $P < 0.001$) and the (e) abundance ($r^2 = 0.43$, $F_{1,10} = 8.16$, $P = 0.017$) and (f) log-transformed biomass ($r^2 = 0.45$, $F_{1,10} = 6.83$, $P = 0.026$) of the fishing spider *Dolomedes aquaticus*, originally measured as g/100-m reach of river across a flood disturbance gradient measured by the river disturbance index. A high river disturbance index score indicates a river frequently or severely disturbed by floods. For all P values, $\alpha = 0.05$, $df = 12$. Data are from the Waimakariri River catchment, New Zealand.

$P = 0.80$), but increased in the habitat addition treatment one month after the manipulation and remained higher than the control treatment for 14 months (Fig. 2d; $F_{1,8} = 6.42$, $P = 0.04$).

The proportion of large females (cephalothorax width > 8 mm), indicating likely breeding females, did not differ between treatments before the habitat manipulation ($F_{1,4} = 0.11$, $P = 0.75$) but differed significantly between treatments after the manipulation ($F_{1,8} = 23.17$, $P = 0.001$). More large females were found where habitat had been added than in habitat reduction and control treatments, and this effect was most marked 14 months after the manipulation (Fig. 2e).

DISCUSSION

Although the influence of some landscape-scale processes on the magnitude and direction of cross-ecosystem subsidies is comparatively well known (e.g., relative productivity [Nakano and Murakami 2000, Cadenasso et al. 2004]), few studies have investigated controls on whether subsidies impact consumer populations. This is crucial for understanding and ultimately predicting how cross-ecosystem transfers of energy alter populations and communities.

Our results demonstrate the influence of large-scale features on both the magnitude of cross-ecosystem

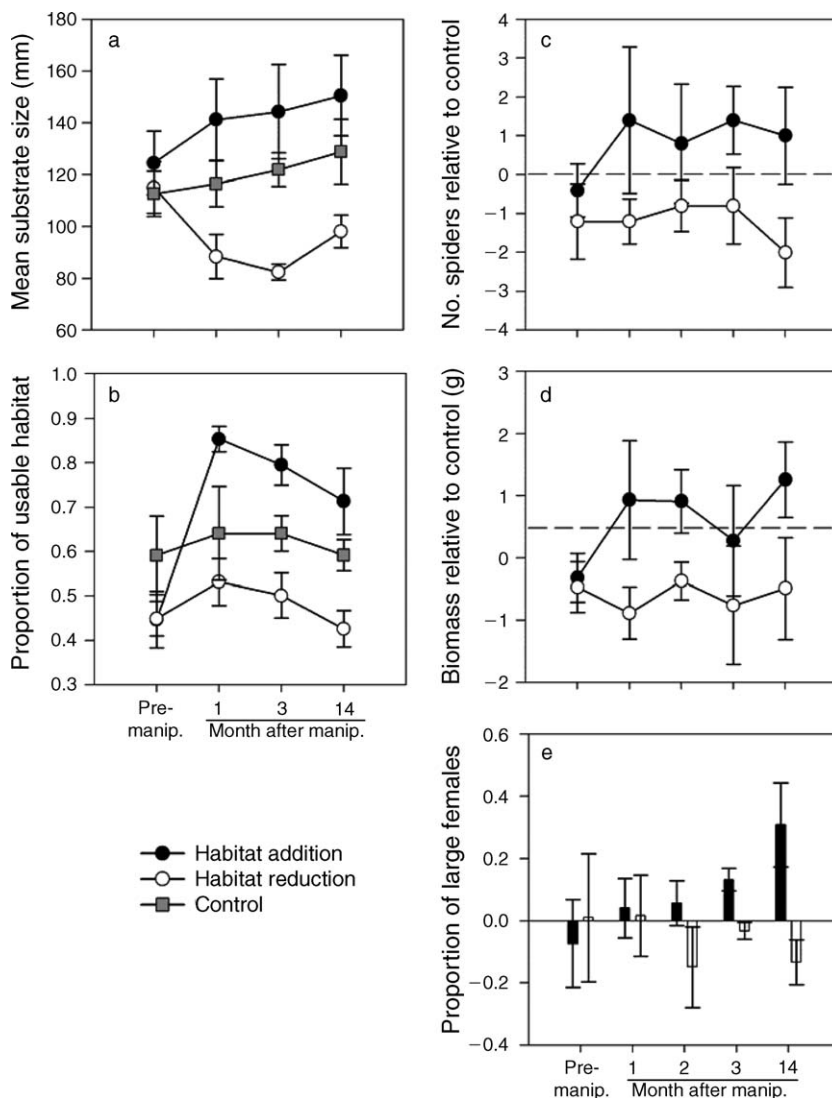


FIG. 2. (a) Substrate size and (b) proportion of usable habitat, i.e., areas of rocks larger than 50 mm embedded no more than one-fifth of their depth, before the habitat manipulation experiment (pre-manip.) and 1, 3, and 14 months after the manipulation. Loose, unembedded rocks >50 mm (longest axis) were removed from the habitat reduction section and added to the habitat addition section. Controls were unmanipulated. (c) Number, (d) biomass, and (e) proportion of *D. aquaticus* spiders that were large females (cephalothorax width >8 mm) before habitat manipulation and 1, 2, 3, and 14 months after rock habitat addition and reduction, relative to the control area at each river. Rivers are replicates ($n = 5$ rivers); values in all panels are shown as mean \pm SE.

resource subsidies and the ability of consumers to utilize those resources by responding numerically. The biomass of winged aquatic insects, which form a high proportion of the diet of many riparian consumers (e.g., Henschel et al. 2001, Akamatsu et al. 2004), was substantially altered by the flooding regime of the rivers studied. In addition, by changing physical habitat characteristics, flood disturbances impacted the ability of the consumer to respond to the subsidy. The interaction of these two processes, (i.e., the subsidy and habitat availability), which were controlled by landscape-scale driven factors, determined the functional and numerical responses of the consumer across the disturbance gradient and resulted in

the observed patterns of highest spider abundance and biomass at intermediately disturbed rivers.

D. aquaticus depend on emerging aquatic insects for a large proportion of their diet (Williams 1979, Collier et al. 2002), and rates of emergence of aerial aquatic insects can be greatly affected by the nature of the riverscape (Power 1990). In concordance with this, we found at stable rivers (≤ 60 RDI) a higher biomass of aquatic larvae with a winged adult stage, indicating a higher abundance of emerging aquatic insects available as prey (Statzner and Resh 1993) to *D. aquaticus*.

However, as well as influencing the abundance of prey from an adjacent ecosystem, the characteristics of the

landscape also affect an organism's ability to make use of the resource. In our case the flooding regime of the river also controlled the physical characteristics of the riparian zone, and therefore the quantity and quality of habitat for spiders (Bonn et al. 2002). Like many riparian cursorial spiders (e.g., Sabo and Power 2002), *D. aquaticus* lives under loose unembedded rocks close to the rivers edge. The lack of scouring floods at stable rivers enables a high proportion of the banks to be vegetated and there are consequently few areas with cobbles unembedded enough to provide habitat for *D. aquaticus*. When we experimentally increased the amount of habitat (loose, unembedded rocks) at stable river to levels similar to disturbed rivers (from 40% usable habitat pre-manipulation to ~80%), the number, biomass, and proportion of spiders that were large females (ct width > 8 mm) increased. These effects persisted, and even increased in strength up to 14 months after the manipulation. At this time the number and biomass of spiders in the habitat addition sites were significantly greater than in the control treatment and nearly twice as high as in the habitat reduction treatment. Terrestrial prey abundance is unlikely to have increased in the habitat addition sites. By adding more rocks to the stable rivers, we modified the habitat characteristics to resemble a disturbed river, yet terrestrial prey availability was not altered across this habitat gradient. These results suggest that habitat limitation at stable rivers suppressed spider population size, preventing the spiders from benefiting from the higher availability of aquatic prey.

The increase in abundance and biomass of *D. aquaticus*, and the higher proportion of large females in the habitat addition sites 14 months after the manipulation, indicates that if habitat is provided, fishing spiders can take advantage of the increased food supply from the aquatic environment and respond numerically. The increase in the number of large females, and the time lag for this increase to occur, suggests that growth or developmental rates may have been influenced by the aquatic subsidy (Kreiter and Wise 2001). In addition, six nests with live young were found 14 months after the manipulation: four in the habitat addition sites, two in the control sites, and none in the habitat reduction areas. The proportion of large females in the habitat addition treatment after 14 months was twice as high as that found at disturbed rivers with similar habitat availability (disturbed river, 0.25 ± 0.09 large females [mean \pm SE]; stable river habitat addition, 0.53 ± 0.13 large females; $n = 5$ rivers for both).

Mortality from floods or food limitation, or a combination of both, are the most likely factors explaining the low abundance and biomass of *D. aquaticus* found at disturbed rivers. The abundance of predators of the spiders is unlikely to vary across the disturbance gradient and is especially unlikely to be highest at more open, flood-prone rivers. There is one record of a *Dolomedes* in the gut of a small owl,

Morepork, *Ninox novaeseelandiae* (Lindsay and Ordish 1964), but these birds do not occur at the study sites (Robertson et al. 2007). Other riverbank-feeding birds are largely day active, when the spiders are hidden beneath rocks. Lizards are also potential predators, but they prefer stable rock banks generally out of the immediate floodplain. A total of three lizards were found in similar habitats to *D. aquaticus* during >500 people-hours of spider searches, and only one of these was at a disturbed river (M. Greenwood, unpublished data). In addition, fishing spiders are well adapted to avoid floods; they build their nests on stable islands that are seldom disturbed, and comparable numbers of spiders have been found in the same locality before and immediately after a flood (M. Greenwood, personal observation). Low food availability could also be a significant factor; for example, Kreiter and Wise (2001) found that food availability limited the fecundity of a North American fishing spider (*Dolomedes triton* Latreille). However, food availability at intermediately disturbed rivers was as low as that in more disturbed rivers, yet *D. aquaticus* biomass was higher at these sites.

Regardless of the mechanism operating at more flood-disturbed rivers, we have shown that landscape-driven factors not only can influence the level of cross-ecosystem subsidies available to consumers, but also can affect the ability of the consumer to respond both functionally and numerically to these variations in allochthonous prey abundance by altering the physical nature of the ecosystem boundary. Thus responses of consumers to such spatial subsidies will vary depending on the propensity and ability of the consumer to utilize the resources as well as its specific habitat requirements. Furthermore, cross-ecosystem subsidies will not always lead to larger consumer populations, and consumer responses may be complicated by interactions between landscape-driven processes. Responses to energy subsidies are often species specific and influenced by seasonal factors (Nakano and Murakami 2000, Kato et al. 2004), and in addition habitat requirements are often specific to a taxon. The importance of landscape-driven effects on the magnitude and importance of cross-ecosystem subsidies of resources has been highlighted but it must also be realized that these factors can also impact other resources important to consumers.

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APPENDIX

Physical characteristics of the study rivers (*Ecological Archives* E089-090-A1).