Dynamics of aquatic insect flux affects distribution of riparian web-building spiders

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The flux of emerging aquatic insects from streams can provide a significant energy subsidy to riparian web-building spiders. However, despite the high temporality of aquatic insect emergence, the effects of such aquatic insect dynamics on spider distribution are poorly understood. To examine the relationship, the aquatic insect flux from a headwater stream in a northern Japanese deciduous forest was experimentally manipulated by using a greenhouse-type covering, during May to July. Under natural conditions, the aquatic and terrestrial insect abundances dramatically decreased and increased from May through July, respectively. The experimental reduction of aquatic insect flux depressed the density of horizontal orb weavers (Tetragnathidae) in both May and June, but not in July when aquatic insects were scarce, indicating a temporal limitation on spider distribution by aquatic insect flux. In contrast, the densities of both vertical orb weavers (Araneidae) and sheet weavers (Linyphiidae) were unaffected by the manipulation throughout the study period. These various responses, differing among months or spider guilds, may be attributed to the degree of specialization for aquatic prey in the spiders and their mobility in response to aquatic insect flux. The experimental results provided direct evidence that the temporal dynamics of aquatic insect flux, as well as spider characteristics, were primary factors determining the distributional patterns of riparian web-building spiders.

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Ecotones, defined as zones of transition between different ecological systems, typically exhibit greater species diversity and abundance than their adjacent systems (MacArthur 1964, diCastri et al. 1988, Smith et al. 1997). Recently, cross-habitat energy transfer occurring at ecotones has been stressed as a major determinant of such patterns of ecological communities (Polis et al. 1997). Spatial flow of detritus or prey organisms from adjacent systems often increases consumer populations by providing alternative resources in recipient systems (Polis and Hurd 1996, Polis et al. 1997, Power and Rainey 2000). Such energy flux is ubiquitous, being predicted to exert critical influences on the ecotone communities in a variety of spatially heterogeneous landscapes (Polis et al. 1997).

There is much circumstantial evidence indicating that cross-habitat energy flux flows from more to less productive systems, influencing the distribution and abundance of generalist consumers in the latter system (Polis and Hurd 1996, Power and Rainey 2000, review by Polis et al. 1997). However, because productivity in a local system generally varies seasonally, the magnitude and direction of the energy flux may also vary seasonally (Ostfeld and Keesing 2000, Nakano and Murakami 2001, Takimoto et al. 2002). For instance, in cool-temperate riparian deciduous forests (forest-stream eco-

tone), the biomass of adult aquatic insects emerging from streams is greatest in spring, which is characterized by a low level of terrestrial production (Nakano and Murakami 2001). Riparian generalist consumers, such as forest birds, heavily depend on the flux of aquatic insects in this season (Keast 1990, Nakano and Murakami 2001). However, the contribution of aquatic insects to the diets of these consumers dramatically decreases with the approach of summer, as aquatic insect flux decreases and terrestrial arthropod production increases with the progression of time (Nakano and Murakami 2001). Thus, the seasonal dynamics of aquatic prey flux, as well as that of terrestrial prey abundance, is a key to determine the degree of dependence of riparian generalist consumers on aquatic insect flux (Nakano and Murakami 2001). Therefore, the possibility exists that the distribution and abundance of riparian generalist consumers can be closely associated with the seasonal dynamics of aquatic prey flux. Nevertheless, few experimental studies have tested for such connection in natural habitats, owing probably to the difficulty of prey flux control at the forest–stream interface (but see Sabo and Power 2002).

The flux of aquatic insects has received much attention as a crucial determinant of the distribution of web-building spiders (Jackson and Fisher 1986, Williams et al. 1995, Henschel et al. 2001). In many regions, web-building spiders are conspicuously abundant along stream edges by numerically tracking high concentrations of emerging aquatic insects (Jackson and Fisher 1986, Williams et al. 1995, Henschel et al. 2001). Moreover, such stream subsidies can have substantial impacts on riparian food web dynamics by intensifying the top-down effects of riparian spiders on terrestrial prey populations (Henschel et al. 2001). Henschel et al. (2001) demonstrated that web-building spiders enhanced by aquatic insects depressed terrestrial herbivore populations (such as leafhoppers), in turn releasing riparian plants from grazing pressure. However, because web-building spiders often switch to capturing more abundant prey items (Wise 1993, Marc et al. 1999), prey dynamics may affect the intensity of spider predation. Therefore, an understanding of the numerical and behavioral responses of web-building spiders to aquatic prey dynamics should be of critical importance to an understanding of the riparian food webs in highly seasonal environments, such as cool-temperate deciduous forests.

In the present study, we conducted a manipulative field experiment to test whether or not temporal dynamics of aquatic insect flux affected the local abundance of riparian web-building spiders in a cool-temperate riparian deciduous forest in northern Japan. The experiment was performed during May to July, because the flux of aquatic insects dramatically decreased and the secondary production of terrestrial arthropods increased during this period in the study forest (Nakano and Murakami 2001).

Methods

Study site

The manipulative field experiment was conducted in 2000 in a riparian deciduous forest plot along the headwater reach of the Horonai stream in the Tomakomai Experimental Forest (TOEF; 42° 43′N, 141° 36′E) in Hokkaido, the northernmost island of the Japanese archipelago. The study area is situated in the cool-temperate region, having a mean annual temperature of about 7°C. This small, cold, spring-fed stream (15.4 km^2 in drainage area, 14 km in total length, 2–5 m width, gradient < 1%) rarely receives flood disturbances, with discharge remaining stable throughout the year (annual average discharge 0.24 m^3 s^{-1}). The stream is not accompanied by fringing floodplains, instead having a well-developed forest along the edges of the active stream channel. The riparian forest is dominated by deciduous species, including oak (*Quercus crispula* Blume), cherry (*Prunus sargentii* Rehder), ash (*Fraxinus mandshurica* Maxim.), painted maple (*Acer mono* Maxim.) and Japanese maple (*Acer palmatum* var. *matsumurae* Makino). The 1–5 m tall understory vegetation mainly consisted of lilac (*Syringa reticulata* Hara) and saplings of the above five species. In the study year, most of the riparian trees produced buds during the period from 25 to 29 May, developed leaves throughout June and leafed out in early July. Forty-nine species of web-building spiders (Araneae) have been recorded from the forest, the former usually emerging from hibernation in early to mid April (C. Kato, unpubl.).

Field experiment

To examine the effects of aquatic insect flux on spider density, two experimental treatments (reduced-flux and natural-flux) were established in the forest plot (Fig. 1). In the reduced-flux treatment, the flux of emerging aquatic insects into the forest was experimentally reduced over a 1.2-km stretch of the stream using a 'greenhouse'-type cover (Fig. 1). The cover (5 m wide and 2.5 m high), which was made of 1-mm mesh plastic nets supported by aluminum frames, was constructed in mid April (one month prior to the experiment) so as to cover the entire stream channel width. Each end of the experimental reach was also covered to the water surface with a 1-mm mesh plastic net. Both sides of the cover along its entire length were fixed to the ground by steel pegs at 2-m intervals, so as to prevent the escape of emerging aquatic insects. Natural-flux treatment was assigned to both the upper and lower reaches (600 m stretch of stream for each), which were 100 m distant from the reduced-flux treatment (Fig. 1). The daily mean air temperature (reduced-flux, 11.0 ± 0.4°C

Experimental plot

Fig. 1. Diagram of the experimental plot with the greenhouse-type cover used for experimental reduction of aquatic insect flux from the Horonai stream. Transects for spider sampling were re-established each month during the experimental period from May to July.
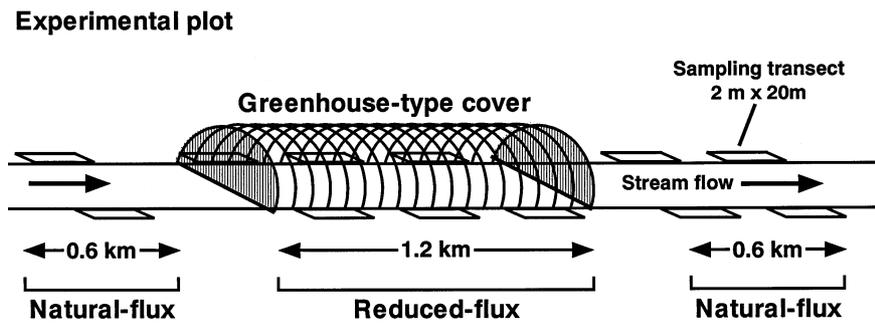
[May], $14.3 \pm 0.4°C$ [June], $18.7 \pm 0.2°C$ [July]; natural-flux, $10.9 \pm 0.4°C$ [May], $14.4 \pm 0.4°C$ [June], $18.9 \pm 0.3°C$ [July]) and the lowest daily relative humidity (reduced-flux, $69 \pm 3\%$ [May], $71 \pm 2\%$ [June], $77 \pm 2\%$ [July]; natural-flux, $65 \pm 3\%$ [May], $72 \pm 2\%$ [June], $82 \pm 2\%$ [July]) did not differ significantly between the two experimental treatments (all comparisons were by unpaired t tests, $P > 0.05$, n = 31 [May], 30 [June], 31 [July]).

The abundance of aquatic and terrestrial insects in the reduced- and natural-flux treatments was estimated each month during the experiment by Malaise-trap sampling (Townes 1972). Three Malaise traps (2 m high, 1.8 m long, 1.2 m wide, 0.5 mm mesh) were placed on stream banks (1 m apart from the active stream channel) in each treatment and operated for one week in each month (18–25 May, 16–23 June and 23–30 July). Insects caught by the Malaise traps were preserved in 70% ethanol until analyzed.

The density of web-building spiders was estimated each month in both the reduced- and natural-flux treatments during the experiment (10–21 May, 10–21 June and 19–28 July). Three transects (2 m wide and 20 m long) were set on both banks along the stream channel in each treatment (n = 6, Fig. 1). The transects were separated by at least 100 m, being re-established each month so as to minimize disturbance effects associated with the previous sampling procedure (18 transects in total for each treatment). The density of > 2-m tall mid-overstory (reduced-flux, 0.58 ± 0.05 trees m^{-2}; natural-flux, 0.60 ± 0.07 trees m^{-2}) and ≤ 2-m tall shrubs (reduced-flux, 0.62 ± 0.07 trees m^{-2}; natural-flux, 0.64 ± 0.08 trees m^{-2}) in the transects did not differ significantly between the two experimental treatments (mid-overstory, t = 0.29, P = 0.771; shrubs, t = 0.15, P = 0.881, n = 18 for both). In each transect, all web-building spiders found at a maximum height of 2 m were collected by hand picking from webs during night time (08:00–10:00 pm), when the spiders were most active, and preserved in 70% ethanol until analyzed. Concurrently, all arthropods recently entangled in spider webs in which spiders were present were collected in the natural-flux treatment, in order to

determine the prey items of web-building spiders under natural conditions. To ensure sufficient sample sizes, additional sampling for spider prey items was also conducted along the stream edges each month (not in the transects established for determining spider density).

Sample analyses

In the laboratory, arthropods collected by the Malaise-traps were identified to at least family level and sorted into aquatic insects or terrestrial arthropods under a binocular microscope. The damp mass of each taxon was measured to the nearest 0.01 mg after blotting for 10 s, and converted into dry mass by multiplying by the taxon-specific damp mass-dry mass ratio (S. Nakano, unpubl.). The abundance of aquatic and terrestrial insects was expressed as dry mass per trap per day (mg $trap^{-1}$ day^{-1}), with only aerial insects being included as the main prey item of web-building spiders. Non-aerial terrestrial arthropods comprised only a small proportion ($< 5\%$) of the total abundance of the Malaise trap samples.

The web-building spiders were identified to species under a binocular microscope according to Chikuni (1989). Spiderlings were excluded from the analyses because of the difficulty of species identification. On the basis of web architecture, spider species were grouped into the following six guilds: horizontal orb-web weavers (Tetragnathidae), vertical orb-web weavers (Araneidae), sheet-web weavers (Linyphiidae), tangle-web weavers (Theridiidae), funnel-web weavers (Agelenidae) and hackle-band weavers (Uloboridae) (Wise 1993). However, tangle-web weavers, funnel-web weavers and hackle-band weavers comprised only a small proportion ($< 5\%$ in each) of total numbers in the web-building spider assemblage. Accordingly, those guilds were excluded from the analyses. Sheet weavers build a horizontal sheet with scaffolding above and below (Wise 1993). The densities of horizontal orb weavers, vertical orb weavers and sheet weavers were determined for each transect each month (spiders m^{-2}).

Table 1. Results of two-way ANOVA for the effects of greenhouse-type cover (flux control) and month on the abundance of aquatic and terrestrial insects.

	Flux control (df = 1, 12)		Month (df = 2, 12)		Flux control × month (df = 2, 12)	
	F	P	F	P	F	P
Aquatic insects	23.5	<0.001	4.83	0.029	3.69	0.056
Terrestrial insects	3.35	0.092	8.72	0.005	0.43	0.661

For the analyses of prey items, arthropods collected from spider webs were sorted into aquatic insects or terrestrial arthropods, the dry mass of each item being determined in the same manner as the Malaise-trap samples. For each of the horizontal orb weaver, vertical orb weaver and sheet weaver groups, the percentage of dry mass contributed by aquatic insect prey was determined for each month by combining all of the samples collected.

Statistical analyses

The abundances of aquatic and terrestrial insects were analyzed using two-way ANOVA, with treatments (reduced- and natural-flux) and months (May, June, and July) as main factors, and traps as replicates. Two-way ANOVA was also performed separately for the density of horizontal orb weavers, vertical orb weavers and sheet weavers, with treatments and months as main factors, and transects as replicates. When the interaction terms in the ANOVAs were significant, multiple comparisons were made after one-way ANOVA, using Fisher's protected least significant difference (PLSD) tests. For all tests, the α value of 0.05 was used for statistical significance. All analyses were conducted using the statistical package StatView Version 5.0 (SAS Institute Inc., Cary, USA).

Results

Aquatic and terrestrial insect abundance

The flux of aquatic insects was significantly reduced by the greenhouse-type cover (Table 1). The abundance of aquatic insects in the natural-flux treatment was 9.8 times greater than that in the reduced-flux treatment when all months were combined (Fig. 2). In addition, a significant 'month' effect was detected (Table 1), reflecting a clear seasonal trend for gradually decreased aquatic insect abundance from May through July (Fig. 2). There was no significant interaction effect of month and treatment on aquatic insect abundance (Table 1).

In contrast to aquatic insects, terrestrial insects were less affected by the greenhouse-type covering. Neither treatment nor interaction effects were significant for terrestrial insect abundance (Table 1). However, a significant 'month' effect was detected (Table 1), the abundance of terrestrial insects increasing from May through July, in contrast to the trend for aquatic insects (Fig. 2).

Spider diets under natural conditions

The proportion of aquatic prey to spider diets in the natural-flux treatment differed considerably both among guilds and months (Table 2). Emerging aquatic insects were a dominant prey item for horizontal orb weavers in both May and June, accounting for >80% of prey dry mass. However, the proportion dropped to 53% in July. In contrast, vertical orb weavers preyed mainly upon terrestrial arthropods throughout the study period. For sheet weavers, emerging aquatic insects comprised nearly half of their diets in May. However, aquatic prey contributed to a small proportion (<15% in dry mass) of their diets in both June and July.
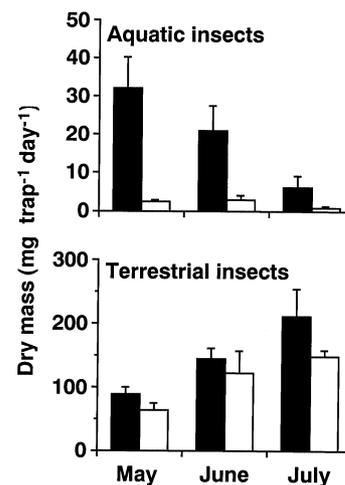

Fig. 2. Abundance of aquatic and terrestrial insects in two treatments with natural- (filled column) and reduced-flux (open column) of aquatic insects from the Horonai stream, during the experimental period from May to July. Mean and SE presented (n = 3).

Table 2. Proportions (% dry mass) of aquatic insects in the diets of horizontal orb weavers, vertical orb weavers and sheet weavers under natural conditions during the experimental period from May to July. Total numbers of prey items collected (n) shown.

	May		June		July	
	n	Proportion	n	Proportion	n	Proportion
Horizontal orb weavers	38	81.0	34	90.6	33	52.6
Vertical orb weavers	32	0.6	39	5.1	36	10.0
Sheet weavers	32	51.5	20	0.7	36	11.8

Spider density

The experimental reduction of aquatic insect flux seasonally depressed the density of horizontal orb weavers (Fig. 3). Two-way ANOVA on the density of horizontal orb weavers revealed that treatment, month and interaction effects were all significant (Table 3). Subsequent one-way ANOVA showed a significant difference in the density of horizontal orb weavers among the six groups (two treatments × three months; $F_{5,30} = 22.40$, $P < 0.0001$). Multiple comparisons (Fisher's PLSD test) showed that the density was significantly lower in the reduced- than in the natural-flux treatments in both May and June, but not in July (Fig. 3). These results indicated that aquatic insect flux influenced the density of horizontal orb weavers during the period from May to June. In contrast, the greenhouse-type cover did not affect the density of the other two guilds (Fig. 3). Neither treatment nor interaction effects were significant regarding the density of both vertical orb weavers and sheet weavers (Table 3). However, significant effects of 'month' on density were detected in both guilds. All guilds exhibited similar seasonal trends in that their density decreased from May through July (Fig. 3).

Discussion

The seasonal dynamics of aquatic insect flux differed considerably from that of terrestrial insect abundance in the riparian forest. The flux of emerging aquatic insects into the riparian forest declined from May through July. In contrast, terrestrial insects increased continuously throughout the study period. Thus, seasonal trends were the exact reverse between aquatic and terrestrial insects. In general, aquatic insect larvae/nymphs inhabiting headwater streams running through temperate deciduous forests develop during the leafless period, owing to increases in leaf-litter inputs and periphyton biomass (Sweeney 1993, Nakano and Murakami 2001). Subsequently, their emergence peaks in spring before canopy closure. In contrast, terrestrial insect abundance increases with increasing terrestrial plant production, peaking in mid-summer after the forest has leafed out (Keast 1990, Nakano and Murakami 2001). Such habitat-specific phenology in secondary production may account for the seasonal contrast between aquatic and terrestrial insect dynamics in the riparian forest (Nakano and Murakami 2001).

The dynamics of aquatic insect flux strongly influenced the seasonal diets of horizontal orb weavers and sheet weavers, whereas vertical orb weavers were less affected. Horizontal orb weavers consumed aquatic prey intensely in both May and June when the aquatic insect flux was abundant, but the aquatic prey contribution to their diets decreased in July. Because terrestrial insects were ≈ 3–7 times more abundant than aquatic insects, even in May and June (Fig. 2), horizontal orb weavers seemed to be selectively utilizing emerging aquatic insects. Although web-building spiders are generally sit-and-wait predators, they select preferred prey by adopting an appropriate web design and location (Olive 1981, Shear 1986, Uetz 1992). In fact, previous studies have reported that horizontal orb weavers inhabiting riparian zone preferentially utilized emerging aquatic insects (Yoshida 1989, Williams et al. 1995, Henschel et al. 2001). These previous findings, being
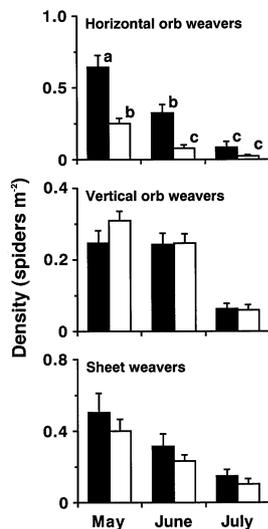

Fig. 3. Density of horizontal orb weavers, vertical orb weavers and sheet weavers in two treatments with natural- (filled column) and reduced-flux (open column) of aquatic insects from the Horonai Stream during the experimental period from May to July. There is no significant difference ($P \geq 0.05$) between bars with the same letter above (assessed by Fisher's PLSD tests). Mean and SE presented (n = 6).

Table 3. Results of two-way ANOVA for the effects of greenhouse-type cover (flux control) and month on the density of horizontal orb weavers, vertical orb weavers and sheet weavers.

	Flux control (df = 1, 30)		Month (df = 2, 30)		Flux control × month (df = 2, 30)	
	F	P	F	P	F	P
Horizontal orb weavers	34.6	<0.001	32.9	<0.001	5.84	0.007
Vertical orb weavers	0.95	0.339	46.3	<0.001	0.95	0.339
Sheet weavers	2.17	0.151	13.8	<0.001	0.13	0.881

consistent with the present study, of the preference of horizontal orb weavers for aquatic prey suggest that their relatively weak dependence on aquatic prey in July can be attributed to the decrease of aquatic insect flux rather than the increase of terrestrial insect abundance. For sheet weavers, aquatic insects were also an important prey item in May, accounting for nearly half of their diets, but the contribution dramatically decreased in June and remained at a low level in July. Sheet webs of entirely non-sticky silk are regarded as having been adapted for the capture of small insects with poor flight ability (Nentwig 1980). Because emerging aquatic insects, such as midges and stoneflies, are weakly-flying prey (Brodsky 1994), sheet weavers may depend on aquatic insects in May when tiny terrestrial prey is less abundant. The present results indicated that despite the small amount, aquatic insect flux into the riparian forest provided significant seasonal subsidies to horizontal orb weavers and sheet weavers. In contrast, vertical orb weavers, of which webs are adapted to the task of capturing large, fast flying insects (Olive 1981, Craig 1987, Uetz and Hartsock 1987, Köhler and Vollrath 1995), mainly consumed terrestrial prey, such as flies or wasps, throughout the study period.

The present experimental study demonstrated that the flux of aquatic insects had prominent effects on the density of riparian web-building spiders, although such effects varied seasonally and differed among guilds. The experimental reduction of aquatic insect flux depressed the density of horizontal orb weavers in May and June. Because the availability of preferred prey strongly influences web-site selection and tenure of web-building spiders (Olive 1982, Uetz 1992, Wise 1993), the reduced aquatic prey decreased the horizontal orb weaver density owing probably to their high emigration or low immigration rates in the reduced-flux treatment (Uetz 1992). However, no significant treatment effect on horizontal orb weavers was detected in July. This may have resulted from the fact that the importance of aquatic insects as a food source declined with the decrease in flux, as revealed by the diet analysis. In contrast, vertical orb weavers, which mainly consumed terrestrial prey, did not exhibit any population change in the reduced-flux treatment throughout the study period. Moreover, sheet weaver density did not decrease as a result of the reduction of aquatic insects, although

aquatic prey contributed a fairly large proportion to their diets in May. Sheet weavers invest so much silk in their webs that moving frequently would be energetically costly (Janetos 1982a, b). The resulting sedentary life style may have prevented them from responding numerically to the experimental reduction of aquatic insect flux (see also Power and Rainey 2000).

The varied effects of stream subsidy among spider guilds or months contrast strikingly with the general argument that energy flux from adjacent productive systems often exerts community-wide influences in recipient systems (Polis and Hurd 1995, Stapp et al. 1999, Sánchez-Piñero and Polis 2000). However, such an argument has been derived largely from research conducted on a landscape comprising arid islands surrounded by productive ocean, where the terrestrial production is nearly equal to zero, excepting in ENSO years (review by Polis et al. 1997). In this extreme landscape type, because of the constant input of large amounts of marine detritus or seabird guano, almost all terrestrial consumers can respond numerically to such marine products, thereby being heavily subsidized. In contrast, in the forest adjacent to the Horonai stream, the amount of aquatic insect flux was relatively small compared with terrestrial insect abundance. Moreover, this forest-stream ecotone is characterized as a highly seasonal environment in which aquatic insect flux provides the temporary availability of higher than normal levels of resources and then decreases with time (Nakano and Murakami 2001). In this temporally heterogeneous landscape, we consider that the degree of specialization on aquatic prey or mobility of generalist consumers should be primary factors determining the numerical response of consumer communities to aquatic insect flux (Ostfeld and Keesing 2000).

The present study provided direct evidence that the local distribution of riparian horizontal orb weavers was controlled by the temporal dynamics of aquatic insect flux. Given that aquatic insect flux depresses a terrestrial prey population by magnifying the predation intensity of riparian subsidized predators (Henschel et al. 2001), the dynamics of aquatic insect emergence may impact riparian food web dynamics through predators' numerical and/or functional responses. A recent theoretical study showed that the stability of food web dynamics in a recipient habitat depends on the tempo-

ral dynamics of energy supply from an adjacent, spatially-linked habitat (Takimoto et al. 2002). We emphasize that an understanding of the dynamic linkages between forest and stream food webs via aquatic insect flux can yield key insights into the maintenance of riparian communities.

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APPENDIX 1: Spider densities (spiders m^{-2}) recorded in the natural- and reduced-flux treatments.

Family	Species	Natural-flux treatment	Reduced-flux treatment
Horizontal orb weavers	*Leucauge subblanda* (Bösenberg and Strand 1906)	0.033 ± 0.010	0.024 ± 0.006
	Metleucauge yunohamensis (Bösenberg and Strand 1906)	0.065 ± 0.018	0.007 ± 0.004
	Tetragnatha maxillosa (Thorell 1895)	0.006 ± 0.004	0.000 ± 0.000
	Tetragnatha pinicola L. (Koch 1870)	0.049 ± 0.015	0.007 ± 0.003
	Tetragnatha praedonia L. (Koch 1878)	0.108 ± 0.027	0.049 ± 0.018
	Tetragnatha yesoensis (Saito 1934)	0.088 ± 0.032	0.028 ± 0.011
Vertical orb weavers	*Araneus ishisawai* (Kishida 1928)	0.013 ± 0.005	0.011 ± 0.004
	Araneus marmoreus (Clerck 1758)	0.003 ± 0.002	0.004 ± 0.002
	Araneus rotundicornis (Yaginuma 1972)	0.012 ± 0.005	0.003 ± 0.002
	Araneus tsuno (Yaginuma 1972)	0.001 ± 0.001	0.003 ± 0.003
	Araneus tsurusakii (Tanikawa 2001)	0.018 ± 0.007	0.006 ± 0.003
	Araneus ventricosus L. (Koch 1878)	0.011 ± 0.005	0.003 ± 0.002
	Araniella sp.	0.011 ± 0.004	0.013 ± 0.006
	Cyclosa kumadai (Tanikawa 1992)	0.056 ± 0.014	0.074 ± 0.015
	Zilla sachalinensis (Saito 1934)	0.058 ± 0.014	0.087 ± 0.022
Sheet weavers	*Linyphia angulifera* (Schenkel 1953)	0.019 ± 0.010	0.017 ± 0.007
	Linyphia nigripectoris (Oi 1960)	0.199 ± 0.054	0.153 ± 0.042
	Linyphia emphana (Walckenaer 1841)	0.025 ± 0.007	0.028 ± 0.006
	Linyphia longipedella (Bösenberg and Strand 1906)	0.078 ± 0.029	0.049 ± 0.014

Notes: means ± SEs determined by pooling data from the overall sampling period (May, June and July; n = 18). Horizontal orb weavers, vertical orb weavers and sheet weavers were the family Tetragnathidae, Araneidae and Linyphiidae, respectively.