

How wide is a stream? Spatial extent of the potential “stream signature” in terrestrial food webs using meta-analysis

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Abstract. The magnitude of cross-ecosystem resource subsidies is increasingly well recognized; however, less is known about the distance these subsidies travel into the recipient landscape. In streams and rivers, this distance can delimit the “biological stream width,” complementary to hydro-geomorphic measures (e.g., channel banks) that have typically defined stream ecosystem boundaries. In this study we used meta-analysis to define a “stream signature” on land that relates the stream-to-land subsidy to distance. The 50% stream signature, for example, identifies the point on the landscape where subsidy resources are still at half of their maximum (in- or near-stream) level. The decay curve for these data was best fit by a negative power function in which the 50% stream signature was concentrated near stream banks (1.5 m), but a non-trivial (10%) portion of the maximum subsidy level was still found >0.5 km from the water’s edge. The meta-analysis also identified explanatory variables that affect the stream signature. This improves our understanding of ecosystem conditions that permit spatially extensive subsidy transmission, such as in highly productive, middle-order streams and rivers. Resultant multivariate models from this analysis may be useful to managers implementing buffer rules and conservation strategies for stream and riparian function, as they facilitate prediction of the extent of subsidies. Our results stress that much of the subsidy remains near the stream, but also that subsidies (and aquatic organisms) are capable of long-distance dispersal into adjacent environments, and that the effective “biological stream width” of stream and river ecosystems is often much larger than has been defined by hydro-geomorphic metrics alone. Limited data available from marine and lake sources overlap well with the stream signature data, indicating that the “signature” approach may also be applicable to subsidy spatial dynamics across other ecosystems.

Key words: aquatic subsidies; dispersal; distance; food webs; insects; meta-analysis; stream.

INTRODUCTION

For almost 20 years, ecologists have recognized the importance of ecological resource subsidies that allow material biomass, organisms, and—fundamentally—energy transfer to food webs across classical ecosystem boundaries (Polis et al. 2004a). In many cases, subsidies provide energy that allows higher trophic level consumers to exist at densities that seem incongruous with in situ basal production (Polis et al. 2004b). They also mediate resource gradients between recipient and donor ecosystems and provide nutrients that facilitate primary production (Henschel 2004). The magnitude of subsidies and their effect on recipient ecosystems can be pronounced at habitat-transitioning ecotones (Nakano

and Murakami 2001), although in some cases (as in bird migrations), subsidies can have ecological effects at landscape and continental scales (Kitchell et al. 1999).

Freshwater ecosystems are disproportionately represented in this literature because they serve as exemplary case studies of cross-ecosystem subsidies: they are recipients of terrestrial inputs of leaves, sediment, and nutrients, which are traditionally characterized as being processed in situ and conveyed downstream. More recently, the multidirectional complexity of material flows to and from river systems has also been recognized, most acutely in the case of “reciprocal subsidies” (sensu Nakano and Murakami 2001), in which aquatic insects, salmon (Helfield and Naiman 2001), otters (Ben-David et al. 1998), birds (Bueno et al. 2011), bats (Power et al. 2004), and other organisms transfer energy back onto floodplains and riparian forests. Whereas the subsidy input to the stream (mostly leaf litter) is of mostly low nutritive quality, reciprocal stream exports back to land (e.g., emergent aquatic

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insects; see Plate 1) generally have much lower carbon:nitrogen (C:N) ratios and affect higher (predator) trophic levels (but see Bastow et al. 2002). The magnitude of this subsidy can be substantial; in one early study, emergent insect flux from the stream transferred $>20 \text{ g/m}^2$ of aquatic secondary production annually to terrestrial desert food webs (Jackson and Fisher 1986). It is now clear that streams subsidize food webs of terrestrial ecosystems, and that the magnitude of these subsidies can be quite large (Baxter et al. 2005).

In contrast to quantifying the magnitude of food web subsidies, spatial considerations of subsidy dynamics have received far less attention (but see Sanzone et al. 2003, Power et al. 2004, Briers et al. 2005, Raikow et al. 2011). Most studies of stream-to-land subsidies focus on organisms and food webs $<10 \text{ m}$ from stream banks (Sabo and Hagen 2012). This ignores the importance of these aquatic resources to food webs in adjacent terrestrial zones, which are intimately connected to in-stream processes (Iwata et al. 2003). Few studies have quantified how far stream subsidies penetrate into the terrestrial landscape and the conditions that affect this transmission, and there have been no efforts to systematically analyze available spatial data.

Results from the studies that have examined distance effects have raised several important issues. Overall, there is no agreement as to which decay curve best fits the distance–subsidy proportion data: many advocate negative power functions ($\text{Subsidy} = \text{Distance}^{-k}$; e.g., Briers et al. 2002), while others support a negative exponential ($\text{Subsidy} = e^{-\text{Distance}}$; e.g., Briers et al. 2005) or even a negative linear function ($\text{Subsidy} = -\text{Distance}$; e.g., Jackson and Resh 1989). The nature of the relationship may have ecological significance (Briers et al. 2002); for example, a negative exponential function indicates that the aquatic subsidy diffuses randomly from the stream and has been suggested as a nondeterministic, null model for dispersal (Rees 1993). In contrast, a negative power curve declines more steeply than does the negative exponential, suggesting that the subsidy is nonrandomly biased toward the stream bank, possibly as a result of stream-aggregating behavior in emergent aquatic adults (Briers et al. 2002). This power decay function also has a “fatter” tail than does the negative exponential, best fitting dispersal data in which a small, but nontrivial, number of organisms (or their energy in a food web) can travel great distances (Baguette 2003).

Factors that may affect subsidy dynamics include in-stream biological variables such as primary production (Power et al. 2004, Ballinger and Lake 2006), productivity or trophic level discontinuities between the stream and its surrounding landscape (Henschel 2004, Marczak et al. 2007), and the behavior of specific emergent taxa (Finn and Poff 2008). Similarly, stream and landscape physical features such as land use (Briers et al. 2002), stream size (Henschel 2004), or channel meandering and valley confinement (Sabo and Hagen

2012) can affect subsidy transmission. Certainly other related factors, such as the methods used for computing the magnitude of subsidies or the design or position of traps can also influence results (Jackson and Resh 1989, Raikow et al. 2011). Nonetheless, the relative importance of these parameters in affecting the distance that stream subsidies penetrate into the landscape is largely unknown.

Throughout this emerging and evolving understanding of subsidies, scale in food web interactions between ecosystems is gaining prominence, especially in the context of delimiting “resource sheds” of carbon and nutrients (analogous to watersheds; Power and Rainey 2000). This is especially true for rivers, which transport pollutants that are incorporated into terrestrial food webs via subsidies (Walters et al. 2010). There are policy and legal contexts to these scientific questions as well: ecological adjacency has been a focus point of U.S. Supreme Court cases (Carr and Wilcox 2006) and within local governments interested in enacting riparian buffer rules and best management practices (Marczak et al. 2010). Regulators tasked with managing stream boundaries are asking, essentially, “Where does a stream begin/end?” or “How wide is a stream?” Just as physical landscape features such as the presence of well-defined banks or surface water may satisfy such questions from a hydro-geomorphic perspective, the spatial extent of stream subsidies to terrestrial food webs could be useful as a tool for delineating the lateral biological boundaries of stream ecosystems (Doyle and Bernhardt 2010). Yet, in spite of this imperative to better understand riverine-terrestrial biological connectivity, few studies have quantified the scale at which these subsidies can meaningfully impact terrestrial food web energetics (Baxter et al. 2005).

In this study, we seek to answer the question “How wide is a stream?” from a biological, food web subsidy perspective, using a global meta-analysis (Appendix A). With this metadata set, we define a “stream signature” as the lateral distance on land at which the stream signal for a given variable is at 50% and 10% of the maximum level found in the stream or at the stream bank. In an idealized case, the biomass of food web components or organisms that act as recipients of aquatic subsidies (e.g., hunting spider groups) would be 100% derived from aquatic sources at the water’s edge. The proportion of aquatic subsidies in the collective biomass of this food web component would then decay with increasing distance from the stream, as individuals feed proportionally less on aquatic subsidies and more on terrestrial prey. The 50% stream signature in this case would thus be the distance at which half the energy in a given food web component is aquatic in origin, and half is terrestrial.

In our analysis, we predicted that distance–subsidy proportion decay curves from the metadata would be best fit by a negative power function, indicating nonrandom dispersal of stream insect subsidies. We

expected the stream signature to increase commensurate with in-stream primary productivity and in open, low-productivity, terrestrial zones, and to be affected by community-specific taxonomic differences (e.g., data on midges vs. caddisflies). We hypothesized that abiotic variables would also explain variation in the distance–proportion data; specifically, that the stream signature would be maximized in mid-order streams due to productivity gradients in larger rivers and size considerations in smaller streams, and that streams with more complex (e.g., sinuous) channels would have larger stream signatures resulting from a greater degree of physical aquatic-terrestrial interaction.

METHODS

Data retrieval and compilation

The objective of the present meta-analysis was to synthesize available data on spatially delimited, stream-to-land food web subsidies in order to determine how far this aquatic subsidy to food webs travels within the terrestrial environment. Data compilation began with the identification of highly relevant papers in ISI Web of Science and Google Scholar (using e.g., “aquatic subsidy distance” as search terms). This method returned four studies of direct relevance with spatially explicit, food web subsidy data (Sanzone et al. 2003, Power et al. 2004, Briers et al. 2005, Raikow et al. 2011). These studies, in combination with review papers on stream subsidies (Baxter et al. 2005, Ballinger and Lake 2006, Marczak et al. 2007, Richardson et al. 2010), became the basis for identification of additional data sets via studies referenced therein. Papers from those collected citations were read, data were extracted, any new relevant references were collected, and the process was then repeated. In the case of particularly relevant papers (~20; those with a more explicit focus on distance–subsidy measurement), “forward citation mapping” in Web of Science and the “cited by” tool in Google Scholar were used to identify new references and data. Aside from one data set (S. Collins, *unpublished data*), all data were from published, peer-reviewed sources.

Inclusion of studies into the metadata set was based on three criteria: (1) the study measured a lateral transect extending perpendicularly from the stream; (2) the first measurement in this transect was taken at or very near the water’s edge; and (3) the study used some metric of aquatic incorporation into the terrestrial environment. This was ideally in the form of true food web incorporation, such as isotope analysis and predator feeding observations. Due to the paucity of such studies, analogues for this process, including abundance of aquatic adult insects (i.e., dispersal onto land), and abundance of terrestrial predators attracted to the stream resource were also included in the metadata.

Data were transcribed from published tables or extracted from figures using DataThief III software (version 1.6; Tummers 2006), compiled, and made

available for future use (Supplement). The final data set contains 31 studies published from 1973–2011 (Appendix A), with 91 unique data subsets and 462 data points across 109 streams and rivers. Studies were primarily carried out in first- to fourth-order streams (87% of data points). Most data subsets were focused on insect dispersal (64% of data points), with food web and predator abundance metrics accounting evenly for the rest.

Available data were predominantly based on arthropods as sources and recipients of aquatic subsidies, with emergent aquatic insects acting as the subsidy donor and terrestrial spiders and beetles acting as recipients. The most commonly studied groups were caddisflies, stoneflies, terrestrial arthropod predators, and taxa generically reported as “all aquatic insects” (each ~20% of data points), with midges (Chironomidae), mayflies (Ephemeroptera), blackflies (Simuliidae), and bats also included in the metadata set. Aside from the data on bat predator abundance, no other available vertebrate data (e.g., salmon carcass translocation, otter latrine usage, water bird activity, amphibian movement, and so on) fit the criteria for inclusion in the data set. Additionally, the bat data were from only two studies (Power et al. 2004, Hagen and Sabo 2011) and represented only 3.5% of the metadata set. Thus, although bat data were retained in the metadata set (Supplement), they were excluded from the meta-analysis to limit excess variation, and the meta-analysis was focused entirely on arthropod taxa as a result. Data subsets with only two data points per transect were similarly excluded, such that the data set used for this meta-analysis was ultimately trimmed from 462 to 417 data points.

Effect size and inclusion of variables

To scale data from disparate sources, the response variable in meta-analysis must be transformed to a standardized “effect size.” This was accomplished by converting all data to a portion of the maximum subsidy value in each unique data subset (hence the second inclusion criterion). Thus, response data were scaled between 0% and 100%, and all unique data subsets had at least one distance measurement for which the response value was 100%, generally the value at or near the stream bank.

A variable separating the different methods used in individual studies was included as a potential explanatory variable. In this way, food web studies using isotopes or percent aquatic vs. terrestrial insects in a diet were isolated from studies of aquatic insect dispersal and others that observed increased terrestrial predator abundance near stream banks. Several other variables that could potentially affect the distance decay curve were also included in the data set. These included physical variables: climate, channel geomorphology (e.g., straight or meandering), bank type (steep or gradual), stream width class (i.e., stream width in log₂ bins), and terrestrial vegetation structure, as well as

biological variables such as focal study organism (aquatic insect or terrestrial predator order) and categorized estimates of in-stream, autotrophic primary productivity (low, medium, or high, often based on estimates of primary producer biomass). This variable was based entirely on autotrophic production and ignored potential heterotrophic, detrital, energy sources. Additional variables could conceivably have been used that might have been relevant or even more directly applicable (such as total autochthonous and allochthonous energy available in-stream, or emergent secondary production), but those included are well represented and supported in the existing literature (e.g., Ballinger and Lake 2006, Marczak et al. 2007). When variables were unspecified, authors of the studies were contacted via e-mail; their responses filled ~50% of the blanks in the datasheet. Remaining data gaps were filled by researching the study site with the use of maps, photographs, and other published studies. For many of these variables, quantitative data (e.g., chlorophyll *a* measurements for primary production) were rarely available and author responses were qualitative (e.g., productivity was low, medium, or high); thus, data were incorporated into the data set as categorical estimates rather than as numerical predictors.

Curve fitting and model analysis

Stream signatures (i.e., the points on distance decay curves where the stream signal for a given metric had decreased to 50% and 10% relative to its maximum observed value near the stream) were calculated using an approach similar to that used by Power and Rainey (2000): by computing a decay function to estimate aquatic energy input to terrestrial food webs at a given distance. Decay curves do not produce sharp breaks that would indicate a distinct point where aquatic subsidy can no longer be located within the terrestrial food web. Thus, the 50% and 10% values were used as surrogates, in keeping with previous studies (Petersen et al. 2004).

Curve fitting and analysis was carried out using R software (version 3.0; R Development Core Team 2013). Simple negative linear, exponential, and power curves were fit for the subsidy proportion effect (i.e., the response) using only one independent variable (distance). These models and all subsequent models were compared using Akaike's information criterion corrected for small sample sizes (AIC_c ; sensu Burnham and Anderson 2002) and were fit using a multilevel, mixed-effects modeling approach, with study stream as the random effect, structural variable. Because the power and exponential curves required log transformations to the independent and/or response variables, a model-optimized constant ($k = 0.05$) was added to eliminate zeros and allow fitting. Using the best of the three simple models as a base, potential physical and biological explanatory variables were then added to the model, first individually and then in concert. Models were compared

primarily using AIC_c , and the validity of adding single variables to the distance-only model was also confirmed using likelihood ratio tests. The nature of multilevel models also allowed the magnitude and direction of fitted coefficients to be assessed within the context of the entire data set, allowing the effect of caddisfly in comparison to mayfly studies to be identified, for example.

RESULTS

Type of curve

Of the three simple models tested for the distance–subsidy proportion data (negative linear, exponential, and power), the negative power function best fit the overall metadata set (Fig. 1). This was also true for unique data subsets on the individual study level, 77% of which were best fit by a negative power function (Table 1). Among studies that explicitly quantified model fit (64 data subsets), 22% reported that a negative power curve fit best, compared to 66% and 13% for negative exponential and linear functions, respectively. However, of the 22 data subsets where both negative power and exponential functions were compared, 64% advocated the negative power function. In fact, 63% of data subsets in which authors did not test a negative power function would actually have been better fit by a negative power curve.

Importance of individual explanatory variables

Additional variables were added individually to the simple negative power model for distance–subsidy proportion (Table 2). Most of these explanatory variables improved upon the fit of the base (distance only) model, particularly variables related to stream width, study method, and organism (type of aquatic insect or terrestrial predator). However, variables for bank type, terrestrial vegetation structure, and climate did not improve upon the base model. For the “study methods” variable, the stream signature was greatest for food web methods (Table 3). In other words, the 50% and 10% decay distances were greater for studies utilizing food web incorporation (e.g., stable isotope data) than for others that measured the dispersal of aquatic insects or the attraction of predators to aquatic resources.

Among physical, habitat-related variables, channel width and its analogues (e.g., stream order) had an effect on stream signatures, which extended farthest into the landscape in third- to fourth-order and seventh- or higher-order stream ecosystems (Table 3). In contrast, the stream signature response to increasingly complex channel geomorphologies was unclear, and channel bank type, climate, and landscape factors (i.e., vegetation structure) were not important to stream signatures (Table 2).

For biotic variables, aquatic primary productivity improved the base model more than did any other individual parameter (Table 2), and stream signatures increased with in-stream productivity (Table 3). The data

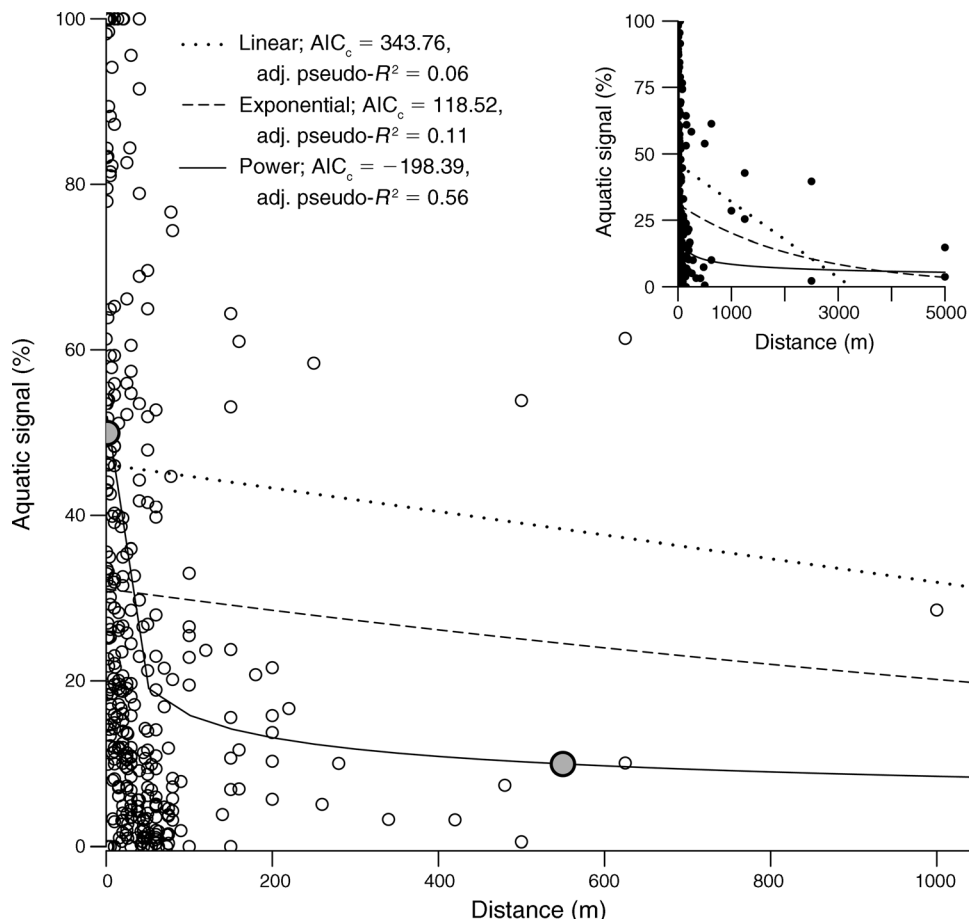


FIG. 1. All data included in the metadata set, plotted as distance from the stream vs. the percentage aquatic signal. The aquatic signal size (%) was calculated as the aquatic value of a given data point, divided by the maximum aquatic value recorded within the given transect. To aid in visualization, the main figure shows only data out to 1 km from stream banks; the inset figure shows all the data (i.e., out to 5 km). Lines represent multilevel, mixed-effects model fits for negative linear, exponential, and power curves. Large gray dots indicate the overall 50% and 10% stream signatures. Adjusted pseudo- R^2 values are based on the log-likelihood improvement of the given model vs. a corresponding null model and use Nagelkerke's adjustment.

also varied according to the studied subsidy donor organism. For example, stream signatures based on emergent caddisfly (Trichoptera) abundance data were greater than corresponding stream signatures based on

mayfly data (Ephemeroptera, Fig. 2). Midges in the family Chironomidae had the largest stream signatures of all groups of study organisms, by an order of magnitude or more.

TABLE 1. Unique data subsets for each study organism in the meta-analysis, according to the number of subsets best fit by a negative power rather than a negative exponential or linear model.

Subset	Negative power	All studies	Negative power (%)	All studies (%)	“Non-power” studies (%)
All aquatic insects	15	16	94	21	6
Stoneflies	15	17	88	22	11
Mayflies	6	7	86	9	6
Caddisflies	12	17	71	22	28
Chironomids	2	6	33	8	22
Terrestrial predators	9	14	64	18	28
Totals	59	77	77	100	100

Notes: Percentage negative power values are the numbers of negative power studies for a given organism as a percentage of all studies for that organism. Percentage of all studies values are the numbers of all studies (all model fits) for a given organism as a percentage of all studies for all organisms. Percentage of “non-power” studies values are the numbers of data subsets that did not fit a negative power curve for a given organism as a percentage of all studies for all organisms that were best fit by negative exponential or linear curves. Combined, these latter two columns give an indication of the representation of each taxon in the metadata set as well as the not necessarily proportional contributions of each taxon to the number of data subsets best fit by something other than a negative power curve (i.e., those that deviate from the overall best model fit).

TABLE 2. Explanatory variables considered in the meta-analysis, with fits compared using Akaike's information criterion corrected for small sample sizes (AIC_c).

Parameter	AIC _c	Likelihood ratio	<i>P</i>	df
Climate	886.71	1.28	0.973	10
Terrestrial vegetation	881.61	2.19	0.701	8
Bank type	877.67	6.13	0.190	8
Distance-only (base model)	875.54	NA	NA	4
Stream order	873.85	14.14	0.028	10
Channel geomorphology	872.62	11.18	0.025	8
Study method	870.28	13.52	0.009	8
Stream width	869.87	9.78	0.007	6
Stream width class	864.82	31.67	<0.001	14
Study organism	858.05	38.44	<0.001	14
Aquatic productivity	854.08	29.71	<0.001	8

Notes: Likelihood-ratio test results, *P* values, and degrees of freedom are from comparisons of a given model vs. the base (distance-only) model with no other predictors. Significant *P* values are in boldface type. "NA" indicates "not applicable."

Overall best model for future prediction

When sensible permutations of models containing multiple explanatory variables were considered in concert (sensu Burnham and Anderson 2002), five superior model options emerged (Appendix B). These best models all contained aquatic productivity, study method, and organism parameters, and the best of these models contained only these three variables, in addition to distance. Nonetheless, most of the best models (three of five) also contained a bank type, stream order, or channel geomorphology parameter.

DISCUSSION

Type of curve

The nature of the negative power curve that best fit most individual studies and the overall metadata indicates that most of the subsidy (or individual organisms) stays very near the water's edge: the overall 50% stream signature was only 1.5 m. Biologically, this suggests that most emergent aquatic insects behave in such a way as to remain near the stream (Briers et al. 2002), and that subsidy donor and recipient organisms aggregate near the water's edge in greater densities than would be expected by random diffusion or a null model

TABLE 3. Stream signatures at the 50% and 10% level for various explanatory factor levels.

Conditions	50% level			10% level		
	Stream signature (m)			Stream signature (m)		
	Mean	CI	Group	Mean	CI	Group
Overall	1.5	1.5–1.5		550	450–680	
Study method						
Dispersal	1.3	1.3–1.4	a	350	240–560	a
Predator abundance	1.3	1.3–1.5	a	570	270–1600	a
Food web	3.0	3.0–3.7	b	7200	3500–17 000	b
Aquatic productivity						
Low	1.6	1.6–1.7	b	110	87–150	a
Medium	1.4	1.4–1.4	a	790	480–1400	b
High	2.9	2.9–3.3	c	5300	3100–9500	c
Stream order						
1–2	1.3	1.3–1.3	c	190	160–250	a
3–4	2.4	2.4–2.9	d	1900	1100–3600	b
5–6	1.1	1.1–1.1	a	1100	430–4400	b
7+	1.2	1.2–1.2	b	2500	1000–8600	b
Channel geomorphology						
Straight	1.6	1.6–1.8	b	850	500–1600	b
Straight/meandering	1.9	1.9–2.1	c	230	160–360	a
Meandering	0.6	0.6–0.6	a	770	470–1400	b

Notes: Stream signatures are from distance–subsidy decay curves derived from fitted multilevel, mixed-effects models computed individually for each explanatory variable and represent the decay distance at which 50% and 10% of the stream signal is retained. The "Overall" row contains overall stream signatures from the entire metadata set, based on the multilevel, mixed-effects model. Upper and lower confidence interval (CI) bounds are included to show variation. Factor levels within a given category with the same group letter had overlapping confidence intervals and are taken to be indistinguishable from one another.

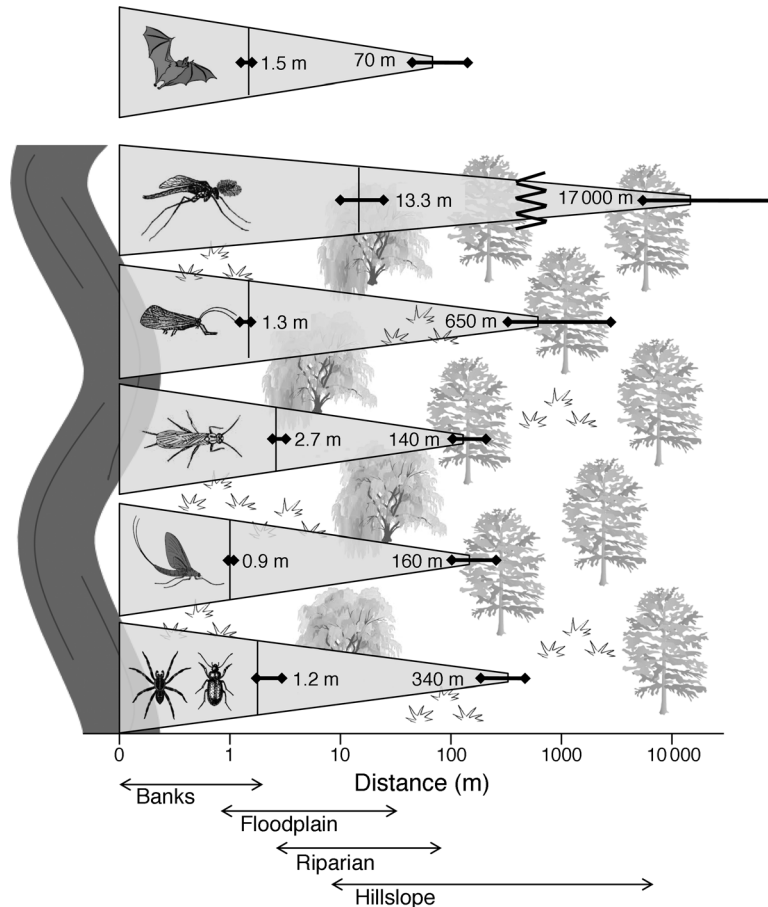


FIG. 2. Stream signature data for different taxa included in the meta-analysis, at the 50% and 10% level (vertical lines and the small end of the wedge, respectively). Stream signature values are from distance–subsidy decay curves derived from a multilevel, mixed-effects model and represent the distance at which abundance of a given organism is at 50% and 10% of its near-stream levels, respectively. Thick horizontal lines represent confidence intervals for each value. The jagged vertical line on the chironomid wedge indicates the farthest distance at which empirical data for chironomids were available; model estimates beyond that distance (e.g., the 10% chironomid stream signature) are likely spurious. Bats were not included in modeling for the overall meta-analysis but are included here for reference. All data shown here are based on group abundance. Ecosystems listed below the x -axis are rough approximations of the location of each ecotone. From bottom to top, the organisms plotted are as follows: terrestrial predators (mostly webbed spiders but also ground/hunting spiders and predaceous Coleoptera), mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), midges (Chironomidae), and bats.

of dispersal (Rees 1993). Near-stream landscape structural conditions related to dense forest edges (Cadenasso et al. 2004), narrow valley confinement (Hagen and Sabo 2011), and associated advective conditions may also inhibit dispersal or attract predators via the provision of arboreal habitat structure.

Power-curve-type stream aggregating behavior may confer benefits to the subsidy donor organisms. Stream banks are zones where mates can be found in locally high abundance (via emergence), and remaining near the stream also reduces transit and concomitant predation risk in the time between mating over land and oviposition back in the natal stream. However, the tail of this distribution also indicates that a small number of organisms disperse over great distances, potentially promoting gene flow within a meta-population (Baguette 2003, Macneale et al. 2005). In ecological terms,

most of the energy exported laterally from streams is incorporated into terrestrial food webs almost immediately. However, as indicated by the 10% stream signatures (550 m overall), a portion of this subsidy travels much farther: out of the riparian zone and into adjacent upland ecosystems.

Importance of biological explanatory variables

Stream signatures generally increased with coarse estimates of in-stream primary productivity, and this variable most strongly improved model fit (Table 2). It is reasonable to expect the magnitude (not necessarily distance) of subsidy transmission to increase when aquatic primary productivity is high, as it presumably feeds the aquatic larvae that become the emergent insect subsidy (Ballinger and Lake 2006). But the metadata also indicate that the aquatic subsidy decays more

gradually with distance from the stream as in-stream productivity increases. It may be that this larger magnitude of subsidies (i.e., emergent aquatic adults) oversaturates the ability of near-stream predators to consume proportionally similar levels of these prey resources, or that higher productivity allows insects to grow larger or promotes shifts in population structure to larger-bodied taxa, making them less vulnerable to near-bank predation (Davis et al. 2011). This pattern was discernible despite the coarse estimates of productivity relied upon in the meta-analysis (i.e., estimates of emergence production would have been ideal to use in these models whereas our estimates of stream productivity relied on categorization based on algal biomass and ignored detrital pathways). Although the metadata set was not designed specifically to test such questions, this result suggests that highly disturbed systems with concomitantly lower levels of production, such as urban streams, may have lower stream signatures than would more stable systems.

The study organism variable also improved model fit, and there were often large differences between stream signatures computed using data from different aquatic taxa (Fig. 2). These results provide some indication of the distance that many emergent aquatic insects are capable of dispersing. The data suggests that in some cases, taxa with shorter terrestrial stages or poor flying ability (e.g., mayflies) remained near the stream, while taxa with longer terrestrial stages or better flying ability, such as caddisflies, have larger stream signatures.

In contrast to these trends, midges (Chironomidae) had very large stream signatures (Fig. 2), despite being short-lived, weak fliers (Armitage et al. 1995). However, the modeled 10% stream signature for chironomids extended far beyond the range of collected distance data, indicating both that calculation of this value involved an extreme amount of extrapolation and that stream signature results for this taxa are likely spurious. A disproportionate number of these data subsets were also best fit by a negative exponential, rather than negative power, distribution (Table 1). In spite of accounting for less than 10% of the data subsets, the chironomid data nonetheless accounted for nearly one-quarter of the subsets that were not best fit by a negative power curve. Combined, these lines of evidence suggest that chironomids somehow differ from other taxa in their dispersal strategies, and possibly that they are dispersed by more passive, nondeterministic processes (sensu Rees 1993). Some chironomid taxa are capable of long-distance dispersal by flying vertically, escaping the aerial boundary layer, and becoming entrained in the wind (Delettre 1988), which could explain our results. Given the difficulty in identifying small Diptera, it is also conceivable that some of the “stream chironomid” densities observed in studies in the metadata set were augmented by non-stream species, such as from the terrestrial subsurface or from ephemeral pools (Armitage et al. 1995).

Different study methods yielded different stream signatures, as both 50% and 10% stream signatures were much larger for food web metrics, such as stable isotopes, than for dispersal and terrestrial predator abundance (Table 3). As with the chironomid data, the 10% food web stream signature is based on extensive model extrapolation beyond the range of empirical data (Fig. 1) and should be interpreted with caution. Similarly, all methods used by the studies in this meta-analysis are susceptible to their own unique sources of error, whether from isotopic mixing models (Sanzone et al. 2003), emergent insect sampling difficulties (Jackson and Resh 1989), or the assumption that terrestrial predators are attracted to stream resources (Henschel 2004). However, the order-of-magnitude increase for the 10% stream signature and the tripling of the 50% stream signature for food web incorporation relative to other methods suggests, at a minimum, that food web stream signatures are legitimately larger than those from other methods. As mobile predators carry energy obtained near the stream back to upland roosting habitats, or as aquatic energy is cycled and recycled through the riparian food web (Power and Rainey 2000, Walters et al. 2010), the effect of this aquatic subsidy can extend farther into adjacent terrestrial ecosystems than would be expected based on emergent insect dispersal alone.

The metadata also indicate that riparian predator densities track the distribution of emergent aquatic insects, as the stream signatures and negative power curves for predator attraction and dispersal were similar (Table 3, Fig. 3). Thus, terrestrial predator abundance may be useful as a surrogate for understanding the dispersal distances of emergent aquatic insects from a stream source. Ecologically, this verifies the subsidy's importance to organisms within the terrestrial food web, particularly to higher trophic levels (Marczak et al. 2007), which can have cascading effects throughout the terrestrial ecosystem (Henschel et al. 2001).

Importance of physical (abiotic) explanatory variables

Channel geomorphology improved model fit, while bank type/steepness did not (Table 2). However, stream signatures for channel geomorphology did not follow any consistent trend with respect to a predicted increase in the stream signature with channel complexity (Table 3). Additional field research and more quantitative assessment will be required to better test both this hypothesis and the hypothesis that steeper banks would impair subsidy connectivity.

For the stream width metrics, in contrast, 10% stream signatures were smallest for the smallest streams, indicating that subsidies extended farther in larger streams and rivers than in headwaters (Table 3). For the 50% stream signature, third- to fourth-order large streams (or small rivers) seem to provide optimum conditions for the spatially extensive transmission of dispersing organisms and subsidies. One explanation for

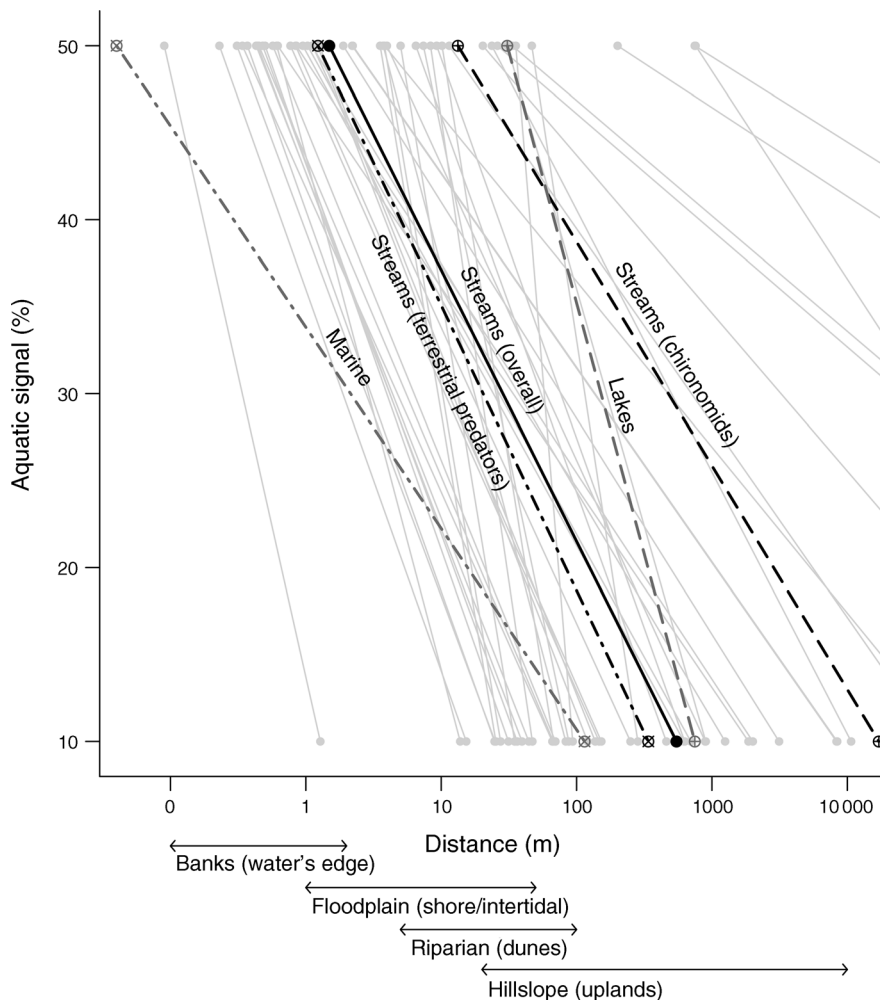


FIG. 3. Signature regression lines from individual case studies containing abundance data in lake and marine ecosystems, compared to the 50% and 10% overall stream signatures from the multilevel, mixed-effects model. The aquatic signal size (%) was calculated as the aquatic value of a given data point, divided by the maximum aquatic value recorded within the given transect. Chironomid and terrestrial predator stream signatures (also both based on abundance data) are included for comparison, as these were the focal organisms of the lake and marine studies, respectively. Gray lines represent individual regression lines for each unique data subset included in the stream meta-analysis to represent the variability in the data. Ecosystems listed below the x -axis are rough approximations of the location of each ecotone for streams, with respective lake and marine analogues in parentheses.

this may be that smaller streams, as physically smaller habitats, may be unable to export much of a subsidy, so predators near the stream banks are able to immediately consume most of the emergence. Subsidy-related predation may also be concentrated very near the banks in larger river ecosystems, before emergent aquatic insects disperse rapidly through expansive large river floodplains and are lost to predators. However, the 10% stream signature increased from the smallest headwater streams to the third- to fourth-order streams, but then plateaued. This suggests that subsidy dynamics are also controlled by ecosystem size such that most of the subsidy remains near the stream irrespective of stream order, but that larger rivers are conducive to allowing more of the subsidy to make it past this bank-side filter. Productivity gradients can also be pronounced in the

case of order-of-magnitude size differences between larger rivers and other lotic freshwaters (Henschel 2004), which may also contribute to stream signature differences. The metadata set is biased toward smaller streams though, so additional studies would be useful in improving the robustness of this result.

Contrary to expectations, neither climate nor terrestrial vegetation structure exerted a control on stream signatures (Table 1). However, these variables were weakly represented in the metadata set (i.e., poorly quantified in included studies), which may explain their lack of apparent effect. Terrestrial vegetation, in particular, should affect terrestrial productivity and consequently the ratio of available terrestrial vs. aquatic energy resources in the food web (Nakano and Murakami 2001), and dense vegetation should reduce



PLATE 1. Emergent aquatic insect taxa can provide resource subsidies to terrestrial food webs far away from the water's edge. This adult mayfly (Heptageniidae) is resting on upland vegetation away from the banks of the North Fork Boise River, Idaho, USA. Photo credit: S. F. Collins.

the dispersal ability of aquatic insects (Jackson and Resh 1989, Cadenasso et al. 2004). Further, vegetation differences might explain some of the variation in stream signatures observed between different stream orders. For example, emergent aquatic insects may disperse farther through open floodplains on large rivers (e.g., Kovats et al. 1996) than through dense forest surrounding headwater streams. In contrast, climate as a master variable may be a poor correlate to variables that affect the stream signature, namely in-stream productivity, which can vary greatly at the meso-scale.

"Stream signatures" in other aquatic environments

Stream and river ecosystems are not unique in providing food web subsidies to a recipient ecosystem. Notably, lake and coastal ecosystems provide similar subsidies (Polis et al. 2004b, Dreyer et al. 2012), and a comparison of different environments in this context can be useful (Gratton and Vander Zanden 2009). The data on subsidy–distance dynamics for these other near-shore ecosystems are not sufficiently comprehensive for meta-analysis, but can be useful to explore (Fig. 3). From these data, the modeled overall stream signatures are generally larger than the corresponding "marine signature" and smaller than the "lake signature," although both curves exist within the range of stream data variability. Data composition helps explain these differences: the lake data are based on chironomid emergence from four lakes in Iceland (Dreyer et al. 2012). Given

that stream chironomid data produced the largest stream signatures (Fig. 2), large lake signatures would also be expected for this taxon. Similarly, the small marine signatures were based on terrestrial predator attraction to marine resources on Gulf of California islands (Polis et al. 2004b), and the stream signatures for predator attraction were also smaller than the overall stream signature values.

Biological "true stream widths"

From a biological, food web, or organismal perspective, stream and river systems are much "wider" than would be expected based only on stream bank location. This is particularly true in the case of the 10% stream signature (550 m overall), but even adding the width of the 50% stream signature (1.5 m) is nontrivial. Median channel width in the metadata set was 3.50 m, so the 50% stream signature across both banks represents a 186% addition to this width. Although larger streams and rivers had larger stream signatures, the proportional increase in biological (relative to hydro-geomorphic) stream width is most pronounced in headwater streams with small channel widths. Because the 50% stream signature represents the distance at which the aquatic resource present is still equivalent to half of the maximum observed subsidy (e.g., the amount above the stream or at the banks), it is reasonable to contend that, biologically, stream widths extend beyond their traditional hydro-geomorphic boundaries.

Applications of the stream signature

The results of this meta-analysis may be of use in informing decision-making concerning riparian buffers. The metadata suggest that most individuals from in-stream populations with terrestrial adult stages do remain near the stream, but many also rely on the riparian zone at distances much greater than the stream channel width. Our anthropocentric, visual definition of a stream's boundary is thus likely inadequate for aquatic macroinvertebrates and their consumers. Failure to establish habitable riparian buffers that allow adequate movement and dispersal of aquatic insects during critical adult mating stages may partially explain why so many stream restorations focused solely on in-channel modifications do not show improvement in aquatic insect bio-indicator metrics (Violin et al. 2011). To allow for ecosystem size that supports the majority of area needed by adult stages of aquatic macroinvertebrates and their consumers, buffer width should at least be equal to the 50% stream signature, although even larger distances such as the 10% stream signature may be required to maintain population viability and gene flow (Macneale et al. 2005, Marczak et al. 2010, but see Finn et al. 2006). Traditional strategies base buffer widths on hydrogeomorphic metrics (e.g., location of channel banks or permanence of flow) or on the composition of riparian vegetation. The stream signature method offers a complementary alternative that focuses specifically on animals such as aquatic Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa or bats that can be the focal points of conservation interest (Lenat and Penrose 1996, Hagen and Sabo 2011).

Model output from this meta-analysis allows the prediction of stream signatures in a wide variety of stream and riparian ecosystems (Appendix B). These models may also be useful for species conservation in predicting dispersal distance requirements for a given taxon, or for predicting riparian habitat needs based on a diverse species assemblage in a given stream. The models should be strongest in predicting stream signatures for food webs in smaller streams that are reliant on emergent aquatic insect taxa, as the majority of studies included in this meta-analysis focused on such systems.

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LITERATURE CITED

- Armitage, P. D., P. S. Cranston, and L. C. V. Pinder. 1995. *The Chironomidae: biology and ecology of non-biting midges*. Chapman and Hall, London, UK.
- Baguette, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography* 26:153–160.
- Ballinger, A., and P. S. Lake. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. *Marine and Freshwater Research* 57:15–28.
- Bastow, J. L., J. L. Sabo, J. C. Finlay, and M. E. Power. 2002. A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. *Oecologia* 131: 261–268.
- Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Ben-David, M., R. T. Bowyer, L. K. Duffy, D. D. Roby, and D. M. Schell. 1998. Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. *Ecology* 79:2567–2571.
- Briers, R. A., H. M. Cariss, and J. H. R. Gee. 2002. Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchments with contrasting land-use. *Archiv für Hydrobiologie* 155:627–644.
- Briers, R. A., H. M. Cariss, R. Geoghegan, and J. H. R. Gee. 2005. The lateral extent of the subsidy from an upland stream to riparian lycosid spiders. *Ecography* 28:165–170.
- Bueno, A. S., R. S. Bruno, T. P. Pimentel, T. M. Sanaiotti, and W. E. Magnusson. 2011. The width of riparian habitats for understory birds in an Amazonian forest. *Ecological Applications* 22:722–734.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- Cadenasso, M. L., S. T. A. Pickett, and K. C. Weathers. 2004. Effects of landscape boundaries on the flux of nutrients, detritus, and organisms. Pages 154–168 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA.
- Carr, D. A., and W. A. Wilcox. 2006. It all depends on what the definition of the word “tributary” is—Supreme Court hears major environmental cases. *Environmental Liability, Enforcement and Penalties Reporter*. April, pp. 147–152.
- Davis, J. M., A. D. Rosemond, and G. E. Small. 2011. Increasing donor ecosystem productivity decreases terrestrial consumer reliance on a stream resource subsidy. *Oecologia* 167:821–834.
- Delettre, Y. R. 1988. Chironomid wing length, dispersal ability and habitat predictability. *Holarctic Ecology* 11:166–170.
- Doyle, M. W., and E. S. Bernhardt. 2010. What is a stream? *Environmental Science and Technology* 45:354–359.
- Dreyer, J., D. Hoekman, and C. Gratton. 2012. Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways. *Oikos* 121:252–258.
- Finn, D. S., and N. L. Poff. 2008. Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. *Arctic, Antarctic, and Alpine Research* 40:638–646.
- Finn, D. S., D. M. Theobald, W. C. Black, and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology* 15:3553–3566.
- Gratton, C., and M. J. Vander Zanden. 2009. Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. *Ecology* 90:2689–2699.
- Hagen, E. M., and J. L. Sabo. 2011. A landscape perspective on bat foraging ecology along rivers: does channel confinement and insect availability influence the response of bats to

- aquatic resources in riverine landscapes? *Oecologia* 166:751–760.
- Helfield, J. M., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82:2403–2409.
- Henschel, J. R. 2004. Subsidized predation along river shores affects terrestrial herbivore and plant success. Pages 189–199 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA.
- Henschel, J. R., D. Mahsberg, and H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93:429–438.
- Iwata, T., S. Nakano, and M. Murakami. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. *Ecography* 26:325–337.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* 67:629–638.
- Jackson, J. K., and V. H. Resh. 1989. Distribution and abundance of adult aquatic insects in the forest adjacent to a northern California stream. *Environmental Entomology* 18:278–283.
- Kitchell, J. F., D. E. Schindler, B. R. Herwig, D. M. Post, M. H. Olson, and M. Oldham. 1999. Nutrient cycling at the landscape scale: the role of diel foraging migrations by geese at the Bosque del Apache National Wildlife Refuge, New Mexico. *Limnology and Oceanography* 44:828–836.
- Kovats, Z. E., J. J. H. Ciborowski, and L. D. Corkum. 1996. Inland dispersal of adult aquatic insects. *Freshwater Biology* 36:265–276.
- Lenat, D. R., and D. L. Penrose. 1996. History of the EPT taxa richness metric. *Bulletin of the North American Benthological Society* 13:305–306.
- Macneale, K. H., B. L. Peckarsky, and G. E. Likens. 2005. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshwater Biology* 50:1117–1130.
- Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. R. Wood, and J. S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecological Applications* 20:126–134.
- Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences USA* 98:166–170.
- Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* 41:934–950.
- Polis, G. A., M. E. Power, and G. R. Huxel, editors. 2004a. *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA.
- Polis, G. A., F. Sánchez-Piñero, P. T. Stapp, W. B. Anderson, and M. D. Rose. 2004b. Trophic flows from water to land: marine input affects food webs of islands and coastal ecosystems worldwide. Pages 200–216 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA.
- Power, M. E., and W. E. Rainey. 2000. Food webs and resource sheds: towards spatially delimiting trophic interactions. Pages 291–313 in M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. *Ecological consequences of habitat heterogeneity*. Blackwell Scientific, Oxford, UK.
- Power, M. E., W. E. Rainey, M. S. Parker, J. L. Sabo, A. Smyth, S. Khandwala, J. C. Finlay, F. C. McNeely, K. Marsee, and C. Anderson. 2004. River-to-watershed subsidies in an old-growth conifer forest. Pages 217–240 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA.
- R Development Core Team. 2013. R version 3.0. R Project for Statistical Computing, Vienna, Austria. www.R-project.org
- Raikow, D. F., D. M. Walters, K. M. Fritz, and M. A. Mills. 2011. The distance that contaminated aquatic subsidies extend into lake riparian zones. *Ecological Applications* 21:983–990.
- Rees, M. 1993. Null models and dispersal distributions: a comment on an article by Caley. *American Naturalist* 141:812–815.
- Richardson, J. S., Y. Zhang, and L. B. Marczak. 2010. Resource subsidies across the land–freshwater interface and responses in recipient communities. *River Research and Applications* 26:55–66.
- Sabo, J. L., and E. M. Hagen. 2012. A network theory for resource exchange between rivers and their watersheds. *Water Resources Research* 48:W04515.
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank, and N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134:238–250.
- Tummers, B. 2006. DataThief III. <http://datathief.org/>
- Violin, C. R., P. Cada, E. B. Sudduth, B. A. Hassett, D. L. Penrose, and E. S. Bernhardt. 2011. Effects of urbanization and urban stream restoration on the physical and biological structure of stream ecosystems. *Ecological Applications* 21:1932–1949.
- Walters, D. M., M. A. Mills, K. M. Fritz, and D. F. Raikow. 2010. Spider-mediated flux of PCBs from contaminated sediments to terrestrial ecosystems and potential risks to arachnidivorous birds. *Environmental Science and Technology* 44:2849–2856.

SUPPLEMENTAL MATERIAL

Appendix A

Literature cited in the stream signature distance–subsidy proportion metadata set ([Ecological Archives E095-006-A1](#)).

Appendix B

Model comparison table and regression coefficients for parameters included in the five best overall stream signature prediction models ([Ecological Archives E095-006-A2](#)).

Supplement

Stream signature metadata set containing all available distance–subsidy proportion data ([Ecological Archives E095-006-S1](#)).