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Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics

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Abstract. Cross-ecosystem movements of material and energy, particularly reciprocal resource fluxes across the freshwater–land interface, have received major attention. Freshwater ecosystems may receive higher amounts of subsidies (i.e., resources produced outside the focal ecosystem) than terrestrial ecosystems, potentially leading to increased secondary production in freshwaters. Here we used a meta-analytic approach to quantify the magnitude and direction of subsidy inputs across the freshwater–land interface and to determine subsequent responses in recipient animals. Terrestrial and freshwater ecosystems differed in the magnitude of subsidies they received, with aquatic ecosystems generally receiving higher subsidies than terrestrial ecosystems. Surprisingly, and despite the large discrepancy in magnitude, the contribution of these subsidies to animal carbon inferred from stable isotope composition did not differ between freshwater and terrestrial ecosystems, likely due to the differences in subsidy quality. The contribution of allochthonous subsidies was highest to primary consumers and predators, suggesting that bottom-up and top-down effects may be affected considerably by the input of allochthonous resources. Future work on subsidies will profit from a food web dynamic approach including indirect trophic interactions and propagating effects.

Key words: allochthonous; autochthonous; bottom-up; cross-ecosystem; food web dynamics; resource subsidy; top-down.

INTRODUCTION

More than half a century ago, Lindeman (1942) suggested two different properties causing structural discrepancy between aquatic and terrestrial ecosystems. The first of these is dominance by unicellular primary producers in aquatic ecosystems vs. multicellular primary producers in terrestrial ecosystems. Second, ecosystems that lie low in the landscape receive more organic and inorganic allochthonous matter (i.e., matter produced outside of the focal ecosystem) than ecosystems in high positions. Since his seminal work, defining differences between aquatic and terrestrial systems has received major attention (e.g., Cyr et al. 1997, Chase 2000, Shurin et al. 2002, 2006). Numerous empirical studies have shown the ecological importance of subsidy (i.e., allochthonous energy) fluxes from aquatic to terrestrial ecosystems and from terrestrial to aquatic ecosystems (reviewed in Polis et al. 1997, Baxter et al. 2005, Richardson et al. 2010, Marcarelli et al. 2011). These reciprocal fluxes might be perceived as a phenomenon that could increase the similarity between terrestrial and aquatic ecosystems by erosion of their boundaries. However, following Lindeman's second hypothesis, aquatic ecosystems are postulated to receive higher amounts of allochthonous energy and material than terrestrial ecosystems. Given that net primary production does not seem to vary systematically between aquatic and terrestrial ecosystems, greater subsidies to aquatic ecosystems might contribute to the tendency for greater secondary production in aquatic ecosystems compared to terrestrial ecosystems (Shurin et al. 2006). It is therefore important to understand if reciprocal subsidies could lead to differences between terrestrial and aquatic ecosystems. Surprisingly, general quantifications and conclusions about the differences in subsidies between terrestrial and aquatic ecosystems, and their potential effects on consumer resource and food web dynamics are still scarce.

Freshwater and terrestrial ecosystems can be linked through several pathways (reviewed in Richardson et al.

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2010). Freshwater ecosystems receive inorganic nutrients and organic matter in dissolved and particulate forms from terrestrial ecosystems (see Plate 1). Aquatic consumers may greatly benefit from the input of such subsidies (Polis et al. 1997). Subsidy fluxes from land to water are largely governed by physical vectors such as gravity, run-off, precipitation, and wind, and perhaps to a lesser extent by biotic vectors such as the dispersal of terrestrial prey organisms. The reversed fluxes from water to land are essentially similar, i.e., terrestrial ecosystems receive nutrients and dissolved and particulate organic matter from freshwater ecosystems (Polis et al. 1997). However, these fluxes need to "overcome" gravity and emerging insects likely play an important role in connecting freshwater to terrestrial ecosystems (Nakano and Murakami 2001, Baxter et al. 2005). Furthermore, terrestrial predators can cross the water–land interface and forage on aquatic prey such as annually returning salmon (Willson and Halupka 1995), and further transport prey carcasses into the riparian ecosystem. Detrital fluxes from water to land have been studied intensively in the case of marine detritus transported to coastal terrestrial ecosystems (Polis et al. 2004). In riparian ecosystems, floods may carry aquatic autochthonous matter onto land, and return allochthonous matter back to terrestrial ecosystems (Nilsson and Grelsson 1990, Jones and Smock 1991, Ben-David et al. 1998). Aquatic insects that die after mass emergence may also be deposited in terrestrial ecosystems (Hoekman et al. 2011).

The consumption of allochthonous energy by recipient animals can result in increased biomass and/or density of the animal population (numerical response). This effect might be referred to as direct, i.e., it solely affects the recipients. Such direct responses in animals are independent of the productivity in donor and recipient systems (Marczak et al. 2007). Numerous empirical examples of direct subsidy effects on recipient animal assemblages have appeared in the last two decades (reviewed in Baxter et al. 2005, Richardson et al. 2010). Yet, numerical responses in animals due to subsidy inputs can spread within the food web beyond the recipient level. These indirect effects are expected to have major consequences for food web dynamics. For instance, Leroux and Loreau (2008) suggested that the amount of subsidy input controlled the strength of trophic cascades, which have been shown to be stronger in aquatic than in terrestrial ecosystems (Shurin et al. 2002). Indirect effects of subsidies are not determined solely by the quantity of the subsidy input, but depend also on the trophic level at which the subsidies enter the food web (Huxel et al. 2002, Leroux and Loreau 2008). Polis and Strong (1996) suggested that bottom-up forces dominated if low trophic levels received subsidies, whereas top-down effects should dominate if high trophic levels were recipients. Several pathways can link freshwater and terrestrial ecosystems (reviewed in Richardson et al. 2010), potentially subsidizing different trophic levels in aquatic and terrestrial ecosystems.

The aims of this study were to quantify (1) the amount of subsidies to freshwater and terrestrial ecosystems, and (2) the responses of aquatic and terrestrial animals to subsidies. We tested (3) whether freshwater and terrestrial ecosystems exhibit systematically different subsidy fluxes, and (4) whether aquatic animals are more strongly subsidized (i.e., show larger responses to subsidies) than terrestrial animals. We provide a framework identifying general differences and similarities of subsidy effects between freshwater and terrestrial ecosystems. In a recent study, Marcarelli et al. (2011) argued to combine quantity and quality estimates of subsidies to investigate the importance of allochthonous resources for aquatic food webs. We extend the perspective of Marcarelli et al. (2011) to terrestrial ecosystems. Further, we incorporate potential consequences of resource subsidies for food web dynamics by estimating the quantitative contribution of subsidies to different trophic levels.

METHODS

We conducted a meta-analysis to achieve our aims. We defined subsidies as any movement of energy in the form of particulate organic carbon (i.e., prey organisms and detritus, but excluding dissolved organic carbon (DOC) and nutrient subsidies) across the freshwater–land interface. DOC subsidies are typically reported as standing stocks rather than input fluxes, and are seldom clearly separated from corresponding autochthonous resources. Hence, we were not able to include DOC in the analysis. We considered multiple results within a single paper as independent observations when they involved different species, life stages of one species, habitats, and subsidy types. Different locations from a single paper were considered independent if they represented different aquatic systems (e.g., different lakes and streams), and different sampling times were considered independent if they represented observations from different seasons. If several measurements were reported from the same location or sampling season, the average over all reported estimates was calculated and used for further analyses.

Data retrieval

We searched *Web of Science* for studies that observationally quantified or manipulated subsidies.[9] The search strategy and list of studies are presented in Appendices A and B. The resulting database included observations focusing on the subsidy, on the recipient community (or species), or both, and also spanned very different methodological approaches. We therefore created four different databases to test the hypotheses.

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[9] http://thomsonreuters.com/products_services/science/science_products/a-z/web_of_science/

First, we used all observations that reported estimates of subsidy inputs (data set 1) as fluxes (e.g., milligrams dry mass per square meter per day, $n = 63$). Second, we used observations reporting the responses of subsidized animals (data set 2) by quantifying the contribution of the subsidy to the animal (assimilation inferred from stable isotope composition of tissues, $n = 221$). Generally, stable isotope analysis integrates resource use over longer time periods compared to stomach content analysis (Tieszen et al. 1983), and therefore provides a more accurate and integrative estimate for utilization of allochthonous resources. A third data set (data set 3) included responses of animals (assimilation inferred from stable isotope composition of tissues, $n = 41$) to salmon subsidies. We treated salmon subsidies separately because (1) salmon are actively foraged by terrestrial animals that cross the freshwater–land boundary (cross-boundary foragers), and (2) the classification of salmon subsidies in the animal's diet as detritus or prey is impaired by their semelparous life cycle (i.e., they die after spawning). Finally, we included field experiments or observations that compared low- and high-subsidy input locations, and that simultaneously reported the responses of subsidized animals either as abundance (number), activity (times spent foraging per hour), biomass (grams per square meter), density (number per square meter), growth rate (millimeters per day), use of foraging space (number per hour) or contribution to diet as inferred from stomach analysis or stable isotope analysis (data set 4). The type of subsidy assessment differed between observations, i.e., low- and high-subsidy input locations were either manipulated experimentally (through removal or exclosure experiments, $n = 12$ and $n = 25$, respectively), or were presented as comparative field assessments (through transects from shore to inland or transects along shore, $n = 54$ and $n = 51$, respectively). Overall, we obtained 467 observations from 71 papers across all four databases.

Predictor and response variables

Across all databases, we categorized each observation by the direction of subsidy input (aquatic to terrestrial or terrestrial to aquatic), type of aquatic ecosystem (lentic or lotic), size of aquatic ecosystem, study location, subsidy category (salmon, detritus, or prey organism), and trophic level of recipient animals (primary consumer, omnivore, or predator), where primary consumers included herbivorous and detritivorous animals. We used log response ratios ($\ln R$) for data derived from data set 4 as a comparable effect size across all studies (as a result, the dimension of the consumer response was irrelevant; $n = 142$):

$$\ln R = \ln \frac{X_{\mathrm{T}}}{X_{\mathrm{C}}}$$

where X_{T} corresponded to the animal response (i.e., abundance, activity, biomass, density, diet inferred from stomach analysis and stable isotope analysis, growth, and use of foraging space) in the treatment (T, high-subsidy input in transects and ambient conditions in exclosure and removal experiments, respectively), and X_{C} corresponded to the animal response in the control (C, low-subsidy input in transects and exclosure and removal treatment, respectively). Mean effect sizes did not differ between type of subsidy assessment ($F_{3,126} = 1.19$, $P = 0.32$) or type of variable quantifying the animal response ($F_{7,122} = 0.98$, $P = 0.76$), and were therefore combined in one data set (hereafter log ratios). We used unweighted meta-analysis because weighing would have emphasized small-scale rather artificial observations over less replicated but perhaps more realistic observations (Osenberg et al. 1999), and because many observations did not report precision estimates.

We used data set 1 to test the following predictions: (1) freshwater ecosystems receive higher inputs of subsidies than terrestrial ecosystems; (2) the input of detritus is higher than the input of prey organisms in freshwater ecosystems; and (3) reciprocal fluxes of prey organisms are similar across the freshwater–land interface. Data sets 2 and 3 and log ratios were used to test the following prediction: (4) aquatic animals are more strongly subsidized (i.e., higher contribution of subsidies and larger log ratios, respectively) than terrestrial animals.

All proportional data (assimilation inferred from stable isotope composition of animal tissue) were arcsine square-root transformed to fit model assumptions. Data of the subsidy input were log-transformed. Analyses were performed with randomized one-way ANOVA in Rundom Pro 3.14 (Jadwitzczak 2010). All other analyses were performed in R 2.10.1 (R Development Core Team 2010).

RESULTS

Overall, observations in lentic ecosystems were highly underrepresented in our data set (only 7.2% of all observations were conducted in or adjacent to lentic ecosystems). Therefore we report here the results from lotic ecosystems; results from lentic ecosystems can be found in Appendix C. The studies reviewed were heterogeneously distributed over the globe (Fig. 1). Most observations were reported from the Northern Hemisphere ($n = 60$ and $n = 218$ for input and contribution, respectively) including Canada, Europe, Eastern Asia, and the United States, whereas the Southern Hemisphere ($n = 3$ and $n = 29$) and equatorial regions (studies for input not available, $n = 1$ for contribution) were highly underrepresented. Lotic systems were generally small, i.e., 38.9% and 23.8% were smaller than 11 m in width or lower than fourth order, respectively. However, 7.4% of the reviewed observations did not report aquatic ecosystem size.

Subsidy input fluxes

Subsidy fluxes across the lotic–terrestrial interface varied over several orders of magnitude, with substan-

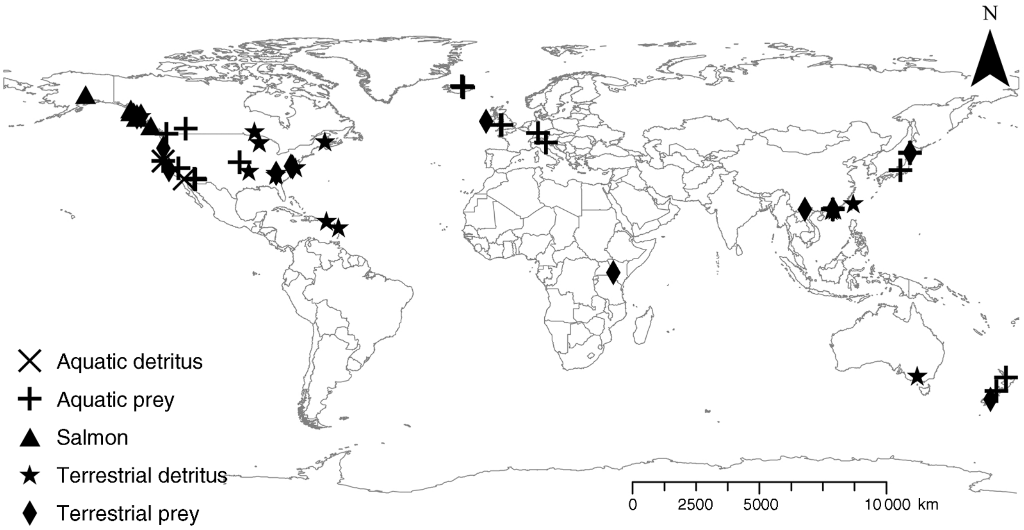

FIG. 1. Distribution map of study locations. Map used with permission: Lantmäteriet Gävle 2010. Medgivande I 2010/0027-0060. Uppsala University Permission No. I 2010/0058.

tially higher variation in fluxes from terrestrial to lotic ecosystems than reciprocal fluxes (Fig. 2A). Fluxes from terrestrial to lotic ecosystems were consistently higher than the reverse ($F_{1,54} = 14.74$, $P < 0.001$; Fig. 2A). The magnitudes of the fluxes of the different subsidy types differed substantially ($F_{2,53} = 30.63$, $P < 0.001$; Fig. 3A). Detrital fluxes from terrestrial to lotic ecosystems were highest, and prey fluxes from lotic to terrestrial ecosystems were lowest (terrestrial detritus, terrestrial prey, $P < 0.001$; terrestrial detritus, lotic prey, $P < 0.001$; terrestrial prey, lotic prey, $P < 0.002$; Fig. 3A). However, we found no measurements of detrital fluxes from lotic to terrestrial ecosystems. Average stream width did not affect the flux of lotic subsidies to terrestrial ecosystems ($r = 0.19$, df = 2, $P = 0.81$) or the flux of terrestrial subsidies to lotic ecosystems ($r = -0.34$, df = 4, $P = 0.51$).

Contribution of subsidies to recipient animals

Overall, the contribution of subsidies to animals was high, constituting on average 39.2% of the animal carbon. In contrast to our prediction, the contribution of subsidies to terrestrial and aquatic animals was similar despite the high discrepancy in subsidy input ($F_{1,246} = 1.90$, $P = 0.17$; Fig. 2B). However, the contribution of different subsidy types to animals varied (Fig. 3B). The contribution of lotic detritus to terrestrial animals was higher than the contribution of terrestrial detritus to lotic animals (post hoc test: $P = 0.005$) and the contribution of terrestrial detritus to lotic animals was higher than the contribution of salmon to terrestrial animals ($P = 0.036$), whereas all other subsidy types contributed similarly to lotic and terrestrial animals ($P > 0.20$; Fig. 3B). Average stream width did not affect the contribution of aquatic subsidies to terrestrial animals ($r = 0.32$, df = 3, $P = 0.59$) or the contribution of terrestrial subsidies to aquatic animals ($r = 0.81$, df = 3, $P = 0.09$).

Contribution to different trophic levels

The contribution of subsidies varied between different trophic levels ($F_{4,243} = 7.07$, $P < 0.001$; Fig. 4). In terrestrial ecosystems, the contribution of subsidies to

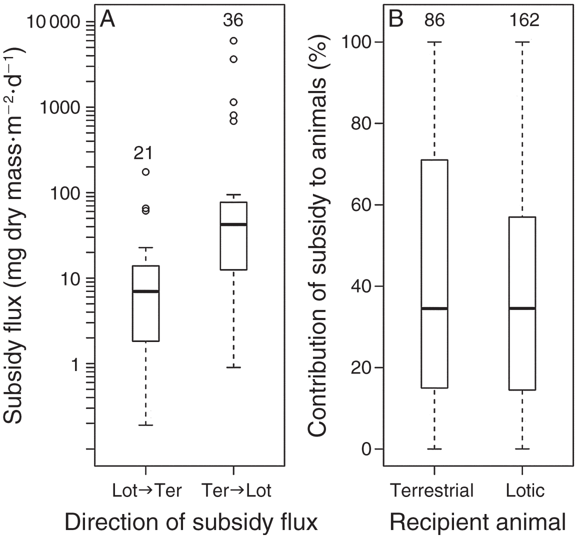

FIG. 2. Overview of (A) subsidy fluxes across the interface between lotic (Lot) and terrestrial (Ter) ecosystems and (B) contribution of subsidies to recipient animals. The numbers above the boxplots denote the number of observations. In the boxplot, the horizontal line shows the median, the bottom and top of the box show the first and third quartiles. The whiskers indicate either the maximum value or, if smaller, 1.5 times the difference in the response variable between its first and third quartiles (i.e., interquartile range). Open circles indicate values that fall outside 1.5 times the interquartile range.

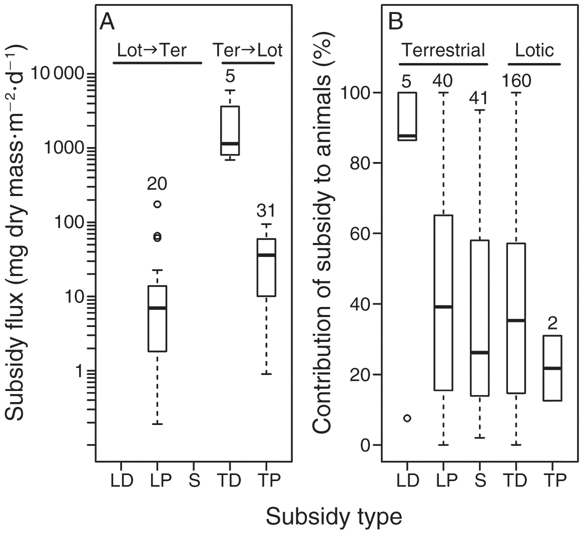

FIG. 3. Overview of different subsidy types. (A) Fluxes of lotic detrital (LD; no data available), lotic prey (LP), and salmon (S; no data available) subsidies to terrestrial (Ter) ecosystems and terrestrial detrital (TD) and terrestrial prey (TP) subsidies to lotic (Lot) ecosystems. (B) Contribution of LD, LP, and S subsidies to terrestrial animals and TD and TP subsidies to lotic animals. The numbers above the boxplots denote the number of observations. In the boxplot, the horizontal line shows the median; the bottom and top of the box show the first and third quartiles. The whiskers indicate either the maximum value or, if smaller, 1.5 times the difference in the response variable between its first and third quartiles (i.e., interquartile range). Open circles indicate values that fall outside 1.5 times the interquartile range.

primary consumers was higher than to predators ($P = 0.028$; Fig. 4A). We did not find any studies that estimated the contribution of subsidies to terrestrial omnivores. In lotic ecosystems, the contribution of subsidies was lowest to omnivores, and did not differ between predators and primary consumers (omnivore–primary consumer, $P = 0.003$; omnivore–predator, $P = 0.012$; primary consumer–predator, $P > 0.99$; Fig. 4B). Across ecosystems, the contribution of subsidies to terrestrial primary consumers was higher than to lotic primary consumers ($P = 0.031$), whereas the contribution of subsidies did not differ between terrestrial and lotic predators ($P > 0.99$).

Responses in recipient animals estimated as log ratios

Overall, animal responses to subsidies were strong as estimated by log ratios. Locations with high-subsidy inputs showed a 2.3-fold greater animal response (mean ln R; 95% bootstrapped confidence intervals (CI): 0.84; 0.66–1.02) compared to locations with low-subsidy input. The responses of animals did not differ between different subsidy types (lotic detritus: 1.32; –0.02–2.66; lotic prey: 0.88; 0.65–1.12; terrestrial detritus: 0.52; 0.03–1.02; terrestrial prey: 0.81; 0.48–1.14; $F_{3,125} = 1.38$, $P = 0.25$). Furthermore, the responses of animals did not differ between aquatic and terrestrial animals (0.68; 0.41–0.95, and 0.93; 0.69–1.19, respectively; t test: $t = 1.39$, $P = 0.17$), whereas the responses of trophic levels differed (lotic primary consumer: 0.41; –0.22–1.05; lotic omnivore: 0.11; –0.71–0.94; lotic predator: 0.88; 0.57–1.19; terrestrial primary consumers: 2.42; –2.06–6.90; terrestrial predator: 0.90; 0.65–1.15; $F_{4,125} = 2.86$, $P = 0.026$). Responses of terrestrial primary consumers to aquatic subsidies were higher than responses of lotic primary consumers ($P = 0.021$), lotic omnivores ($P = 0.032$), and marginally higher than terrestrial predators ($P = 0.09$).

DISCUSSION

Our study shows that the lotic ecosystems reviewed receive substantially higher amounts of subsidies than terrestrial ecosystems. In some geographic regions, however, cross-boundary foragers and physical processes such as floods may play an exceptional role in that they can transfer considerable amounts of aquatic subsidies to terrestrial ecosystems, likely exceeding other fluxes from lotic to terrestrial ecosystems by several orders of magnitude. Despite the high discrepancy in subsidy input, animal responses, i.e., both the contribution of subsidies to animal carbon and log ratios, were similar across lotic and terrestrial ecosystems. Generally, the contribution of subsidies was higher for primary consumers and predators than for omnivores.

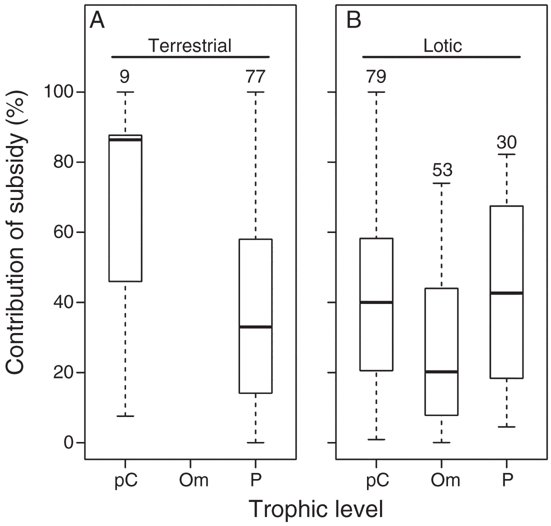

FIG. 4. Overview of the contribution of subsidies to different trophic levels in (A) terrestrial and (B) lotic ecosystems. Key to abbreviations: pC, primary consumer; Om, omnivore; P, predator. Data for terrestrial omnivores were not available. The numbers above the boxplots denote the number of observations. In the boxplot, the horizontal line shows the median; the bottom and top of the box show the first and third quartiles. The whiskers indicate either the maximum value or, if smaller, 1.5 times the difference in the response variable between its first and third quartiles (i.e., interquartile range).

Discrepancy in subsidy input

As proposed by Lindeman (1942), input fluxes of allochthonous resources from terrestrial to freshwater ecosystems often exceed the opposite fluxes from freshwater to terrestrial ecosystems. Fluxes from terrestrial to aquatic ecosystems are dominated by physical processes such as run-off, airborne input, precipitation, and gravity. The input of prey organisms to water bodies is likely a combination of active dispersal and physical transport (e.g., wind-blown input of aerial insects). In contrast, reciprocal fluxes from freshwater to terrestrial ecosystems need to flow "uphill." Biotic vectors such as emerging insects can transport aquatic carbon into riparian ecosystems (Nakano and Murakami 2001). Furthermore, aquatic detritus can be transported by cross-boundary foragers and physical processes such as floods to adjacent terrestrial ecosystems (Nilsson and Grelsson 1990, Ben-David et al. 1998). However, we did not find any estimates of the magnitude of such fluxes. The input of marine carrion and algal wrack to coastal ecosystems through wave movements is well studied (Polis et al. 2004, Orr et al. 2005), and those fluxes have been measured repeatedly (Heck et al. 2008). Our data on contribution of freshwater subsidies to terrestrial animals indicate that terrestrial primary consumers receive aquatic detritus. Our study highlights, however, that fluxes of aquatic detritus to riparian ecosystems have largely been neglected, suggesting that these fluxes are difficult to measure, that ecologists assume that these fluxes are insignificant, and/or that they have simply been ignored. Future studies need to estimate the amount of aquatic detritus that is transported to terrestrial ecosystems.

In some geographic regions, aquatic-to-terrestrial fluxes might exceed terrestrial–to-aquatic fluxes due to the migration of anadromous fish (i.e., fish migrating from the ocean to freshwater to spawn). Anadromy is widespread in northern cool-temperature and subarctic regions of the Northern Hemisphere and less common in south-temperate regions (McDowall 1987). The total flux of salmon transported to terrestrial ecosystems is likely a function of salmon-spawning density, fish size, density of foragers, and habitat (Quinn and Kinnison 1999, Gende et al. 2001, 2004). Although our study is biased towards published data and chosen study locations, the distribution of salmon as a subsidy is restricted to particular geographic regions. Therefore, the massive input of salmon carcasses through cross-boundary foragers or physical processes to adjacent terrestrial ecosystems might be an exception to the general pattern of fluxes between freshwater and terrestrial ecosystems.

Responses of recipient animals

In contrast to our prediction, the contribution of subsidies to terrestrial and aquatic animals was similar despite the large discrepancy in subsidy input. Overall, the input of subsidies resulted in a more than twofold increase in animal response, similar to responses reported by other studies on resource subsidies (Marczak et al. 2007). The reviewed terrestrial–aquatic fluxes were mainly driven by the transport of detritus, whereas aquatic–terrestrial fluxes were dominated by prey organisms. This also means that the overall nutritional quality of the subsidy differs as the stoichiometry of detritus and living organisms differs, potentially by several orders of magnitude (Cross et al. 2005). The terrestrial environment receives high N and P supply per unit of C derived from freshwater, whereas freshwater systems mainly receive C and low amounts of mineral nutrients through the detrital input. In a recent study, Marcarelli et al. (2011) showed that aquatic animals select for high-quality food. Thus the difference in quality might explain the low aquatic animal responses despite high detrital inputs. Terrestrial consumers, in contrast, receive primarily high-quality food through the input of prey organisms. The similar responses in aquatic and terrestrial animals to subsidies despite the large discrepancy in subsidy input are therefore largely governed by the quality of the subsidy.

Freshwater and terrestrial ecosystems did not systematically differ in recipient trophic levels. However, predators and primary consumers generally showed stronger responses to subsidies than omnivores, although we did not find any measurements on terrestrial omnivores consuming aquatic subsidies. Primary consumers are likely the main entrance channel for detrital subsidies, whereas prey subsidies primarily enter recipient food webs at the predator level. The contribution to terrestrial primary consumers was higher than to terrestrial predators and lotic primary consumers. However, only one study was responsible for this difference (five observations; Bastow et al. 2002) and might therefore not be representative. The impact of allochthonous input on food web dynamics is largely determined by the specific trophic level receiving the input, where top-down effects should be influenced if predators receive subsidies, and bottom-up effects should dominate if primary consumers receive subsidies (Polis and Strong 1996). Whether subsidies change the top-down control or cause trophic cascades remains controversial, since the input of subsidies to top consumers has been suggested to both dilute and strengthen top-down effects (Leroux and Loreau 2008). Few studies have specifically addressed the impact of allochthonous resources on the strength of top-down effects, and results are inconsistent (e.g., Nakano et al. 1999, Murakami and Nakano 2002, Sabo and Power 2002*a*, *b*). Bottom-up effects following the input of allochthonous detritus have been repeatedly demonstrated in freshwater ecosystems (Wallace et al. 1997, 1999), and in coastal ecosystems (e.g., Polis and Hurd 1995); however, there is a lack of such studies for riparian ecosystems. Aquatic and terrestrial ecosystems do not differ systematically in primary production (Shurin et al. 2006). At the level of secondary

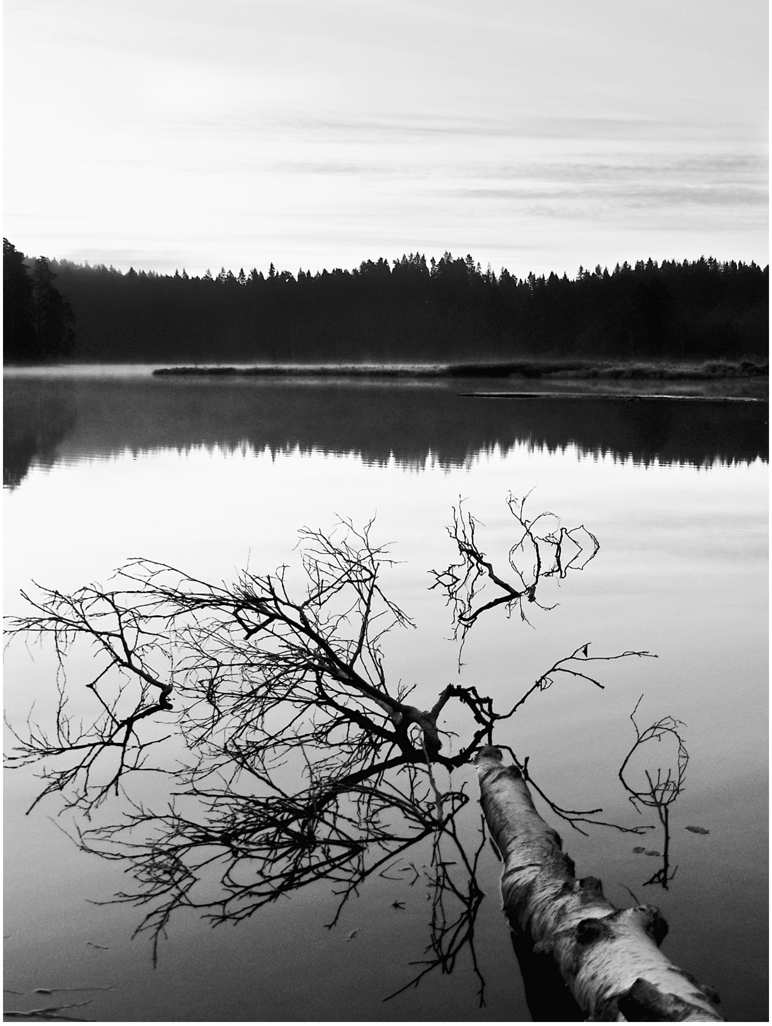

PLATE 1. The relevance of coarse organic matter for food web dynamics remains underappreciated in lake ecosystems: toppled birch tree in a lake in central Sweden. Photo credit: Cristian Gudasz.

production, the detrital pathway dominates over the herbivore pathway in both ecosystems (Cebrian and Duarte 1998, Cebrian 1999), but the level of detritivore production has been suggested to be similar in aquatic and terrestrial ecosystems (Cebrian and Lartigue 2004). However, previous studies were primarily focused on autochthonous detrital production, and might therefore have underestimated the potential of higher decomposition in aquatic ecosystems. If detrital fluxes from freshwater to terrestrial ecosystems are negligible, bottom-up effects caused by the input of terrestrial subsidies to freshwater ecosystems might potentially explain the tendency of higher secondary production in aquatic ecosystems. Empirical studies on propagating effects of subsidies are scarce, and we encourage future research to address propagating food web effects caused by allochthonous resources.

Sources of caveat and future perspectives

There could be a publication bias in that studies only report animals of a community that utilized allochthonous resources, whereas animals that do not consume subsidies despite constant availability of subsidies are not reported. In our literature survey, only one study (Nakano and Murakami 2001) reported that some animals exploited subsidies only temporarily despite constant availability of subsidies. We encourage researchers to report complete results including lack of subsidy consumption to minimize bias against cases of no or little importance of subsidies.

Greater attention to detrital fluxes from freshwater to terrestrial ecosystems is needed. Fluxes of marine detritus to coastal ecosystems have been studied intensively (Polis et al. 2004, Orr et al. 2005, Heck et al. 2008), but little is known about equivalent limnic fluxes and their contribution to recipient terrestrial animals (but see Bastow et al. 2002). Although we found a few measurements of the contribution of freshwater detritus to terrestrial consumers, we did not find any quantitative estimate of the spatial and temporal availability of such detrital fluxes from freshwater to terrestrial ecosystems. Empirical studies are clearly needed to investigate the magnitude of detrital fluxes from freshwater to terrestrial ecosystems and the importance of such fluxes to terrestrial consumers.

The reviewed literature is extremely biased toward lotic ecosystems. Studies on lake ecosystems have mainly focused on DOC subsidies. Heterotrophic bacteria utilize allochthonous DOC as an energy source (Tranvik 1988), and its incorporation in bacterioplankton biomass is a major entry route of externally produced organic carbon into lake food webs (Jansson et al. 2007), although some studies suggest that much of the production does not reach higher trophic levels (Cole et al. 2002, Karlsson 2007). The potential role of other carbon subsidies to lake food webs has largely been neglected (but see, e.g., Pace et al. 2004, Cole et al. 2006; Bartels et al. 2012). Marcarelli et al. (2011) showed that the ratio of gross primary production to ecosystem respiration was comparable in lentic and lotic systems, suggesting similar extents of subsidies. However, the contribution of different subsidy types to respiration processes was not investigated. The exclusion of DOC from our study, necessitated by the lack of input rate data, likely resulted in a significant underestimation of the importance of terrestrial subsidies to freshwater, and in particular to lake ecosystems.

Evidence shows that prey fluxes from either lentic or lotic to terrestrial ecosystems can vary substantially and can be more than three times higher from lotic than from lentic ecosystems (Gratton and Vander Zanden 2009). In our study there was a clear dominance of studies examining lotic ecosystems. Regardless of this bias, the dominating input of subsidies seems to be in the direction from terrestrial to freshwater (lentic or lotic) ecosystems, rather than a reciprocal flux. Whether lentic and lotic animals might be differently subsidized still remains an open question, and further empirical studies investigating the importance of carbon subsidies other than DOC in lentic ecosystems are clearly needed.

We further detected a strong bias of study location. Most reviewed studies concern sites in the Northern Hemisphere, in particular in temperate and subarctic regions. Although we suggest that the observed patterns are likely present in other geographic regions, there is clearly a need for investigation in different climate zones. For instance, in semiarid and arid ecosystems where vegetation is sparse, fluxes from aquatic ecosystems can play an important role, while reciprocal fluxes from terrestrial ecosystems might be weak.

Most lakes worldwide are small, and most of the stream channel length consists of headwater streams (Leopold et al. 1964, Downing et al. 2006). Therefore, our study likely represents the majority of inland freshwater systems. However, since the strength of aquatic–terrestrial linkages depends on ecosystem geometry, i.e., size and shape of the ecosystem (Polis and Hurd 1996, Gratton and Vander Zanden 2009, Vander Zanden and Gratton 2011), more attention needs to be paid to larger aquatic systems. In our study, stream size did not affect the flux of subsidies between terrestrial and lotic ecosystems and the contribution to recipient animals, but the majority of the reviewed streams were small (median 4.35 m; range 1–300 m). Small aquatic ecosystems are governed by edge effects due to the close proximity of the entire ecosystem to the shoreline. In contrast, large aquatic ecosystems are likely less affected by edge effects. Fluxes of coarse detritus and prey from adjacent terrestrial ecosystems to large aquatic ecosystems are probably weak, but subsidies originating farther up in the catchment such as DOC and fine particulate organic matter may still be important. Future studies should compare different subsidy types across small and large aquatic ecosystems.

Human alteration of subsidy flows

Few studies address the effect of human alteration on cross-ecosystem subsidies. Pollution in streams can affect abundance and community composition of terrestrial riparian predators (Paetzold et al. 2011). The removal or addition of species may affect resource fluxes across ecosystems (Baxter et al. 2004, Epanchin et al. 2010, Wesner 2010). Furthermore, changes in the magnitude and composition of subsidies due to species introduction or removal are likely to cascade through the food web in recipient ecosystems (Knight et al. 2005). Alterations in shoreline development such as deforestation or urbanization can reduce the input of terrestrial prey organisms and detritus (France and Peters 1995, England and Rosemond 2004) but can increase the input of dissolved and fine particulate organic matter (Lal 2003). In spite of the differences we discussed in subsidy input and trophic level of recipient animals, aquatic and terrestrial ecosystems are similarly susceptible to anthropogenic changes, and their consequences are poorly explored. Human domination does not stop at the ecosystems' boundaries, but likely alters the amount and quality of material and organisms translocated between them.

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Literature Cited

Bartels, P., J. Cucherousset, C. Gudasz, M. Jansson, J. Karlsson, L. Persson, K. Premke, A. Rubach, K. Steger, L. J. Tranvik, and P. Eklöv. 2012. Terrestrial subsidies to lake food webs: an experimental approach. Oecologia 168:807–818.

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, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656–2663.

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., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83:47–55.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. American Naturalist 154:449–468.

Cebrian, J., and C. M. Duarte. 1998. Patterns in leaf herbivory on seagrasses. Aquatic Botany 60:67–82.

Cebrian, J., and J. Lartigue. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecological Monographs 74:237–259.

Chase, J. M. 2000. Are there real differences among aquatic and terrestrial food webs? Trends in Ecology and Evolution 15:408–412.

Cole, J. J., S. R. Carpenter, J. F. Kitchell, and M. L. Pace. 2002. Pathways of organic carbon utilization in small lakes: results from a whole-lake C-13 addition and coupled model. Limnology and Oceanography 47:1664–1675.

Cole, J. J., S. R. Carpenter, M. L. Pace, M. C. Van de Bogert, J. L. Kitchell, and J. R. Hodgson. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecology Letters 9:558–568.

Cross, W. F., J. P. Benstead, P. C. Frost, and S. A. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. Freshwater Biology 50:1895–1912.

Cyr, H., R. H. Peters, and J. A. Downing. 1997. Population density and community size structure: comparison of aquatic and terrestrial systems. Oikos 80:139–149.

Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, P. Kortelainen, N. F. Caraco, J. M. Melack, and J. J. Middelburg. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51:2388–2397.

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

Epanchin, P. N., R. A. Knapp, and S. P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology 91:2406–2415.

France, R. L., and R. H. Peters. 1995. Predictive model of the effects on lake metabolism of decreased airborne litterfall through riparian deforestation. Conservation Biology 9:1578–1586.

Gende, S. M., T. P. Quinn, R. Hilborn, A. P. Hendry, and B. Dickerson. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos 104:518–528.

Gende, S. M., T. P. Quinn, and M. F. Willson. 2001. Consumption choice by bears feeding on salmon. Oecologia 127:372–382.

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.

Heck, K. L., T. J. B. Carruthers, C. M. Duarte, A. R. Hughes, G. Kendrick, R. J. Orth, and S. W. Williams. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems 11:1198–1210.

Hoekman, D., J. Dreyer, R. D. Jackson, P. A. Townsend, and C. Gratton. 2011. Lake to land subsidies: Experimental addition of aquatic insects increases terrestrial arthropod densities. Ecology 92:2063–2072.

Huxel, G. R., K. McCann, and G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. Ecological Research 17:419–432.

Jadwitzczak, P. 2010. Rundom Pro 3.14. http://www.pjadw.tripod.com

Jansson, M., L. Persson, A. M. De Roos, R. I. Jones, and L. J. Tranvik. 2007. Terrestrial carbon and intraspecific size-variation shape lake ecosystems. Trends in Ecology and Evolution 22:316–322.

Jones, J. B., and L. A. Smock. 1991. Transport and retention of particulate organic matter in 2 low-gradient headwater streams. Journal of the North American Benthological Society 10:115–126.

Karlsson, J. 2007. Different carbon support for respiration and secondary production in unproductive lakes. Oikos 116:1691–1696.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature 437:880–883.

Lal, R. 2003. Soil erosion and the global carbon budget. Environment International 29:437–450.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W.H. Freeman, San Francisco, California, USA.

Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecology Letters 11:1147–1156.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Marcarelli, A. M., C. V. Baxter, M. M. Madeleine, and R. O. Hall. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92:1215–1225.

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.

McDowall, R. M. 1987. The occurrence and distribution of diadromy among fishes. American Fisheries Society Symposium 1:1–13.

Murakami, M., and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through predation by birds. Ecology Letters 5:333–337.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

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.

Nilsson, C., and G. Grelsson. 1990. The effects of litter displacement on riverbank vegetation. Canadian Journal of Botany 68:735–741.

Orr, M., M. Zimmer, D. E. Jelinski, and M. Mews. 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86:1496–1507.

Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology 80:1105–1117.

Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell, J. R. Hodgson, M. C. Van de Bogert, D. L. Bade, E. S. Kritzberg, and D. Bastviken. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427:240–243.

Paetzold, A., M. Smith, P. H. Warren, and L. Maltby. 2011. Environmental impact propagated by cross-system subsidy: Chronic stream pollution controls riparian spider populations. Ecology 92:1711–1716.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands–flow of energy from the marine to terrestrial food webs and the absence of predation. Proceedings of the National Academy of Sciences USA 92:4382–4386.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147:396–423.

Polis, G. A., F. Sánchez-Piñero, P. T. Stapp, W. B. Anderson, and M. D. Rose. 2004. Trophic flows from water to land: Marine inputs affect 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. The University of Chicago Press, Chicago, Illinois, USA.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813–846.

Quinn, T. P., and M. T. Kinnison. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. Oecologia 121:273–282.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richardson, J. S., Y. X. 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 M. E. Power. 2002*a*. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 83:3023–3036.

Sabo, J. L., and M. E. Power. 2002*b*. River–watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860–1869.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Shurin, J. B., D. S. Gruner, and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. Proceedings of the Royal Society B 273:1–9.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal-tissues–implications for delta-C-13 analysis of diet. Oecologia 57:32–37.

Tranvik, L. J. 1988. Availability of dissolved organic carbon for planktonic bacteria in oligotrophic lakes of different humic content. Microbial Ecology 16:311–322.

Vander Zanden, M. J., and C. Gratton. 2011. Blowin' in the wind: reciprocal airborne carbon fluxes between lakes and land. Canadian Journal of Fisheries and Aquatic Sciences 68:170–182.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Wesner, J. S. 2010. Aquatic predation alters a terrestrial prey subsidy. Ecology 91:1435–1444.

Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489–497.

SUPPLEMENTAL MATERIAL

Appendix A

Search strategy (*Ecological Archives* E093-100-A1).

Appendix B

Tables listing studies that observationally quantified or manipulated subsidies for testing our hypotheses (*Ecological Archives* E093-100-A2).

Appendix C

Results for lentic ecosystems (*Ecological Archives* E093-100-A3).