

CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Synthesis: comparing effects of resource and consumer fluxes into recipient food webs using meta-analysis

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Abstract. Here we synthesize empirical research using meta-analysis to compare how consumer and resource fluxes affect recipient food webs. We tested the following hypotheses: (H₁) The direct effects of resource fluxes (bottom-up) should be stronger than the direct effects of consumer fluxes (top-down), because resource fluxes are permanent (do not return to the food web in which they were produced) but consumer fluxes may not be (consumers can leave). (H₂) Following H₁, the indirect effects should attenuate (weaken) more quickly for consumer fluxes than for resource fluxes due to their direct effects being weaker. (H₃) The effects of resource fluxes should be stronger when recipient food webs are in different ecosystems than donor food webs due to differences in elevation that accompany cross-ecosystem food web interfaces, often increasing flux quantity due to gravity, while the effects of consumer fluxes should be stronger when donor and recipient food webs are in the same ecosystem as they should more easily assimilate into the recipient food web. We found no differences in the magnitude of bottom-up and top-down direct effects for resource and consumer fluxes, but top-down direct effects were 122% stronger than top-down indirect effects. Indirect effects of prey and predator fluxes quickly attenuated while indirect effects of non-prey resource and herbivore fluxes did not, as the overall direct effects of prey and predator fluxes were 123% and 163% stronger than their indirect effects, respectively. This result suggests that the magnitude of indirect effects decrease as the trophic level of resource and consumer fluxes increases, and also contrasts with results from studies showing in situ top-down indirect effects are stronger than in situ bottom-up indirect effects. We found that resource and consumer flux effect sizes were similar when they occurred between ecosystems, but when they occurred within ecosystems predator flux effects were 107% stronger than nutrient flux effects. Finally, we found that observational studies had higher effect sizes than manipulative studies. Future research should focus on how resource and consumer fluxes might interact and generate feedbacks in empirical studies of natural food webs, and what ecological factors might affect their relative strength.

Key words: *cross-ecosystem flux; cross-habitat foraging; edge effect; metacommunity; meta-ecosystem; resource subsidy; spatial subsidy; spillover predation; top-down vs. bottom-up control; trophic cascade.*

INTRODUCTION

Ecosystems and habitats are open to fluxes of materials, organisms, and energy, and understanding the effects of these *fluxes* between *local food webs* has been a central goal of recent ecological research (see glossary of italicized terms in Table 1). Theoretical

approaches have used metacommunity and meta-ecosystem models to investigate the effects of simultaneous *resource fluxes* and *consumer fluxes* from one food web to another (Gravel et al. 2010, Leroux and Loreau 2012, Marleau et al. 2014). Yet empirical approaches have studied resource fluxes in isolation from consumer fluxes, and vice versa. Resource fluxes have been studied in the context of *resource subsidies* (Polis et al. 1997, Nakano and Murakami 2001, Bartels et al. 2012), while consumer fluxes have been studied in the context of *edge effects* and *spillover consumers*

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TABLE 1. Glossary of key terms used in this paper (in order of appearance).

Term	Definition
Ecosystem	A community of living organisms interacting with each other and the nonliving components of their environment. Here we define ecosystems as terrestrial, freshwater, or marine, which have fundamentally different abiotic conditions (presence/absence of air, and/or low/high salinity levels) that limit the ability of organisms in one ecosystem to interact in the food web of another ecosystem.
Habitat	An area within an ecosystem comprised of a distinct community type due to environmental heterogeneity. <i>Terrestrial example:</i> in arid systems, deciduous trees dominate the composition of primary producers in riparian habitats while succulents and small shrubs are dominant in upland habitats. <i>Freshwater example:</i> pelagic (open-water) habitats are composed of different algae, invertebrate, and fish species than benthic (bottom-dwelling) habitats. <i>Marine example:</i> coral reef habitats are comprised of different primary producer and invertebrate species than sea grass habitats.
Flux	A flow of materials, organisms, or energy from one ecosystem or habitat to another.
Local food web	A food web whose permeable boundaries are defined by the edge of a given habitat or ecosystem.
Resource flux	A flux of materials, organisms, or energy produced in the donor food web that is transported in some way to a recipient food web in a different ecosystem or habitat, where it becomes a resource used by consumers. <i>Between-ecosystem example:</i> trees produce leaves in terrestrial food webs, which fall into streams and are used as a resource in by detritivores in aquatic food webs. <i>Within-ecosystem example:</i> freshwater mussels filter water-column algae produced in pelagic habitats, and excrete pelagic-derived nutrients that are used as a resource by algae in benthic habitats where mussels live.
Consumer flux or spillover consumer	A flux of organisms from a donor food web that consume resources in a recipient food web. <i>Between-ecosystem example:</i> dragonflies are produced in stream food webs as larvae, but emerge as adults in terrestrial food webs where they feed on terrestrial prey. <i>Within-ecosystem example:</i> nest predators that live in forest habitats often predate nests in grassland habitats near grassland–forest edges.
Edge effect	Changes in abiotic or biotic conditions that occur at the boundaries of habitats or ecosystems.
Recipient food web	A food web that receives a flux from another food web.
Donor food web	A food web from which a flux flows to another food web.
Bottom-up force/effect	An effect on higher trophic levels from lower trophic levels, moving up the food web.
Top-down force/effect	An effect on lower trophic levels from higher trophic levels, moving down the food web.
Direct effect	An effect of a flux on the trophic level that directly interacts with the flux.
Indirect effect	An effect of a flux mediated by intermediate trophic levels between the trophic level directly affected by the flux and the focal trophic level (we did not consider horizontal indirect effects).

(Andren and Angelstam 1988, Rand et al. 2006, Magrath et al. 2014, Martinson and Fagan 2014). Thus, empirical studies have yet to incorporate recent metacommunity and meta-ecosystem theory and simultaneously examine or even compare the relative effects of resource and consumer fluxes in *recipient food webs*.

There is good reason to expect that resource and consumer fluxes should have different effects on recipient food webs, as they represent influxes to a recipient food web at different trophic levels and induce different types of effects. Resource fluxes include flows of nonliving material (nutrients, detritus) or living organisms (producers or prey) from a *donor food web* and can subsidize multiple trophic levels in a recipient food web. They are a *bottom-up force* and tend to have positive effects, increasing recipient food web productivity (Polis et al. 1997, Marczak et al. 2007, Leroux and Loreau 2008). On the other hand, consumer fluxes enter a recipient food web only at upper trophic levels, representing a *top-down force* that can

generate negative effects via consumption (Fagan et al. 1999, Magrath et al. 2014, Martinson and Fagan 2014) or positive effects via increasing prey persistence in metacommunities and increasing recipient food web productivity via nutrient recycling (Orrock et al. 2008, Gravel et al. 2010, Leroux and Loreau 2010). But while theoretical food web studies often investigate simultaneous resource and consumer fluxes between food webs (Holt 2004, Gravel et al. 2010, Marleau et al. 2014), few empirical studies have directly compared the effects of resource and consumer fluxes in recipient food webs.

The relative strengths of bottom-up forces due to increases in in situ production and top-down forces due to increases in in situ consumer abundance in food webs have been well studied (Power 1992, Borer et al. 2006, Gruner et al. 2008). However, resource and consumer fluxes originate outside of a focal food web, and their dynamics (e.g., amount, timing, and duration) are controlled externally (at least partially),

and are thus unique relative to the internal dynamics of a local food web (Polis et al. 1997, Nakano and Murakami 2001, Wesner 2010). This distinguishes fluxes between food webs from simple increases in in situ resource or consumer density, potentially leading to different effects than might be expected from traditional in situ food web models (Huxel and McCann 1998, Leroux and Loreau 2008, Orrock et al. 2008). Therefore, it is important to understand the relative effects of resource and consumer fluxes in recipient food webs, and how they might differ from in situ resource and consumer dynamics.

Here we synthesize studies that examined the effects of resource or consumer fluxes in recipient food webs using meta-analysis. We compile data from empirical studies to test the following hypotheses: (H₁) The *direct effects* of resource fluxes (bottom-up) should be stronger than the direct effects of consumer fluxes (top-down), because resource fluxes are permanent (resource fluxes do not return to the food web in which they were produced) but consumer fluxes may not be (as they often result from a consumer foraging in multiple habitats or ecosystems, so their effects on any given food web may be temporary as their long-term effects are spread throughout multiple food webs). (H₂) The direct effects of resource and consumer fluxes will indirectly affect other trophic levels. However, following H₁, these *indirect effects* should attenuate (weaken) more quickly for consumer fluxes than for resource fluxes due to their direct effects being weaker. And finally, (H₃) the effects of resource fluxes should be stronger when recipient food webs are in different ecosystems than donor food webs, due to differences in elevation that accompany cross-ecosystem food web interfaces, which should increase flux quantity due to gravity (e.g., terrestrial fluxes to aquatic food webs are typically aided by gravity, while fluxes between two different terrestrial food webs are not [Leroux and Loreau 2008]). In contrast, the effects of consumer fluxes should be stronger when crossing within-ecosystem food web interfaces, as they should more easily assimilate into the recipient food web.

METHODS

Literature search

We conducted two separate literature searches using Thomson Reuters Web of Science to collect articles that could be suitable for data extraction. Search 1 was aimed at collecting articles examining resource fluxes between food webs in adjacent habitats or ecosystems, and used the Boolean phrases: “food web subsid*” OR “energy subsid*” OR “resource subsid*” OR “spatial subsid*” OR “allocthonous subsid*” OR “allocthonous input*” OR “cross ecosystem” OR “across ecosystem” OR “cross habitat” OR “across

habitat.” Search 2 was aimed at collecting articles examining consumer fluxes between food webs in adjacent habitats or ecosystems, and used the Boolean phrases: (“ecotone” OR “edge effect*” OR “spillover”) AND (“food web*” OR “trophic” OR “predat*” OR “herbivor*” OR “consumer”). The results of both searches were further refined using the Web of Science “ecology” category and the range of publication years of 1900–2013; these methods yielded 348 results for search 1 and 487 results for search 2. We then selected papers from these search results that used empirical approaches (manipulative or observational) to examine the effects of any type of nutrient, detritus, primary producer, primary consumer, and predator flux between food webs. For results from search 2, we only included studies that either (1) actually documented spillover consumers (i.e., increase in consumer movement from one habitat to another) *and* measured a response of spillover consumers in the recipient food web, or (2) measured consumer effects (e.g., predation/herbivory rates) in *both* the donor and recipient ecosystems. Our rationale for doing so was that increased predation or herbivory in “edge” habitats can be a result of factors unrelated to spillover consumers, such as increased consumer activity due to changes in environmental conditions associated with the edge habitat (Marini et al. 1995). We only wanted to include studies that presented data demonstrating the presence of spillover consumers. Studies that measured consumer effects in a recipient food web without measuring concurrent changes in spillover consumer abundance or measuring consumer effects in both donor and recipient food webs did not meet this standard.

Data extraction

After literature sources were compiled, we extracted data from text, tables, or graphs. We extracted any data that presented the central tendency (mean or median if no mean was presented) in response to a resource subsidy or spillover consumer. If the study was an experimental manipulation, we extracted data from the treatments containing the manipulation and the control. If a manipulation presented time-series data, we extracted data from whichever time point showed the maximum effect in the response. We did so because time lag or seasonal effects could differ depending on trophic level or organism type, and we wanted to measure the greatest response of the focal organism to a consumer or resource flux (e.g., the rate at which predators respond to bottom-up indirect effects from detritus subsidies might lag behind the response of primary consumers, or vertebrate consumer activity might have different seasonal dynamics than invertebrate consumer activity). If the study was observational through a temporal or spatial gradient of resource or consumer flux, we extracted data from periods or locations of the highest and lowest flux following Marczak et al. (2007). If a

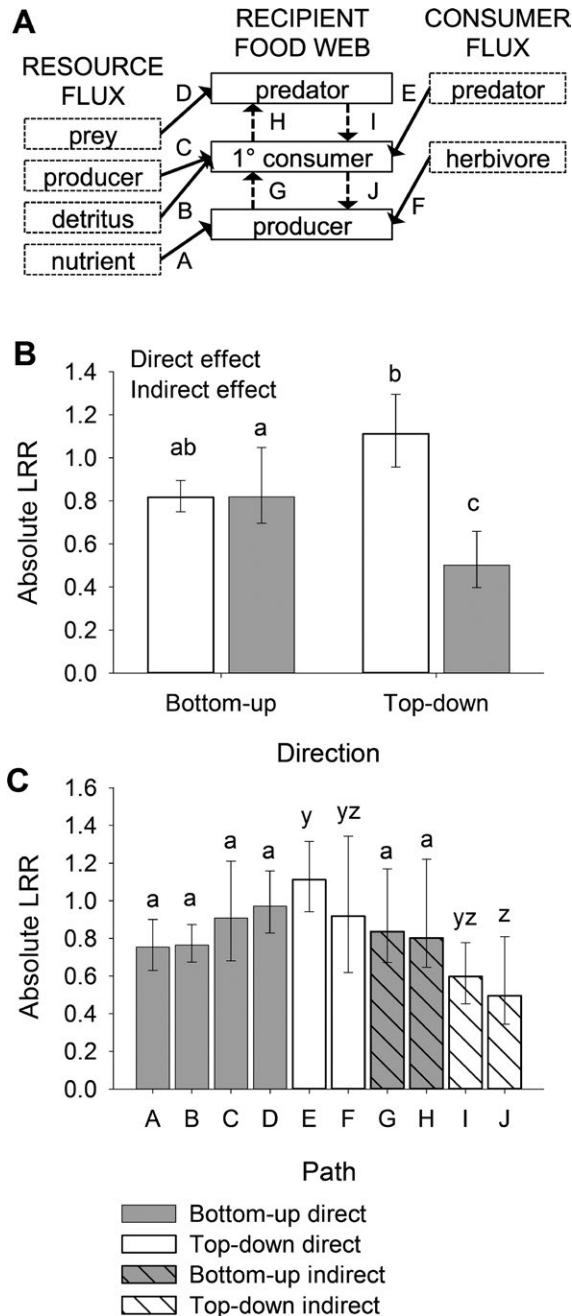


FIG. 1. Panel (A) is a diagram showing potential pathways for food web flux effects in a simplified tritrophic recipient food web. Solid arrows indicate direct effects of a resource or consumer flux (A–F), and dashed arrows indicate indirect effects that propagate from the trophic level receiving a resource or consumer flux (G–J). Paths A–D and G–H represent bottom-up effects, and paths E–F and I–J represent top-down effects. Panels (B–C) show effect sizes (absolute log-response ratio [LRR]) for bottom-up and top-down effects in recipient food webs separated by direct and indirect effects (panel B), and for individual paths that comprise those effects (panel C). Bars are means, and error bars are bootstrapped nonparametric 95% confidence intervals. In panel (B), bars that do not share a letter are significantly different ($P < 0.05$). In panel (C), path labels A–J refer to paths in panel A, and bars within bottom-up or top-down effects that do not share a letter are significantly different ($P < 0.05$).

reference measured the response of a consumer or resource flux on multiple taxa within the recipient food web we considered data from each taxon as a separate study (i.e., individual datum), and if a reference presented data from multiple study sites we treated each site as a separate study as well.

We quantified the log-response ratio (LRR) as our metric of the flux effect size:

$$\ln\left(\frac{\text{treatment mean with flux or highest flux}}{\text{treatment mean with no flux or lowest flux}}\right)$$

(Hedges et al. 1999). For example, in a manipulation of aquatic insect subsidies to riparian food webs, a direct effect on a riparian predator would be measured as the LRR using means of riparian predator abundance with and without the aquatic insect resource flux, while its indirect effect on a terrestrial prey species mediated by the riparian predator would use the means of the terrestrial prey with and without the aquatic insect flux. We corrected for zeros in LRRs by adding the lowest value observed in the study to the zero value following Viola et al. (2010). If no suitable replacement was available, the comparison was removed from the data set. We classified each direct and indirect effect of resource or consumer fluxes in our data set as one of 10 possible paths in a simplified three trophic level food web (primary producer, primary consumer, and predator) receiving different fluxes (Fig. 1A). We chose not to weight LRRs by a measure of precision (i.e., variance) as many studies did not report sample sizes or a measurement of error, and this would have removed ~40% of our data set. Moreover weighting effect sizes does not eliminate bias, but rather is used to transform the data to simpler sampling distributions and increase statistical power (Gurevitch and Hedges 1999). Finally, we used absolute values of LRRs for comparing effects of resource subsidies and spillover consumers against another, as resource and consumer fluxes can generate positive or negative effects in recipient food webs, and we were only interested in differences in magnitude and not differences in sign.

Our literature search yielded studies with a range of response variables for a given trophic level in a food web. We only included response variables most strongly related to abundance, growth, or biomass, and grouped different specific response variables into representative general categories. The most common response variable was abundance (e.g., raw counts of individuals per sample, transect, or unit area, or measurements of biomass per sample, transect, or unit area), but we also included variables related to taxonomic richness, consumption, growth, reproduction, and survival in our analysis (Appendix S1). For each study, we documented the following: (1) the flux type (nutrient, detritus, primary producer, prey, primary consumer, or predator), (2) the response variable measured (as above), (3) the trophic level of the response variable,

simplified into either a predator, primary consumer, primary producer (omnivores were classified to their lowest possible trophic level), (4) whether the effect was a direct effect of the flux or an indirect effect mediated by another trophic level, (5) if it was an indirect effect, we recorded the number of trophic levels between the direct effect of the flux and the indirect effect of interest, (6) the ecosystem that contained the donor food web, (7) the ecosystem that contained the recipient food web, and (8) whether it was an experimental or observational study.

Data analyses

For all analyses, we used a general linear mixed modeling (GLMM) approach using Proc GLIMMIX in SAS 9.4 (SAS Institute, Inc., Cary, NC). Many of our analyses of fixed effects were unbalanced, so we modeled restricted maximum likelihood F tests to determine significance of fixed effects following the framework of Bolker et al. (2009). Following Albertson and Allen (2015), in all GLMMs described below, we accounted for potential bias of multiple studies from a single reference by using the reference ID as a random effect on the intercept, and accounted for potential bias from different response variables and study approaches (experimental vs. observational) by including response variable as a random effect (effect sizes for different response variables and study approaches were significantly different, (Appendix S2). Absolute LRRs were not normally distributed, so we modeled lognormal or Poisson distributions depending on which best fit the data. We calculated nonparametric bootstrapped 95% confidence intervals (10 000 bootstraps) on means of all response variables of interest using the “boot” package in R (R Development Core Team, www.r-project.org), which we present in our figures.

To test H_1 , that the direct bottom-up effects of resource fluxes should be stronger than the direct top-down effects of consumer fluxes, we created a pooled data set containing absolute LRRs from all studies. We used a GLMM with direction (bottom-up [paths A–D, G–H in Fig. 1A] or top-down [paths E–F, I–J in Fig. 1A]) and effect type (direct [paths A–F in Fig. 1A] or indirect [G–J in Fig. 1A]) as fixed effects crossed with each other. We then evaluated the differences between individual paths (as in Fig. 1A) using a GLMM on absolute LRRs with path as a fixed effect. Because we were only interested in differences between paths within the broader categories of bottom-up or top-down effects and not all possible comparisons between paths, if we found a significant effect of path we conducted a priori planned multiple comparisons to test for significant differences between path within bottom-up and top-down effects with Cicchetti’s method to control for alpha for multiple comparisons (Toothaker 1993).

To test H_2 , that indirect effects should attenuate (weaken) more quickly for consumer fluxes than for resource fluxes, we tested for differences in absolute LRRs for each path (as in Fig. 1A) using GLMMs on subsets of our data for each flux type (nutrient, detritus, primary producer, prey, primary consumer, or predator). We followed any significant effect of path with post hoc contrasts using Tukey’s method to control for alpha for multiple comparisons.

To test H_3 , that the effects of resource fluxes should be stronger in ecosystems that are “downhill” from donor ecosystems, while the effects of consumer fluxes should be stronger when crossing food web interfaces within the same ecosystem, we conducted two analyses. Our data set contained studies documenting resource flux effects at all ecosystem interfaces, but did not contain studies documenting consumer flux effects at all interfaces. Therefore we first created a data subset containing only resource flux effects and used a GLMM with interface type (categorized by donor–recipient ecosystems: freshwater-freshwater, freshwater-marine, freshwater-terrestrial, marine-freshwater, marine-marine, marine-terrestrial, terrestrial-freshwater, terrestrial-marine, terrestrial-terrestrial) as the fixed effect and flux type (nutrient, detritus, producer, prey) as a blocking random effect. Second, to allow for a direct comparison between resource and consumer fluxes, we classified food web boundaries as “within” if the flux occurred between food webs in different habitats but *within* the same ecosystem, and as “between” if the flux occurred between food webs *between* different ecosystems. Our data set contained data from all flux types, but only contained studies of primary producer subsidies in food webs within and not between ecosystems, and only two spillover herbivore studies conducted between ecosystems, so we excluded these data and only included studies on nutrient, detritus, and prey and predator fluxes in this analysis. We then used a GLMM with boundary type (within or between) and flux type (nutrient, detritus, producer, prey) as fixed effects. Because we were not interested in all possible pairwise multiple comparisons, we performed two sets of a priori planned contrasts using Cicchetti’s method to control for alpha (Toothaker 1993): (1) we tested for significant differences between resource subsidy/spillover consumer types within each boundary type and (2) we tested for differences between boundary type for each resource subsidy/spillover consumer type.

RESULTS

Our meta-analysis yielded 1029 different studies from 130 references (Supplement). The general linear mixed model (GLMM) with direction (bottom-up/top-down) and effect type (direct/indirect) showed an insignificant effect of direction ($F_{1, 878} = 0.47$, $P = 0.90$), a

significant effect of effect type ($F_{1, 878} = 27.13$, $P < 0.0001$), and a significant direction \times effect type interaction ($F_{1, 878} = 13.29$, $P = 0.0003$). Direct top-down effects were 122% greater in magnitude than indirect top-down effects, while direct and indirect bottom-up effects did not differ in strength (Fig. 1B). When we analyzed effect sizes of individual food web paths, we found that they also significantly differed in magnitude ($F_{9, 872} = 2.73$, $P = 0.0032$, Fig. 1C). A priori planned contrasts showed no significant differences between the bottom-up effects (paths A–D, G–H), but did show significant differences between top-down effects (paths E–F, I–J). Namely, the effect size of Path E (predator flux to primary consumer direct effect, Fig. 1C) was 125% greater than path J (primary consumer to primary producer indirect effect).

We found significant differences between individual food web paths for some flux types, but not for others (Fig. 2). We did not observe significant differences between food web paths for nutrient ($F_{2, 152} = 0.41$, $P = 0.6653$), detritus ($F_{2, 360} = 0.56$, $P = 0.6436$), and primary producer ($F_{1, 30} = 0.01$, $P = 0.9089$) subsidies, or for spillover herbivores ($F_{1, 37} = 0.74$, $P = 0.3944$). However, we did observe significant differences between food web paths for prey subsidies ($F_{2, 125} = 4.64$, $P = 0.0114$) and spillover predators ($F_{2, 133} = 4.47$, $P = 0.0133$). For prey subsidies, the effect size of path D (direct effect) was 65% greater than path I and 2.4-fold greater than path J (both indirect effects), and paths I and J were not significantly different. For spillover predators, the effect of path E (direct effect) was three-fold greater than path G (indirect effect), but path J (indirect effect) was not significantly different from path E or G. Therefore, we found evidence that as indirect effects propagate in a recipient food web from influxes of resources or consumers, indirect effects attenuate (weaken) for prey subsidies and spillover predators, but not for nutrient, detritus, or primary producer subsidies, nor for spillover herbivores.

We found no significant differences between food web interface types on the effects of resource subsidies in recipient food webs when controlling different for resource subsidy types ($F_{8, 693} = 0.90$, $P = 0.5152$, Fig. 3A). When we analyzed how resource subsidy and spillover consumer effects might vary depending on if they crossed ecosystem boundaries or not (i.e., food webs between ecosystems vs. within the same ecosystem), we found an insignificant effect of boundary ($F_{1, 796} = 2.00$, $P = 0.1574$), a significant effect of flux type ($F_{3, 796} = 4.45$, $P = 0.0041$), and an insignificant boundary \times flux type interaction ($F_{3, 797} = 2.54$, $P = 0.0555$). However, a priori planned contrasts showed significant differences between flux types when the donor and recipient food webs were in the same ecosystem (within ecosystem predator fluxes were 107% greater than within ecosystem nutrient fluxes), but not when they were in different ecosystems (Fig. 3B). Yet

contrasts comparing the effect of boundary type for each flux type individually were not significant. This suggests that predators had the strongest effects when the donor and recipient food webs were in the same ecosystem, but effects of all flux types were similar when donor and recipient food webs were in different ecosystems.

DISCUSSION

Here we compared the effects of resource and consumer fluxes in recipient food webs using meta-analysis. Our most striking result was that resource and consumer fluxes have similar direct effect sizes, but different indirect effect sizes. Namely, bottom-up indirect effects were greater in magnitude than top-down indirect effects. Indeed, when we analyzed effects of each flux type individually, we found evidence for attenuation (weakening) of indirect effects for prey and predator fluxes, but not for nutrient, detritus, producer, or herbivore fluxes. This suggests that fluxes which enter at lower trophic levels in a recipient food web and produce bottom-up effects elicit stronger indirect effects than fluxes that enter at higher trophic levels and cascade down. This result is particularly interesting as it contrasts with the effects of in situ top-down and bottom-up forces, as top-down forces tend to have stronger indirect effects than bottom-up forces when they are manipulated within the same food web (Borer et al. 2006). Further, it suggests that it may be reasonable to model consumer responses to resource fluxes as a donor controlled functional response (Poggiale et al. 1998), which has important implications for food web models of resource subsidy effects. Surprisingly, the effects of resource fluxes were similar in magnitude across all ecosystem interfaces, regardless of the direction of the flux (e.g., freshwater-terrestrial vs. terrestrial-freshwater). Moreover, consumer and resource flux effects were similar in size when they occurred between food webs in different ecosystems. In contrast, when fluxes occurred between food webs in the same ecosystem, the effects of predator fluxes were stronger than the effects of nutrient fluxes. Overall these findings have important implications for our understanding of ecosystems as open systems, and are relevant to recent advances in food web, metacommunity, and meta-ecosystem theory.

Consumer fluxes may have weaker indirect effects in recipient food webs than resource fluxes because their effects may be less permanent in a recipient food web, as they often can forage in multiple food webs (most studies on consumer fluxes in our analysis focused on mobile vertebrates or flying insects). Thus their direct effects in any given food web may be temporary, dampening the potential for strong indirect effects that may have delayed responses to direct effects. Indeed, theoretical studies suggest that when top consumers couple multiple local food webs, or different food web

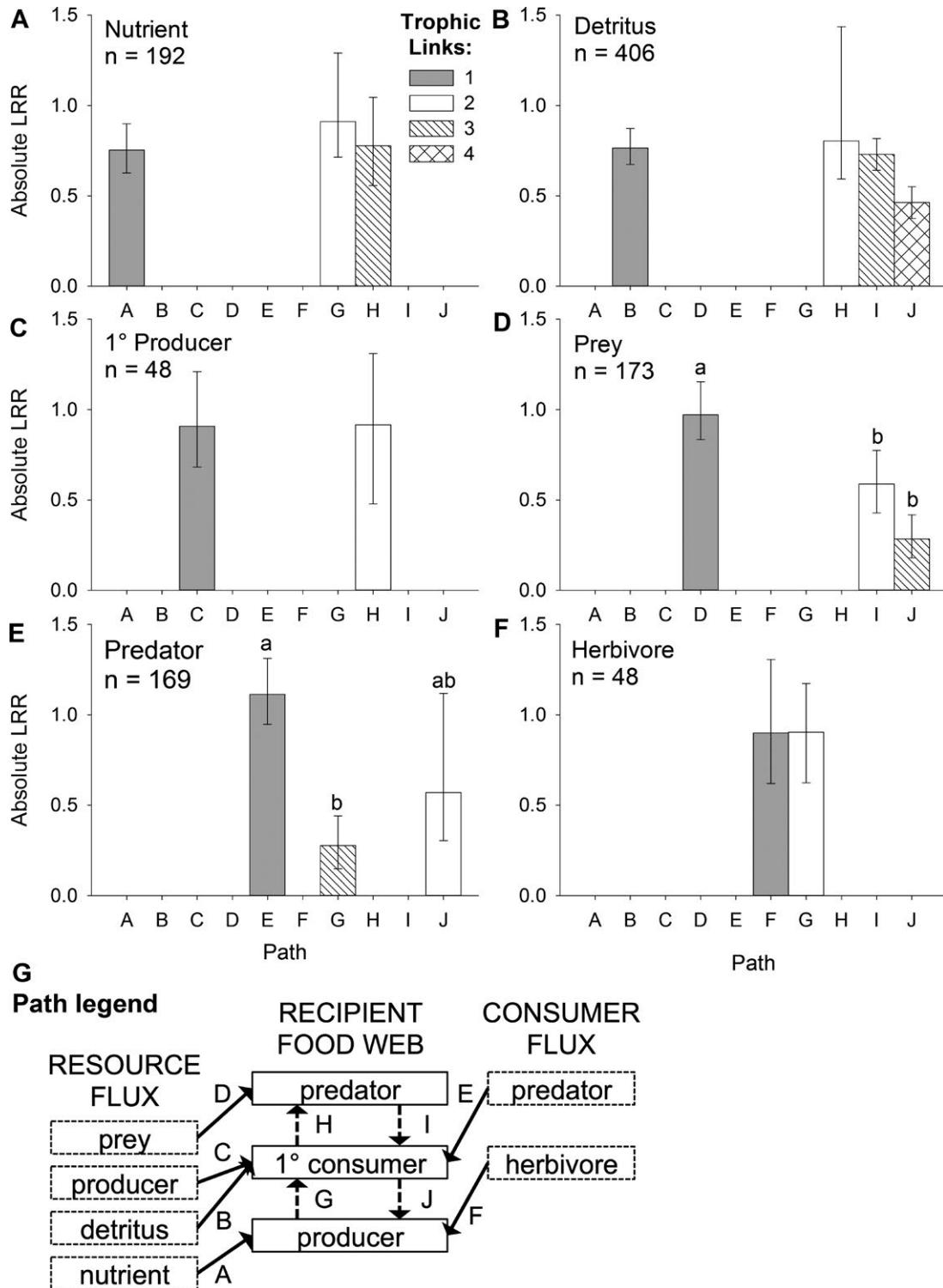


FIG. 2. Effect sizes (absolute log-response ratio [LRR]) for individual food web paths by different flux types: (A) nutrient, (B) detritus, (C) primary producer, (D) prey, (E) predator, and (F) herbivore. Legend for food web paths is shown in G. For panels (A–F), bars are means and error bars are bootstrapped nonparametric 95% confidence intervals, and bars are shaded according to the number of trophic links between the resource or consumer influx and the measured effect (one link [direct effect], solid gray; two links [indirect effect], white; three links [indirect], hatched; four links [indirect], cross-hatched). In panels (D) and (E), bars that do not share a letter are significantly different ($P < 0.05$).

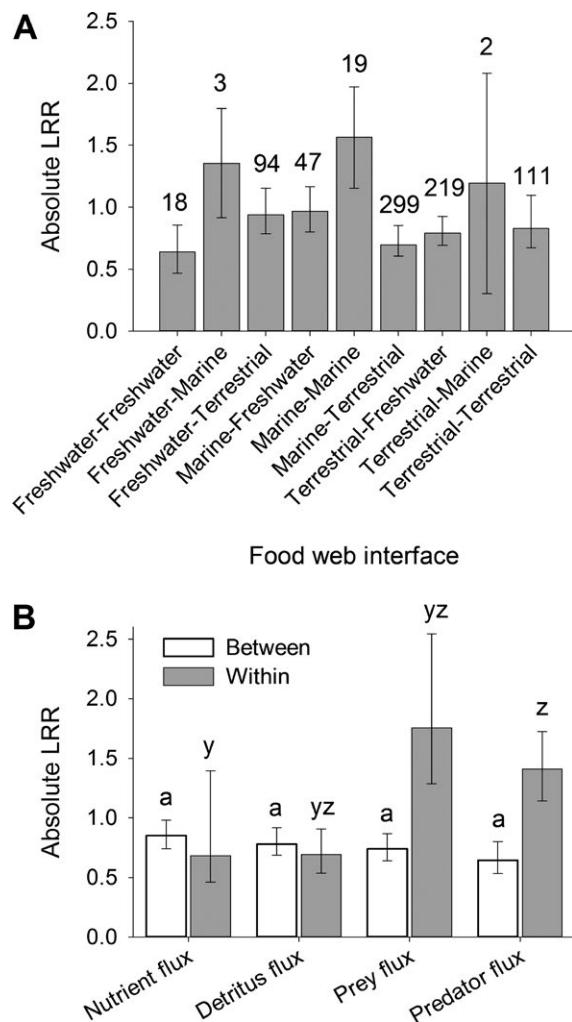


FIG. 3. Effect sizes (absolute log-response ratio [LRR]) of resource and consumer flux effects on recipient food webs for different food web interfaces: (A) effect sizes for resource flux effects across ecosystem types (donor-ecosystem–recipient-ecosystem), (B) effect sizes for nutrient, detritus, prey, and predator fluxes for food web interfaces that occur between or within the same ecosystem type. Bars are means and error bars are bootstrapped nonparametric 95% confidence intervals, and bars that do not share a letter within the between and within categories are significantly different ($P < 0.05$). In (A), sample size (n) is listed above each bar.

compartments fed by different energy channels (e.g., primary producer channel vs. detritus channel), food webs are more stable and less susceptible to runaway consumption (McCann et al. 2005, Rooney et al. 2006, Rooney and McCann 2012). Mobile consumers thus have the luxury of moving when resources become depleted in one food web, or if foraging efforts are more profitable in another, which could dampen the strength of their indirect effects in any given local food web. For example, many waterfowl migrate to productive breeding grounds to match the increased resource demand they might have during mating and

rearing (Polis et al. 1997), and glaucous-winged gulls (*Larus glaucescens*) and coastal brown bears (*Ursus arctos*) move among headwater streams to track migrating salmon (Schindler et al. 2013). Therefore, even if the direct effects of consumer fluxes are strong in a local food web they may be short lived, preventing strong indirect effects from developing over time. On the other hand, resources and prey are typically less mobile than their consumers (Polis et al. 1997), often flowing in the direction of gravity (Leroux and Loreau 2008), and thus typically do not return to their donor food web. For example, even though some adult aquatic insects that emerge from streams return to streams to oviposit, approximately 97% of emergent aquatic insect biomass does not (Jackson and Fisher 1986) and is then instead incorporated into terrestrial food webs as either prey or detritus (Nakano and Murakami 2001, Dreyer et al. 2012). Thus, effects of resource fluxes may simply be stronger because the energy and nutrients contained in their flux remain in the recipient food web, while consumptive or nutrient recycling effects of consumer fluxes may not.

Our meta-analysis also showed different indirect effects of resource fluxes depending on the trophic level that receives it. We showed evidence for attenuation of indirect effects initiated by prey fluxes, but not for nutrient, producer, or detritus fluxes. Several theoretical models have found that the trophic level that receives the flux can have strong implications for food web dynamics, and can point to some likely explanations of our results. Huxel and McCann (1998) and Huxel et al. (2002) used tritrophic food web models that allowed resource fluxes to enter the food web at different trophic levels. They found that when resource subsidies were given to top trophic levels and top predators preferred resource subsidies to in situ prey, food webs became compartmentalized and top predators became decoupled from in situ prey. Hence, the removal of that resource subsidy would likely have little effect on in situ prey if the subsidized predators were decoupled from them. For example, riparian tetragnathid spiders spin horizontal webs over water to catch aquatic insects, receiving nearly 100% of their energy from aquatic sources (Sanzone et al. 2003), and are thus decoupled from in situ terrestrial insect prey. Rather than switch to feeding on terrestrial insects when subsidies are reduced, tetragnathids simply migrate to more profitable areas (Baxter et al. 2004). Thus the potential for apparent mutualisms between aquatic insects and terrestrial insects mediated through tetragnathids may be weak, and while the removal of an aquatic insect subsidy would have strong effects on tetragnathid abundance, that effect would not likely cascade down to terrestrial insects.

Conversely, a model developed by Takimoto et al. (2002) suggests that if a consumer feeds on both prey subsidies and in situ prey, then removal of prey subsidies can have strong indirect effects on in situ prey

if the consumer switches to feeding on in situ prey instead. For example, many fish can feed on both terrestrial invertebrate prey subsidies and in situ benthic invertebrate prey (even though they might prefer the terrestrial subsidy). When terrestrial subsidies are removed, the abundance of benthic invertebrate prey can decrease if fish feed on them instead (Nakano et al. 1999). Yet producers and detritivores may be less likely to specialize on a specific nutrient or detritus subsidy relative to in situ nutrients or detritus. Indeed, Anderson and Polis (1999) found that marine nutrients were incorporated into a wide variety of terrestrial plants, and Polis and Hurd (1996) observed that marine detritus subsidies increased the abundance of many different detritivorous arthropod species. This should lead to an increased potential for indirect effects of resource fluxes to be incorporated by lower trophic levels relative to higher trophic levels. For example, in a long-term manipulation of marine detritus subsidies to terrestrial food webs, Spiller et al. (2010) showed that seaweed additions increased herbivory on in situ producers through a complex multitrophic pathway mediated by four trophic links. Therefore, indirect effects of prey fluxes may be weaker than other types of resource fluxes due to the increased potential to generate compartmentalized food webs, where in situ and subsidized energy channels become decoupled from each other.

Interestingly, our meta-analysis showed that the magnitude of resource flux effects did not vary between ecosystem interface types. Models developed by Leroux and Loreau (2008) suggest that the effects of resource fluxes should be greater when the donor food web is greater in elevation than the recipient food web, as gravity should increase the quantity of resource fluxes to the recipient food web, generating stronger indirect effects. Accordingly we expected the effect of resource fluxes to be greater at interfaces that typically have such a difference in elevation (fluxes from terrestrial-to-freshwater, terrestrial-to-marine, freshwater-to-marine food webs) Yet we found no difference in effect size between any ecosystem interface types. However, we did not measure if the quantity of resource fluxes actually increased at these interfaces, which is a central assumption of the theory posited by Leroux and Loreau (2008). Additionally, this result also contrasts with the results of a previous meta-analysis on resource subsidies, as Marczak et al. (2007) found that resource subsidy effect sizes differed across different freshwater-terrestrial recipient habitat types. But our analysis of interface types was at a larger ecosystem-level scale and we did not specifically consider different habitats within ecosystems, so our results may not be mutually exclusive with the findings of Marczak et al. (2007). Finally, our findings that predator fluxes have stronger effects than nutrient fluxes within the same ecosystem is broadly consistent with what has been observed in studies that manipulate predator abundance and nutrient levels in in situ (Borer et al. 2006).

Nevertheless, our meta-analysis provided evidence that consumer and resource flux effects can differ depending on food web interface type. Predator flux effects were strongest when comparing fluxes occurring between food webs within the same ecosystem, but did not differ when fluxes occurred between food webs in different ecosystems. This is likely because prey and predator fluxes occurring between food webs within the same ecosystem may be more easily assimilated into food webs occurring in the same ecosystem, since their respective predators and prey in the recipient food web are more likely to be more similar to the predators and prey in the donor food web. However, this distinction is not often considered in meta-ecosystem studies.

Future considerations and conclusions

Of the 800+ research articles that our search terms provided, there was not a single empirical study that manipulated resource and consumer fluxes simultaneously. This is striking given the recent theoretical advances in our understanding of spatially linked food webs using models where both resources and consumers flow between food webs within metacommunities and meta-ecosystems (Gravel et al. 2010, Leroux and Loreau 2012, Marleau et al. 2014). Empirical studies of in situ bottom-up and top-down effects in food webs have a long history of manipulating the presence of both basal resources and top consumers simultaneously to investigate interactions between bottom-up and top-down effects (Hillebrand 2002, Borer et al. 2006, Gruner et al. 2008). Accordingly there is both a clear need and a clear precedent to suggest that empirical food web ecologists studying resource or consumer fluxes between food webs ought to consider studying them both simultaneously to better understand the dynamics of food webs linked in space. Moreover, feedbacks are a key component of meta-ecosystem theory (Leroux and Loreau 2012), so future research should also investigate how reciprocal fluxes of resources and consumers may generate feedback loops between ecosystems. Of particular importance might be discerning under what conditions feedbacks caused by resource and consumer fluxes produce positive, negative, or net-neutral effects in local ecosystems.

Although empirical ecologists have studied resource and consumer fluxes separately for the past 20 years, here we explicitly integrate them and compare their relative effects on recipient food webs using meta-analysis. In doing so we were able to test various aspects of spatial food web, metacommunity, and meta-ecosystem theory, which have considered simultaneous resource and consumer fluxes in mathematical models for some time. Importantly we found that resource and consumer flux effects behave differently in recipient food webs, and that the type of interface between the donor and recipient food web has implications for the effects of

predator fluxes, but perhaps not for other flux types. We argue that future research should focus on how resource and consumer fluxes might interact, and what ecological factors might affect their relative strength and the feedbacks between them. The findings reported here add to a number of recent meta-analyses of resource subsidy and spillover consumer effects on food webs, as well as to recent developments in metacommunity and meta-ecosystem theory, which in sum suggest that flows of materials, organisms and energy are ubiquitous across many different ecosystems and strongly affect community dynamics in recipient ecosystems.

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