


# Context dependency of animal resource subsidies

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## ABSTRACT

The transport of resource subsidies by animals has been documented across a range of species and ecosystems. Although many of these studies have shown that animal resource subsidies can have significant effects on nutrient cycling, ecosystem productivity, and food-web structure, there is a great deal of variability in the occurrence and strength of these effects. Here we propose a conceptual framework for understanding the context dependency of animal resource subsidies, and for developing and testing predictions about the effects of animal subsidies over space and time. We propose a general framework, in which abiotic characteristics and animal vector characteristics from the donor ecosystem interact to determine the quantity, quality, timing, and duration (QQTd) of an animal input. The animal input is translated through the lens of recipient ecosystem characteristics, which include both abiotic and consumer characteristics, to yield the QQTd of the subsidy. The translated subsidy influences recipient ecosystem dynamics through effects on both trophic structure and ecosystem function, which may both influence the recipient ecosystem's response to further inputs and feed back to influence the donor ecosystem. We present a review of research on animal resource subsidies across ecosystem boundaries, placed within the context of this framework, and we discuss how the QQTd of resource subsidies can influence trophic structure and ecosystem function in recipient ecosystems. We explore the importance of understanding context dependency of animal resource subsidies in increasingly altered ecosystems, in which the characteristics of both animal vectors and donor and recipient ecosystems may be changing rapidly. Finally, we make recommendations for future research on animal resource subsidies, and resource subsidies in general, that will increase our understanding and predictive capacity about their ecosystem effects.

*Key words:* allochthonous input, animal movement, ecosystem function, food web, migration, spatial subsidy, stoichiometry.

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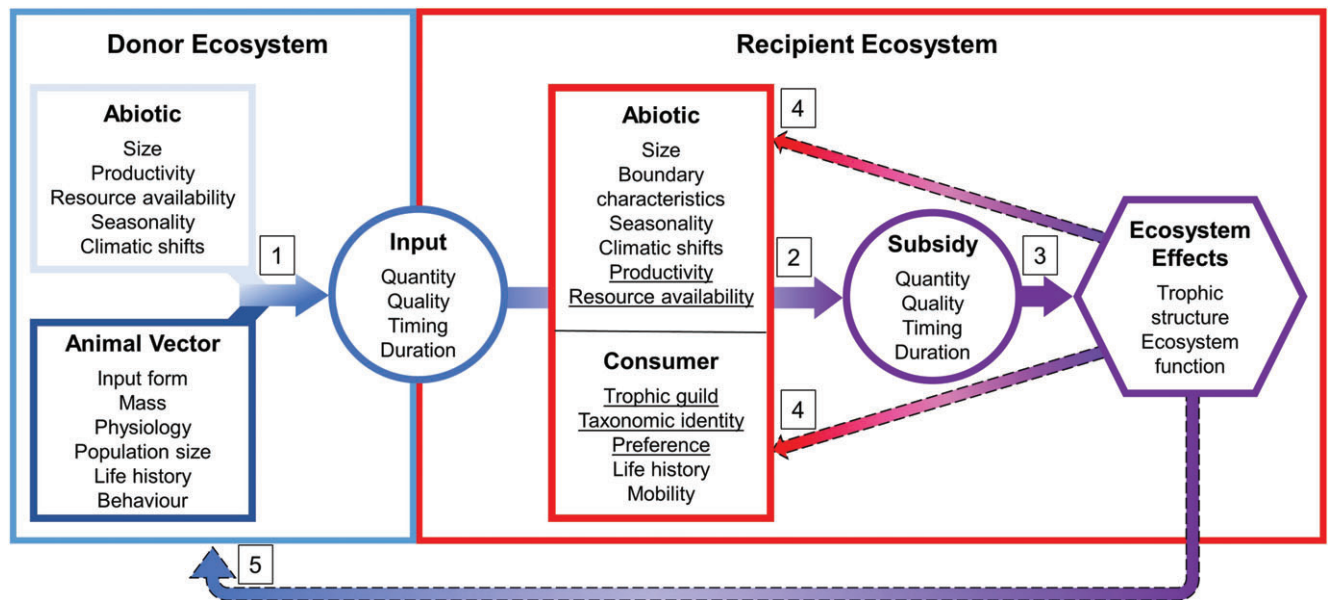
## I. INTRODUCTION

Allochthonous organic matter, produced in one ecosystem and transferred into another, has long been known to play potentially important roles in food-web and ecosystem dynamics (Summerhayes & Elton, 1923; Lindeman, 1942; Likens & Bormann, 1974; Polis, Anderson, & Holt, 1997a). Polis *et al.* (1997a, p. 290) first formally defined spatial subsidies as ‘a donor-controlled resource (prey, detritus, nutrients) from one habitat to a recipient (plant or consumer) from a second habitat which increases population productivity of the recipient, potentially altering consumer–resource dynamics in the recipient ecosystem.’ This landmark paper generated a substantial amount of interest in documenting the occurrence of spatial subsidies and quantifying their ecosystem effects. Twenty years later, we know that spatial subsidies are an important feature of many if not all landscapes, and that they can have strong and complex effects on the recipient ecosystem, altering nutrient cycling (Kitchell *et al.*, 1999; Vanni, 2002), increasing (Marcarelli *et al.*, 2011; Samways & Cunjak, 2015) or decreasing ecosystem productivity (Menninger *et al.*, 2008; Kelly *et al.*, 2013), subsidizing consumer populations (Polis *et al.*, 1997a; Sabo & Power, 2002), and altering food web structure and stability (Huxel & McCann, 1998; Nowlin *et al.*, 2007; Leroux & Loreau, 2008). In some cases, spatial subsidies can move in opposing directions between ecosystems (reciprocal subsidies) (Nakano & Murakami, 2001; Baxter, Fausch, & Saunders, 2005), leading to complex cross-system dynamics that can increase the challenge of untangling the drivers of ecosystem function.

Resource transfers between ecosystems can occur through passive processes, such as wind, atmospheric deposition, overland flow, and riverine flow, but the transfer of resources by animals is particularly interesting because (i) animal resources are often rich in limiting nutrients, (ii) animals can move resources either more quickly along or against naturally established gradients (e.g. upstream or upslope transfers) (Vanni, 2002; Lundberg & Moberg, 2003; Bauer & Hoye, 2014; Earl & Zollner, 2017), and (iii) animals tend to aggregate in space and time, which can lead to ‘hot spots’ and ‘hot moments’ of biogeochemical cycling (McClain *et al.*, 2003; McIntyre *et al.*, 2008). Animal resource inputs also directly link animal population dynamics with

dynamics of both the donor and recipient ecosystems, which adds increasing levels of complexity to ecosystem dynamics (Kitchell *et al.*, 1979; Vanni, 2002). The transfer of allochthonous resources through animal movement has been documented for a range of animal taxa, from zooplankton to salmon to whales, moving resources by excretion, egestion, gametes and/or carcasses. These movements can occur on hourly and daily time scales (as animals move between ecosystems for feeding and roosting), on a monthly to yearly basis (as animals move between ecosystems during different life-history stages or during long-distance migrations), or on multi-year or decadal time scales (as animal populations cycle across years or emerge periodically, e.g. cicada emergence events). The resulting transfer of resources can have large effects on ecosystem function, driving overall metabolism through increased productivity or heterotrophy (Naiman *et al.*, 2009; Holtgrieve & Schindler, 2011; Bellmore *et al.*, 2014; Samways & Cunjak, 2015), and on trophic structure, providing a pulse in high-quality resources that may be selected for by local consumers regardless of relative magnitude of the input (e.g. terrestrial insects falling into streams) (Marcarelli *et al.*, 2011). Animals can also have ecosystem effects through their role as herbivores, predators, or prey, which have been referred to as trophic effects or process subsidies; in this review, we focus on transport effects *via* material or resource subsidies (Flecker *et al.*, 2010; Bauer & Hoye, 2014).

It is now generally accepted that animal resource inputs can provide an important part of the nutrient budget for many ecosystems, but the degree to which their relative importance can vary and the drivers of this variability are not well understood. Difficulties explaining and predicting the relative importance of inputs are likely due to the large number and wide range of variables that influence their magnitude and impacts. Previous syntheses have primarily focused on characteristics of the animal vector (Kitchell *et al.*, 1979; Vanni, 2002; Wardle & Bardgett, 2004; Schmitz, Hawlena & Trussell, 2010; Sitters *et al.*, 2017) or characteristics of the donor and recipient ecosystems (Polis *et al.*, 1997a; Marczak, Thompson & Richardson, 2007; Richardson, Zhang & Marczak, 2010; Marcarelli *et al.*, 2011; Sitters *et al.*, 2015), but not often on interactions between them (although see Atkinson *et al.*, 2016). What is missing, to understand and predict the variability inherent



**Fig. 1.** Conceptual framework illustrating the influence of animal resource subsidies on ecosystem dynamics. 1, Abiotic characteristics of the donor ecosystem (light blue box/arrow) interact with characteristics of the animal vector (dark blue box/arrow) to influence the quantity, quality, timing and duration (QQTd) of a resource input (blue circle) to a recipient ecosystem. 2, Input QQTd are translated through the lens (blue-purple arrow) of both abiotic and consumer characteristics of the recipient ecosystem (red box) to yield the QQTd of the resource subsidy (purple circle). 3, Subsidy QQTd (purple circle/purple arrow) determine ecosystem effects (purple hexagon) in the recipient ecosystem. 4, Recipient ecosystem effects can alter the lens through which future inputs are translated (purple-red dashed arrows) through changes in certain abiotic and consumer characteristics (underlined characteristics are responsive to feedbacks). 5, Recipient ecosystem effects also can feed back into the donor ecosystem to influence future inputs (purple-blue dashed arrow).

in animal resource inputs and their ecosystem effects fully, is a framework for integrating the range of both animal vector and donor and recipient ecosystem characteristics and their interactions with one another.

Our goal herein is to develop a conceptual framework for understanding and predicting the effects of animal resource subsidies on ecosystem dynamics. We propose a general framework, in which (i) abiotic and animal vector characteristics in the donor ecosystem interact to determine the quantity, quality, timing, and duration (QQTd) of an animal input; (ii) the animal input is translated through the lens of recipient ecosystem characteristics, which include both abiotic and consumer characteristics, to yield the QQTd of the subsidy; (iii) the translated subsidy influences the recipient ecosystem through effects on trophic structure and ecosystem function; (iv) these ecosystem effects may influence the recipient ecosystem's response to further inputs; and (v) these effects may feed back to influence the donor ecosystem (Fig. 1, Table 1). Here, we place into this framework the considerable research on animal resource subsidies across ecosystem boundaries. We also provide a set of examples spanning several orders of magnitude of animal body mass to illustrate how subsidy magnitude, stoichiometry and relative importance in the recipient ecosystem can vary by system in sometimes unexpected ways (Table 2). Finally, we explore how this framework might be particularly helpful in studying animal subsidies in a changing world.

## II. SUBSIDY DEFINITION AND CHARACTERISTICS

There has been some discussion in the literature about what constitutes a resource subsidy (Jones, Solomon & Weidel, 2012; Kelly *et al.*, 2013), so we start by clarifying our use of terminology. In the original definition, Polis *et al.* (1997a) specified that a subsidy *increases* consumer production. Anderson, Wait & Stapp (2008, p. 660) modified that definition to include subsidies that 'alter the dynamics of recipient populations and communities', which includes instances in which the subsidy either *promotes* or *inhibits* production. We incorporate the language of the latter in our definition, as inhibited productivity can have strong ecosystem and trophic effects, and we argue that both outcomes could occur in the same recipient ecosystem for a given subsidy, depending on variability in subsidy and ecosystem characteristics. We also recognize that identification of subsidies depends upon delineation of the boundaries between donor and recipient ecosystems. Interestingly, both Polis *et al.* (1997a) and Anderson *et al.* (2008) use 'habitat' to refer to donor and recipient systems. Here we use 'ecosystem', in which ecosystem boundaries are defined functionally as discontinuities or steep gradients in the flux of material and energy or the physical parameters that drive those fluxes (Post *et al.*, 2007). Our definition of a resource subsidy, then, is a resource that originates from

Table 1. Animal and ecosystem characteristics and their primary influence on subsidy quantity (Qt), quality (Ql), timing (T), and duration (D)

Component	Factor	Effect on subsidy	References
Animal characteristics	Input form	Qt, Ql, D	Childress & McIntyre (2015), Vanni (2002) and Wotton & Malmqvist (2001)
	Animal mass	Qt, Ql	Allgeier <i>et al.</i> (2015), Elser <i>et al.</i> (1996), Gillooly <i>et al.</i> (2001), Pershing <i>et al.</i> (2010) and Vanni & McIntyre (2016)
	Physiology	Qt, Ql	Brown <i>et al.</i> (2004), Liess <i>et al.</i> (2015) and Vanni & McIntyre (2016)
	Stoichiometry	Ql	Atkinson <i>et al.</i> (2016), Capps & Flecker (2013a), Dalton & Flecker (2014), Sterner & Elser (2002) and Vanni <i>et al.</i> (2002)
	Population size	Qt	Bump <i>et al.</i> (2009a), Fey <i>et al.</i> (2015b), Habeck & Meehan (2008) and Post <i>et al.</i> (1998)
	Life history	Qt, Ql, T, D	Capps <i>et al.</i> (2015), Luhring <i>et al.</i> (2017), Regester <i>et al.</i> (2006) and Twining <i>et al.</i> (2017)
	Behaviour	Qt, Ql, T, D	Ben-David <i>et al.</i> (1998), Bilby <i>et al.</i> (2003), Meyer <i>et al.</i> (1983), Post <i>et al.</i> (1998) and Subalusky <i>et al.</i> (2015)
Donor ecosystem characteristics	Animal mobility	T, D	Earl & Zollner (2014), Kitchell <i>et al.</i> (1999) and Post <i>et al.</i> (1998)
	Size	Qt, Ql	Gratton & Vander Zanden (2009) and Polis <i>et al.</i> (1997a)
	Productivity	Qt, Ql	Gratton & Vander Zanden (2009) and Polis & Hurd (1996)
	Resource availability	Qt, Ql	Bump <i>et al.</i> (2009b), Elser <i>et al.</i> (2000) and Martin-Creuzburg <i>et al.</i> (2017)
	Seasonality	Qt, T	Baxter <i>et al.</i> (2005), Füreder <i>et al.</i> (2005) and Rundio & Lindley (2008)
Recipient ecosystem characteristics – abiotic	Climatic shifts	Qt, T	Finney <i>et al.</i> (2000), Larsen <i>et al.</i> (2016) and Naiman <i>et al.</i> (2002)
	Size	Qt, D	Hocking & Reimchen (2009) and Polis & Hurd (1995)
	Boundary characteristics	Qt, D	Cadenasso <i>et al.</i> (2004), Polis <i>et al.</i> (1997a) and Post <i>et al.</i> (2007)
	Retention	Qt, D	Harding <i>et al.</i> (2004), Janetski <i>et al.</i> (2009) and Tiegs <i>et al.</i> (2011)
	Productivity	Qt, Ql	Nakano & Murakami (2001), Paetzold <i>et al.</i> (2008) and Polis & Hurd (1996)
	Resource availability	Qt, Ql	Adams <i>et al.</i> (2010), Bellmore <i>et al.</i> (2014) and Marczak <i>et al.</i> (2007)
Recipient ecosystem characteristics – consumer	Seasonality	T	Giroux <i>et al.</i> (2012), Janetski <i>et al.</i> (2009) and Tiegs <i>et al.</i> (2011)
	Climatic shifts	Qt, T	Polis <i>et al.</i> (1997b) and Stapp & Polis (2003a)
	Trophic guild	Ql	Huxel <i>et al.</i> (2002), Leroux & Loreau (2008) and Stapp & Polis (2003b)
	Taxonomic identity	Ql, D	Kendall <i>et al.</i> (2012) and Smith & Baco (2003)
	Preference	Ql, D	Gende <i>et al.</i> (2004) and Shaner & Macko (2011)
	Life history	Qt, D	Anderson <i>et al.</i> (2008) and Levi <i>et al.</i> (2015)
	Mobility	Qt, D	McCann <i>et al.</i> (2005), Paetzold <i>et al.</i> (2008) and Payne & Moore (2006)

production in a donor ecosystem, moves into a recipient ecosystem, and alters the dynamics of a consumer in that recipient ecosystem. This definition still implies knowing something about the effects of a resource in the recipient ecosystem before it can be called a subsidy. Thus, we use the more general term ‘input’ in our conceptual framework (and throughout the majority of this review) to refer to a resource that is produced in a donor ecosystem and transported to a recipient ecosystem, and we use the term ‘subsidy’ to refer to an input that has been incorporated into the recipient ecosystem and has subsequent effects on trophic structure and ecosystem function (Fig. 1).

We propose there are four primary, non-orthogonal axes of variability that can be used to describe an animal input or subsidy: quantity, quality, timing and duration (QQTd). These four variables can be directly influenced by the animal

vector transporting the input and the donor ecosystem from which it emerges, and these variables are also relative to, and can be shaped by, the recipient ecosystem it enters. Examples of animal vector characteristics and donor and recipient ecosystem characteristics and how they influence each of these four parameters are provided in Table 1.

*Quantity* is the total amount of resources moved from the donor to recipient ecosystem, typically measured as biomass. Quantity was the focus of many early studies of spatial subsidies and continues to be the focus of many ecosystem studies (Marcarelli *et al.*, 2011). However, inputs also vary widely in their *quality*, which is typically defined by the chemical characteristics of the resource (lability, stoichiometry, etc.) (Marcarelli *et al.*, 2011; Sitters *et al.*, 2015). In general, higher quality resources have a higher ratio of macro- and micronutrients relative to overall C or biomass.

Table 2. Examples of animal resource subsidies across several orders of magnitude of body size, with the carbon, nitrogen, and phosphorus they move from donor to recipient ecosystems listed as total loading ( $\text{kg yr}^{-1}$ ), aerial loading ( $\text{g m}^{-2} \text{yr}^{-1}$ ) and % of recipient ecosystem levels

Organism	Input type	Donor ecosystem	Recipient ecosystem	C loading $\text{kg year}^{-1}$ $\text{g m}^{-2} \text{year}^{-1}$ % recipient system levels	N loading $\text{kg year}^{-1}$ $\text{g m}^{-2} \text{year}^{-1}$ % recipient system levels	P loading $\text{kg year}^{-1}$ $\text{g m}^{-2} \text{year}^{-1}$ % recipient system levels	References
Aquatic insects	Carcasses	Lakes ( $N=28$ ), streams ( $N=21$ )	Riparian zones	– $0.021, 0.002$	–	–	Gratton & Vander Zanden (2009)
	Carcasses	Lake ( $N=1$ )	Riparian zones	–	$310-7,600$ $0.04-1.0$	$31-760$ $0.004-0.1$	Dreyer <i>et al.</i> (2015)
Snails ( <i>Euchondrus albulus</i> )	Excretion, egestion	Endolithic lichens	Desert soils	–	– $0.02-0.03$ 11%	–	Jones & Shachak (1990)
Cicadas ( <i>Magicicada</i> spp.)	Carcasses	Belowground	Small ponds and low-order streams	– $0.07-28.90$	– $0.02-5.43$ $1.4-105\%^a$	– $0.003-0.35$ $0.3-86\%^a$	Nowlin <i>et al.</i> (2007)
Wood frogs ( <i>Lithobates sylvaticus</i> )	Excretion, egg masses	Forest	Pond	$0.42$ $0.15$	$0.10$ $0.03$	$0.01$ $0.003$	Capps <i>et al.</i> (2015)
	Juvenile emergence	Pond	Forest	$1.0$ $0.35$	$0.26$ $0.09$	$0.06$ $0.02$	
Alewife ( <i>Alosa pseudoharengus</i> ) (present – pre-colonial) <sup>b</sup>	Carcasses, gametes, excretion	Ocean	Lake	–	$252-4,193$ $0.9-14.6$	$36-13$ $0.1-1.8$	West <i>et al.</i> (2010) and Twining <i>et al.</i> (2013)
Grunts ( <i>Haemulon flavolineatum</i> and <i>H. plumieri</i> ) <sup>c</sup>	Excretion, egestion	Sea grass beds	Coral reef heads	–	$5-68\%$	$23-95\%$	Meyer & Schultz (1985)
Bonneville cut-throat trout ( <i>Oncorhynchus clarkia utah</i> ) and Kokanee salmon ( <i>O. nerka</i> ) <sup>d</sup>	Excretion	Reservoir	Tributaries	–	$19.9-49.1$ $1.0-1.4\%$	$2.1-6.9$ $2.6-4.4\%$	Wheeler <i>et al.</i> (2015)
Sockeye salmon ( <i>Oncorhynchus nerka</i> )	Adult carcasses	Ocean	Rivers ( $N=4$ )	– $59.9-91.6$	– $2.5-4.7$ $6-859\%$	– $0.3-0.8$ $1-388\%$	Moore & Schindler (2004)
	Juvenile export	Rivers ( $N=4$ )	Ocean	–	$6,645-29,054$	$1,150-5,000$	
Lesser snow geese ( <i>Chen caurulegens caurulegens</i> ) and Ross' geese ( <i>C. rossii</i> )	Excretion	Agricultural fields	Wetlands	–	$8,780$ $17.5$ $40\%$	$1,090$ $2.2$ $75\%$	Post <i>et al.</i> (1998)
Alligators ( <i>Alligator mississippiensis</i> )	Excretion	Streams	Seasonal wetlands	–	$27$ $0.03$	$9$ $0.01$	Subalasky, Fitzgerald & Smith (2009)
Loggerhead sea turtles ( <i>Caretta caretta</i> ) <sup>f</sup>	Eggs	Ocean	Beach	–	$0.7\%^c$ $734.4$ $3.0$	$2.3\%^c$ $56.8$ $0.3$	Bouchard & Bjorndal (2000)



Table 2. Continued

Organism	Input type	Donor ecosystem	Recipient ecosystem	C loading		N loading		P loading		References
				kg year <sup>-1</sup>	g m <sup>-2</sup> year <sup>-1</sup>	kg year <sup>-1</sup>	g m <sup>-2</sup> year <sup>-1</sup>	kg year <sup>-1</sup>	g m <sup>-2</sup> year <sup>-1</sup>	
Wildebeest ( <i>Connochaetes taurinus</i> ) <sup>g</sup>	Carcasses	Savanna grasslands	River	107,000	141.4	25,000	32.6	13,000	16.7	Subalusky <i>et al.</i> (2017)
Grizzly bears ( <i>Ursus arctos</i> ) <sup>h</sup>	Excretion, egestion	Marine-derived nutrients from salmon in streams	Riparian white spruce	–	–	6–78%	23.1–56.3	31–451%	–	Hilderbrand <i>et al.</i> (1999)
Hippopotami ( <i>Hippopotamus amphibius</i> )	Excretion, egestion	Savanna grasslands	River	1,277,000	502.3	179,600	70.6	17,600	6.9	Subalusky <i>et al.</i> (2015)
Marine mammals	Excretion, egestion	Deep ocean zone	Phototrophic ocean zone	–	–	27%	23 × 10 <sup>6</sup>	29%	–	Roman & McCarthy (2010)
Whales (present – pre-whaling)	Carcasses	Ocean	Sea floor	29 × 10 <sup>6</sup> –193 × 10 <sup>6</sup>	–	1%	–	–	–	Pershing <i>et al.</i> (2010)

<sup>a</sup>Compared to inputs from autumn leaf senescence.  
<sup>b</sup>Estimates are net nutrient flux, as the sum of nutrients from adult carcasses, excretion and gametes minus those exported by juveniles.  
<sup>c</sup>Values are given for particulate organic carbon and total soluble N and P.  
<sup>d</sup>All N and P values given are for ammonium (NH<sub>4</sub>-N) and soluble reactive phosphorus (SRP).  
<sup>e</sup>Compared to inputs from litterfall.  
<sup>f</sup>Estimates are net nutrient flux, as the sum of nutrients from eggs minus those exported by hatchlings.  
<sup>g</sup>Annual loading for all drownings; aerial extent and % recipient levels for individual drownings.  
<sup>h</sup>Values are given per individual bear.

Both the quantity and quality of an input are fundamentally linked to the animal making the movements, but they are also shaped directly by the donor ecosystem from which the animals emanate and are ultimately measured relative to characteristics of the recipient ecosystem (Table 1).

The timing of the input and the duration over which it is available to the recipient ecosystem can also shape an input's effect and, as with quantity and quality, these two variables are inter-related. *Timing* refers to when the input enters the recipient ecosystem relative to other environmental factors (temperature, rainfall, etc.) and is therefore often related to seasonal variability. *Duration* is the length of time for which an input is available to the recipient ecosystem. Duration may be influenced by the frequency and length of loading events, and by retention of the input in the recipient ecosystem (i.e. time to complete utilization). These factors are largely shaped by the animal vector and donor ecosystem, as timing and seasonality vary with species and geographic location; however, timing and duration also may be influenced by both abiotic and consumer characteristics in the recipient ecosystem (Table 1).

### III. ANIMAL VECTOR CHARACTERISTICS

#### (1) Input form

Animal inputs typically are one or a combination of four primary forms: egestion, excretion, gametes and carcasses. Carbon and nutrients that are ingested but not assimilated are released through egestion (faeces) (Wotton & Malmqvist, 2001). Material that is assimilated can be excreted through kidneys or similar organs (e.g. as urine, guano), can be used for secondary production through growth or reproduction, or, for carbon, can be lost through respiration (Vanni, 2002; Schmitz *et al.*, 2010). Material incorporated into animal tissue can ultimately become available through production of gametes or as a carcass when the animal dies. We include as resource subsidies both carcasses of animals that died outside the recipient ecosystem and were transported in, and those of animals that died within the recipient ecosystem, provided the majority of the carcass biomass originated from the donor ecosystem. The form of input an animal vector contributes is largely determined by the animal's behaviour and life-history patterns.

The input form can influence its quantity, quality, and duration. Excretion supplies soluble nutrients, which are often inorganic, and can be easily assimilated by primary producers or bacterial communities, making it a relatively high-quality resource (Vanni, 2002). However, excretion is usually present in lower quantities than egestion or carcasses, and due to its solubility, may be transported out of the system quickly. Egestion supplies some particulate nutrients, but is typically high in carbon and requires mineralization, making it a relatively lower quality resource. However, egestion typically persists in the ecosystem for longer time periods than excretion (Wotton & Malmqvist, 2001; Joyce & Wotton,

2008). A number of studies have examined the influence of animal excretion on ecosystem function (Atkinson *et al.*, 2016). Far fewer have studied the influence of egestion, largely due to difficulties estimating it in the field, although research that has explicitly investigated egestion has shown it can play an important role in biogeochemical cycles and food webs (Joyce, Warren & Wotton, 2007; Halvorson *et al.*, 2015; Masese *et al.*, 2015; Atkinson *et al.*, 2016; Stears *et al.*, 2018; Subalusky *et al.*, 2018). Animal tissue, primarily through gametes and carcasses, is typically high in nutrients as well as carbon, but also requires mineralization for uptake and may break down over a longer time, providing a high-quality but potentially more complex resource than excretion and egestion (Wipfli *et al.*, 2010). Input form interacts with a range of other animal characteristics ultimately to influence input characteristics.

#### (2) Animal mass and physiology

Animal mass, metabolic type and whether they are invertebrates or vertebrates are primary determinants of input quantity because they directly determine carcass size, regulate egestion and excretion rates by setting an animal's daily energy requirements, and ultimately influence population size (Tables 1, 2) (Gillooly *et al.*, 2001; Brown *et al.*, 2004). Two recent meta-analyses of excretion rates of aquatic ectotherms found that body mass explained a large amount of variation in excretion rates (Allgeier *et al.*, 2015; Vanni & McIntyre, 2016), and that vertebrates had higher rates of excretion than invertebrates even when accounting for body mass (Vanni & McIntyre, 2016). In a sensitivity analysis of alewife (*Alosa pseudoharengus*) nutrient loading estimates, animal mass had the largest effect *via* its impact on excretion rate and carcass mass (West *et al.*, 2010). When the input is excretion and egestion, the *per capita* input is determined by the amount of food consumed, nutritional content of the food, assimilation efficiency of the animal and amount of time excreting/egesting in the recipient ecosystem. Body mass and metabolic type are the primary determinants of daily energetic requirements, which interact with the energetic content of the diet to determine the amount of food consumed and assimilation efficiency. Nutrient excretion rates usually scale allometrically with body mass, although there is variation in scaling rates across species and between N and P excretion (Vanni, 2002; Allgeier *et al.*, 2015 ; Vanni & McIntyre, 2016). Endothermic animals typically have higher metabolic demands, meaning higher turnover rates of consumed and metabolized resources (Brown *et al.*, 2004), although endotherms in cold regions can have lower excretion rates due to increased growth efficiency (Liess *et al.*, 2015). When the input is carcasses, *per capita* input quantity is equivalent to the animal's body mass. Animal mass also may influence input duration, as larger carcasses will take longer to decompose.

Animal mass and whether they are vertebrates or invertebrates also may influence the stoichiometry of both carcasses and excretion/egestion, and therefore input quality (Table 1). As vertebrate animals grow larger, the relative

proportion of skin, muscle and bone changes, leading to a general increase in P relative to C and N with increasing body size, largely due to the high P concentration in bones (Elser *et al.*, 1996). This could make large vertebrate carcasses a higher quality resource than small vertebrate carcasses, and vertebrate carcasses in general a higher quality resource than invertebrate ones, if P is a limiting nutrient in the ecosystem. However, because much of the P is in bones or scales, both of which have a much lower decay rate than soft tissues, the P may not be readily or rapidly available to the recipient ecosystem (Vanni, Boros & McIntyre, 2013). Almost half of the dry mass and 95% of the P in a wildebeest (*Connochaetes taurinus*) carcass is bone, but it takes 170 times longer to decay than muscle tissue (Subalusky *et al.*, 2017). The elevated dietary need for P to build and maintain bone may also negatively impact the quality of excretion. According to stoichiometric theory, an animal with a lower body N:P ratio will excrete nutrients with a higher N:P ratio (Sturner & Elser, 2002; McIntyre & Flecker, 2010). However, there was little support for this prediction in two meta-analyses of animal excretion rates (Allgeier *et al.*, 2015; Vanni & McIntyre, 2016). This relationship may be largely influenced by the rate at which animals are growing and allocating resources to different tissues and whether the tissues are metabolically active or not (Atkinson *et al.*, 2016).

There are other factors that may influence the nutritional status or body content of an animal and thus the amount and/or stoichiometry of resources it excretes. Animals that are growing, reproducing, migrating, or reserving nutrients for other purposes may excrete or egest relatively fewer or lower quality resources (Brown *et al.*, 2004; Liess *et al.*, 2015). Although many estimates of animal excretion assume homeostasis, or the relative constancy of the nutrient content of animal tissue, there is increasing evidence showing that tissue stoichiometry within a species may be variable over time (Small & Pringle, 2010; Atkinson *et al.*, 2016). Body stoichiometry may be influenced by different growth rates or resource-use patterns associated with different ontogenetic stages or life-history strategies (Werner & Gilliam, 1984; Elser *et al.*, 1996; Atkinson *et al.*, 2016). Ecological stoichiometry also predicts a positive relationship between dietary and waste stoichiometric ratios, suggesting that animals feeding at higher trophic levels are likely to excrete/egest higher quality resources than primary consumers, which have relatively high C:nutrient ratios for consumption and egestion (Sturner & Elser, 2002). However, in a meta-analysis of aquatic animals, Vanni & McIntyre (2016) found that primary consumers excreted as much nutrients as carnivores. Species-specific differences also may be important, such as the relatively high amounts of P sequestered for armour growth in loriciid catfish, and their subsequently high N:P ratio for excretion (Vanni *et al.*, 2002; Knoll *et al.*, 2009; Capps & Flecker, 2013a). Changes in an animal's physiology in response to fear of predation can also influence input quality *via* influences on body stoichiometry

(Hawlena & Schmitz, 2010; Schmitz *et al.*, 2010; Dalton & Flecker, 2014).

Body mass also influences animal mobility, which can influence the timing and duration of an input, in addition to the scale of connection between donor and recipient systems (Table 1) (Paetzold, Lee & Post, 2008; Earl & Zollner, 2014, 2017). Small-bodied animals are more likely to make shorter-distance movements that connect proximate donor and recipient systems that may already be linked by passive transport of resources. Insect emergence inputs to riparian zones are highest immediately adjacent to the donor ecosystem and decline inland (Gratton & Vander Zanden, 2009; Muehlbauer *et al.*, 2014; Dreyer *et al.*, 2015). Migration distances tend to increase with body size, from 12 km for black-tailed jackrabbits (*Lepus californicus*) to over 4000 km for caribou (*Rangifer tarandus*) (Berger, 2004); however, there are many exceptions to this generalization, particularly for animals that swim or fly.

### (3) Population size

Population size is a major driver of input quantity because it determines the number of animals serving as nutrient vectors (Table 1). Population size had the greatest effect on estimates of nutrient loading by excretion for waterfowl in wetlands (Post *et al.*, 1998) and moose (*Alces alces*) in boreal forests (Bump, Peterson & Vucetich, 2009a) and was second only to the effect of animal mass for loading by alewife in lakes (West *et al.*, 2010), both because these estimates were very sensitive to changes in population size and because there can be considerable variation in population size relative to other drivers of inputs. Population size can offset the effect of small body size and lead to equivalent or even higher overall loading levels. The largest estimated flux of energy transported by a single population ( $1.3 \times 10^6$  tons) is *via* reproductive output from a spawning herring (*Clupea harengus*) migration (Varpe, Fiksen & Slotte, 2005). Habeck & Meehan (2008) showed that the trade-off between animal mass and population density led to population-level nitrogen flux being independent of species mass.

Excretion and egestion rates are typically proportional to population size when the entire population follows the same movement patterns into the recipient ecosystem, as has been seen for geese (Post *et al.*, 1998). Carcass inputs are generally proportional to population size when an age class experiences consistent levels of mortality, for example for semelparous fish (Naiman *et al.*, 2009) or iteroparous fish where spawning mortality is similar across variation in population size (Walters, Barnes & Post, 2009). Where mortality rates are more variable, due to individual variation in behaviour or the occurrence of catastrophic events (Fey *et al.*, 2015b), input quantity is likely variable but generally positively correlated with population size. For example, a large population of birds could experience a large or small mortality event during migration that could contribute a wide range of a number of carcasses, but a small population can only contribute so many carcasses before it goes extinct (Fey *et al.*, 2015b). Mortality events that have a small impact on



the animal population may have large impacts on recipient ecosystems, particularly for large-bodied animals in small recipient ecosystems (Subalusky *et al.*, 2017).

#### (4) Life history and behaviour

Life history and behaviour can modify quantity, quality, timing and duration of inputs largely through their effect on input form (excretion, egestion, gametes and carcasses) (Table 1) (Twining *et al.*, 2017). Daily feeding migrations, when animals feed in a habitat distinct from where other activities such as breeding or resting occur, typically result in inputs *via* excretion and egestion. Large life-history changes (often driven by ontogenetic niche shifts) and long-distance migrations (often driven by reproduction) typically put great mortality pressure on individuals and often result in gamete and carcass inputs. Animals undergoing life-history shifts and/or long-distance migrations are also excreting/egesting, but excretion/egestion often happen within hours of consumption and do not result in an input to a different ecosystem. For both types of animal movement pattern and input form, it is a species' tendency to aggregate on feeding, resting, or breeding grounds that contributes to the overall quantity and effect of the input, both through concentrating it in space and time (Post *et al.*, 1998; McIntyre *et al.*, 2008; Post & Walters, 2009; Holdo *et al.*, 2011) and through facilitating its use by consumers (Bilby *et al.*, 2003).

Some of the earliest recognized examples of animal inputs are due to daily feeding migrations, including those by bats (Hutchinson, 1950), coral reef fish (Meyer, Schultz & Helfman, 1983; Meyer & Schultz, 1985), seabirds (Bosman & Hockey, 1986; Sanchez-Pinero & Polis, 2000; Stapp & Polis, 2003b), and waterfowl (Manny, Johnson & Wetzel, 1994; Post *et al.*, 1998; Kitchell *et al.*, 1999). Other behaviours, such as scent marking at latrine sites by river otters (*Lutra canadensis*), also can lead to cross-ecosystem transfer of excretion/egestion (Ben-David *et al.*, 1998). Inputs from feeding migrations usually occur daily when animals move into resting habitat, although movement between ecosystems could be triggered by a range of factors (fear of predation, thermoregulation, respiration) that influence the input's timing and duration. For some animals (e.g. bats, hippos), daily feeding movements and their associated inputs occur throughout the year in one general location, allowing the daily inputs to accrue in the recipient ecosystem (Duchamp, Sparks & Swihart, 2010; Subalusky *et al.*, 2015). For other animals (geese, whales), these daily feeding migrations are couched within larger long-distance migrations, so daily inputs occur for focused periods of time (days to months) and then cease (Post *et al.*, 1998; Kitchell *et al.*, 1999; Roman & McCarthy, 2010).

Life-history shifts are often accompanied by reproduction and considerable mortality, and when those shifts are accompanied by movement across ecosystem boundaries, they can transfer large quantities of gametes and carcasses into the recipient ecosystem (Wilbur, 1980). One of the best-known examples is the migration of anadromous, semelparous salmon (*Oncorhynchus* spp.) (Naiman *et al.*, 2009),

although it has also been documented in other diadromous and potamodromous fish species (Nislow, Armstrong & McKelvey, 2004; Walters *et al.*, 2009; Wheeler, Miller & Crowl, 2015; Twining *et al.*, 2017). In diadromous fish, life-history traits like semelparity and iteroparity have strong impacts on whether inputs are primarily *via* carcasses (semelparity) or a combination of carcasses, gametes, and excretion/egestion (iteroparity) (Janetski *et al.*, 2009; Walters *et al.*, 2009; Childress, Allan & McIntyre, 2014; Childress & McIntyre, 2015; Twining *et al.*, 2017). In both cases, life-history strategy interacts strongly with population size to determine the overall quantity and quality of inputs. Metamorphosis and associated migrations of animals with complex life histories are often associated with adult excretion, gamete deposition and larval mortality in one ecosystem and juvenile export into another (Schreiber & Rudolf, 2008), as has been shown for amphibians (Capps, Berven & Tiegs, 2015) moving between aquatic and terrestrial ecosystems, and salmon (*Oncorhynchus nerka*) moving between marine and freshwater ecosystems (Moore & Schindler, 2004) (Table 2). In these cases, the magnitude and direction of net flux may be element-dependent (i.e. the net flux of C, N and P may not always be in the same direction) and may depend on characteristics of the animals, such as adult population size, juvenile recruitment, ontogenetic shifts in stoichiometry, and mobility (Jackson & Fisher, 1986; Capps *et al.*, 2015; Luhring, DeLong & Semlitsch, 2017), as well as characteristics of the ecosystems, such as size, perimeter to area ratio and boundary characteristics (Jackson & Fisher, 1986; Regester, Lips & Whiles, 2006). Theory suggests that gradual changes in ecosystem productivity or consumer mortality can lead to abrupt regime shifts in ecosystems coupled by consumers with complex life histories (Schreiber & Rudolf, 2008).

During long-distance migrations, which may be driven by a range of behavioural (e.g. reproduction) or environmental factors (e.g. rainfall, temperature), animal mortality can be elevated due to physical and environmental challenges of migration (Sillert & Holmes, 2002; Milner-Gulland, Fryxell & Sinclair, 2011; Klaassen *et al.*, 2014). When mortality is particularly high in one ecosystem along the migratory route, carcass inputs may constitute a subsidy from the ecosystem in which most resources were consumed. The length of the migration and where mortality occurs along it may impact the quality of the carcass input, as use of fat stores, altered feeding patterns and nutrient excretion may alter carcass stoichiometry throughout the migration (Tiegs *et al.*, 2011; Sitters *et al.*, 2015).

When inputs are in the form of carcasses from mortality during a life-history shift and/or long-distance migration, timing is often linked to seasonal shifts in temperature, light or rainfall regimes. For life-history shifts and reproductive migrations that are cued by warmer temperatures and longer days (Milner-Gulland *et al.*, 2011; Winkler *et al.*, 2014), the resulting carcasses enter a recipient ecosystem primed to use added nutrients for production. Because the phenology of these events is often conserved across individuals of a species,

mortality events are often experienced by large numbers of individuals at the same time, which can result in a major pulse of carcasses (Baxter *et al.*, 2005; Uno & Power, 2015). A similar pulse of carcasses can occur due to mass mortality from a catastrophic event or disease outbreak, the latter of which is the factor most often associated with mass mortality events across all animal taxa (Fey *et al.*, 2015*b*). The duration of carcasses in an ecosystem depends on the decomposition rate of different carcass components (Vanni *et al.*, 2013; Keenan *et al.*, 2018), which is days to weeks for muscle tissue and years for bones (Subalusky *et al.*, 2017); thus, the carcasses of larger animals, of which nearly 50% of the dry mass may be bones, may last significantly longer than those of smaller animals. The duration of an input may in turn influence its quality, as variable decomposition and leaching rates influence stoichiometric ratios (Sitters *et al.*, 2015).

#### IV. DONOR ECOSYSTEM CHARACTERISTICS

##### (1) Size, productivity and resource availability

The size and productivity of donor ecosystems, which influence the degree to which potential animal vectors acquire resources, interact to impact strongly the quantity and quality of inputs to the recipient ecosystem (Table 1). Ecosystems with high rates of either primary production or detrital inputs can support high levels of secondary production and potentially increase the number and/or biomass of individuals available as vectors. Small ecosystems may have higher rates of secondary productivity per unit area, partially due to their own receipt of subsidies (Polis *et al.*, 1997*a*); however, large ecosystems may have larger net productivity. For example, streams have more productive zoobenthos than lakes, but due to higher rates of insect emergence and larger size, lakes have approximately 2.5 times greater flux of insects to land (Gratton & Vander Zanden, 2009) (Table 2). Several studies have proposed that donor ecosystem productivity is particularly important in producing large subsidy effects when it is greater than productivity in the recipient ecosystem (Polis *et al.*, 1997*a*; Witman, Ellis & Anderson, 2004). When productivity in donor and recipient ecosystems is equivalent, subsidy influence appears to be predominantly an edge effect (Paetzold *et al.*, 2008). A meta-analysis of resource subsidies on food webs did not find a significant effect of donor ecosystem productivity on consumer effects in the recipient ecosystem, but hypothesized that the other variables that influence subsidy transport, including landscape features, boundaries between the donor and recipient ecosystem and subsidy characteristics may have obscured effects of productivity (Marczak *et al.*, 2007). For example, geomorphological features like stream meanders can increase aquatic insect flux into riparian habitats and increase insectivorous bird abundance, likely due to increased amount of stream edge and surface in meandering reaches (Iwata, Nakano & Murakami, 2003). Habitat structure in the

donor ecosystem also may influence input quantity. Fluxes of terrestrial insects into streams are higher from closed-canopy deciduous riparian zones, although the scale at which these effects are evident is unclear (Baxter *et al.*, 2005). Trophic dynamics in the donor ecosystem also may influence the quantity of animal vectors. Several studies have shown that non-native stream fishes significantly reduce emerging aquatic insects, which subsequently reduce riparian spider populations (Baxter *et al.*, 2004; Benjamin, Fausch & Baxter, 2011).

Donor ecosystems may influence input quantity and quality through variations in resource availability. For example, most aquatic ecosystems are considered P limited (Schindler, 1977; Elser, Marzolf & Goldman, 1990; Elser *et al.*, 2000) while terrestrial systems are N limited (Elser *et al.*, 1990). However, primary consumers in both systems were found to have very similar body N:P ratios, suggesting that N may be available in excess for aquatic consumers, leading to elevated N:P excretion/egestion ratios (Elser *et al.*, 2000). Higher nutrient or fatty acid availability in the donor ecosystem also may increase the nutrient or fatty acid content in the body tissues of animal consumers in that ecosystem, with subsequent effects on the quality of their excretion/egestion and carcasses (Heintz *et al.*, 2004; Small & Pringle, 2010; Twining *et al.*, 2016; Martin-Creuzburg, Kowarik & Straile, 2017). Animals' diet in the donor ecosystem also may interact with animals' body stoichiometry, as an animal with a low body N:P ratio feeding on a diet with a high N:P ratio will have to consume more food to obtain sufficient P, thus excreting a larger amount of N (Vanni, 2002). For example, at low N concentration in forage, large mammalian herbivores primarily egest N to maximize retention, and at high N concentration, they primarily excrete N as urea to remove excesses (Hobbs, 1996; Bump *et al.*, 2009*a*).

##### (2) Seasonal and large-scale climatic shifts

Seasonality in the donor ecosystem can be important for determining the quantity and timing of inputs (Table 1). Seasonal variations in temperature can have large effects on productivity, which may increase the production of animal vectors and their subsequent transport to recipient ecosystems. Fluxes of terrestrial insects into streams, which can be important prey for fishes, typically coincide with higher temperatures in summer and early autumn (Nakano & Murakami, 2001; Baxter *et al.*, 2005). This timing is seasonally offset from aquatic insect biomass and emergence in temperate regions, which may increase the relative importance of terrestrial prey, but timing of aquatic and terrestrial insects is more synchronous in Mediterranean regions (Rundio & Lindley, 2008; Larsen, Muehlbauer & Marti, 2016).

Seasonal increases in production also may influence the time animal vectors spend foraging in the donor ecosystem, which may influence the time they spend excreting/egesting in the recipient ecosystem. For example, dry conditions tend to increase the amount of time many animals spend

near watering holes and riparian areas, which increases the amount of resources transferred from terrestrial to aquatic systems (Jacobs *et al.*, 2007). Seasonality in the donor ecosystem also may interact with life-history traits of the animal vectors, as when changes in temperature and discharge trigger aquatic insect emergence (Füreder, Wallinger & Burger, 2005). Large-scale climatic shifts that increase (El Niño events) or decrease (major droughts) the productivity of the donor ecosystem also may alter the quantity and timing of animal vectors (Finney *et al.*, 2000; Naiman *et al.*, 2002). Donor ecosystem characteristics are not likely to have substantial effects on the duration of inputs in a recipient ecosystem, although they may influence the length of time high secondary production and movement out of the donor ecosystem can be sustained.

## V. RECIPIENT ECOSYSTEM – PHYSICAL/CHEMICAL CHARACTERISTICS

### (1) Size and location

Characteristics of the animal vector and donor ecosystem interact to determine the QQTD of an *input*, and that input is translated through the lens of recipient ecosystem characteristics to determine the QQTD of the *subsidy*. The size and location of the recipient ecosystem are primary determinants that influence the relative quantity of the input (Table 1). A given number of animal vectors will yield a relatively larger input in a small ecosystem than in a large ecosystem, in which their inputs may be minimal compared to the ecosystem's overall resource budget (Post *et al.*, 2007; Hocking & Reimchen, 2009). This influence of ecosystem size can be seen in the difference between total and areal loading rates for a given input (Table 2). However, a larger recipient ecosystem may be able to support a larger population of animal vectors once they arrive, which may increase the relative quantity and duration of inputs compared to small ecosystems, particularly when animals arrive by active means or tend to aggregate. Size, in addition to the ecosystem's shape and the fractal irregularity of its edges, also influences the perimeter:area (P:A) ratio of a recipient ecosystem, and smaller systems tend to have higher P:A ratios. The increased amount of edge in small systems increases their connection with adjacent systems, which often leads to higher input rates of allochthonous resources, particularly when animals arrive by passive means (e.g. wind or water currents) (Polis & Hurd, 1995, 1996; Polis *et al.*, 1997a; Iwata *et al.*, 2003). The probability that an animal migrating across a landscape will encounter the recipient ecosystem is also directly related to the perimeter of the recipient ecosystem and inversely related to its distance from the donor ecosystem (Polis *et al.*, 1997a; Power & Rainey, 2000; Gratton & Vander Zanden, 2009), although the relative importance of distance will vary for animal vectors with different mobility. Recipient ecosystem size also may influence the trophic structure of the ecosystem in a way that influences input quantity. Small islands in the

Gulf of California were less likely than large islands to have predators of marine nesting birds, which resulted in their use as nesting sites by seabirds and the subsequent transfer of large amounts of allochthonous marine resources (Polis & Hurd, 1995).

In some cases, these characteristics may be variable over time, as seasonal or climatic shifts may alter the size of recipient systems or their proximity to donor systems. For example, periods of high or low discharge in river systems due to seasonal events (e.g. snowmelt) or large-scale climatic events (e.g. drought or monsoonal rains) can change the effective size of the river ecosystem by several orders of magnitude as well as its connectivity to seasonal waterways. The interaction of input timing with timing of variability in the recipient ecosystem can have significant effects on the relative size of the input (Chaloner *et al.*, 2007; Janetski *et al.*, 2009; Wheeler *et al.*, 2015). For example, Wheeler *et al.* (2015) suggest the ratio of potamodromous fish biomass to ecosystem size, as measured by discharge, can help determine the contribution of migrant excretion to river nutrient cycling.

### (2) Boundary characteristics

Boundary characteristics that influence the permeability and retention of the recipient ecosystem can influence relative quantity and duration of an input (Table 1) (Polis *et al.*, 1997a; Cadenasso, Pickett & Weathers, 2004; Post *et al.*, 2007). Typically, boundary permeability is positively related to relative quantity of the input, but because highly permeable boundaries lead to low retention times, boundary permeability may be inversely related to duration. Low boundary permeability may directly block inputs, or may lengthen the transport time between ecosystems such that resulting biogeochemical transformations influence the quantity of the input (Harding *et al.*, 2004). Whether a boundary is permeable depends both on the time scale of analysis and the animal vector under consideration (Post *et al.*, 2007). For example, lakes are often considered to be closed systems at short time scales, but open to water and nutrient inputs at longer time scales. Lakes with alewife migrating between them and the ocean on an annual basis are relatively open systems, but they could be considered closed systems for some questions at short time scales. The transition from terrestrial to aquatic systems (or *vice versa*) may be a highly impermeable barrier to some animals or specific age classes, while being highly permeable to others undergoing metamorphosis. In some cases, highly impermeable boundaries may lead to increases in relative quantity of an input. When animal migrations encounter an impermeable boundary, mass mortality may occur and result in a large input of carcasses. This type of mortality has been documented in response to both anthropogenic barriers, such as fences and dams (Bolger *et al.*, 2008) and natural boundaries, such as water crossings by migrating ungulates (Capaldo & Peters, 1995, 1996; Hummel & Ray, 2008; Subalusky *et al.*, 2017) and mass stranding of marine animals (Brownell *et al.*, 2005; Mazzariol *et al.*, 2011).



Boundary permeability also may be altered by seasonal or climatic events, such as increased rainfall that increases aquatic–terrestrial linkages through floodplain inundation and increases the relative quantity of inputs entering a recipient ecosystem (Junk, Bayley & Sparks, 1989; Junk, 1999). There also may be complex interactions between the timing of inputs and the permeability of the ecosystem which influence the duration of time the input is in the recipient ecosystem. For example, if an input coincides with low rates of retention (high rainfall in terrestrial systems, or high discharge in aquatic systems), the relative effect of the input on the recipient ecosystem may be diminished (Chaloner *et al.*, 2007; Janetski *et al.*, 2009).

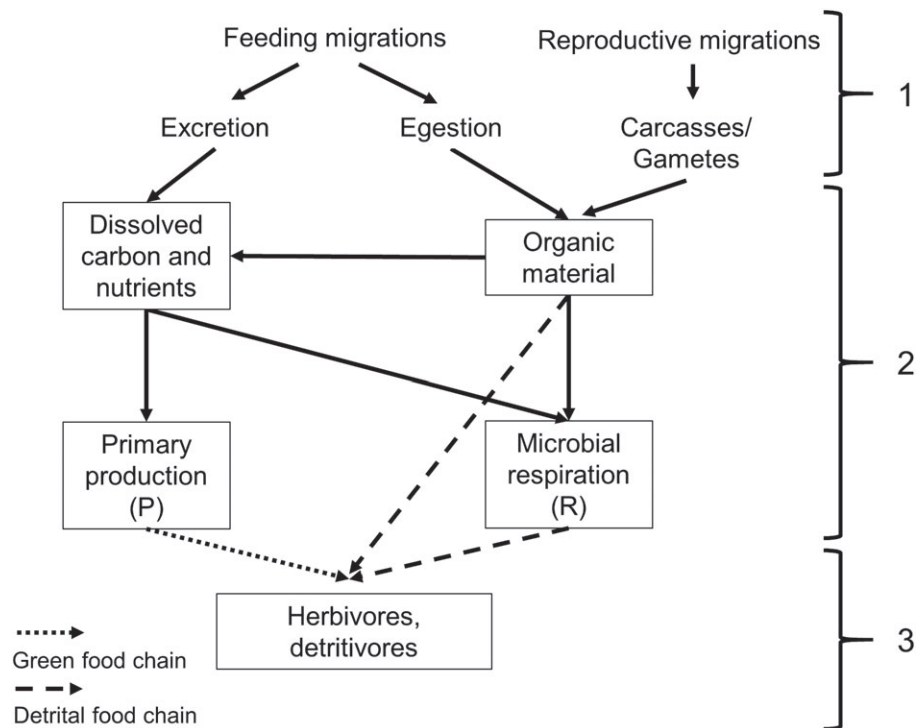
### (3) Productivity and resource availability

The productivity and resource availability of a recipient ecosystem ultimately determines the relative quantity and quality of the input in that ecosystem, although resource availability appears to be a better tool for predicting subsidy effects (Marczak *et al.*, 2007) (Table 1). A given input will generally have a larger effect in a resource-poor ecosystem than in a resource-rich one (Polis *et al.*, 1997a; Post *et al.*, 2007; Atkinson *et al.*, 2016). These differences are illustrated by the difference in total loading estimates for a given input as compared to the per cent of recipient ecosystem levels they comprise (Table 2). For example, snails load  $0.02\text{--}0.03\text{ g m}^{-2}\text{ year}^{-1}$  of N to desert soils, but these soils are so low in nutrients that snail loading comprises 11% of the total soil nitrogen input (Jones & Shachak, 1990) (Table 2). By contrast, all the marine mammals in the Gulf of Maine contribute  $23 \times 10^6$  kg of N to the phototrophic zone of oceans through faecal plumes, but this only accounts for 1% of the N influx for that area (Roman & McCarthy, 2010) (Table 2). Nutrient limitation in an ecosystem tends to promote the importance of resource inputs (Bellmore *et al.*, 2014), while nutrient enrichment decreases it (Carpenter *et al.*, 2005), and this pattern is especially pronounced when the input provides resources similar to those already abundant in the recipient ecosystem (Marczak *et al.*, 2007; Adams *et al.*, 2010). Arctic foxes (*Vulpes lagopus*) were more dependent on proximity to colonies of greater snow geese (*Anser caerulescens atlanticus*) for denning and cub rearing when abundance of lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) was low (Giroux *et al.*, 2012). By contrast, inputs that provide complementary resources to those available in the recipient ecosystem could be disproportionately important (Kominoski *et al.*, 2015; Rosemond *et al.*, 2015). Whales in the Southern Ocean stimulate carbon export through consumption of prey at depth and provision of iron-rich faecal plumes to the iron-limited photosynthetic zone (Lavery *et al.*, 2010). Provision of complementary resources may be more likely when the donor and recipient ecosystems differ substantially from one another. For example, because aquatic and terrestrial systems often differ in stoichiometry and limiting resources, inputs that move from an aquatic ecosystem into a terrestrial ecosystem, or *vice versa*, may be more likely to

provide different resources than those already available in the recipient ecosystem (Elser *et al.*, 2000; Nowlin, Vanni & Yang, 2008; Sitters *et al.*, 2015; Twining *et al.*, 2016; Martin-Creuzburg *et al.*, 2017).

The relative quality of an input, and thus the degree to which it influences an ecosystem, will be largely determined by its timing relative to other recipient ecosystem dynamics that are shaped by seasonal variability or large-scale climatic events (Table 1). Inputs are more likely to be important when the demand for that resource is high relative to the supply (Wheeler *et al.*, 2015; Wheeler, Miller & Crowl, 2017). Inputs that enter the recipient ecosystem when *in situ* sources of productivity are low are more likely to be utilized by consumers and may help stabilize the food web (Nakano & Murakami, 2001; Takimoto, 2002). However, inputs that enter during periods when abiotic factors promote increased productivity (e.g. warmer temperatures, more light), may be more likely to be transformed and assimilated into primary or secondary production (Tiegs *et al.*, 2011). Large-scale climatic events also may influence the relative quality of an input in a recipient ecosystem. Climatic events like the El Niño Southern Oscillation (ENSO) may bring additional rainfall or drought conditions, depending on the region, which may have contrasting effects in terrestrial *versus* aquatic systems. Additional rainfall may reduce water limitation and allow nutrient inputs to be utilized more fully in terrestrial systems (Anderson *et al.*, 2008), while increasing discharge may decrease input duration and effect in aquatic systems (Stears *et al.*, 2018). By contrast, drought conditions may limit terrestrial production regardless of input, while they may decrease ecosystem size and increase input duration and effect in aquatic ecosystems.

There are other characteristics of recipient ecosystems that can influence input quality and duration (Table 1). Temperature is an important variable that both increases metabolism and excretion/egestion rates of animals, potentially increasing input quantity (Allen & Gillooly, 2009; Liess *et al.*, 2015; Vanni & McIntyre, 2016), and increases decomposition rates in both aquatic (Paudel *et al.*, 2015) and terrestrial ecosystems (Zhang *et al.*, 2008), potentially decreasing input duration. Decomposition rates also can be influenced by whether the recipient ecosystem is aquatic or terrestrial. Carcass decomposition tends to occur faster in aquatic ecosystems, as decomposition is influenced by a range of additional physical factors (Beasley, Olson & Devault, 2012; Muhametsafina *et al.*, 2014). In cases where inputs are being provided by living animals (*via* excretion and egestion), input duration may also be influenced by resource availability in the recipient ecosystem that determines how long that ecosystem can sustain or support the animal vectors. The resource being provided by the recipient ecosystem to the animal vector may vary, although it is often habitat or space. For example, migratory waterfowl will only utilize certain agricultural wetlands that provide sufficient roosting habitat, limiting the wetlands to which they transport terrestrial resources (Post *et al.*, 1998).



**Fig. 2.** Flow chart depicting the fate of animal resource subsidies in a recipient ecosystem. 1, There are several primary forms of animal input – excretion and egestion resulting from daily feeding migrations, and carcasses and gametes resulting from life-history shifts or long-distance migrations. 2, These inputs provide carbon and nutrients that can subsidize autotrophic and/or heterotrophic production through a range of pathways and influence the balance of autotrophic to heterotrophic production [often measured as the ratio of primary production (P) to respiration (R)]. 3, Resulting changes in autotrophic and heterotrophic production can influence trophic dynamics in the recipient ecosystem through the green and detrital food chains, respectively.

## VI. RECIPIENT ECOSYSTEM – CONSUMER CHARACTERISTICS

### (1) Taxonomic identity and trophic guild

The ultimate fate of inputs in the recipient ecosystem is their transformation and uptake by a range of consumers, which may include microbial decomposers, primary producers, and primary and secondary consumers. The taxonomic identity and trophic guild of a given consumer compared to where in the food chain the input enters influences the relative quality and duration of the input (Table 1). While primary producers may be able to respond rapidly to limiting nutrients in excretion, nutrients from carcasses and egestion are not available until initial decomposition and mineralization has occurred. Microbial communities may be able to respond rapidly to carcasses and egestion, which provide nutrients and carbon, but they also may utilize soluble nutrients from excretion (Fig. 2). Microbial processing of detritus may further increase input quality and increase its likelihood of assimilation by other consumers (France, 2011; Sitters *et al.*, 2015). However, stimulation of microbial growth by labile carbon may immobilize other nutrients in the input and make them unavailable to other consumers (Lovett & Ruesink, 1995; Christenson *et al.*, 2002). Many invertebrate and vertebrate consumers consume faeces

or carcasses directly, particularly after microbial processing, thus incorporating inputs directly into the detrital food chain (DeVault, Rhodes & Shivik, 2003; Moore *et al.*, 2004; Wilson & Wolkovich, 2011) and subsequently mineralizing them for use in stimulating primary production (Fittkau, 1973). Whether primary producers, primary consumers, secondary consumers or some combination of these are feeding on the input can have significant impacts on food-web and ecosystem effects (Fig. 2), such as altering the strength of resulting trophic cascades (Huxel, McCann & Polis, 2002; McCann, Rasmussen & Ulanowicz, 2005; Leroux & Loreau, 2008). Top predator consumers can have a range of both consumptive and non-consumptive effects on ecosystem nutrient dynamics (Bump *et al.*, 2009a; Schmitz *et al.*, 2010). Some inputs may be utilized by consumers at multiple trophic levels. Marine inputs to islands, either *via* seaweed deposition or seabird colonies, both fertilize plants and provide alternative insect prey for resident predators (Polis & Hurd, 1995; Spiller *et al.*, 2010).

Consumer preference can also mediate input effects (Table 1). Consumers that are generalists may be better adapted to switching to animal inputs during times when they become available (Shaner & Macko, 2011), while specialists may not be able to take advantage of this new resource; complete switching of a consumer from an autochthonous to an allochthonous resource can decouple indirect dynamics



between consumers and primary producers (Leroux & Loreau, 2008). Preferential prey selection by consumers can influence the pathway through which an input is incorporated. For example, brown bears (*Ursus arctos*) and black bears (*Ursus americanus*) selectively feed on salmon (*Oncorhynchus* spp.) with the highest energy content (large individuals that have spent the fewest number of days on the spawning grounds), which increases the likelihood of transport of those salmon into the riparian zone (Gende *et al.*, 2004; Hocking & Reimchen, 2009). Bear-killed salmon that are left in the river are preferentially colonized by caddisfly larvae compared to senesced carcasses, possibly due to their higher energetic content, improved accessibility, or extended temporal availability (Winder *et al.*, 2005). This prey selection is also mediated by stream habitat structure, and in complex habitats where preferred salmon are difficult to catch, bears selectively kill older, more senesced individuals (Gende *et al.*, 2004). Increases in input quality may also preclude certain consumers – nutrient enrichment in a stream increased the biomass of emerging insects, thus decreasing the consumption efficiency of the spiders that were their primary predators and decreasing their reliance on this resource (Davis, Rosemond & Small, 2011). Competitive interactions also may determine which consumers are able to benefit from inputs, and competition may be particularly strong when the input is of high quality (DeVault *et al.*, 2003; Stapp & Polis, 2003a). There may also be complex interactions between abiotic and biotic characteristics in the recipient ecosystem; for example, depth of snow pack influences carcass remains from wolf (*Canis lupus*) predation that are available for scavengers (Wilmers *et al.*, 2003) and rainfall influences the effect of reindeer (*Rangifer tarandus platyrhynchus*) faecal pellets on the balance between grass and moss (van der Wal *et al.*, 2004).

Taxonomic identity of the consumer is often less important than trophic guild in determining relative quality of an input, however, there are species-specific differences that can impact the timing and degree to which an input is utilized (Table 1). Whale falls, which decompose over years to decades, can host a succession of scavenger species that range from necrophages consuming the carcass flesh, to bone specialists consuming the lipid-rich bones, to chemoautotrophic bacteria using the sulphur from the decomposing skeleton (Bennett *et al.*, 1994; Smith & Baco, 2003; Lundsten *et al.*, 2010; Amon *et al.*, 2013). In sub-Saharan Africa, white-backed vultures (*Gyps africanus*) arrive early at carcass sites and use their sharp beaks to tear into carcasses and expose the muscle and internal organs, which are a higher quality resource and easier to digest than the skin (Kendall *et al.*, 2012). Marabou storks (*Leptoptilos crumenifer*) have bulkier and less sharp bills and must rely on openings in the carcass created by vultures or other decomposition processes to feed on the high-quality portions inside the carcass (C. Kendall, personal observations). Hyenas (*Crocuta crocuta*) are able to feed on carcasses throughout a range of decomposition stages, due to their strong jaws and associated ability to consume bone and

skin (Cooper, Holekamp & Smale, 1999; Wambuguh, 2008). These taxonomic differences in scavenger feeding structures establish a succession of carcass consumption that determines the timing of input utilization and its relative quality along that trajectory.

## (2) Life history and mobility

The number of consumers present and how quickly they can take advantage of a new resource input determines its relative quantity and duration in a recipient ecosystem (Table 1). Initial consumer abundance may be determined by their ability to exist on other resources in the absence of the input, and this will help determine the input's initial rate of utilization (Levi *et al.*, 2015). If an input is of sufficiently high quality, its appearance may cause consumers to switch resources to take advantage of it, or to increase their population in response to it. Inputs can alter these dynamics themselves, such as through the priming effect, when inputs high in labile organic matter increase mineralization rates of more recalcitrant organic matter (Guenet *et al.*, 2010). The rate of consumer response to the input is shaped by the consumer's life history, feeding strategy, and mobility (Nowlin *et al.*, 2008; Paetzold *et al.*, 2008; Levi *et al.*, 2015). Consumers that can reproduce quickly, or switch resources readily, will be able to take full advantage of a pulse in a new resource. For plant consumers, annual species may have life-history characteristics that are more able to take advantage of pulsed resources, which can lead to a shift in community composition and diversity in recipient ecosystems (Anderson *et al.*, 2008). For animal consumers, mobility may be a key feature allowing animals to change foraging strategies to take advantage of new resource inputs (Stapp, Polls & Pinero, 1999; Power & Rainey, 2000; Stapp & Polis, 2003a; Levi *et al.*, 2015). The rate of consumer response to an input may influence the duration of the input in the recipient ecosystem. When consumers can respond quickly, *via* high mobility or life histories that support rapid reproduction, inputs may be consumed quickly and entirely. Consumer mobility also may influence the spatial scale of an input's influence, if highly mobile consumers in the recipient ecosystem are able to transport inputs into other ecosystems. For example, the transport of salmon carcasses by bears and birds into freshwater and terrestrial ecosystems the salmon otherwise wouldn't have reached extends the spatial influence of this input (Hilderbrand *et al.*, 1999; Helfield & Naiman, 2006; Payne & Moore, 2006; Levi *et al.*, 2015).

## VII. THE EFFECTS OF SUBSIDY CHARACTERISTICS ON TROPHIC DYNAMICS AND ECOSYSTEM FUNCTION

The range of examples cited above illustrate how interactions between the animal vector and donor ecosystem can influence the QOTD of animal resource inputs, and how the characteristics of these inputs can be further mediated

by interactions with the recipient ecosystem. The resulting variability in subsidy QQTd is manifest in the variability of subsidy impacts on trophic structure and ecosystem function in the recipient ecosystem. Several theoretical studies have formulated hypotheses about how subsidy characteristics may impact food webs and ecosystem processes (Huxel & McCann, 1998; Huxel *et al.*, 2002; Leroux & Loreau, 2008), although considering the four characteristics of QQTd together presents a formidable level of complexity. Furthermore, challenges in manipulating these subsidy characteristics in the field have made it difficult to test these relationships empirically. Here we present a summary of predictions from theoretical research and meta-analyses of empirical research on how subsidy QQTd may impact trophic dynamics and ecosystem function, and we use case studies to illustrate the variable effects subsidies can have even within a single ecosystem.

### (1) Trophic structure

Animal subsidies often have strong, positive direct effects on consumers in the recipient ecosystem. Studies have shown that animal subsidies can account for 25–100% of the energy or carbon to consumers and may increase consumer growth and reproduction (Baxter *et al.*, 2005). Animal subsidies also can have negative indirect effects on trophic dynamics, by increasing the density of subsidized predators that in turn increase predation on *in situ* prey (Polis & Hurd, 1996; Huxel & McCann, 1998), although experiments testing these interactions have produced a range of results (Baxter *et al.*, 2005). Theoretical modelling suggests that subsidy quantity is important in determining the impact on food-web stability, with low levels of subsidies stabilizing food webs and increasing community persistence, and high levels of subsidies decreasing food-web stability and increasing the strength of trophic cascades (Huxel & McCann, 1998; Huxel *et al.*, 2002; Leroux & Loreau, 2008). The timing and duration of a subsidy also influence its effects on trophic structure. Theory suggests that subsidies that occur when other *in situ* sources of productivity are low are more likely to stabilize food-web dynamics (Takimoto, 2002).

Due to their relatively high quality, animal subsidies are often incorporated into the food web even if they occur in relatively low quantities (Marcarelli *et al.*, 2011). However, the pathway through which they are incorporated depends on the subsidy form and its effects on ecosystem function. As illustrated in Fig. 2, animal excretion rich in inorganic nutrients may be taken up readily by autotrophic producers and incorporated into higher trophic levels *via* grazing by primary consumers (green food chain). Animal egestion or carcasses may be either mineralized to inorganic nutrients and assimilated *via* the same pathways or consumed directly by heterotrophic consumers (detrital food chain). Larger carcasses in particular provide a fairly complex resource that decomposes over long time scales, so trophic uptake is often *via* a range of consumers (Bennett *et al.*, 1994; Smith & Baco, 2003; Lundsten *et al.*, 2010; Kendall *et al.*, 2012). Characteristics of the ecosystem in which the carcass is

deposited also influence these dynamics. Carcasses tend to decompose faster in aquatic than terrestrial systems (Muhametsafina *et al.*, 2014), however, in marine systems, the less-important role of bacterial communities and the decreased stability of environmental conditions as compared to terrestrial systems can lead to an increase in the diversity of macrofauna that utilize the carcass resource (Beasley *et al.*, 2012).

### (2) Ecosystem function

Animal subsidies can have a range of effects on ecosystem function, as illustrated in Fig. 2. Animal subsidies typically increase nutrient concentrations in recipient ecosystems (Anderson & Polis, 1999), which often results in increased primary production and a shift towards increased net ecosystem production [NEP; the difference between gross primary production (GPP) and ecosystem respiration (R)] (Kitchell *et al.*, 1999; Naiman *et al.*, 2009). When subsidies are in the form of organic nutrients (e.g. carcasses) or are high in carbon (e.g. hippo faeces), mineralization of these subsidies could shift the ecosystem towards increased heterotrophy and a decline in NEP (Christenson *et al.*, 2002; Marcarelli *et al.*, 2011; Subalusky *et al.*, 2018), although the effect of subsidies on heterotrophic communities has been studied much less frequently (Atkinson *et al.*, 2016). The release of inorganic nutrients after mineralization may then stimulate either autotrophs or heterotrophs, and the resulting outcome may be mediated by other factors, including temperature, light and nutrient availability and community composition (Roberts & Howarth, 2006).

Examples from the literature on migratory salmonids illustrate how characteristics of the animal vector and donor and recipient ecosystems may interact to determine subsidy impact on ecosystem function. Large-scale shifts in ocean–atmosphere patterns lead to fluctuations in salmon abundance and the number of salmon (*Oncorhynchus* spp.) moving from marine to freshwater ecosystems to spawn and die (Finney *et al.*, 2000; Naiman *et al.*, 2002). Salmon carcasses contribute high levels of nutrients, and depending on ecosystem nutrient demand, these can be assimilated by primary producers and increase primary production (Mitchell & Lamberti, 2005; Wheeler *et al.*, 2017). However, the disruption of substrate by live salmon during redd construction can decrease benthic algal biomass and drive the ecosystem from a net autotrophic to a net heterotrophic state during salmon spawning runs (Holtgrieve & Schindler, 2011; Wheeler *et al.*, 2017). The ecological effects of live salmon, through excretion and gamete release, can exceed those of carcasses, partly due to the corresponding abiotic characteristics of the river (Tiegs *et al.*, 2011). River discharge tends to be lower and water temperature higher earlier in the spawning season when most fish are still alive, and these characteristics are more likely to promote primary production.

Recent research on hippos (*Hippopotamus amphibius*) has also shown how interactions between the subsidy and donor and recipient ecosystem characteristics can drive variability

in ecosystem effects. Hippopotami graze 1–10 km inland from rivers, and they tend to graze further inland during drier seasons when grass is sparser (Field, 1970; Kanga *et al.*, 2011). By travelling further inland in response to lower donor ecosystem productivity, hippos spend a longer time feeding in the grasslands, which leads to less time spent in the river and therefore less excretion/egestion in the aquatic ecosystem (Subalusky *et al.*, 2015). The magnitude of hippo inputs entering the recipient ecosystem appears to drive large differences in effects on ecosystem function, with low levels of input increasing primary and secondary production, and high levels decreasing production, particularly during low discharge when inputs concentrate on the river bottom (Masese *et al.*, 2015, 2018; McCauley *et al.*, 2015; Dawson *et al.*, 2016; Stears *et al.*, 2018; Dutton *et al.*, 2018b; Subalusky *et al.*, 2018). Hippo inputs can become so concentrated they lead to hypoxic conditions in the hippo pools and hypoxic floods and fish kills downstream, a condition Dutton *et al.* (2018b) termed ‘subsidy overload’. Hippos can also influence characteristics of the river ecosystem by increasing turbidity in the river directly, through bioturbation, but also indirectly, through decomposition of faeces into fine particulates (Dutton *et al.*, 2018a). Increased turbidity causes light limitation to the benthos, which likely influences the degree to which hippo faeces are used by autotrophs. This case study illustrates how animal inputs can alter recipient ecosystem characteristics in a way that influences the recipient ecosystem’s response to further inputs.

### (3) Feedbacks

Some animal subsidies increase productivity of a component of the recipient ecosystem that in turn provides a subsidy back to the donor ecosystem, potentially establishing feedbacks between the donor and recipient systems. For example, when salmon carcasses promote biofilm growth that is consumed by aquatic insects that ultimately provide the diet for salmon hatchlings, they can promote higher survivorship of young salmon that return to the ocean (Giannico & Hinch, 2007; Naiman *et al.*, 2009). These feedback loops can increase the complexity of untangling drivers of food-web structure across ecosystems. These feedbacks may be widespread, but they are poorly documented and are an important avenue for future research.

## VIII. IMPLICATIONS FOR ALTERED ECOSYSTEMS

Many animal populations have declined or been lost in response to anthropogenic change, with the accompanying loss of their role in resource transport (Moss, 2015; Malhi *et al.*, 2016). Late Pleistocene extinctions of megafauna across much of the world removed most of the largest species from all continents except Africa (Barnosky *et al.*, 2004; Lyons, Smith & Brown, 2004). Research on nutrient transport capacity of megafauna has shown the substantial impacts

that megafaunal species can have, due to their large size, high consumption rate, and widespread movement patterns (Wolf, Doughty & Malhi, 2013; Subalusky *et al.*, 2015). Modelling approaches show that the loss of Amazonian megafauna led to a 98% decrease in the lateral flux of phosphorous away from fertile floodplains, with similar decreases in all continents except Africa (Doughty, Wolf & Malhi, 2013). Estimates of nutrient transport from before the Quaternary megafauna extinctions suggest that nutrient transport by animals has dropped to 4–8% of pre-extinction levels (Doughty *et al.*, 2015). Present-day population declines have contributed further to the loss of species, due to a range of drivers including habitat loss, direct mortality, over-exploitation, climate change and increased barriers to migration (Finney *et al.*, 2000; Hilborn *et al.*, 2003; Allan *et al.*, 2005; Varpe *et al.*, 2005; Harris *et al.*, 2009; West *et al.*, 2010; Dirzo *et al.*, 2014; Ceballos *et al.*, 2015). In a range of species subjected to human exploitation, there also has been a general decline in body size over time, which interacts with declining population numbers to further decrease subsidy quantity (McIntyre *et al.*, 2007; Pershing *et al.*, 2010; West *et al.*, 2010; Twining *et al.*, 2017). This pattern has been further compounded by global reductions in the extent of animal movements in response to anthropogenic development (Tucker *et al.*, 2018). Other animal species are increasing in response to anthropogenic activities, such as invasive species that have colonized novel habitats with potentially large impacts on ecosystem nutrient cycling (Capps *et al.*, 2012; Capps & Flecker, 2013b) and cross-system nutrient transport (Baxter *et al.*, 2004; Middleton *et al.*, 2013; Gergs *et al.*, 2014; Twining *et al.*, 2017). Some animal vectors have been subsidized themselves, as is the case with geese feeding in agricultural fields (Jeffries, Henry & Abraham, 2004). The geese in turn subsidize wetlands through daily feeding migrations (Post *et al.*, 1998; Kitchell *et al.*, 1999) and Arctic predators through seasonal reproductive migrations (Giroux *et al.*, 2012).

As many animal subsidies have decreased, anthropogenic resource subsidies have increased and may have essentially replaced those lost by animal movements in some ecosystems (Twining, West & Post, 2013). Common forms of anthropogenic inputs include sewage waste from humans and livestock and fertilizer run-off from agricultural fields. These forms are often high in inorganic nutrients, particularly N, and are often associated with large increases in algal growth in aquatic ecosystems (Sitters *et al.*, 2015). Humans also provide large amounts of food subsidies, either intentionally through bird and game feeders, or unintentionally through dumps, fishing discards, and restaurants, among other sources (Oro *et al.*, 2013). These anthropogenic food subsidies can have substantial direct and indirect effects at the individual, community and ecosystem scale (Oro *et al.*, 2013; Newsome *et al.*, 2015; Winton & River, 2017). Increasing anthropogenic subsidies could decrease the relative size and impact of animal subsidies due to elevated background nutrient levels or could compound the influence of animal subsidies and push ecosystems closer to a tipping point of eutrophication.



Anthropogenic changes are also often associated with increasing pollutant loads, which can become coupled to animal resource transport (Walters *et al.*, 2010).

In addition to changing nutrient levels, many ecosystems are also experiencing increased temperatures, changes in the timing of temperature and precipitation regimes, and higher levels of variability in a range of environmental factors due to climate change and other anthropogenic factors, which may influence the QOTD of subsidies in complex ways (Karl, Knight & Plummer, 1995; Verboom *et al.*, 2010; Schulz *et al.*, 2015; Sitters *et al.*, 2015; Larsen *et al.*, 2016). Increased temperatures may influence the phenology of animal vectors, potentially altering the quantity and timing of their inputs to recipient ecosystems. Increased temperatures also may influence subsidy quality. For example, increasing temperatures have been shown to decrease the quality of leaf litter subsidies to aquatic systems, with negative impacts on nutrient levels but positive impacts on zooplankton due to decreased shading (Fey *et al.*, 2015a). Increased variability also may change the way recipient ecosystems interact with animal subsidies (Larsen *et al.*, 2016). For example, higher rainfall may increase recipient ecosystem productivity and decrease its retention rate, both of which would minimize the effect of an animal subsidy, or rainfall could enhance the decomposition and uptake of a subsidy and increase its effect. Changes in the physical structure of recipient ecosystems that conflict with changes in the physiology and phenology of animal vectors may lead to trophic mis-matches with long-term consequences (Larsen *et al.*, 2016). The interaction between changing recipient systems and changing animal vector populations will likely have complex effects that vary across systems.

## IX. RECOMMENDATIONS FOR FUTURE RESEARCH

Here we have presented a framework that can be used both to develop predictions about the role of different animal subsidies in space and time, and to guide research programs aimed at understanding the ecosystem and trophic effects of animal subsidies. We also present several recommendations to aid future studies in following this framework and developing research that is directly comparable to other studies. First, we recommend measuring and reporting both the magnitude and stoichiometry of resource subsidies, as well as the rate and aerial extent of loading, which reflects the relative quantity of the subsidy. We also recommend measuring the availability of similar resources in the recipient ecosystem and, when possible, the ecosystem demand for those resources, to present subsidies as a proportion of *in situ* resource supply and demand, which reflects the relative quality of the subsidy. Although obtaining all these data for every study may be expensive and difficult, measuring only a subset of these variables can make it difficult to compare findings across studies (Table 2).

Second, we recommend developing study designs that allow animal subsidies and their impacts to be measured at spatial and temporal scales that capture relevant environmental variability. Variability of animal subsidy effects is important to document, as it can increase spatial and temporal heterogeneity to which other consumer guilds in turn respond. Furthermore, understanding how variability in animal and ecosystem characteristics influence subsidy effects will be particularly important in a changing world, as these characteristics continue to change even in well-studied systems.

Third, we recommend studying the role of animals in transporting resource subsidies within the broader context of understanding how animal movement and behaviour can influence food webs and ecosystems. Animals can have an array of transport and trophic effects in ecosystems in which they reside (Bauer & Hoyer, 2014), and they can physically alter their environments (Jones, Lawton & Shachak, 1997). These various roles may have ecological effects that either surpass or alter the impact of any resource subsidies they transport. Research on animal resource subsidies should consider, if not explicitly address, the additional roles an animal vector may be playing in the recipient ecosystem that may influence interpretation of the results.

Fourth, we recommend using this conceptual framework to guide research on resource subsidies in general, even when transported by abiotic vectors. This will simplify the component of the framework devoted to characteristics of the animal vector (Fig. 1), but the proposed characteristics of the donor and recipient systems will still be important to understanding context dependency of resource subsidies in general. As cross-system resource subsidies are an important feature of ecosystems in every biome, and perhaps more the rule than the exception in influencing ecosystem dynamics, predicting when and where they are likely to be most important can inform our broader understanding of ecosystem function.

Finally, we propose following the more general definition of resource subsidies set forth above that includes instances in which the subsidy either promotes or inhibits production in the recipient ecosystem. The trophic and ecosystem effects of a subsidy may be highly variable in time and space for a given subsidy and may influence a range of consumers in the recipient ecosystem in complex and dynamic ways across variable time scales. A given resource may increase primary production over days to weeks, secondary production over weeks to months and secondary consumers over months to years. With a slight change in environmental conditions, it may decrease primary production but increase secondary production through the detrital food web. With a sufficient decrease in animal populations, the subsidy may still impact primary producers or microbes, but have no effect on secondary production. We believe a broader definition of resource subsidy better reflects the range of outcomes that can occur in the same recipient ecosystem for any given subsidy, depending on how that subsidy is translated through the ever-changing lens of recipient ecosystem characteristics.

## X. CONCLUSIONS

(1) Animals can play an important role in shaping trophic structure and ecosystem function through the transport of resources across ecosystem boundaries, but the importance of these resource inputs is context dependent and is shaped by characteristics of the animal vector and the donor and recipient ecosystems.

(2) The trophic and ecosystem effects of animal resource subsidies can influence how the recipient ecosystem responds to additional inputs and can feed back to influence the donor ecosystem.

(3) Animal subsidies, and resource subsidies in general, must be studied in the context of donor and recipient ecosystem dynamics to understand and predict their ecosystem effects fully, and this context is particularly important in a rapidly changing world.

(4) Future research should work towards measuring and reporting the magnitude, stoichiometry and temporal and spatial scale of resource inputs, as well as their proportion of *in situ* resource supply and demand, in order to facilitate comparisons both within and across taxa and ecosystems.

(5) Resource subsidies may have positive, negative and/or neutral effects on different components of the recipient ecosystem across different time scales, and future research should utilize this range of ecosystem effects to improve our understanding and predictive capacity of when and where subsidies will be important.

## XI. ACKNOWLEDGEMENTS

We are grateful to two anonymous reviewers for helpful comments that greatly improved this manuscript. Work on this manuscript was funded by grants from the National Science Foundation (DEB 0924393, 1343920, 1354053, 1556848, and 1753727).

## XII. REFERENCES

- ADAMS, L. G., FARLEY, S. D., STRICKER, C. A., DEMMA, D. J., ROFFLER, G. H., MILLER, D. C. & RYE, R. O. (2010). Are inland wolf–ungulate systems influenced by marine subsidies of Pacific salmon? *Ecological Applications* **20**, 251–262.
- ALLAN, J. D., ABELL, R., HOGAN, Z., REVENGA, C., TAYLOR, B. W., WELCOMME, R. L. & WINEMILLER, K. (2005). Overfishing of inland waters. *BioScience* **55**, 1041–1051.
- ALLEN, A. P. & GILLOOLY, J. F. (2009). Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecology Letters* **12**, 369–384.
- ALLGEIER, J. E., WENGER, S. J., ROSEMOND, A. D., SCHINDLER, D. E. & LAYMAN, C. A. (2015). Metabolic theory and taxonomic identity predict nutrient recycling in a diverse food web. *Proceedings of the National Academy of Sciences* **112**, E2640–E2647.
- AMON, D. J., GLOVER, A. G., WIKLUND, H., MARSH, L., LINSE, K., ROGERS, A. D. & COPLEY, J. T. (2013). The discovery of a natural whale fall in the Antarctic deep sea. *Deep Sea Research Part II: Topical Studies in Oceanography* **92**, 87–96.
- ANDERSON, W. B. & POLIS, G. A. (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **118**, 324–332.
- ANDERSON, W. B., WAIT, D. A. & STAPP, P. (2008). Resources from another space and time: responses to pulses in a spatially subsidized system. *Ecology* **89**, 660–670.
- ATKINSON, C. L., CAPPS, K. A., RUGENSKI, A. T. & VANNI, M. J. (2016). Consumer-driven nutrient dynamics in freshwater ecosystems: from individuals to ecosystems. *Biological Reviews* **92**, 2003–2023.
- BARNOSKY, A. D., KOCH, P. L., FERANEC, R. S., WING, S. L. & SHABEL, A. B. (2004). Assessing the causes of late Pleistocene extinctions on the continents. *Science* **306**, 70–75.
- BAUER, S. & HOYE, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552.
- BAXTER, C. V., FAUSCH, K. D., MURAKAMI, M. & CHAPMAN, P. L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* **85**, 2656–2663.
- BAXTER, C. V., FAUSCH, K. D. & SAUNDERS, W. C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* **50**, 201–220.
- BEASLEY, J. C., OLSON, Z. H. & DEVAULT, T. L. (2012). Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos* **121**, 1021–1026.
- BELLMORE, J. R., FREMIER, A. K., MEJIA, F. & NEWSOM, M. (2014). The response of stream periphyton to Pacific salmon: using a model to understand the role of environmental context. *Freshwater Biology* **59**, 1437–1451.
- BEN-DAVID, M., BOWYER, R. T., DUFFY, L. K., ROBY, D. D. & SCHELL, D. M. (1998). Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. *Ecology* **79**, 2567–2571.
- BENJAMIN, J. R., FAUSCH, K. D. & BAXTER, C. V. (2011). Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. *Oecologia* **167**, 503–512.
- BENNETT, B. A., SMITH, C. R., GLASER, B. & MAYBAUM, H. L. (1994). Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. *Marine Ecology-Progress Series* **108**, 205–223.
- BERGER, J. (2004). The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* **18**, 320–331.
- BILBY, R. E., BEACH, E. W., FRANSEN, B. R., WALTER, J. K. & BISSON, P. A. (2003). Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. *Transactions of the American Fisheries Society* **132**, 733–745.
- BOLGER, D. T., NEWMARK, W. D., MORRISON, T. A. & DOAK, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* **11**, 63–77.
- BOSMAN, A. L. & HOCKEY, P. A. R. (1986). Seabird guano as a determinant of rocky intertidal community structure. *Marine Ecology Progress Series* **32**, 247–257.
- BOUCHARD, S. S. & BJORNDAAL, K. A. (2000). Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**, 2305–2313.
- BROWN, J. H., GILLOOLY, J. F., ALLEN, A. P., SAVAGE, V. M. & WEST, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.
- BROWNELL, R. L., MEAD, J. G., VAN HELDEN, A. L., YAMADA, T. K. & FRANTZIS, A. (2005). Worldwide mass strandings of beaked whales: retrospective review and causes. In *19th Annual Conference of the European Cetacean Society*, La Rochelle, France.
- BUMP, J. K., PETERSON, R. O. & VUCETICH, J. A. (2009a). Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* **90**, 3159–3167.
- BUMP, J. K., TISCHLER, K. B., SCHRANK, A. J., PETERSON, R. O. & VUCETICH, J. A. (2009b). Large herbivores and aquatic–terrestrial links in southern boreal forests. *Journal of Animal Ecology* **78**, 338–345.
- CADENASSO, M. L., PICKETT, S. T. A. & WEATHERS, K. C. (2004). Effect of landscape boundaries on the flux of nutrients, detritus, and organisms. In *Food Webs at the Landscape Level* (eds G. A. POLIS, M. E. POWER and G. R. HUXEL), pp. 263–267. University of Chicago Press, Chicago.
- CAPALDO, S. D. & PETERS, C. R. (1995). Skeletal inventories from wildebeest drownings at Lakes Masek and Ndutu in the Serengeti Ecosystem of Tanzania. *Journal of Archaeological Science* **22**, 385–408.
- CAPALDO, S. D. & PETERS, C. R. (1996). Observations of wildebeest, *Connochaetes taurinus* (Artiodactyla, Bovidae), crossing Lake Masek (Serengeti ecosystem, Tanzania), including one small drowning. *Mammalia* **60**, 303–306.
- CAPPS, K. A., ATKINSON, C. L., RUGENSKI, A., BAXTER, C., BOERSMA, K. S., CAREY, C. C., MCINTYRE, P. B., MOORE, J. W., NOWLIN, W. H. & VAUGHN, C. C. (2012). Impacts of species addition and species loss on ecosystem function in freshwater systems. *Bulletin of the Ecological Society of America* **93**, 402–408.
- CAPPS, K. A., BERVEN, K. A. & TIEGS, S. D. (2015). Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. *Freshwater Biology* **60**, 500–511.
- CAPPS, K. A. & FLECKER, A. S. (2013a). Invasive aquarium fish transform ecosystem nutrient dynamics. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20132418.
- CAPPS, K. A. & FLECKER, A. S. (2013b). Invasive fishes generate biogeochemical hotspots in a nutrient-limited system. *PLoS One* **8**, e54093.
- CARPENTER, S. R., COLE, J. J., PACE, M. L., VAN DE BOGERT, M., BADE, D. L., BASTVIKEN, D., GILLE, C. M., HODGSON, J. R., KITCHELL, J. F. & KRITZBERG, E. S. (2005). Ecosystem subsidies: terrestrial support of aquatic food webs from C-13 addition to contrasting lakes. *Ecology* **86**, 2737–2750.



- CEBALLOS, G., EHRLICH, P. R., BARNSKY, A. D., GARCÍA, A., PRINGLE, R. M. & PALMER, T. M. (2015). Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances* **1**: e1400253.
- CHALONER, D. T., LAMBERTI, G. A., CAK, A. D., BLAIR, N. L. & EDWARDS, R. T. (2007). Inter-annual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. *Freshwater Biology* **52**, 478–490.
- CHILDRESS, E. S., ALLAN, J. D. & MCINTYRE, P. B. (2014). Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems* **17**, 522–534.
- CHILDRESS, E. S. & MCINTYRE, P. B. (2015). Multiple nutrient subsidy pathways from a spawning migration of iteroparous fish. *Freshwater Biology* **60**, 490–499.
- CHRISTENSON, L. M., LOVETT, G. M., MITCHELL, M. J. & GROFFMAN, P. M. (2002). The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. *Oecologia* **131**, 444–452.
- COOPER, S. M., HOLEKAMP, K. E. & SMALE, L. (1999). A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). *African Journal of Ecology* **37**, 149–160.
- DALTON, C. M. & FLECKER, A. S. (2014). Metabolic stoichiometry and the ecology of fear in Trinidadian guppies: consequences for life histories and stream ecosystems. *Oecologia* **176**, 691–701.
- DAVIS, J. M., ROSEMOND, A. D. & SMALL, G. E. (2011). Increasing donor ecosystem productivity decreases terrestrial consumer reliance on a stream resource subsidy. *Oecologia* **167**, 821–834.
- DAWSON, J., PILLAY, D., ROBERTS, P. J. & PERISSINOTTO, R. (2016). Declines in benthic macroinvertebrate community metrics and microphytobenthic biomass in an estuarine lake following enrichment by hippo dung. *Scientific Reports* **6**, 37359.
- DEVVAULT, T. L., RHODES, O. E. JR. & SHIVIK, J. A. (2003). Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234.
- DIRZO, R., YOUNG, H. S., GALETTI, M., CEBALLOS, G., ISAAC, N. J. B. & COLLEN, B. (2014). Defaunation in the Anthropocene. *Science* **345**, 401–406.
- DOUGHTY, C. E., ROMAN, J., FAURBY, S., WOLF, A., HAQUE, A., BAKKER, E. S., MALHI, Y., DUNNING, J. B. & SVENNING, J. C. (2015). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences* **113**, 868–873.
- DOUGHTY, C. E., WOLF, A. & MALHI, Y. (2013). The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience* **6**, 761–764.
- DREYER, J., TOWNSEND, P. A. III, HOOK, J. C., HOEKMAN, D., VANDER ZANDEN, M. J. & GRATTON, C. (2015). Quantifying aquatic insect deposition from lake to land. *Ecology* **96**, 499–509.
- DUCHAMP, J. E., SPARKS, D. W. & SWIHART, R. K. (2010). Exploring the “nutrient hot spot” hypothesis at trees used by bats. *Journal of Mammalogy* **91**, 48–53.
- DUTTON, C. L., SUBALUSKY, A. L., ANISFELD, S. C., NJOROGE, L., ROSI, E. J. & POST, D. M. (2018a). The influence of a semi-arid sub-catchment on suspended sediments in the Mara River, Kenya. *PLoS One* **13**, e0192828.
- DUTTON, C. L., SUBALUSKY, A. L., HAMILTON, S. K., ROSI, E. J. & POST, D. M. (2018b). Organic matter loading by hippopotami causes subsidy overload resulting in downstream hypoxia and fish kills. *Nature Communications* **9**: 1951.
- EARL, J. E. & ZOLLNER, P. A. (2014). Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecological Modelling* **283**, 45–52.
- EARL, J. E. & ZOLLNER, P. A. (2017). Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *Journal of Animal Ecology* **86**, 987–997.
- ELSER, J. J., DOBBERFUHL, D. R., MACKAY, N. A. & SCHAMPEL, J. H. (1996). Organism size, life history, and N:P stoichiometry. *BioScience* **46**, 674–684.
- ELSER, J. J., FAGAN, W. F., DENNO, R. F., DOBBERFUHL, D. R., FOLARIN, A., HUBERTY, A., INTERLANDI, S., KILHAM, S. S., MCCAULEY, E., SCHULZ, K. L., SIEMANN, E. H. & STERNER, R. W. (2000). Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408**, 578–580.
- ELSER, J. J., MARZOLF, E. R. & GOLDMAN, C. R. (1990). Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1468–1477.
- FEY, S. B., MERTENS, A. N., BEVERS DORF, L. J., MCMAHON, K. D. & COTTINGHAM, K. L. (2015a). Recognizing cross-ecosystem responses to changing temperatures: soil warming impacts pelagic food webs. *Oikos* **124**, 1473–1481.
- FEY, S. B., STEPIELSKI, A. M., NUSSLÉ, S., CERVANTES-YOSHIDA, K., HWAN, J. L., HUBER, E. R., FEY, M. J., CATENAZZI, A. & CARLSON, S. M. (2015b). Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences* **112**, 1083–1088.
- FIELD, C. R. (1970). A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius* Linn.) in the Queen Elizabeth National Park, Uganda, with some management implications. *Zoologica Africana* **5**, 71–86.
- FINNEY, B. P., GREGORY-EAVES, I., SWEETMAN, J., DOUGLAS, M. S. V. & SMOL, J. P. (2000). Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. *Science* **290**, 795–799.
- FITTKAU, E. J. (1973). Crocodiles and the nutrient metabolism of Amazonian waters. *Amazoniana* **4**, 102–133.
- FLECKER, A., MCINTYRE, P. B., MOORE, J. W., ANDERSON, J., TAYLOR, B. & HALL, R. (2010). Migratory fishes as material and process subsidies in riverine ecosystems. *American Fisheries Society Symposium* **73**, 559–592.
- FRANCE, R. L. (2011). Leaves as “crackers”, biofilm as “peanut butter”: exploratory use of stable isotopes as evidence for microbial pathways in detrital food webs. *Oceanological and Hydrobiological Studies* **40**, 110.
- FÜREDER, L., WALLINGER, M. & BURGER, R. (2005). Longitudinal and seasonal pattern of insect emergence in alpine streams. *Aquatic Ecology* **39**, 67–78.
- GENDE, S. M., QUINN, T. P., HILBORN, R., HENDRY, A. P. & DICKERSON, B. (2004). Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. *Oikos* **104**, 518–528.
- GERGS, R., KOESTER, M., SCHULZ, R. S. & SCHULZ, R. (2014). Potential alteration of cross-ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the terrestrial food web. *Freshwater Biology* **59**, 2645–2655.
- GIANNICO, G. R. & HINCH, S. G. (2007). Juvenile coho salmon (*Oncorhynchus kisutch*) responses to salmon carcasses and in-stream wood manipulations during winter and spring. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 324–335.
- GILLOOLY, J. F., BROWN, J. H., WEST, G. B., SAVAGE, V. M. & CHARNOV, E. L. (2001). Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251.
- GIROUX, M. A., BERTEAUX, D., LECOMTE, N., GAUTHIER, G., SZOR, G. & BETY, J. (2012). Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an Arctic predator. *Journal of Animal Ecology* **81**, 533–542.
- GRATTON, C. & VANDER ZANDEN, M. J. (2009). Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. *Ecology* **90**, 2689–2699.
- GUENET, B., DANGER, M., ABBADIE, L. & LACROIX, G. (2010). Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology* **91**, 2850–2861.
- HABECK, C. W. & MEEHAN, T. D. (2008). Mass invariance of population nitrogen flux by terrestrial mammalian herbivores: an extension of the energetic equivalence rule. *Ecology Letters* **11**, 898–903.
- HALVORSON, H. M., FULLER, C., ENTREKIN, S. A. & EVANS-WHITE, M. A. (2015). Dietary influences on production, stoichiometry and decomposition of particulate wastes from shredders. *Freshwater Biology* **60**, 466–478.
- HARDING, J. S., HAWKE, D. J., HOLDAWAY, R. N. & WINTERBOURN, M. J. (2004). Incorporation of marine-derived nutrients from petrel breeding colonies into stream food webs. *Freshwater Biology* **49**, 576–586.
- HARRIS, G., THIRGOOD, S., HOPCRAFT, J. G. C., CROMSIGT, J. P. G. M. & BERGER, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research* **7**, 55–76.
- HAWLENA, D. & SCHMITZ, O. J. (2010). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences* **107**, 15503–15507.
- HEINTZ, R. A., NELSON, B. D., HUDSON, J., LARSEN, M., HOLLAND, L. & WIPFLI, M. (2004). Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. *Transactions of the American Fisheries Society* **133**, 559–567.
- HELFIELD, J. M. & NAIMAN, R. J. (2006). Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* **9**, 167–180.
- HILBORN, R., BRANCH, T. A., ERNST, B., MAGNUSSON, A., MINTE-VERA, C. V., SCHEUERRELL, M. D. & VALERO, J. L. (2003). State of the world’s fisheries. *Annual Review of Environment and Resources* **28**, 359–399.
- HILDERBRAND, G. V., HANLEY, T. A., ROBBINS, C. T. & SCHWARTZ, C. C. (1999). Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* **121**, 546–550.
- HOBBS, N. T. (1996). Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**, 695–713.
- HOCKING, M. D. & REIMCHEN, T. E. (2009). Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos* **118**, 1307–1318.
- HOLDO, R. M., HOLT, R. D., SINCLAIR, A. R. E., GODLEY, B. J. & THIRGOOD, S. (2011). Migration impacts on communities and ecosystems: empirical evidence and theoretical insights. In *Animal Migration: A Synthesis* (eds E. J. MILNER-GULLAND, J. M. FRYXELL and A. R. E. SINCLAIR), pp. 131–143. Oxford University Press Inc., New York.
- HOLTGRIEVE, G. W. & SCHINDLER, D. E. (2011). Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology* **92**, 373–385.
- HUMMEL, M. & RAY, J. C. (2008). *Caribou and the North: A Shared Future*. Dundurn, Toronto.
- HUTCHINSON, G. E. (1950). *3. The Biogeochemistry of Vertebrate Excretion*. American Museum of Natural History, New York.
- HUXEL, G. R. & MCCANN, K. (1998). Food web stability: the influence of trophic flows across habitats. *American Naturalist* **152**, 460–469.
- HUXEL, G. R., MCCANN, K. & POLIS, G. A. (2002). Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research* **17**, 419–432.
- IWATA, T., NAKANO, S. & MURAKAMI, M. (2003). Stream meanders increase insectivorous bird abundance in riparian deciduous forests. *Ecography* **26**, 325–337.

- JACKSON, J. K. & FISHER, S. G. (1986). Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* **67**, 629–638.
- JACOBS, S. M., BECHTOLD, J. S., BIGGS, H. C., GRIMM, N. B., LORENTZ, S., MCCLAIN, M. E., NAIMAN, R. J., PERAKIS, S. S., PINAY, G. & SCHOLES, M. C. (2007). Nutrient vectors and riparian processing: a review with special reference to African semiarid Savanna ecosystems. *Ecosystems* **10**, 1231–1249.
- JANETSKI, D. J., CHALONER, D. T., TIEGS, S. D. & LAMBERTI, G. A. (2009). Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* **159**, 583–595.
- JEFFRIES, R. L., HENRY, H. A. L. & ABRAHAM, K. F. (2004). Agricultural nutrient subsidies to migratory geese and change in Arctic coastal habitats. In *Food Webs at the Landscape Level* (eds G. A. POLIS, M. E. POWER and G. R. HUXEL), pp. 268–283. Chicago University Press, Chicago.
- JONES, C. G., LAWTON, J. H. & SHACHAK, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–1957.
- JONES, C. G. & SHACHAK, M. (1990). Fertilization of the desert soil by rock-eating snails. *Nature* **346**, 839–841.
- JONES, S. E., SOLOMON, C. T. & WEIDEL, B. C. (2012). Subsidy or subtraction: how do terrestrial inputs influence consumer production in lakes? *Freshwater Reviews* **5**, 37–49.
- JOYCE, P., WARREN, L. L. & WOTTON, R. S. (2007). Faecal pellets in streams: their binding, breakdown and utilization. *Freshwater Biology* **52**, 1868–1880.
- JOYCE, P. & WOTTON, R. S. (2008). Shredder fecal pellets as stores of allochthonous organic matter in streams. *Journal of the North American Benthological Society* **27**, 521–528.
- JUNK, W. J. (1999). The flood pulse concept of large rivers: learning from the tropics. *Archiv für Hydrobiologie Supplement* **115/3**, Large Rivers 11, 261–280.
- JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. (1989). The flood pulse concept in river-floodplain systems. In *International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences (Volume 106)*, pp. 110–127. Canada Department of Fisheries and Oceans, Ottawa.
- KANGA, E. M., OGUTU, J. O., OLFF, H. & SANTEMA, P. (2011). Population trend and distribution of the vulnerable common hippopotamus *Hippopotamus amphibius* in the Mara Region of Kenya. *Oryx* **45**, 20–27.
- KARL, T. R., KNIGHT, R. W. & PLUMMER, N. (1995). Trends in high-frequency climate variability in the twentieth century. *Nature* **377**, 217–220.
- KEENAN, S. W., SCHAEFFER, S. M., JIN, V. L. & DEBRUYN, J. M. (2018). Mortality hotspots: nitrogen cycling in forest soils during vertebrate decomposition. *Soil Biology and Biochemistry* **121**, 165–176.
- KELLY, P. T., SOLOMON, C. T., WEIDEL, B. C. & JONES, S. E. (2013). Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. *Ecology* **95**, 1236–1242.
- KENDALL, C., VIRANI, M. Z., KIRUI, P., THOMSETT, S. & GITHIRU, M. (2012). Mechanisms of coexistence in vulture: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. *Condor* **114**, 523–531.
- KITCHELL, J. F., O'NEILL, R. V., WEBB, D., GALLEPP, G. W., BARTELL, S. M., KOONCE, J. F. & AUSMUS, B. S. (1979). Consumer regulation of nutrient cycling. *BioScience* **29**, 28–34.
- KITCHELL, J. F., SCHINDLER, D. E., HERWIG, B. R., POST, D. M., OLSON, M. H. & OLDHAM, M. (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.
- KLAASSEN, R. H. G., HAKE, M., STRANDBERG, R., KOKS, B. J., TRIERWEILER, C., EXO, K. M., BAIRLEIN, F. & ALERSTAM, T. (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology* **83**, 176–184.
- KNOLL, L. B., MCINTYRE, P. B., VANNI, M. J. & FLECKER, A. S. (2009). Feedbacks of consumer nutrient recycling on producer biomass and stoichiometry: separating direct and indirect effects. *Oikos* **118**, 1732–1742.
- KOMINOSKI, J. S., ROSEMOND, A. D., BENSTEAD, J. P., GULIS, V., MAERZ, J. C. & MANNING, D. W. P. (2015). Low-to-moderate nitrogen and phosphorus concentrations accelerate microbially driven litter breakdown rates. *Ecological Applications* **25**, 856–865.
- LARSEN, S., MUEHLBAUER, J. D. & MARTI, E. (2016). Resource subsidies between stream and terrestrial ecosystems under global change. *Global Change Biology* **22**, 2489–2504.
- LAVERY, T. J., ROUDNEW, B., GILL, P., SEYMOUR, J., SEURONT, L., JOHNSON, G., MITCHELL, J. G. & SMETACEK, V. (2010). Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proceedings of the Royal Society B-Biological Sciences* **277**, 3527–3531.
- LEROUX, S. J. & LOREAU, M. (2008). Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* **11**, 1147–1156.
- LEVI, T., WHEAT, R. E., ALLEN, J. M. & WILMERS, C. C. (2015). Differential use of salmon by vertebrate consumers: implications for conservation. *PeerJ* **3**, 15.
- LISS, A., GUO, J., LIND, M. I. & ROWE, O. (2015). Cool tadpoles from Arctic environments waste fewer nutrients - high gross growth efficiencies lead to low consumer-mediated nutrient recycling in the North. *Journal of Animal Ecology* **84**, 1744–1756.
- LIKENS, G. E. & BORMANN, F. H. (1974). Linkages between terrestrial and aquatic ecosystems. *BioScience* **24**, 447–456.
- LINDEMAN, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology* **23**, 399–418.
- LOVETT, G. M. & RUESINK, A. E. (1995). Carbon and nitrogen mineralization from decomposing gypsy moth frass. *Oecologia* **104**, 133–138.
- LUHRING, T. M., DELONG, J. P. & SEMLITSCH, R. D. (2017). Stoichiometry and life-history interact to determine the magnitude of cross-ecosystem element and biomass fluxes. *Frontiers in Microbiology* **8**, 814.
- LUNDBERG, J. & MOBERG, F. (2003). Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* **6**, 87–98.
- LUNDSTEN, L., SCHLINING, K. L., FRASIER, K., JOHNSON, S. B., KUHNZ, L. A., HARVEY, J. B., CLAGUE, G. & VRIJENHOEK, R. C. (2010). Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. *Deep Sea Research Part I: Oceanographic Research Papers* **57**, 1573–1584.
- LYONS, S. K., SMITH, F. A. & BROWN, J. H. (2004). Of mice, mastodons and men: human-mediated extinctions on four continents. *Evolutionary Ecology Research* **6**, 339–358.
- MALHI, Y., DOUGHTY, C. E., GALETTI, M., SMITH, F. A., SVENNING, J. C. & TERBORGH, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences* **113**, 838–846.
- MANNY, B. A., JOHNSON, W. C. & WETZEL, R. G. (1994). Nutrient additions by waterfowl to lakes and reservoirs: predicting their effects on productivity and water quality. *Hydrobiologia* **279/280**, 121–132.
- MARCARELLI, A. M., BAXTER, C. V., MINEAU, M. M. & HALL, R. O. (2011). Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* **92**, 1215–1225.
- MARZAK, L. B., THOMPSON, R. M. & RICHARDSON, J. S. (2007). Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* **88**, 140–148.
- MARTIN-CREUZBURG, D., KOWARIK, C. & STRAILE, D. (2017). Cross-ecosystem fluxes: export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. *Science of the Total Environment* **577**, 174–182.
- MASESE, F. O., ABRANTES, K. G., GETTEL, G. M., BOUILLON, S., IRVINE, K. & MCCLAIN, M. E. (2015). Are large herbivores vectors of terrestrial subsidies for riverine food webs? *Ecosystems* **18**, 686–706.
- MASESE, F. O., ABRANTES, K. G., GETTEL, G. M., IRVINE, K., BOUILLON, S. & MCCLAIN, M. E. (2018). Trophic structure of an African savanna river and organic matter inputs by large terrestrial herbivores: a stable isotope approach. *Freshwater Biology* doi: 10.1111/fwb.13163.
- MAZZARIOL, S., DI GUARDO, G., PETRELLA, A., MARSILI, L., FOSSI, C. M., LEONZIO, C., ZIZZO, N., VIZZINI, S., GASPARI, S., PAVAN, G., PODESTÀ, M., GARIBALDI, F., FERRANTE, M., COPAT, C., TRAVERSA, D., et al. (2011). Sometimes sperm whales (*Physeter macrocephalus*) cannot find their way back to the high seas: a multidisciplinary study on a mass stranding. *PLoS One* **6**, e19417.
- MCCANN, K. S., RASMUSSEN, J. B. & UMBANHOWAR, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters* **8**, 513–523.
- MCCAULEY, D. J., DAWSON, T. E., POWER, M. E., FINLAY, J. C., OGADA, M., GOWER, D. B., CAYLOR, K., NYINGI, W. D., GITHAIGA, J. M., NYUNJA, J., JOYCE, F. H., LEWISON, R. L. & BRASHARES, J. S. (2015). Carbon stable isotopes suggest that hippopotamus-vectored nutrients subsidize aquatic consumers in an East African river. *Ecosphere* **6**, art52.
- MCCLAIN, M. E., BOYER, E. W., DENT, C. L., GERGEL, S. E., GRIMM, N. B., GROFFMAN, P. M., HART, S. C., HARVEY, J. W., JOHNSTON, C. A., MAYORGA, E., MCDOWELL, W. H. & PINAY, G. (2003). Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* **6**, 301–312.
- MCINTYRE, P. B. & FLECKER, A. S. (2010). Ecological stoichiometry as an integrative framework in stream fish ecology. *American Fisheries Society Symposium* **73**, 539–558.
- MCINTYRE, P. B., FLECKER, A. S., VANNI, M. J., HOOD, J. M., TAYLOR, B. W. & THOMAS, S. A. (2008). Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? *Ecology* **89**, 2335–2346.
- MCINTYRE, P. B., JONES, L. E., FLECKER, A. S. & VANNI, M. J. (2007). Fish extinctions alter nutrient recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 4461–4466.
- MENNINGER, H. L., PALMER, M. A., CRAIG, L. S. & RICHARDSON, D. C. (2008). Periodical cicada detritus impacts stream ecosystem metabolism. *Ecosystems* **11**, 1306–1317.
- MEYER, J. L. & SCHULTZ, E. T. (1985). Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography* **30**, 146–156.
- MEYER, J. L., SCHULTZ, E. T. & HELFMAN, G. S. (1983). Fish schools - an asset to corals. *Science* **220**, 1047–1049.
- MIDDLETON, A. D., MORRISON, T. A., FORTIN, J. K., ROBBINS, C. T., PROFFITT, K. M., WHITE, P. J., MCWHIRTER, D. E., KOEL, T. M., BRIMEYER, D. G., FAIRBANKS, W. S. & KAUFFMAN, M. J. (2013). Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20130870.
- MILNER-GULLAND, E. J., FRYXELL, J. M. & SINCLAIR, A. R. E. (2011). *Animal Migration: A Synthesis*. Oxford University Press, Oxford.
- MITCHELL, N. L. & LAMBERTI, G. A. (2005). Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. *Limnology and Oceanography* **50**, 217–227.



- MOORE, J. C., BERLOW, E. L., COLEMAN, D. C., DE RUITER, P. C., DONG, Q., HASTINGS, A., JOHNSON, N. C., MCCANN, K. S., MELVILLE, K., MORIN, P. J., NADELHOFFER, K., ROSEMOND, A. D., POST, D. M., SABO, J. L., SCOW, K. M., et al. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**, 584–600.
- MOORE, J. W. & SCHINDLER, D. E. (2004). Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 1582–1589.
- MOSS, B. (2015). Mammals, freshwater reference states, and the mitigation of climate change. *Freshwater Biology* **60**, 1964–1976.
- MUEHLBAUER, J. D., COLLINS, S. F., DOYLE, M. W. & TOCKNER, K. (2014). How wide is a stream? Spatial extent of the potential “stream signature” in terrestrial food webs using meta-analysis. *Ecology* **95**, 44–55.
- MUHAMMETSAFINA, A., MIDWOOD, J. D., BLISS, S. M., STAMPLECOSKIE, K. M. & COOKE, S. J. (2014). The fate of dead fish tagged with biotelemetry transmitters in an urban stream. *Aquatic Ecology* **48**, 23–33.
- NAIMAN, R. J., BILBY, R. E., SCHINDLER, D. E. & HELFIELD, J. M. (2002). Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**, 399–417.
- NAIMAN, R. J., HELFIELD, J. M., BARTZ, K. K., DRAKE, D. C. & HONEA, J. M. (2009). Pacific salmon, marine-derived nutrients, and the characteristics of aquatic and riparian ecosystems. In *Challenges for Diadromous Fishes in a Dynamic Global Environment* (American Fisheries Society Symposium (Volume 69, eds A. HARO, K. L. SMITH, R. A. RULIFSON, C. L. MOFFITT, R. J. KLAUDA, M. J. DADSWELL, R. A. CUNJAK, J. E. COOPER, K. L. BEAL and T. S. AVERY), pp. 395–425. American Fisheries Society, Bethesda.
- NAKANO, S. & MURAKAMI, M. (2001). Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 166–170.
- NEWSOME, T. M., DELLINGER, J. A., PAVEY, C. R., RIPPLE, W. J., SHORES, C. R., WIRSING, A. J. & DICKMAN, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography* **24**, 1–11.
- NISLOW, K., ARMSTRONG, J. & MCKELVEY, S. (2004). Phosphorus flux due to Atlantic salmon (*Salmo salar*) in an oligotrophic upland stream: effects of management and demography. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2401–2410.
- NOWLIN, W. H., GONZALEZ, M. J., VANNI, M. J., STEVENS, M. H. H., FIELDS, M. W. & VALENTEI, J. J. (2007). Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. *Ecology* **88**, 2174–2186.
- NOWLIN, W. H., VANNI, M. J. & YANG, L. H. (2008). Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology* **89**, 647–659.
- ORO, D., GENOVART, M., TAVECCHIA, G., FOWLER, M. S. & MARTÍNEZ-ABRAÍN, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters* **16**, 1501–1514.
- PAETZOLD, A., LEE, M. & POST, D. M. (2008). Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. *Oecologia* **157**, 653–659.
- PAUDEL, E., DOSSA, G. G. O., DE BLÉCOURT, M., BECKSCHÄFER, P., XU, J. & HARRISON, R. D. (2015). Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. *Ecosphere* **6**, 1–20.
- PAYNE, L. X. & MOORE, J. W. (2006). Mobile scavengers create hotspots of freshwater productivity. *Oikos* **115**, 69–80.
- PERSHING, A. J., CHRISTENSEN, L. B., RECORD, N. R., SHERWOOD, G. D. & STETSON, P. B. (2010). The impact of whaling on the ocean carbon cycle: why bigger was better. *PLoS One* **5**, e12444.
- POLIS, G. A., ANDERSON, W. B. & HOLT, R. D. (1997a). Toward 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. & HURD, S. D. (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 of the United States of America* **92**, 4382–4386.
- POLIS, G. A. & HURD, S. D. (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., HURD, S. D., JACKSON, C. T. & PINERO, F. S. (1997b). El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* **78**, 1884–1897.
- POST, D. M., DOYLE, M. W., SABO, J. L. & FINLAY, J. C. (2007). The problem of boundaries in defining ecosystems: a potential landmine for uniting geomorphology and ecology. *Geomorphology* **89**, 111–126.
- POST, D. M., TAYLOR, J. P., KITCHELL, J. F., OLSON, M. H., SCHINDLER, D. E. & HERWIG, B. R. (1998). The role of migratory waterfowl as nutrient vectors in a managed wetland. *Conservation Biology* **12**, 910–920.
- POST, D. M. & WALTERS, A. W. (2009). Nutrient excretion rates of anadromous alewives during their spawning migration. *Transactions of the American Fisheries Society* **138**, 264–268.
- POWER, M. E. & RAINEY, W. E. (2000). Food webs and resource sheds: towards spatially delimiting trophic interactions. In *Ecological Consequences of Habitat Heterogeneity* (eds M. J. HUTCHINGS, E. A. JOHN and A. J. A. STEWART), pp. 291–314. Blackwell Scientific, Oxford.
- REGESTER, K. J., LIPS, K. R. & WHILES, M. R. (2006). Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia* **147**, 303–314.
- RICHARDSON, J. S., ZHANG, Y. X. & MARCZAK, L. B. (2010). Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications* **26**, 55–66.
- ROBERTS, B. J. & HOWARTH, R. W. (2006). Nutrient and light availability regulate the relative contribution of autotrophs and heterotrophs to respiration in freshwater pelagic ecosystems. *Limnology and Oceanography* **51**, 288–298.
- ROMAN, J. & MCCARTHY, J. J. (2010). The whale pump: marine mammals enhance primary productivity in a coastal basin. *PLoS One* **5**, e13255.
- ROSEMOND, A. D., BENSTEAD, J. P., BUMPERS, P. M., GULIS, V., KOMINOSKI, J. S., MANNING, D. W. P., SUBERKROPP, K. & WALLACE, J. B. (2015). Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science* **347**, 1142–1145.
- RUNDIO, D. E. & LINDLEY, S. T. (2008). Seasonal patterns of terrestrial and aquatic prey abundance and use by *Oncorhynchus mykiss* in a California coastal basin with a Mediterranean climate. *Transactions of the American Fisheries Society* **137**, 467–480.
- SABO, J. L. & POWER, M. E. (2002). River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* **83**, 1860–1869.
- SAMWAYS, K. M. & CUNJAK, R. A. (2015). Increases in benthic community production and metabolism in response to marine-derived nutrients from spawning Atlantic salmon (*Salmo salar*). *Freshwater Biology* **60**, 1647–1658.
- SANCHEZ-PINERO, F. & POLIS, G. A. (2000). Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* **81**, 3117–3132.
- SCHINDLER, D. W. (1977). Evolution of phosphorus limitation in lakes. *Science* **195**, 260–262.
- SCHMITZ, O. J., HAWLENA, D. & TRUSSELL, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.
- SCHREIBER, S. & RUDOLF, V. H. W. (2008). Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecology Letters* **11**, 576–587.
- SCHULZ, R., BUNDSCHUH, M., GERGS, R., BRÜHL, C. A., DIEHL, D., ENTILING, M. H., FAHSE, L., FRÖR, O., JUNGKUNST, H. F., LORKE, A., SCHÄFER, R. B., SCHAUMANN, G. E. & SCHWENK, K. (2015). Review on environmental alterations propagating from aquatic to terrestrial ecosystems. *Science of the Total Environment* **538**, 246–261.
- SHANER, P. J. L. & MACKO, S. A. (2011). Trophic shifts of a generalist consumer in response to resource pulses. *PLoS One* **6**, e17970.
- SILLETT, T. S. & HOLMES, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* **71**, 296–308.
- SITTERS, J., ATKINSON, C. L., GUELZOW, N., KELLY, P. & SULLIVAN, L. L. (2015). Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* **124**, 920–930.
- SITTERS, J., BAKKER, E., VELDHUIS, M., VEEN, C., OLDE VENTERINK, H. & VANNI, M. (2017). The stoichiometry of nutrient release by terrestrial herbivores and its ecosystem consequences. *Frontiers in Earth Science* **5**, 32.
- SMALL, G. E. & PRINGLE, C. M. (2010). Deviation from strict homeostasis across multiple trophic levels in an invertebrate consumer assemblage exposed to high chronic phosphorus enrichment in a Neotropical stream. *Oecologia* **162**, 581–590.
- SMITH, C. R. & BACO, A. R. (2003). Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology* **41**, 311–354.
- SPILLER, D. A., PIOVIA-SCOTT, J., WRIGHT, A. N., YANG, L. H., TAKIMOTO, G., SCHOENER, T. W. & IWATA, T. (2010). Marine subsidies have multiple effects on coastal food webs. *Ecology* **91**, 1424–1434.
- STAPP, P. & POLIS, G. A. (2003a). Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos* **102**, 111–123.
- STAPP, P. & POLIS, G. A. (2003b). Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia* **134**, 496–504.
- STAPP, P., POLIS, G. A. & PINERO, F. S. (1999). Stable isotopes reveal strong marine and El Niño effects on island food webs. *Nature* **401**, 467–469.
- STEARNS, K., MCCAULEY, D. J., FINLAY, J. C., MPEMBA, J., WARRINGTON, I. T., MUTAYOBA, B. M., POWER, M. E., DAWSON, T. E. & BRASHARES, J. S. (2018). Effects of the hippopotamus on the chemistry and ecology of a changing watershed. *Proceedings of the National Academy of Sciences* **115**, E5028–E5037.
- STERNER, R. W. & ELSEY, J. J. (2002). *Ecological Stoichiometry - The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.
- SUBALUSKY, A. L., DUTTON, C. L., NJOROGE, L., ROST, E. J. & POST, D. M. (2018). Organic matter and nutrient inputs from large wildlife influence ecosystem function in the Mara River, Africa. *Ecology* doi: 10.1002/ecy.2509.
- SUBALUSKY, A. L., DUTTON, C. L., ROST, E. J. & POST, D. M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 7647–7652.
- SUBALUSKY, A. L., DUTTON, C. L., ROST-MARSHALL, E. J. & POST, D. M. (2015). The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshwater Biology* **60**, 512–525.

- SUBALUSKY, A. L., FITZGERALD, L. A. & SMITH, L. L. (2009). Ontogenetic niche shifts in the American Alligator establish functional connectivity between aquatic systems. *Biological Conservation* **142**, 1507–1514.
- SUMMERHAYES, V. S. & ELTON, C. S. (1923). Contributions to the ecology of Spitsbergen and Bear Island. *Journal of Ecology* **11**, 214–216.
- TAKIMOTO, G. (2002). Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. *Ecological Research* **17**, 433–439.
- TIEGS, S. D., LEVI, P. S., RUEGG, J., CHALONER, D. T., TANK, J. L. & LAMBERTI, G. A. (2011). Ecological effects of live salmon exceed those of carcasses during an annual spawning migration. *Ecosystems* **14**, 598–614.
- TUCKER, M. A., BÖHNING-GAESE, K., FAGAN, W. F., FRYXELL, J. M., VAN MOORTER, B., ALBERTS, S. C., ALI, A. H., ALLEN, A. M., ATTIAS, N., AVGAR, T., BARTLAM-BROOKS, H., BAYARBAATAR, B., BELANT, J. L., BERTASSONI, A., BEYER, D., et al. (2018). Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469.
- TWINING, C. W., BRENNAN, J. T., LAWRENCE, P., SHIPLEY, J. R., TOLLEFSON, T. N. & WINKLER, D. W. (2016). Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *Proceedings of the National Academy of Sciences* **113**, 10920–10925.
- TWINING, C. W., PALKOVCAS, E. P., FRIEDMAN, M. A., HASSELMAN, D. J. & POST, D. M. (2017). Nutrient loading by anadromous fishes: species-specific contributions and the effects of diversity. *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 609–619.
- TWINING, C. W., WEST, D. C. & POST, D. M. (2013). Historical changes in nutrient inputs from humans and anadromous fishes in New England's coastal watersheds. *Limnology and Oceanography* **58**, 1286–1300.
- UNO, H. & POWER, M. E. (2015). Mainstem-tributary linkages by mayfly migration help sustain salmonids in a warming river network. *Ecology Letters* **18**, 1012–1020.
- VANNI, M. J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**, 341–370.
- VANNI, M. J., BOROS, G. & MCINTYRE, P. B. (2013). When are fish sources vs. sinks of nutrients in lake ecosystems? *Ecology* **94**, 2195–2206.
- VANNI, M. J., FLECKER, A. S., HOOD, J. M. & HEADWORTH, J. L. (2002). Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters* **5**, 285–293.
- VANNI, M. J. & MCINTYRE, P. B. (2016). Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis. *Ecology* **97**, 3460–3471.
- VARPE, Ø., FIRSEN, Ø. & SLOTTE, A. (2005). Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* **146**, 443.
- VERBOOM, J., SCHIPPERS, P., CORMONT, A., STERK, M., VOS, C. & OPDAM, P. M. (2010). Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria. *Landscape Ecology* **25**, 1289–1298.
- VAN DER WAL, R., BARDGETT, R. D., HARRISON, K. A. & STIEN, A. (2004). Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. *Ecography* **27**, 242–252.
- WALTERS, A. W., BARNES, R. T. & POST, D. M. (2009). Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 439–448.
- WALTERS, D. M., MILLS, M. A., FRITZ, K. M. & RAIKOW, D. F. (2010). Spider-mediated flux of PCBs from contaminated sediments to terrestrial ecosystems and potential risks to arachnivoracious birds. *Environmental Science & Technology* **44**, 2849–2856.
- WAMBUGUH, O. (2008). Dry wildebeest carcasses in the African savannah: the utilization of a unique resource. *African Journal of Ecology* **46**, 515–522.
- WARDLE, D. A. & BARDGETT, R. D. (2004). Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Frontiers in Ecology and the Environment* **2**, 145–153.
- WERNER, E. E. & GILLIAM, J. F. (1984). The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics* **15**, 393–425.
- WEST, D. C., WALTERS, A. W., GEPHARD, S. & POST, D. M. (2010). Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1211–1220.
- WHEELER, K., MILLER, S. W. & CROWL, T. A. (2015). Migratory fish excretion as a nutrient subsidy to recipient stream ecosystems. *Freshwater Biology* **60**, 537–550.
- WHEELER, K., MILLER, S. W. & CROWL, T. A. (2017). Adfluvial salmonids have engineering but not fertilization impacts in tributaries of a central Utah reservoir. *Canadian Journal of Fisheries and Aquatic Sciences* doi: 10.1139/cjfas-2016-0462.
- WILBUR, H. M. (1980). Complex life cycles. *Annual Review of Ecology and Systematics* **11**, 67–93.
- WILMERS, C. C., CRABTREE, R. L., SMITH, D. W., MURPHY, K. M. & GETZ, W. M. (2003). Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* **72**, 909–916.
- WILSON, E. E. & WOLKOVICH, E. M. (2011). Scavenging: how carnivores and carrion structure communities. *Trends in Ecology & Evolution* **26**, 129–135.
- WINDER, M., SCHINDLER, D. E., MOORE, J. W., JOHNSON, S. P. & PALEN, W. J. (2005). Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2285–2293.
- WINKLER, D. W., JORGENSEN, C., BOTH, C., HOUSTON, A. I., MCNAMARA, J. M., LEVEY, D. J., PARTECKE, J., FUDICKAR, A., KACELNIK, A., ROSHIER, D. & PIERSMA, T. (2014). Cues, strategies, and outcomes: how migrating vertebrates track environmental change. *Movement Ecology* **2**, 10.
- WINTON, R. S. & RIVER, M. (2017). The biogeochemical implications of massive gull flocks at landfills. *Water Research* **122**, 440–446.
- WIPPLI, M. S., HUDSON, J. P., CAOUILLE, J. P., MITCHELL, N. L., LESSARD, J. L., HEINTZ, R. A. & CHALONER, D. T. (2010). Salmon carcasses increase stream productivity more than inorganic fertilizer pellets: a test on multiple trophic levels in streamside experimental channels. *Transactions of the American Fisheries Society* **139**, 824–839.
- WITMAN, J. D., ELLIS, J. C. & ANDERSON, W. B. (2004). The influence of physical processes, organisms, and permeability on cross-ecosystem fluxes. In *Food webs at the Landscape Level* (eds G. A. POLIS, M. E. POWER and G. R. HUXEL), pp. 335–358. University of Chicago Press, Chicago, Illinois.
- WOLF, A., DOUGHTY, C. E. & MALHI, Y. (2013). Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. *PLoS One* **8**, e71352.
- WOTTON, R. S. & MALMQVIST, B. (2001). Feces in aquatic ecosystems. *BioScience* **51**, 537–544.
- ZHANG, D., HUI, D., LUO, Y. & ZHOU, G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology* **1**, 85–93.

(Received 21 November 2017; revised 24 August 2018; accepted 30 August 2018; published online 24 September 2018)