

IDEA AND
PERSPECTIVESubsidy hypothesis and strength of trophic cascades
across ecosystems

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Abstract

Ecosystems are differentially open to subsidies of energy, material and organisms. This fundamental ecosystem attribute has long been recognized but the influence of this property on community regulation has not been investigated. We propose that this environmental attribute may explain variation in the strength of trophic cascades among ecosystems. Simply because of gravity, we should predict that systems with convex profiles receive low amounts of subsidies whereas systems with concave profiles act as spatial attractors, and receive high amounts of subsidies. The subsidy hypothesis states that ecosystems with high amounts of allochthonous inputs will experience the strongest trophic cascades. To test this hypothesis, we derive ecosystem models and investigate the effect of location and magnitude of subsidies on the strength of trophic cascades. Predictions from our models support the subsidy hypothesis and highlight the need to consider ecosystems as open to allochthonous flows.

Keywords

Allochthonous, control, exogenous, flows, functioning, inputs, log–response ratio, regulation, top–down.

Ecology Letters (2008) 11: 1147–1156

INTRODUCTION

The flow of energy, material and organisms across ecosystems, most commonly referred to as allochthonous inputs or spatial subsidies, is ubiquitous (Polis *et al.* 1997; Loreau *et al.* 2003; Loreau & Holt 2004). Such flows are a major determinant of ecosystem functioning in many systems, including coastal areas (Rose & Polis 1998), inland forests (Yang 2004), islands (Polis & Hurd 1995), lentic systems (Pace *et al.* 2004; Knight *et al.* 2005), lotic systems (Vannote *et al.* 1980; Bastow *et al.* 2002) and riparian forests (Murakami & Nakano 2002; Willson *et al.* 2004). Despite the ubiquity of allochthonous inputs, classic theories of community regulation (e.g. Hairston *et al.* 1960; Oksanen *et al.* 1981) are based on *in situ* productivity. Consequently, their predictions may not apply to open ecosystems.

Top–down community regulation, which often results in trophic cascades (Carpenter *et al.* 1985), has been extensively studied, and recent meta-analyses have demonstrated that aquatic systems generally experience stronger trophic cascades than terrestrial systems (Schmitz *et al.* 2000; Shurin *et al.* 2002; Stibor *et al.* 2004). A mechanistic understanding

of the variation in the strength of trophic cascades among ecosystems is emerging (Borer *et al.* 2005; Shurin & Seabloom 2005; Hall *et al.* 2007) but general predictions remain elusive. The leading hypotheses to explain variation in trophic cascade strength among ecosystems are (i) the relative body sizes of consumers and their resources (body size hypothesis, Shurin & Seabloom 2005), (ii) the metabolic efficiency of primary consumers (primary consumer efficiency hypothesis, Borer *et al.* 2005), (iii) system productivity (primary productivity hypothesis, Borer *et al.* 2005; Shurin & Seabloom 2005), (iv) the resource quality of primary producers (food quality hypothesis, Borer *et al.* 2005; Hall *et al.* 2007), (v) the diversity of primary producers (producer diversity hypothesis, Hillebrand & Cardinale 2004; Hillebrand *et al.* 2007) and (vi) key functional traits of predators (foraging–predation risk trade-off hypothesis, Schmitz *et al.* 2004; Schmitz 2008). These hypotheses, derived from recent theoretical work and meta-analyses of trophic cascade experiments, do not consider a fundamental property of ecosystems – differential rates of exogenous inputs – as a potential mechanism for the variation in the strength of trophic cascades.

Subsidy hypothesis

Lindeman (1942) first hypothesized differential rates of spatial subsidies as a mechanism for differences in the structure and productivity of ecosystems but this hypothesis has rarely been investigated theoretically or empirically (Polis & Strong 1996; Shurin *et al.* 2006; but see Huxel & McCann 1998; Nakano *et al.* 1999; Henschel *et al.* 2001). We consider ecosystems to lie along a continuum of allochthonous inputs (Fig. 1; Lindeman 1942; Polis & Strong 1996). Simply because of gravity, systems with convex profiles (e.g. mountains) will receive low amounts of subsidies and subsequently lie at the low end of the continuum, whereas systems with concave profiles act as spatial attractors to receive high amounts of subsidies and therefore lie at the high end of the continuum (e.g. lakes). In general, waterbodies receive higher flows of allochthonous inputs than terrestrial ecosystems (Vannote *et al.* 1980; Power *et al.* 2004; Ballinger & Lake 2006). For example, mean flows of N and P can be up to an order of magnitude larger in aquatic ($1.7\text{--}27.5\text{ g N m}^{-2}\text{ year}^{-1}$, $0.05\text{--}1.2\text{ g P m}^{-2}\text{ year}^{-1}$) than terrestrial ($0.22\text{--}4.25\text{ g N m}^{-2}\text{ year}^{-1}$, $0.016\text{--}0.2\text{ g P m}^{-2}\text{ year}^{-1}$) ecosystems (Wetzel 1975; OECD 1982, Webster *et al.* 1995; Venterink *et al.* 2002; Billen *et al.* 2007). Similarly, in a review, Baxter *et al.* (2005) reported high herbivorous insect flows to streams during the summer ($450\text{ mg m}^{-2}\text{ day}^{-1}$); however, herbivorous insect flows vary seasonally and, during the spring or fall, reciprocal flows to riparian forests can also be high ($130.4\text{ mg m}^{-2}\text{ day}^{-1}$, Jackson & Fisher 1986). In addition, several river continuum studies have quantified fluxes of organic C (e.g. detritus, litterfall, wood) to streams to be as large as $700\text{ g C m}^{-2}\text{ year}^{-1}$ (Caraco & Cole 2004).

We propose differential subsidization rates as a mechanism to explain the variation in the relative strength of trophic cascades among ecosystems and, in particular, why aquatic systems generally have stronger trophic cascades

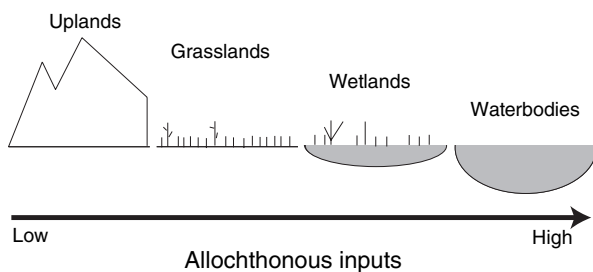


Figure 1 Natural ecosystems are open to allochthonous inputs but areas that are low lying receive high levels of allochthonous inputs (Lindeman 1942; Polis & Strong 1996). The variation in subsidization rates among ecosystems may explain the variation in the strength of trophic cascades among ecosystems.

than terrestrial systems. This subsidy hypothesis states that ecosystems at the high end of the allochthonous input continuum will experience the strongest trophic cascades. This relationship, however, will depend on which trophic level receives the most subsidies. Differential subsidization rates are a fundamental property of ecosystems but because of the complexity in gathering data on the relationship between allochthonous inputs and the strength of trophic cascades (reviewed in Baxter *et al.* 2005), few data are available for cross-system comparisons. However, theory has been critical in examining the generality and robustness of ecological hypotheses even in light of abundant empirical data; therefore, we use simple ecosystem models to investigate the subsidy hypothesis.

ECOSYSTEM MODELS

We derive nutrient-limited ecosystem models with exploitation ecosystem dynamics (Oksanen *et al.* 1981). Our baseline model has three biotic modules: primary producers (P), primary consumers (H) and predators (C), and one abiotic module: inorganic nutrients (N). All modules describe stocks of a limiting inorganic nutrient with explicit nutrient flows that link them. The ecosystems are always open at the basal level through a constant and independent input of inorganic nutrient, I . Biotic modules recycle nutrients at rates d_i but only a fraction, m_b , of recycled nutrients reaches the soil nutrient pool. Nutrients are lost from the basal level with a constant rate, m_N . We use Type II functional responses for each consumer with attack rate, a_j , total available time, T_b , and handling time, V_j . Consumer uptake is converted to stock j with efficiency, ϵ_j .

We present models with two types of allochthonous inputs; inputs that are functionally equivalent and functionally distinct to autochthonous resources and organisms. Allochthonous nutrient inputs that are additional to the ambient nutrient inputs are modelled as functionally equivalent through a constant input rate, w_N (Fig. 2a). This assumption is reasonable for many natural cases such as nutrient flows between aquatic and terrestrial ecosystems initiated by floods (Ballinger & Lake 2006), or rain (Meserve *et al.* 2003). Allochthonous predator inputs are also modelled as functionally equivalent with a constant input rate, w_C (Fig. 2d); for example, consumer species that have complex life cycles in different ecosystems such as amphibians or salmonids (Polis *et al.* 1997; Schreiber & Rudolf 2008). Allochthonous primary producer, A (Fig. 2b), and primary consumer, L (Fig. 2c), subsidies are modelled as functionally distinct modules, which we assume do not feed in the recipient ecosystems; for example, leaf litter (i.e. A inputs) that falls into streams (Vannote *et al.* 1980) or emergent aquatic insects (i.e. L inputs) that flow into surrounding terrestrial ecosystems (Henschel *et al.* 2001; Nakano &

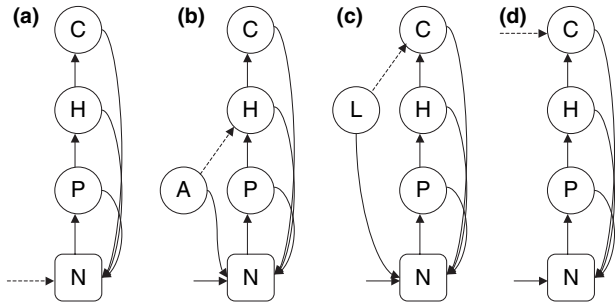


Figure 2 The ecosystem models described in the text. (a) and (d) models with functionally equivalent subsidies; (b) and (c) models with functionally distinct subsidies. Circles represent biotic modules and the square represents the abiotic module. *N*, *P*, *A*, *H*, *L* and *C* are inorganic nutrients, autochthonous primary producers, allochthonous primary producers, autochthonous primary consumers, allochthonous primary consumers and predators respectively. The dashed lines represent the location of allochthonous inputs for each model.

Murakami 2001). Flows of *A* and *L* are modelled with constant inputs rates, w_A and w_L . For models with functionally distinct prey, we assume that their consumer is a generalist and introduce a parameter describing the preference of consumer *j* for the autochthonous prey, π_j . We incorporate recipient consumer preference into a multispecies functional response (McCann *et al.* 1998, 2005; Huxel *et al.* 2002). The general ecosystem model is described by the dynamical equations:

$$\frac{dN}{dt} = I + w_N + (1 - m_P)d_P P + (1 - m_A)d_A A + (1 - m_H)d_H H + (1 - m_L)d_L L + (1 - m_C)d_C C - m_N N - P \left(\frac{a_P T_i N}{1 + a_P V_P N} \right) \tag{1}$$

$$\frac{dP}{dt} = \epsilon_P P \left(\frac{a_P T_i N}{1 + a_P V_P N} \right) - d_P P - H \left(\frac{\pi_H a_H T_i P}{1 + \pi_H a_H V_H P + (1 - \pi_H) a_H V_H A} \right) \tag{2}$$

$$\frac{dA}{dt} = w_A - d_A A - H \left(\frac{(1 - \pi_H) a_H T_i A}{1 + \pi_H a_H V_H P + (1 - \pi_H) a_H V_H A} \right) \tag{3}$$

$$\frac{dH}{dt} = \epsilon_H H \left(\frac{\pi_H a_H T_i P + (1 - \pi_H) a_H T_i A}{1 + \pi_H a_H V_H P + (1 - \pi_H) a_H V_H A} \right) - d_H H - C \left(\frac{\pi_C a_C T_i H}{1 + \pi_C a_C V_C H + (1 - \pi_C) a_C V_C L} \right) \tag{4}$$

$$\frac{dL}{dt} = w_L - d_L L - C \left(\frac{(1 - \pi_C) a_C T_i L}{1 + \pi_C a_C V_C H + (1 - \pi_C) a_C V_C L} \right) \tag{5}$$

$$\frac{dC}{dt} = w_C + \epsilon_C \times C \left(\frac{\pi_C a_C T_i H + (1 - \pi_C) a_C T_i L}{1 + \pi_C a_C V_C H + (1 - \pi_C) a_C V_C L} \right) - d_C C \tag{6}$$

To recover models that describe ecosystems with functionally equivalent subsidies, set $w_A = w_L = 0$ and $\pi_j = 1$. Models with allochthonous primary producer and primary consumer subsidies correspond to $w_N = w_C = w_L = 0$ and $\pi_C = 1$, and $w_N = w_C = w_A = 0$ and $\pi_H = 1$ respectively.

We analyse long-term dynamics of ecosystems with increasing allochthonous inputs at a single trophic level (i.e. $w_i = 0$ to 1) as well as the interaction between allochthonous inputs at the primary producer, primary consumer, or predator module and moderate and high allochthonous nutrient inputs (i.e. $I = 1$, $w_N = 1$ or 2). By investigating the effect of increasing allochthonous inputs, we are modelling a range of different ecosystems along an allochthonous input continuum (Fig. 1). Because we use Type II functional responses, the model exhibits a range of dynamical behaviour from stable equilibria to chaos. We chose parameters that allowed for the persistence of the predator in the baseline model as we are interested in the relative strength of trophic cascades originating from the predator.

MEASURING THE STRENGTH OF TROPHIC CASCADES

Trophic indices

Different metrics are used to quantify the strength of trophic cascades. Huxel and colleagues used theoretical stability as a measure of the effect of predators in food webs (Huxel & McCann 1998; Huxel *et al.* 2002). They equated trophic cascades with unstable dynamics but metrics of theoretical stability can be difficult to measure in nature (McCann 2000), and there is no definite quantitative measure, which can identify the existence of a trophic cascade (Polis *et al.* 2000). Most experimental and empirical studies of community regulation use log-response ratios to quantify the relative strength of top-down effects in food webs (Shurin *et al.* 2002). We follow their lead and use response ratios to determine the relative strength of predator regulation under different allochthonous input treatments because response ratios have clear biological meaning (i.e. proportional change

in the response variable, Hedges *et al.* 1999; Shurin *et al.* 2002), are directly analogous to the metrics of response sizes used in experiments (Schmitz *et al.* 2000; Shurin *et al.* 2002; Borer *et al.* 2005) and have previously been used in theoretical studies on the mechanisms of community regulation (Shurin & Seabloom 2005; Hall *et al.* 2007).

Specifically, the strength of trophic cascades is determined by the log-ratio of the average biomasses of autochthonous primary producers (PTI) and primary consumers (HTI) in the presence (subscript 4) and absence (subscript 3) of predators. For example,

$$\text{PTI} = \ln \frac{\bar{P}_4}{\bar{P}_3}, \quad (7)$$

$$\text{HTI} = \ln \frac{\bar{H}_4}{\bar{H}_3}. \quad (8)$$

Higher values of PTI and lower values of HTI indicate stronger predator regulation (Shurin *et al.* 2002). The interaction between allochthonous primary producer, primary consumer or predator inputs and relatively high external nutrient inputs (w_N) is determined by calculating the PTI and HTI indices for models that incorporate this interaction. To compute the trophic indices, we simulated model dynamics for 2000 time steps, and calculated the average stock of autochthonous primary producers and primary consumers during the last 1000 time steps.

Attenuation plots

The above indices provide information on the strength of predator regulation but another key determinant of the influence of the predator is the relative strength with which top-down forces are passed on to adjacent vs. non-adjacent trophic levels (e.g. Schmitz *et al.* 2000; Hebblewhite *et al.* 2005). Attenuation plots can be used to determine if predator regulation is stronger on adjacent or non-adjacent trophic levels with allochthonous inputs at different locations and different magnitudes (Schmitz *et al.* 2000). To assess the attenuation of predator regulation, we plot PTI vs. HTI for increasing allochthonous inputs. Data on the 45° line (i.e. ratio of absolute direct to indirect effects tests = 1) represent equivalent predator effects on adjacent and non-adjacent trophic levels; therefore, predator regulation does not attenuate along the food chain. Data clustered near the adjacent trophic level axis (i.e. H , response ratio > 1) indicates attenuation of cascades and data clustered near the non-adjacent trophic level axis (i.e. P , response ratio < 1) indicates intensifying or cascading regulation. Oksanen *et al.* (1981) did not specifically investigate attenuation but analysis of our baseline model with linear functional responses and ambient nutrient inputs (i.e. $I = 1$,

$w_N = 0$) indicates that a classic exploitation ecosystem model would predict equivalent predator effects on H and P .

MODEL PREDICTIONS

Increasing allochthonous inputs at any trophic level increased the strength of trophic cascades (Fig. 3). At low inputs ($w_i \leq 0.5$), models with predator subsidies led to the strongest trophic cascades, followed by models with primary producer, primary consumer and nutrient inputs. However, at high inputs ($w_i > 0.5$), models with primary producer subsidies led to the strongest trophic cascades, followed by models with predator, primary consumer and nutrient inputs. Models with increasing primary producer, primary consumer or predator subsidies combined with moderate nutrient inputs (i.e. $I = 1$, $w_N = 1$) resulted in stronger trophic cascades, than similar models with ambient nutrient levels (i.e. $I = 1$, $w_N = 0$; Fig. 3).

Our models can exhibit a range of dynamical behaviour and we observed that increasing allochthonous nutrient or primary producer inputs induces cycles in primary producer stocks in models with predators present. In contrast, increasing primary consumer or predator subsidies stabilizes primary producer stocks and enables high primary producer stocks in models with predators present.

Attenuation plots

Increasing nutrient inputs weakly enhanced the cascading effects of predators in the ecosystem. Similarly, allochthonous primary producer inputs enhanced the cascading effect of the predator in the ecosystem (Fig. 4a). The interaction of increasing primary producer inputs and high nutrient inputs intensified the cascading effects of primary producer subsidies and resulted in stronger predator cascades than similar models with ambient or moderate nutrient levels (Fig. 4a). In contrast, increasing allochthonous primary consumer inputs attenuated the cascading effects of the predator in the ecosystem (Fig. 4b). However, the interaction between increasing primary consumer inputs and high nutrient inputs decreased the overall attenuating effect of primary consumer inputs compared to similar models with ambient or moderate nutrient levels (Fig. 4b). Increasing predator inputs led to stronger direct than indirect effects in the ecosystem and for $w_C > 0.2$ significantly depressed primary consumer stocks. However, the interaction between increasing predator subsidies and high nutrient inputs decreased the overall effect of predator flows.

Consumer preference

In models with functionally distinct prey, we investigated the effect of consumer preference for autochthonous

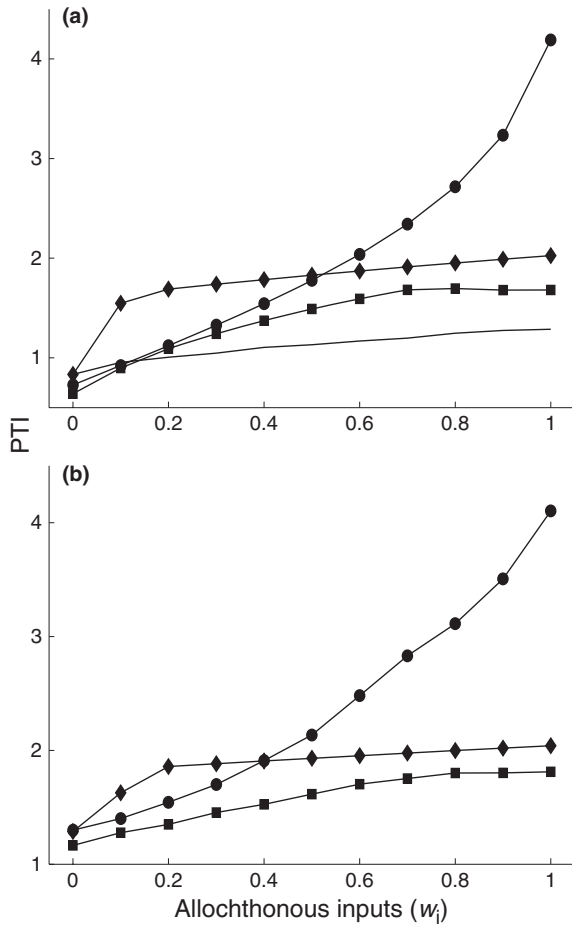


Figure 3 Effect of increasing allochthonous inputs at different trophic levels on the strength of trophic cascades (PTI). Lines without symbols, with circles, squares and diamonds are models with N , A , L and C inputs respectively. (a) Models with A , L and C inputs have ambient nutrient levels ($I = 1$, $w_N = 0$) and (b) models with A , L and C inputs have moderate nutrient levels ($I = 1$, $w_N = 1$). All other parameters are $\epsilon_P = 0.5$, $\epsilon_H = \epsilon_C = 0.75$, $m_N = 0.1$, $m_P = m_A = m_H = m_L = m_C = 0.5$, $d_i = 0.2$, $a_P = a_H = V_i = 0.5$, $T_i = 1$, $a_C = 0.75$, $\pi_i = 0.8$.

prey (π) on the strength of trophic cascades. Our models with primary producer and primary consumer subsidies predict a unimodal relationship between the strength of trophic cascades and consumer preference for autochthonous prey. The strength of trophic cascades is strongest at intermediate consumer preference for autochthonous prey ($0.5 \leq \pi \leq 0.8$) and weakest at low consumer preference for autochthonous prey ($\pi < 0.4$). Low ($w_i = 0.4$) and moderate ($w_i = 0.8$) allochthonous primary producer and primary consumer inputs led to similar-shaped preference curves. However, models with moderate allochthonous primary producer or primary consumer inputs had stronger

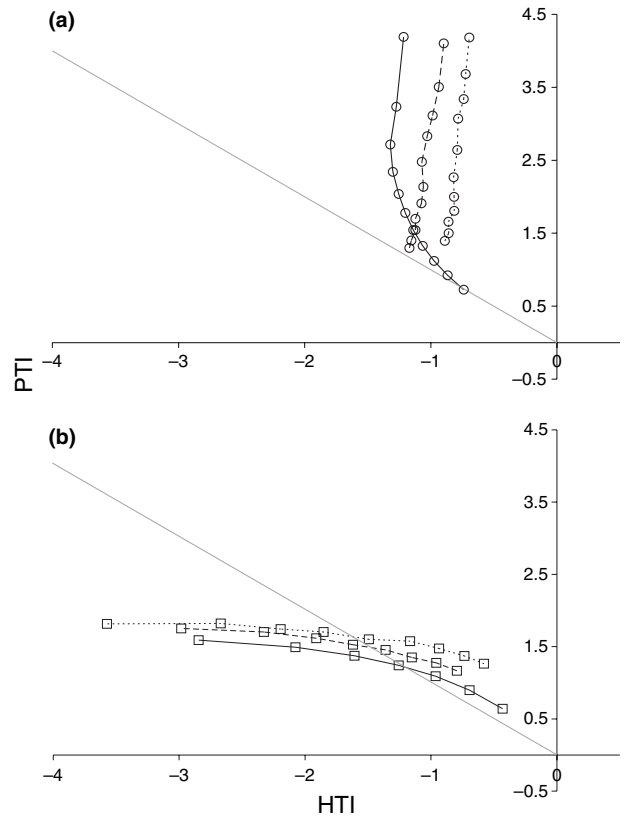


Figure 4 Attenuation plots of PTI vs. HTI for the interaction between allochthonous (a) primary producer (A) and (b) primary consumer (L) inputs and ambient ($I = 1$, $w_N = 0$; solid line), moderate ($I = 1$, $w_N = 1$; dashed line) and high nutrient (N) inputs ($I = 1$, $w_N = 2$; dotted line). w_i inputs increase from 0 to 1 from bottom to top and right to left. The grey line is the 1 : 1 line and all other parameters are as described in Fig. 3.

cascades than models with low inputs as consumer preference for autochthonous resources increased (Fig. 5).

DISCUSSION

Lindeman (1942) suggested that variation in the profile of natural systems can account for structural and dynamical differences between ecosystems. We propose, more specifically, that this fundamental property of ecosystems – differential rates of allochthonous inputs – may explain the variation in the strength of trophic cascades among ecosystems. We elaborate the subsidy hypothesis; that ecosystems with high allochthonous inputs will experience stronger trophic cascades than ecosystems with low allochthonous inputs, and evaluate this hypothesis with ecosystem models that are open to allochthonous flows. Classic theories of community regulation (e.g. Hairston *et al.*

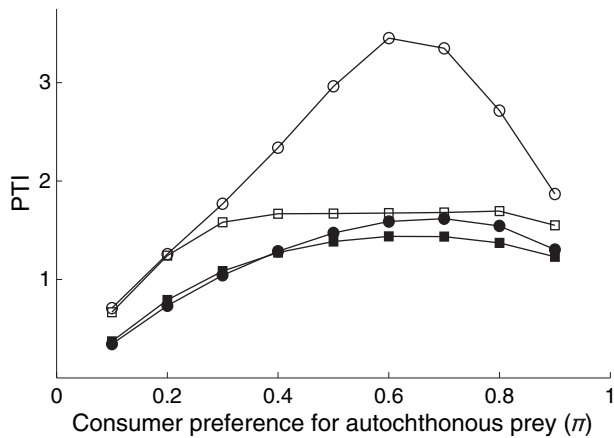


Figure 5 Effect of consumer preference for autochthonous prey (π) on the strength of trophic cascades (PTI) for models with ambient nutrient levels and primary producer (A , circles) and primary consumer (L , squares) inputs. Solid symbols are for allochthonous inputs, $w_A = w_L = 0.4$, and open symbols are for autochthonous inputs, $w_A = w_L = 0.8$. All other parameters are as described in Fig. 3.

1960; Oksanen *et al.* 1981) are based on *in situ* productivity but we know from recent theory that models of closed ecosystems can lead to ecologically inconsistent results (Loreau & Holt 2004). Our model predictions support the subsidy hypothesis and suggest that the prevalence of strong cascades in aquatic systems may result from relatively greater allochthonous input into those systems.

In general, our models predict that increasing allochthonous inputs at the nutrient, primary producer, primary consumer or predator level will increase the strength of trophic cascades. These results suggest that ecosystems that lie at the high end of the allochthonous input continuum will experience the strongest regulation from predators. Lakes, for example, are at the high end of the allochthonous input continuum because they experience strong flows of energy and material between pelagic and benthic habitats (Schindler & Scheuerell 2002) and they receive significant detrital flows from terrestrial ecosystems (Pace *et al.* 2004). Based on our model predictions, it is not surprising then that trophic cascade theory was developed from observations of lake ecosystems (Carpenter *et al.* 1985).

Our models predict that inputs at the predator and primary producer level will result in larger cascading interactions than inputs at other trophic levels. In models with predators present, primary consumers are regulated, and primary producers are able to thrive. Additional predator inputs will lead to increased primary consumer regulation and functionally distinct primary producer subsidies may reduce the overall pressure of primary consumers on autochthonous primary producers. In models without

predators, primary producer subsidies can stabilize the ecosystem by providing a constant and alternative food source for primary consumers. The river continuum concept states that small, headwater streams generally receive more terrestrial organic inputs such as leaf litter and detritus than large streams (Vannote *et al.* 1980). We demonstrate that ecosystems with high primary producer inputs, such as headwater streams, may experience strong trophic cascades relative to ecosystems with low primary producer inputs such as lower-order streams.

In addition, our models predict stronger trophic cascades in recipient systems with moderate-to-high external nutrient inputs and inputs at the primary producer, primary consumer or predator trophic levels. Similarly, Oksanen *et al.* (1981) predict that predator regulation would become more important with increased potential productivity but their predictions are only based on *in situ* productivity. In contrast to our prediction, a recent meta-analysis found no significant interaction between the presence of predators and fertilization on primary producers and primary consumers (Borer *et al.* 2006). However, the experiments used in this meta-analysis were mostly short term and did not investigate continuous variation in predator and nutrient additions, as we have. Ecosystems are open to flows at different trophic levels, but few theoretical or empirical studies have investigated the interaction between flows at multiple levels. Ecosystems that receive high external nutrient inputs may be less nutrient-limited, which may enable higher secondary production and consumption (Shurin *et al.* 2006). Additional inputs at higher trophic levels (e.g. L), however, may intercept the nutrient inputs and modify the effects of nutrients on the predator. McQueen *et al.* (1986) hypothesized complex reciprocal effects between predators and resources but few studies have investigated this interaction in detail.

The strength of trophic cascades is a relative measure, without an explicit quantitative definition. The key element of a cascade is the effect of the predator on non-adjacent or indirect trophic levels (i.e. primary producers). Shurin *et al.* (2002) showed that, regardless of ecosystem, the direct effects of predators were always stronger than their indirect effects. For example, Marquis & Whelan (1994) observed stronger effects of birds and Schmitz (1994) observed stronger effects of spiders on primary consumers than primary producers. We used attenuation plots to investigate the relative strength of the predator's direct and indirect effects when external nutrient inputs and allochthonous inputs at other trophic levels increased. In models with increasing primary consumer or predator inputs, we also observed stronger effects of predators on primary consumers (i.e. direct) than primary producers (i.e. indirect); however, models with increasing nutrients or primary producer subsidies produce stronger effects of predators

on primary producers than primary consumers. Food chain length may influence the strength and prevalence of trophic cascades (Thompson *et al.* 2007) and because we modelled consumers with saturating functional responses, nutrient inputs are dampened before they reach the predator. Consequently, inputs at lower trophic levels have a weaker influence on the direct effects of the predator than inputs at higher trophic levels.

Our models are very simple representations of ecosystems but these simple models allowed us to investigate some general predictions on the relative strength of trophic cascades in open ecosystems. In our models, subsidies increase the total amount of energy in the recipient ecosystems and the effect of subsidies depends on the shape of consumer-functional responses, the efficiency of consumers and the number of trophic levels in the ecosystem. A decrease in the attack rate or conversion efficiency would lead to weaker cascades overall but the main predictions of our models would be qualitatively similar. We investigated the average dynamics of our model, which enabled us to use log–response ratios. These metrics are widely used in experiments, and therefore the predictions of our models may be experimentally tested. We assumed that allochthonous flows are constant but, in many natural systems, these flows can be temporally variable (Polis *et al.* 1997; Yang *et al.* 2008). What is more, we model the response of recipient systems, but subsidies may be reciprocal, which can result in strongly coupled ecosystems (Nakano & Murakami 2001). Despite the assumptions and limitations listed above, our general predictions are robust to different model formulations. For example, analytic analyses of the models (Fig. 2) with linear functional responses and of models that assume all allochthonous inputs are functionally equivalent to autochthonous resources, also provide qualitative support for the subsidy hypothesis.

Subsidies and trophic cascades in natural ecosystems

Many field studies have investigated the direct effects of subsidies on recipient consumers or competitors but few studies have examined the indirect effects of subsidies in recipient ecosystems (Baxter *et al.* 2005; Marczak *et al.* 2007). In freshwater–terrestrial ecotones, Henschel *et al.* (2001) observed positive indirect effects of aquatic subsidies to consumers in an exploitative riparian food web whereas Knight *et al.* (2005) found negative indirect effects of aquatic subsidies in a mutualistic riparian food web. In marine–terrestrial ecotones, Polis *et al.* (2004) reported a wide range of indirect effects of marine subsidies to islands and coastal areas because subsidies allowed higher consumer population densities than could be supported from *in situ* terrestrial resources alone. Similarly, Kurle *et al.* (2008) discussed the cascading effects of an invasive rat species on

the Aleutian Island marine rocky intertidal community. These studies demonstrate that subsidies at different trophic levels and in different ecosystems may lead to strong trophic cascades. The main result of our model is in accord with these experimental results and also provides additional insight on the influence of the magnitude of subsidies on the strength of trophic cascades. Other experimental work, however, contrasts with the predictions of our models.

In the Tomakomai experimental forest in Japan, Nakano *et al.* (1999) and Baxter *et al.* (2004) observed strong trophic cascades in native trout species of Honorai stream in the absence of terrestrial arthropod subsidies. Similarly, Halaj & Wise (2002) observed that experimental additions of detritus altered the direct effects but did not influence indirect effects in recipient ecosystems. In these experiments, however, the generalist predator may have switched completely to feed on an alternative resource, thereby decoupling the dynamics of the primary producers and predator. In our models with functionally distinct prey, we allow the predator to exploit two prey sources but we also observed a strong effect of consumer preference on the strength of trophic cascades. The results from these experiments and our models suggest that the behaviour of generalist consumers may play a key role in determining the strength of trophic cascades in subsidized ecosystems.

In a mesocosm experiment, Howeth & Leibold (2008) show that plankton dispersal does not change the magnitude of spatial trophic cascades. However, their experimental design focused on flows within a single ecosystem. Our models are derived to investigate spatial subsidies; therefore, their exact formulation may not be useful to investigate within-system flows. Nevertheless, by reformulating the models presented in this manuscript, one could evaluate the potential of the subsidy hypothesis to explain intra-ecosystem variation in the strength of trophic cascades. Finally, Gratton & Denno (2003) demonstrated donor-control effects of nutrient pulses in their terrestrial ecosystem. Our models are derived with prey-dependent functional responses, therefore they exhibit baseline predator regulation and their predictions may not apply to ecosystems with consumers that are donor-controlled.

Subsidies and trophic cascades in theory

In models with functionally distinct allochthonous inputs, we observed that intermediate consumer preference for autochthonous prey led to the strongest trophic cascades, particularly when subsidies were high. These results are in agreement with previous models by Huxel & McCann (1998) and Huxel *et al.* (2002). Intermediate preference may lead to a strong numerical response in the consumer, which, in the case of primary producer inputs, transfers energy to

the predator, or in the case of primary consumer inputs, leads to apparent competition through the shared predator. Conversely, high preference for one resource may decouple the interaction between the consumer and the alternative resource, therefore leading to weaker cascades.

Empirical data demonstrates that high allochthonous flows are ubiquitous and can form a large component of a consumer's diet (Polis & Hurd 1995; Nakano & Murakami 2001; Nowlin *et al.* 2007). In contrast to Huxel & McCann (1998) and Huxel *et al.* (2002), our models predict the weakest trophic cascades when consumers prefer allochthonous inputs. However, our models differ from both Huxel & McCann (1998) and Huxel *et al.* (2002) through several assumptions. First, we model nutrients explicitly, and therefore allow for recycling in our model. Second, we use log–response ratios as our metric of trophic cascades whereas they use measures of theoretical stability. Finally, our models and those of Huxel *et al.* (2002) assume that allochthonous inputs can be functionally distinct from autochthonous resources. Consequently, we believe our models are complementary to Huxel & McCann (1998) and Huxel *et al.* (2002). Our theoretical contribution also complements additional theory that has investigated other potential mechanisms to explain variation in the strength of trophic cascades among ecosystems.

Shurin & Seabloom (2005) and Hall *et al.* (2007) models predict that increasing $H : P$ body size ratio, invertebrate and ectotherm predators and primary consumers, increasing system productivity, ecosystems with more easily digested primary producers and lower nutrient : carbon ratio of H will magnify trophic cascades. Our models predict that ecosystems with high allochthonous inputs will have strong trophic cascades and that input location will influence the magnitude of the effect. Future models should investigate multiple hypotheses in order to more comprehensively understand the driving forces of the variation in the strength of trophic cascades among ecosystems.

CONCLUSION

The allochthonous input continuum and the subsidy hypothesis supports the empirical observation that aquatic ecosystems have stronger trophic cascades than terrestrial ecosystems. Concave systems may be spatial subsidy attractors, which may facilitate higher secondary production and consumption. We provide some data in our introduction in support of the allochthonous input continuum, but further data are required to corroborate this relationship. In particular, coastal ecotones and open oceans may be difficult to classify along the allochthonous input continuum. Coastal ecotones will likely fall at the high end of the allochthonous input continuum (Polis & Hurd 1995; Rose & Polis 1998), but open oceans are relatively isolated from terrestrial

sources of allochthonous inputs; therefore, despite their concave profile, they behave more like uplands and may be net donors of energy to other systems. The large salmon runs from oceans can have significant effects on stream, lake and riparian forest ecosystem structure and function (Zhang *et al.* 2003; Moore *et al.* 2007), and this is evidence for placing oceans at the low end of the continuum. However, salmon behaviour, such as nest digging, may stimulate nutrient and matter export from freshwater streams to depositional zones in lakes or oceans (Moore *et al.* 2007). As a result, depending on the stream, salmon may be net importers or exporters of nutrients and matter (Moore *et al.* 2007).

Based on our theoretical analysis, allochthonous flows may be a key component that explains variation in the strength of trophic cascades among ecosystems. Experiments on allochthonous flows, especially at the ecosystem and across ecosystem scale, are relatively rare because of their complexity (Ballinger & Lake 2006; Marczak *et al.* 2007). Our results may help to guide future experiments by suggesting that studies focus on where, trophically, the majority of inputs occur, and how these inputs influence the distribution of standing stocks across trophic levels. Experimental techniques such as the use of stable isotopes of hydrogen can provide reliable methods for partitioning energy flow across ecosystems (Doucett *et al.* 2007).

Differential rates of spatial subsidies is a fundamental property of ecosystems and, in this manuscript, we have only begun to explore the role of this attribute on ecosystem functioning. Human activities are modifying the strength of top–down forces across the planet (e.g. predator exploitation via commercial fishing, Pauly *et al.* 1998) and interrupting natural flows of energy, material and organisms across ecotones (e.g. agrochemical pollutant runoff, Burcher *et al.* 2007). Therefore, a better understanding of the mechanisms responsible for variation in the strength of predator regulation may be crucial for predicting the effects of, and managing, current and future human activities in open ecosystems (Hebblewhite *et al.* 2005; Borer *et al.* 2006; Burcher *et al.* 2007).

ACKNOWLEDGEMENTS

We thank M. Cherif, G. Fussmann, A. Gonzalez, F. Guichard, A. Hurford and P. Pillai for discussions. R. Feldman, G. Kylafis, Z. Long, O. Schmitz and three anonymous referees provided constructive comments on earlier drafts of the manuscript. S. Leroux was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and McGill University. This work was also supported by a Discovery Grant from NSERC and a team research project from the Quebec Nature and Technologies Research Fund to M. Loreau.

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Editor, Oswald Schmitz

Manuscript received 25 June 2008

First decision made 15 July 2008

Manuscript accepted 21 July 2008