

Dynamics of Reciprocal Pulsed Subsidies in Local and Meta-Ecosystems

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ABSTRACT

Temporally variable and reciprocal subsidies between ecosystems are ubiquitous. These spatial flows can generate a suite of direct and indirect effects in local and meta-ecosystems. The focus of most subsidy research, however, has been on the response of consumers in recipient ecosystems to constant subsidies over very short or very long time scales. We derive a meta-ecosystem model to explicitly consider the dynamic feedbacks between local ecosystems coupled through reciprocal pulsed subsidies. We predict oscillating reinforcing and dampening effects of reciprocal pulsed herbivore flows. Maximum reinforcing effects between reciprocal pulsed herbivore flows occur when these flows are in phase with the dynamics of neighboring predators. This prediction is robust to a range of pulse quantities and frequencies. Reciprocal pulsed herbivore subsidies lead to spatial and temporal variability in the strength of trophic cascades in local and meta-ecosystems but these

cascading effects are the strongest when reciprocal pulsed subsidies are temporally concentrated. When predators demonstrate a behavioral response to prey abundance, reciprocal pulsed subsidies dampen the strength of local trophic cascades but lead to strong trophic cascades across local ecosystems. The timing of reciprocal pulsed subsidies is a critical component that determines the cascading effects of spatial flows. We show that spatial and temporal variabilities in resources and consumers can have a significant influence on the strength of cascading trophic interactions; therefore, our ability to detect and understand trophic cascades may depend on the scale of inquiry of ecological studies.

Key words: Allochthonous; apparent competition; apparent mutualism; exogenous; flows; functioning; predators; regulation; resource pulse; top-down control.

INTRODUCTION

Ecosystems are open and coupled through spatial subsidies (Polis and others 1997). Most spatial

subsidies are temporally variable, ranging from very frequent subsidies, such as marine wrack, arising from wave action linking oceans to islands (Polis and Hurd 1995) to infrequent subsidies like mass emergence of cicadas every 15–17 years linking belowground and aboveground temperate forest ecosystems (Yang 2004). Many subsidies are also reciprocal, which can generate dynamic feedbacks between coupled ecosystems (Baxter and others 2005). Most empirical and theoretical research studies, however, focus on the response of consumers in recipient ecosystems to constant

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spatial subsidies over very short or very long time scales (but see Nakano and Murakami 2001). Specifically, the median duration of empirical studies of subsidies is three months (Marczak and others 2007), and the majority of theoretical research on subsidies investigates long-term equilibrium dynamics of ecosystems (for example, Polis and others 1997). Consequently, most studies are not likely capturing the feedbacks and inherent variability of subsidized ecosystems.

Yang and others (2008) identify four main causal processes of resource pulses: climatic and environmental causes (for example, El Niño Southern Oscillation (ENSO)), temporal accumulation and release (for example, mast seeding), spatial accumulation and release (for example, marine wrack), and outbreak population dynamics (for example, mass emergence of forest insects). Pulsed subsidies are resource pulses that are accumulated and transported over space (sensu Yang and others 2008). Reciprocal pulsed subsidies are broadly defined as temporally variable spatial flows occurring between two ecosystems—from local ecosystem 1 to local ecosystem 2 and vice versa. For example, there are reciprocal seasonal invertebrate fluxes between streams and riparian forests (see Nakano and Murakami 2001). The effects of subsidies in recipient ecosystems are well studied but the feedbacks and indirect effects generated from reciprocal pulsed subsidies are not well understood (Baxter and others 2005; Anderson and others 2008; Nowlin and others 2008).

The total quantity (Leroux and Loreau 2008) and timing (Takimoto and others 2009) of subsidies will influence the dynamics of the recipient predator. The response of subsidized predators can then cascade to influence whole ecosystem dynamics. Theory on apparent competition and apparent mutualism (Holt 1977; Holt and Lawton 1994; Abrams and others 1998) provides a framework for understanding the potential feedbacks between reciprocal subsidies and the indirect, cascading effects originating from these feedbacks. Negative feedbacks between two prey species that share a predator often occur when the shared predator shows a strong numerical response to a prey species, whereas positive feedbacks between prey species that share a predator occur if the shared predator switches to feed primarily on one prey species, thereby, releasing the other prey from predation (Holt 1977; Abrams and Matsuda 1996; Abrams and others 1998). These predator–prey interactions also can exert a suite of indirect effects on producers. For example, recent meta-analyses demonstrate the occurrence of trophic cascades in a

range of terrestrial and aquatic ecosystems (Shurin and others 2002; Borer and others 2005).

In this study, we build a meta-ecosystem model; a model of a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries (sensu Loreau and others 2003), to investigate feedbacks and indirect effects generated by reciprocal pulsed prey subsidies. We focus on the effects of reciprocal herbivore flows because they are the most widely studied reciprocal pulsed subsidies. We use this as a case study to derive general predictions on the feedbacks and indirect effects of reciprocal pulsed subsidies in local and meta-ecosystems. Our objective is to determine how the total quantity and timing of flows across local ecosystem boundaries are impacted by reciprocal coupling between ecosystems and how these reciprocal flows affect cascading trophic interactions in local and meta-ecosystems. For the remainder of this article, we refer to positive feedbacks between reciprocal flows as reinforcing, and negative feedbacks between reciprocal flows as dampening.

ECOSYSTEM MODELS

We derive a nutrient-limited meta-ecosystem model with two local ecosystems (Table 1; Figure 1). Each local ecosystem has three biotic modules: primary producers (P_i), herbivores (H_i), and predators (C_i), and one abiotic module, inorganic nutrient (R_i), where the subscript i identifies the local ecosystem. We include three biotic compartments in each local ecosystem because we are interested in the direct response of local predators and herbivores and the indirect cascading response in producers to reciprocal pulsed subsidies. All modules describe stocks of a limiting inorganic nutrient with explicit nutrient flows that link them. Each module also follows nutrient mass-balance constraints. The ecosystems are open at the basal level through a constant and independent input of inorganic nutrient, I_i . Nutrients are lost from the basal module with constant rate, l_i , and from the biotic modules with constant rates, d_i . The plant rate of nutrient stock uptake is a_{P_i} , and the herbivore rate of plant stock uptake is a_{H_i} . These are resource-dependent feeding relationships that obey the laws of mass action and are proportional to both consumer and resource stocks. We assume that predator uptake of herbivores follows a saturating, Type II functional response with attack rate a_{C_i} , total available time, T , and handling time, V . Consumer uptake is converted to stock i with efficiency e_i . A fraction of what is released by each biotic module is lost from the system, and the rest, including nutrients not converted to

Table 1. Meta-ecosystem Model Equations and Parameter Definitions

Local ecosystem 1	Local ecosystem 2
$\frac{dR_1}{dt} = I_1 - l_{R_1}R_1 - a_{P_1}R_1P_1 + m_2H_{2A} + \delta_{P_1}d_{P_1}P_1 + \delta_{H_{1L}}H_{1L}[(1 - e_{H_{1L}})a_{H_{1L}}P_1 + d_{H_{1L}}]$ $+ \delta_{C_1}C_1[(1 - e_{C_1})\left(\frac{s_{1L}a_{C_1}TH_{1L} + s_{1A}a_{C_1}TH_{2A}}{1 + s_{1L}a_{C_1}VH_{1L} + s_{1A}a_{C_1}VH_{2A}}\right) + d_{C_1}]$ $\frac{dP_1}{dt} = a_{P_1}R_1P_1 - d_{P_1}P_1 - a_{H_{1L}}P_1H_{1L}$ $\frac{dH_{1L}}{dt} = e_{H_{1L}}a_{H_{1L}}P_1H_{1L} - d_{H_{1L}}H_{1L} - C_1\left(\frac{s_{1L}a_{C_1}TH_{1L}}{1 + s_{1L}a_{C_1}VH_{1L} + s_{1A}a_{C_1}VH_{2A}}\right) - W_{H_{1L}}[f]H_{1L}$ $\frac{dH_{1A}}{dt} = W_{H_{1L}}[f]H_{1L} - m_1H_{1A} - C_2\left(\frac{s_{2A}a_{C_2}TH_{1A}}{1 + s_{2L}a_{C_2}VH_{2L} + s_{2A}a_{C_2}VH_{2A}}\right)$ $\frac{dC_1}{dt} = e_{C_1}C_1\left(\frac{s_{1L}a_{C_1}TH_{1L} + s_{1A}a_{C_1}TH_{2A}}{1 + s_{1L}a_{C_1}VH_{1L} + s_{1A}a_{C_1}VH_{2A}}\right) - d_{C_1}C_1$	$\frac{dR_2}{dt} = I_2 - l_{R_2}R_2 - a_{P_2}R_2P_2 + m_1H_{1A} + \delta_{P_2}d_{P_2}P_2 + \delta_{H_{2L}}H_{2L}[(1 - e_{H_{2L}})a_{H_{2L}}P_2 + d_{H_{2L}}]$ $+ \delta_{C_2}C_2[(1 - e_{C_2})\left(\frac{s_{2L}a_{C_2}TH_{2L} + s_{2A}a_{C_2}TH_{1A}}{1 + s_{2L}a_{C_2}VH_{2L} + s_{2A}a_{C_2}VH_{1A}}\right) + d_{C_2}]$ $\frac{dP_2}{dt} = a_{P_2}R_2P_2 - d_{P_2}P_2 - a_{H_{2L}}P_2H_{2L}$ $\frac{dH_{2L}}{dt} = e_{H_{2L}}a_{H_{2L}}P_2H_{2L} - d_{H_{2L}}H_{2L} - C_2\left(\frac{s_{2L}a_{C_2}TH_{2L}}{1 + s_{2L}a_{C_2}VH_{2L} + s_{2A}a_{C_2}VH_{1A}}\right) - W_{H_{2L}}[f]H_{2L}$ $\frac{dH_{2A}}{dt} = W_{H_{2L}}[f]H_{2L} - m_2H_{2A} - C_1\left(\frac{s_{1A}a_{C_1}TH_{2A}}{1 + s_{1L}a_{C_1}VH_{1L} + s_{1A}a_{C_1}VH_{2A}}\right)$ $\frac{dC_2}{dt} = e_{C_2}C_2\left(\frac{s_{2L}a_{C_2}TH_{2L} + s_{2A}a_{C_2}TH_{1A}}{1 + s_{2L}a_{C_2}VH_{2L} + s_{2A}a_{C_2}VH_{1A}}\right) - d_{C_2}C_2$
<p><i>State variables:</i></p> <p>R_i, inorganic nutrients; P_i, primary producers; H_{iL}, local herbivores; H_{iA}, allochthonous herbivores; C_i, predators, where the subscript i identifies the local ecosystem</p> <p><i>Parameters:</i></p> <p>I_i, constant and independent input rate of inorganic nutrient; l_i, nutrient loss rate from the basal module; d_i, detritus loss rate from biotic modules; a_i, consumer attack rate; e_i, consumer conversion efficiency; T, total available time of predator functional response; V, handling time of predator functional response; δ_i, recycling efficiency; m_i, rate for allochthonous herbivores returning to the neighboring resource pool.</p> <p><i>Rectangular pulse subsidy function:</i></p> $W_{H_i}[f] = \begin{cases} z & fn \leq t \leq fn + u \\ 0 & \text{otherwise} \end{cases} \text{ for } n = \{0, 1, 2, 3, \dots\}$ <p>where z is the pulse magnitude, u is the pulse duration, and $1/f$ is the pulse frequency.</p> <p><i>Predator preference functions:</i></p> $S_{iL} = \frac{\pi_i H_{iL}}{\pi_i H_{iL} + (1 - \pi_i) H_{iA}}, \quad S_{iA} = \frac{(1 - \pi_i) H_{iA}}{\pi_i H_{iL} + (1 - \pi_i) H_{iA}}$ <p>where π_i ($0 \leq \pi_i \leq 1$) is the relative preference of the local predator (i) for the local herbivore (i) when local and allochthonous herbivores have equal stocks.</p>	<p><i>See Figure 1 for a conceptual diagram, and the text for a full description of the meta-ecosystem.</i></p>

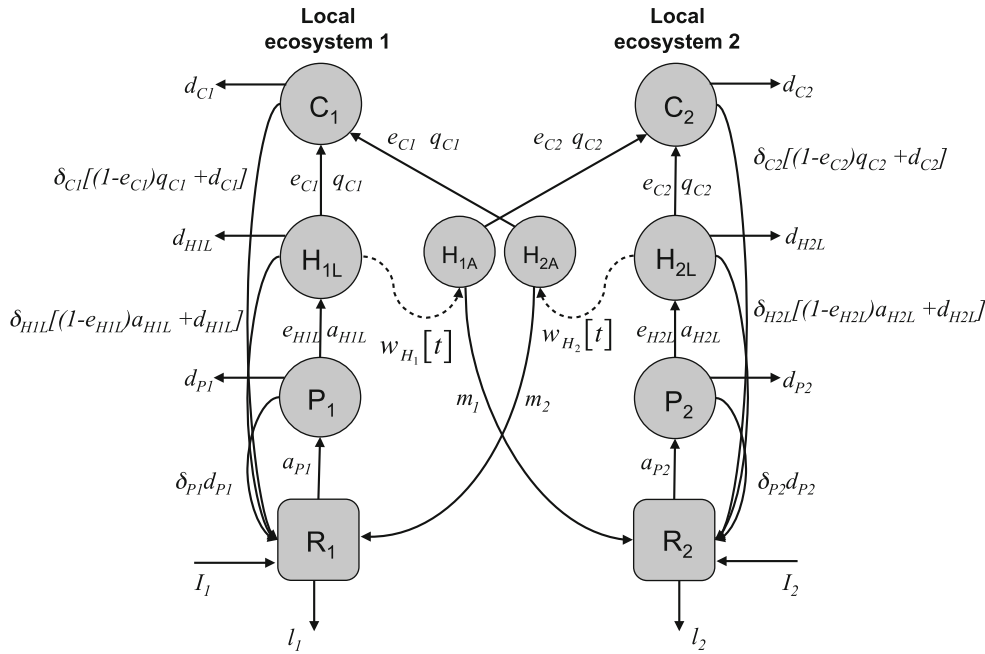


Figure 1. Diagram of our meta-ecosystem model of coupled local ecosystems each with inorganic nutrients (R_i), primary producers (P_i), local herbivores (H_{iL}), allochthonous herbivores (H_{iA}), and predators (C_i). The two local ecosystems are linked through reciprocal pulsed herbivore subsidies (H_{iA}). Model parameters are as defined in Table 1. q_i are the predator functional responses.

consumer biomass ($1 - e_i$), are recycled within the system with efficiency δ_i (Table 1; Figure 1). We include recycling fluxes in our model because consumer-mediated recycling can be a key mechanism of trophic cascades (Leroux and Loreau 2010).

We focus on the spatial flows of herbivores between the two local ecosystems as these are very common reciprocal flows at the aquatic and terrestrial ecotone which is a common and well-studied meta-ecosystem (reviewed in Schindler and others 2003; Baxter and others 2005; Gratton and Vander Zanden 2009). Herbivores are separated into two compartments: a local herbivore compartment (H_{iL}), and an allochthonous herbivore compartment (H_{iA}). Herbivore subsidies are donor controlled from the local herbivores in each ecosystem to the allochthonous herbivores from each ecosystem according to a rectangular pulse subsidy function; $w_{H_i}[t]$ (Table 1). We assume that the allochthonous herbivores do not feed in the neighboring ecosystem. Most of the herbivore flows (H_{iA}) are available for the neighboring predator (C_j) but a portion, m_i , flows directly to the neighboring resource pool (R_j) as detritus. For example, some beetles may fall in shallow water where they will not be consumed by fish but will instead flow directly to the stream detrital pool. We use these simplifying assumptions to capture the essential dynamics of these flows, while maintaining some generality in our model.

When allochthonous flows occur, we assume that predators are generalists and able to consume two different resources. We incorporate prey

selection by predators with prey-switching functions (Post and others 2000; McCann and others 2005; Table 1). Prey switching occurs such that, as the abundance of one prey declines, more of the predator's diet is derived from the other prey (Post and others 2000). Prey-switching functions allow predators to exploit pulsed subsidies. The meta-ecosystem model is described in Table 1 and Figure 1.

METHODS

We model subsidies as a rectangular pulse with variable pulse and interpulse periods. The rectangular pulse function is defined by a pulse magnitude (z), duration (u), and frequency ($1/f$). We parameterized the model so that one time step is equivalent to 1 month. We standardized the rectangular pulse so that $z \cdot u \cdot \frac{1}{f} = c$, where c is a constant quantity of subsidy per unit time, and $u \leq f$. For our analyses, $c = 1/6$. For example, if $c = 1/6$, $f = 1/12$, and $u = 1$, then $z = 2$. We standardized the pulse function to avoid confounding the effects of magnitude, frequency, and duration when we vary each parameter individually. We investigate the influence of the total quantity of subsidies (that is, keep f constant and vary z or u) and the timing (that is, keep z and u constant and vary f) of subsidies on the dynamics of our local and meta-ecosystem. The model with recurrent pulsed subsidies eventually settles into periodic dynamics. We simulate the model for 500 months to remove transient dynamics and report results for one period—months 504–540.

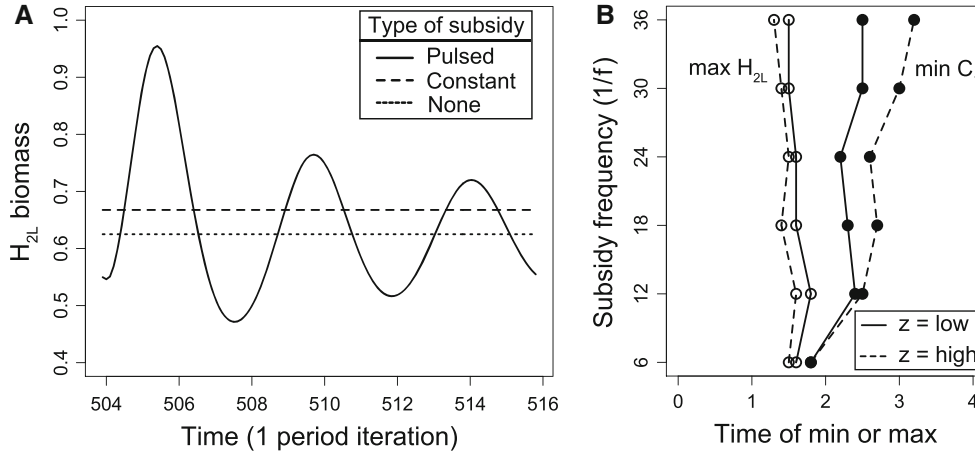


Figure 2. Results for models with unidirectional herbivore subsidies from local ecosystem 1 to local ecosystem 2. **A** Recipient herbivore (H_{2L}) biomass in models with pulsed (solid line), constant (dashed line), and no subsidies (dotted line). The total biomass of subsidies for the pulsed and constant case is standardized over a frequency of $1/12$ (that is, for pulsed subsidies $z = 2$ and $u = 1$ and for constant subsidies $z = 0.167$ and $u = 12$). **B** Time of recipient herbivore (H_{2L}) maximum and donor predator (C_1) minimum biomass relative to the start of one subsidy period for a range of subsidy frequencies and standardized total subsidy quantity. Low subsidy biomass (solid line) is when $u = 1$ and $z = 0.5, 1, 1.5, 2, 2.5,$ and 3 and high subsidy biomass (dashed line) is when $u = 1$ and $z = 1, 2, 3, 4, 5,$ and 6 for $f = 6, 12, 18, 24, 30,$ and 36 , respectively. Other parameters are $I_i = 2, l_i = 0.15, a_P = a_H = 1, a_C = 0.8, T = 1, V = 0.5, \delta_i = 0.5, d_i = 0.3, e_i = 0.75, \pi_i = 0.75, m_i = 0.2$.

We used the `odesolve` package in R for our numerical simulations. We chose baseline parameter values that allow for the persistence of the predators as we are interested in the direct effects of reciprocal pulsed subsidies on predators and herbivores, and the indirect, cascading effects of reciprocal pulsed subsidies originating from the predators. The parameter space is too large for a systematic investigation, but our results are robust to a range of different parameter values and assumptions regarding the two local ecosystems (see sensitivity analyses in Appendix A in Supplementary Material and our summary in the “Results” section). The exact parameter values for our figures were informed by our extensive analytic and numerical analyses of similar local ecosystem models (see Leroux and Loreau 2008; Leroux and Loreau 2010).

We sequentially analyze more complex models to build our predictions on the effects of reciprocal pulsed flows in local and meta-ecosystems. Our baseline is a model with no spatial subsidies at the herbivore level ($w_{H_1}[t] = w_{H_2}[t] = 0$); this establishes H stocks in the absence of flows. We begin by analyzing the response of recipient prey to unidirectional constant ($w_{H_1} > 0$) and pulsed ($w_{H_1}[t] > 0$) subsidies from local ecosystem 1 to 2 to understand the effects of pulsed subsidies relative to constant subsidies. Then, we examine a full model with reciprocal pulsed flows ($w_{H_1}[t] > 0$ and $w_{H_2}[t] > 0$) to

determine if prey subsidies feedback to have reinforcing or dampening effects on each other. We measure reinforcing and dampening effects of herbivore subsidies relative to herbivore biomass in the absence of subsidies. Reinforcing (dampening) effects occur when local herbivore biomass in the presence of subsidies is higher (lower) than the local herbivore biomass in the absence of subsidies. We create asynchrony between the reciprocal flows by having $w_{H_2}[t + \tau] = w_{H_1}[t]$, where τ is the number of months between the start of the two pulse periods. We end by detailing the indirect cascading effects of reciprocal pulsed subsidies at local and meta-ecosystem extents. The strength of cascades (PTI_i) in local ecosystem i can be measured with log response ratios: the biomass of producers in local ecosystem i in the presence (subscript C) and the absence (subscript NC) of the predator in local ecosystem i ; $PTI_i = \ln(P_{iC_i}/P_{iNC_i})$. The strength of cascades at the meta-ecosystem scale is the sum of producer biomasses in the presence and the absence of both predators; $PTI_{ME} = \ln[(P_{1C_1} + P_{2C_2})/(P_{1NC_1} + P_{2NC_2})]$.

RESULTS

Constant and Pulsed Unidirectional Subsidies

Low quantities of constant herbivore subsidies from local ecosystem 1 reinforce recipient (that is, local

ecosystem 2) herbivore biomass (Figure 2A). At low amounts of subsidy, we observe a reinforcing effect on the recipient herbivore because the predator switches to feed on the subsidy (Appendix B in Supplementary Material). However, with the long-term provisioning of constant subsidies and high preference for local prey, the recipient predator demonstrates a strong numerical response to subsidies, and a negative indirect effect on the local herbivore stock emerges (Appendix C in Supplementary Material).

Pulsed subsidies from local ecosystem 1 generate periodic dynamics in the recipient ecosystem as the predator responds functionally by switching between the most abundant prey: the local one and the subsidy (Appendix B in Supplementary Material). The periodical dynamics driven by pulsed subsidies oscillate between reinforcing and dampening effects on the recipient herbivore biomass (see max and min in Figure 2A). This temporally variable response is in stark contrast to the equilibrium response of the recipient herbivore to constant subsidies.

The donor and recipient ecosystems respond to pulsed subsidies similarly irrespective of the pulse quantity or frequency (Figure 2B). Donor predator biomass (C_1) is at a minimum 1.8–3.2 months after the loss of local herbivores, and recipient herbivores (H_{2L}) peak 1.3–1.8 months after receiving herbivore subsidies (Figure 2B).

Based on these results for unidirectional pulsed subsidies, we hypothesize that the strongest reinforcing feedbacks between reciprocal prey flows will occur when the return herbivore flows from local ecosystem 2 to 1 are in phase with the internal dynamics of the donor ecosystem. In our model, this occurs approximately 2 months after the initial herbivore flow from local ecosystem 1 to 2 (Figure 2B). If the herbivore in the recipient ecosystem flows back when the donor predator biomass is at or near a minimum, then the subsidies will complement local resource deficiencies and provide a temporal predation refuge for local herbivores as the donor predator switches to feed on herbivore subsidies. This will result in strong reinforcing reciprocal prey flows.

Reciprocal Pulsed Subsidies

Effects of Frequency

In this section, we investigate the hypothesis from the previous section (that is, strong reinforcing effects between prey flows when they occur ~ 2 months apart) in a full model with reciprocal pulsed herbivore subsidies. We begin by describing

the general dynamics of the meta-ecosystem with reciprocal pulsed subsidies (Figure 3A).

Reciprocal pulsed subsidies lead to periodic variation in the donor and recipient ecosystems. Consequently, reciprocal pulsed herbivore subsidies are reinforcing or dampening (that is, lead to local herbivore biomass that is higher or lower than in the absence of subsidies, Figure 3A). The biomasses of predators and herbivores in both local ecosystems decrease and the biomasses of producers in both local ecosystems increase in response to the loss of herbivores via spatial subsidies (see dynamics at t_1 in Figure 3A). Predators switch to consume the pulsed subsidies, which leads to an increase in predator biomass in response to the gain of subsidies. This switching behavior leads to an increase in the local herbivore biomass and a subsequent decline in the local producer biomass (see dynamics at t_2 in Figure 3). H_{2A} pulsed subsidies that are in phase with the local ecosystem 1 predator dynamics (that is, ~ 2 months apart, Figure 3D) lead to the strongest reinforcing effects between herbivores (dashed line in Figure 3A).

Effects of Duration

Overall, temporally concentrated pulses can increase the extreme minima and maxima of producer, herbivore, and predator biomass. We focus on the effects of pulse duration on producer biomass because high producer biomass can indicate strong trophic cascades, whereas low producer biomass can indicate dampened cascades. Mean producer biomass is relatively invariant under a range of pulse durations (Figure 4). Minimum producer biomasses in both local ecosystems increase with pulse duration and the maximum producer biomasses in both local ecosystems decrease with pulse duration (Figure 4).

Strength of Trophic Cascades

With reciprocal pulsed subsidies, predators switch to feed on herbivore subsidies, resulting in cascading effects in the local and neighboring ecosystems. In the local ecosystem, predator switching creates a refuge for the local prey, enabling it to benefit from the presence of the subsidy from the neighboring ecosystem. These reinforcing effects between herbivore flows lead to higher herbivory and weaker cascading effects on primary producers in local ecosystems (see t_2 in Figure 3A). By switching to feed on herbivore subsidies, predators contribute to the reduction of neighboring herbivores, which leads to strong cascading effects on

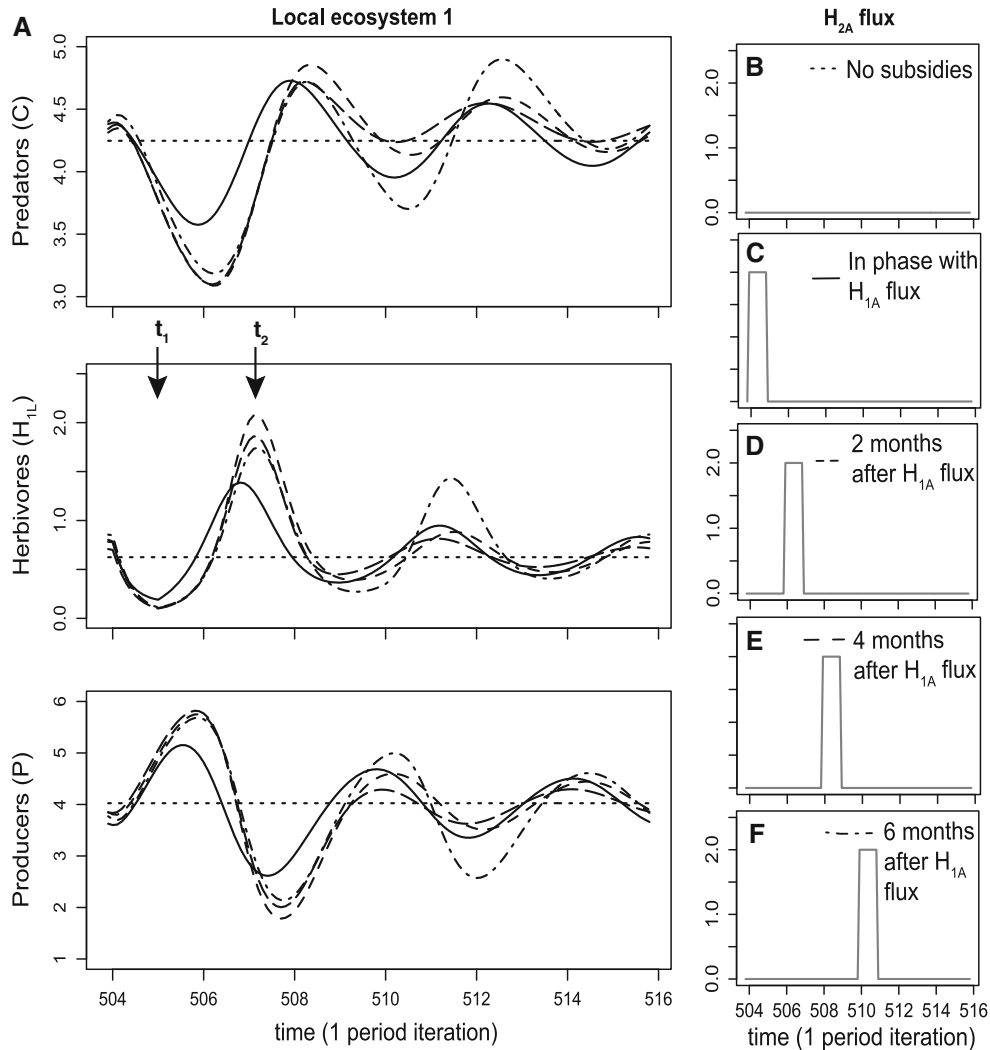


Figure 3. **A** Predator (C), herbivore (H_L), and producer (P) biomass in local ecosystem 1 over one period iteration (time = 504–516) for reciprocal pulsed subsidies. The model displays periodic variation; therefore, we only show results for one period. The results for local ecosystem 2 are similar to the results shown here for local ecosystem 1. The different lines represent cases where we model no subsidies (*dotted line*, **B**) and where the reciprocal flows are out of phase by zero ($\tau = 0$ *solid line*, **C**), 2 months ($\tau = 2$ *dashed line*, **D**), 4 months ($\tau = 4$ *long-dashed line*, **E**), and 6 months ($\tau = 6$ *dot-dashed line*, **F**). The series of panels to the right (**B–F**) depict the timing of the H_{2A} flux. In all cases, we kept the timing of the H_{1L} flow constant (**C**) and varied the timing of the H_{2L} flow to create the phase shift between flows. The *dotted line* in **A** represents C_i , H_{1L} , and P_i biomass in absence of subsidies. Results for $z = 2$, $u = 1$, and $f = 12$. All other parameters are as described in Figure 2.

producers in the adjacent ecosystem. Reciprocal pulsed subsidies of short duration increase the extreme maxima and decrease the extreme minima of producer biomasses (Figure 4), which suggests that temporally concentrated reciprocal pulsed subsidies can increase variability in the strength of trophic cascades.

Reciprocal pulsed subsidies have the potential to generate shifting trophic cascades over short time scales (that is, strength of cascades oscillates between strong and weak, Figure 5). Reciprocal pulsed flows that occur in phase lead to similar

temporal signatures in the strengths of local and meta-ecosystem trophic cascades (Figure 5A). Reciprocal pulsed subsidies that occur out of phase lead to asynchronous strength of cascades in local ecosystems and intermediate strength of cascades at the meta-ecosystem scale (Figure 5B). For example, when flows occur two months apart, the time of maximum strength of cascades in local ecosystem 1 corresponds to the time of minimum strength of cascades in local ecosystem 2 and an intermediate strength of cascades in the meta-ecosystem (see t_1 in Figure 5B).

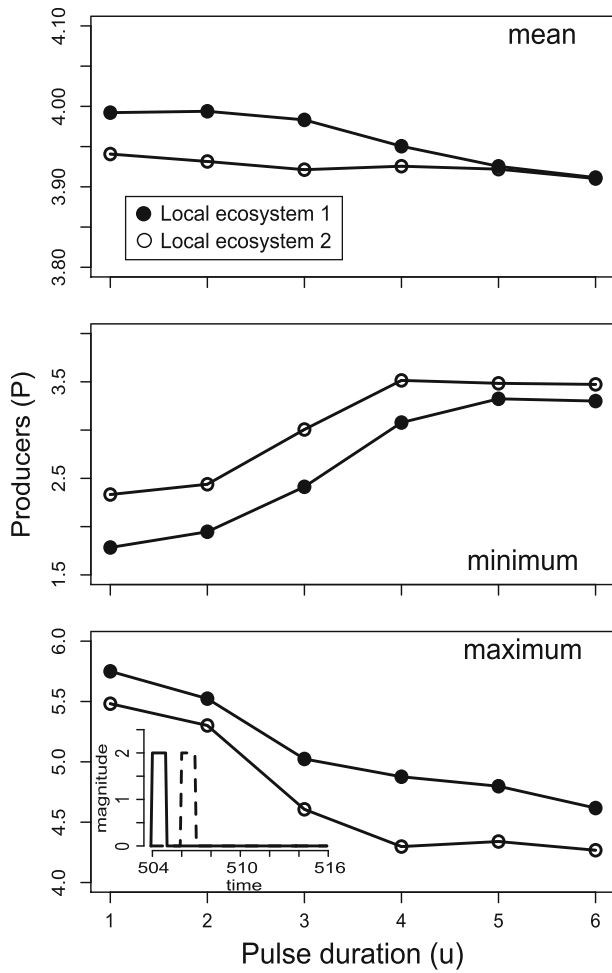


Figure 4. Mean, minimum and maximum producer biomass over one period in local ecosystem 1 (filled circle) and local ecosystem 2 (open circle) for increasing reciprocal pulsed subsidy duration (u). Herbivore subsidies start two months apart. For example, the inset figure shows when $u = 1$, flows from local ecosystem 1 (solid line of inset) occur at time 504 and herbivore subsidies from local ecosystem 2 (dashed line of inset) occur at time 506. Results are for $f = 12$. All other parameters are the same as defined in Figure 2.

Model Sensitivity

Most of our model predictions are not sensitive to the 74 different parameter sets we evaluated in our sensitivity analysis (Appendix A in Supplementary Material). A total of 91.6% of our parameter simulations yielded qualitatively similar results as our main model predictions. The model is least sensitive to changes in recycling (δ_i) and turnover rates (l_i and d_i) and most sensitive to changes in conversion efficiency (e_i), attack rates (a_i), and nutrient input rate (I_i). High herbivore and predator conversion efficiencies and attack rates in one local ecosystem lead to an increase in the variabilities of

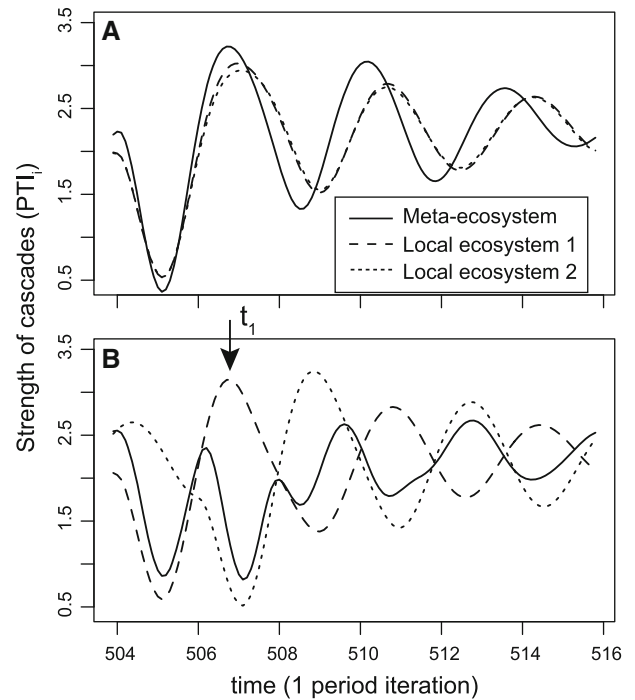


Figure 5. Strengths of cascades in local ecosystem 1 (dashed line), local ecosystem 2 (dotted line), and the meta-ecosystem (solid line), through time when reciprocal pulsed subsidies are **A** in sync (that is, both occur at the same time, see Figure 3C) and **B** 2 months out of phase (for example, see inset of Figure 4). Reciprocal pulsed subsidies lead to asynchronous cascade strength at the local ecosystem scale (for example, see t_1 : when cascades are high in local ecosystem 1, they are low in local ecosystem 2) and intermediate strength of cascades in meta-ecosystems. Results are for $z = 2$, $u = 1$, and $f = 12$. All other parameters are the same as defined in Figure 2.

the producer, herbivore, and predator biomass in this ecosystem.

DISCUSSION

Reciprocal pulsed subsidies are common in nature (see examples in Takimoto and others 2009; Yang and others 2010), and they can create strong responses in predators, and negative or positive competitive interactions between subsidies and local prey through shared predators (Holt 1977; Holt and Lawton 1994; Abrams and others 1998). We observe that reciprocal pulsed herbivore subsidies can reinforce or dampen each other and that the reinforcing effects are maximized when the flows are phase locked to the frequency of the local donor ecosystem dynamics. We also observed shifting in the strengths of trophic cascades in local and meta-ecosystems under reciprocal pulsed subsidies with

the strongest cascades occurring for subsidies of short duration. Predator switching reduces local cascade strength but leads to strong cascading effects across local ecosystems.

Effects of Pulsed Subsidy Characteristics on Ecosystem Dynamics

Spatial subsidies can occur with variable magnitudes, durations, and frequencies; yet, most empirical and theoretical research on subsidies considers them to be constant (for example, Huxel and McCann 1998; Knight and others 2005). As such, our current knowledge may only be capturing the mean response of ecosystems to subsidies. We show that accounting for the temporal variability in reciprocal pulsed subsidies can lead to complex dynamics at local and meta-ecosystem extents. Local predator biomass is at a minimum approximately 2 months after the loss of local herbivores, and the recipient herbivore biomass peaks around 2 months after the gain of herbivore subsidies to its ecosystem. Both these patterns are robust to a range of pulse quantities and frequencies (Figures 2, 3). Therefore, for equivalent total quantity, pulsed subsidies with very different characteristic temporal scales, such as those caused by infrequent events like ENSO (for example, floods; Andrews and others 2004) or frequent events like seasonality (for example, emergent aquatic insects; Nakano and Murakami 2001), may lead to similar temporal responses of organisms. Our analysis of the temporal response of organisms to pulsed subsidies is similar to Neubert and Caswell's (1997) reactivity and time of maximum amplification metrics for measuring the response of ecological systems to perturbations. Our combined results suggest that the short-term dynamics of systems experiencing single perturbations or recurrent "perturbations," such as recurrent pulsed subsidies, may be governed by the same parameters. In our model, however, we kept the total quantity of subsidy (that is, $z \cdot u \cdot \frac{1}{f} = c$) constant across different subsidy frequencies, whereas in nature, resource pulses of longer duration may often have larger overall magnitudes (Yang and others 2010).

Peak reciprocal herbivore biomasses in Honorai stream and the adjacent riparian forest in the Tomakomai Experimental Forest occur 2 months apart (Figure 1 in Nakano and Murakami 2001). These empirical results are qualitatively similar to our predictions on the timing required to maximize the reinforcing effects of reciprocal flows (Figures 2, 3). We predict maximum reinforcing effects of reciprocal herbivore flows when the time of

maximum recipient herbivore biomass is in phase with the timing of minimum donor predator biomass. Under this scenario, reciprocal subsidies complement the local resource deficiencies because of the loss of local herbivores and provide a temporal predation refuge for local herbivores (Takimoto and others 2002). Unfortunately, Nakano and Murakami (2001) do not provide sufficient empirical data to evaluate this hypothesis fully. The asynchrony of reciprocal pulsed subsidies is an intriguing feature of natural systems, which deserves further study in a range of coupled ecosystems with different temporally variable environments.

Holt (2008) investigated the effect of pulse duration in a simple predator-prey model and demonstrated that the predator-prey response to prey pulses is more dramatic when the pulse is temporally concentrated. Specifically, a predator's maximum biomass is the largest and a predator's minimum biomass is the smallest for short prey pulses (Holt 2008). We find qualitatively similar results in our meta-ecosystem model and extend these results to show that cascading effects of predators are also more extreme in their maxima and minima when reciprocal pulsed subsidies are temporally concentrated (Figures 4). These results suggest a synergistic effect of pulsed subsidy magnitude and duration in structuring ecosystem dynamics.

In a model with a single recipient consumer with fast reproduction and fast aggregation, Takimoto and others (2009) predicted either a negative or positive effect of pulsed subsidies on the local prey depending on the timing of the subsidy relative to the dynamics of the local prey. Other studies suggest that population cycles should dampen negative effects between prey that share a predator (Abrams and others 1998; Holt and Barfield 2003; Sacks and Neale 2007). Our approach differs from those studies in that we explicitly consider reciprocity between coupled ecosystems with distinct predators. We also observe the potential for reinforcing and dampening effects between prey that share a predator for models with unidirectional pulsed subsidies. However, in models with reciprocal pulsed subsidies, positive or reinforcing effects between prey are most prevalent. Reinforcing effects between prey that share a predator are contingent upon rapid behavioral response of predators in response to prey abundance, which can balance the overall predation pressure on multiple prey. Aggregative behavioral responses of predators to subsidies are common in many ecosystems. For example, spider densities are high near the sources of marine (Polis and Hurd 1995) and freshwater

(Paetzold and others 2005) subsidies. We focus on the aquatic–terrestrial ecotone because it is common in many biomes, but our modeling framework can be applied to other meta-ecosystems structured by reciprocal pulsed subsidies and predators with behavioral responses to prey abundance.

Reciprocal Pulsed Subsidies and Trophic Cascades

Top predators are often mobile specialists or opportunistic residents, which enable them to effectively exploit resource pulses and link distinct ecosystems (McCann and others 2005; Yang and others 2008). We demonstrate the occurrence of shifting trophic cascades generated by subsidized consumers over short time scales driven by variability in reciprocal pulsed subsidies and a strong behavioral response of predators to prey subsidies (Figure 5, Appendix B in Supplementary Material). In one of the few studies to investigate cascading trophic interactions across ecosystem boundaries, Knight and others (2005) observed a strong effect of fish on riparian shrubs because of fish consumption of larval dragonflies in adjacent ponds. Similarly, Schreiber and Rudolf (2008) and McCoy and others (2009) showed that predators with complex life histories can influence the structure and dynamics of neighboring ecosystems. Juvenile amphibians feeding on aquatic invertebrates have a direct impact on the biomass of emergent aquatic invertebrates and an indirect effect on herbivory in riparian zones (McCoy and others 2009). Strong cascades can be driven by neighboring consumers, yet most cascade experiments and theory focus on the indirect effects of consumers in local ecosystems (for example, Huxel and McCann 1998; Shurin and others 2002; Leroux and Loreau 2008). Our ability to detect and understand trophic cascades, however, may depend on the scale of inquiry of ecological studies (Hastings 2004; Stibor and others 2004).

The median duration of empirical studies of subsidies is three months (Marczak and others 2007), and most of these studies focus their sampling around the peak time of subsidies. The response of ecosystems to subsidies, however, can persist long after the subsidy peaks (Gratton and Denno 2003; Verspoor and others 2010). We show that pulsed subsidies can generate a transient response in the donor and recipient ecosystems that can last throughout the entire interpulse period (Figure 3). Although we are developing a good understanding of the short term and direct impact of subsidies, we need to better understand the

intermediate, long-term, and indirect effects of subsidies. Empirical studies can achieve this by reducing sampling intensity during peak subsidy periods to extend their sampling over interpulse periods. Theoretical studies can contribute by investigating ecosystem dynamics at multiple temporal scales and by incorporating dynamic feedbacks that may be common but often overlooked in meta-ecosystems (Gravel and others 2010; Massol and others 2011).

In our analysis, we chose to focus on reciprocal herbivore flows because these are very common fluxes in the aquatic–terrestrial ecotone. Although the predictions of our model relating to the effect of reciprocal pulsed subsidies on ecosystem dynamics are fairly general, there are some important limitations. Many ecosystems are coupled through flows from multiple trophic levels. For example, aquatic–terrestrial ecotones have not only reciprocal invertebrate flows but also nutrient flows due to flooding (Witman and others 2004) and runoff (Burcher and others 2007), as well as predator flows due to species with complex life histories, such as dragonflies (for example, Knight and others 2005) and amphibians (for example, Semlitsch 2000). Meta-ecosystem models can be useful for understanding the dynamics emerging from such complex ecotones with multiple feedbacks (Loreau and others 2003; Gravel and others 2010). As well, species with complex life histories may be prey as juveniles in one ecosystem and become predators as adults in another ecosystem. The modeling approaches of Schreiber and Rudolf (2008) and McCoy and others (2009) for species with complex life histories can be integrated with our meta-ecosystem approach to further understand the effects of these complex life strategies on ecosystem functioning.

CONCLUSION

We derived a model to explicitly consider the dynamic feedbacks between local ecosystems coupled through reciprocal pulsed subsidies. We predict that reciprocal pulsed subsidies can reinforce or dampen each other and lead to spatial and temporal variabilities in the strength of trophic cascades. Predators that demonstrate a behavioral response to prey abundance are reactive to pulsed subsidies, which leads to transient dynamics in local and meta-ecosystems following resource pulses. Reciprocal flows also can lead to strong trophic cascades across local ecosystems boundaries, particularly when these flows are in phase with the local dynamics of neighboring predators. Future research can build on our model by considering a

broader suite of predator functional responses and spatially extended systems. Ecosystems are inherently variable in both space and time, but few studies have jointly investigated the effects of variation in space and time on ecosystem dynamics (Holt and Barfield 2003; McCann and Rooney 2009). Ecologists must broaden their scope to consider the spatial and temporal mechanisms for variation in the strength of trophic cascades (Howeth and Leibold 2008).

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