# Transient top-down and bottom-up effects of resources pulsed to multiple trophic levels

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*Abstract.* Pulsed fluxes of organisms across ecosystem boundaries can exert top-down and bottom-up effects in recipient food webs, through both direct effects on the subsidized trophic levels and indirect effects on other components of the system. While previous theoretical and empirical studies demonstrate the influence of allochthonous subsidies on bottom-up and top-down processes, understanding how these forces act in conjunction is still limited, particularly when an allochthonous resource can simultaneously subsidize multiple trophic levels. Using the Lake Mývatn region in Iceland as an example system of allochthony and its potential effects on multiple trophic levels, we analyzed a mathematical model to evaluate how pulsed subsidies of aquatic insects affect the dynamics of a soil–plant–arthropod food web. We found that the relative balance of top-down and bottom-up effects on a given food web compartment was determined by trophic position, subsidy magnitude, and top predators' ability to exploit the subsidy. For intermediate trophic levels (e.g., detritivores and herbivores), we found that the subsidy could either alleviate or intensify top-down pressure from the predator. For some parameter combinations, alleviation and intensification occurred sequentially during and after the resource pulse. The total effect of the subsidy on detritivores and herbivores, including top-down and bottom-up processes, was determined by the rate at which predator consumption saturated with increasing size of the allochthonous subsidy, with greater saturation leading to increased bottom-up effects. Our findings illustrate how resource pulses to multiple trophic levels can influence food web dynamics by changing the relative strength of bottom-up and top-down effects, with bottom-up predominating top-down effects in most scenarios in this subarctic system.

*Key words: allochthonous inputs; bottom-up; food webs; resource pulses; subsidy; top-down.*

## Introduction

Temporal variation in the availability of either internally (autochthonous) or externally (allochthonous) derived resources can alter the dynamics of ecological systems (Anderson et al. 2008, Yang et al. 2010, Hastings 2012). Resource pulses are episodic, short-duration events of enhanced resource availability that can exert both direct and indirect bottom-up effects on recipient ecosystems (Yang et al. 2008). Pulsed allochthonous resources to terrestrial ecosystems (e.g., seabird guano on subarctic islands) can increase primary production by plants, which in turn leads to elevated biomass and diversity at higher trophic levels (Sanchez-Pinero and Polis 2000). They can also affect top-down control on lower trophic levels by increasing predator populations (Henschel et al. 2001, Luskin et al. 2017). For example, aquatic insects moving from water to land can subsidize diverse communities of terrestrial predators such as spiders (Power et al. 2004) and birds (Nakano and Murakami 2001), enhancing top-down control on local herbivores and thereby increasing plant productivity. Resource pulses potentially exert multiple direct and indirect effects on recipient systems, making them a valuable context in which to study temporal variation in the strength of bottom-up and top-down control, a topic of recent and general ecological interest (Meserve et al. 2003, Fath et al. 2004, Polishchuk et al. 2013, Leroux and Loreau 2015, Vidal and Murphy 2018, Piovia-Scott et al. 2019).

The influence of resource pulses on bottom-up and top-down effects depends on a variety of factors,

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including the magnitude of the pulse, the trophic position of recipient populations, the structure of the recipient food web, and the relative propensity of the recipient population to exploit the allochthonous resource (Huxel and McCann 1998, Leroux and Loreau 2012, Miller et al. 2019). Theoretical models show that allochthonous subsidies can increase the strength of trophic cascades in simple food webs, with the strength of the cascade being mediated by consumers with an intermediate preference for allochthonous vs. autochthonous resources (Leroux and Loreau 2008). Temporal shifts in the strength of top-down and bottom-up effects due to subsidies have also been observed empirically. For example, island lizards temporarily reduced predation on local herbivores when pulsed seaweed subsidies increased detritivorous prey, but after the pulse-associated period of enhanced resource availability, top-down pressure on herbivores strengthened due to elevated lizard abundance (Piovia-Scott et al. 2019).

While previous theoretical (Huxel and McCann 1998, Leroux and Loreau 2012, Miller et al. 2019) and empirical (Nowlin et al. 2007, Hoekman et al. 2011, Yee and Juliano 2012) studies demonstrate the influence of allochthonous subsidies on bottom-up and top-down processes, our understanding of how allochthony influences these forces in conjunction is still poor. Moreover, an allochthonous resource may also simultaneously subsidize multiple trophic levels, a research topic that has also received limited attention. To address these issues, we developed a mathematical model that reflects the terrestrial food web adjacent to Lake Mývatn in northeastern Iceland (Fig. 1). Mývatn is naturally eutrophic and sustains large populations of midges (Diptera: Chironomidae), which emerge as adults for several weeks each year and form mating swarms over the surrounding heathland landscape. When not swarming, the adult midges settle in the vegetation where they become an abundant food resource for predatory arthropods (Dreyer et al. 2016, Sanchez-Ruiz et al. 2018). In addition, when the midges die uneaten, their carcasses enter the detrital food web and subsidize the soil biota (Hoekman et al. 2011), ultimately leading to the remineralization of nitrogen (N) and other nutrients that affect plant productivity and community composition (Gratton et al. 2017). Because midges subsidize both upper (as prey) and lower (as detritus) trophic levels (Fig. 1), this resource pulse potentially exerts both bottom-up and top-down effects on the intermediate trophic levels, such as detritivorous and herbivorous arthropods. While Mývatn has particularly large aquatic insect emergences, the general phenomenon of allochthony having an effect as both a prey item and as a detrital input is not unique. For example, the 13- or 17-yr periodical cicada (*Magicicada* spp.) can fall prey to many terrestrial predators (e.g., birds, reptiles, and rodents) during emergences in North American forests (Karban 1982, Williams et al. 1993, Koenig and
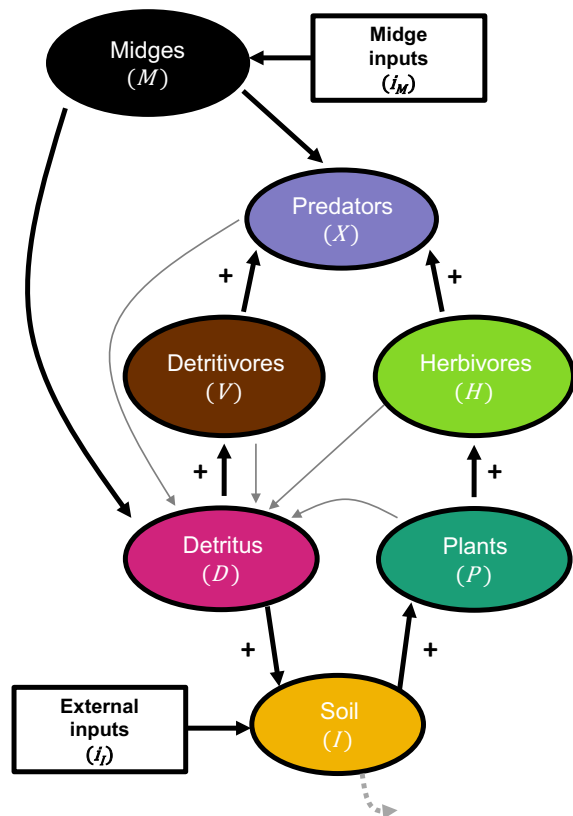


Fig. 1. Conceptual diagram showing how midge pulses are incorporated into the Mývatn terrestrial food web for our model, with arrows showing the flow of N. Black arrows illustrate the movement of N (i.e., consumption, remineralization, and uptake) through the food web. Solid gray arrows indicate the loss of N via mortality; the gray dotted arrow denotes N loss from the system from the soil compartment. Other model parameters are omitted for simplicity. [Color figure can be viewed at wileyonlinelibrary.com]

Liebhold 2005); however, most cicadas escape predation and become deposited as detritus following death (Yang 2004, Nowlin et al. 2007).

We analyzed a mathematical model of a soil–plant–arthropod food web receiving an allochthonous resource that directly subsidizes both predators (as live prey) and detritus (as carcasses). We asked three questions: (1) How do allochthonous pulses entering multiple compartments affect transient top-down and bottom-up effects on recipient food webs? (2) Does the relative strength of top-down and bottom-up effects induced by resource pulses differ between intermediate trophic levels (i.e., detritivores and herbivores)? (3) Under what conditions do bottom-up vs. top-down effects dominate when an allochthonous pulse enters multiple entry points? To address these questions, we examined the responses of intermediate trophic levels that are not directly subsidized by the allochthonous resource, which allowed us to examine the indirect effects of subsidies that propagate throughout the food web.

## METHODS

### Model structure

We analyzed a model informed by the terrestrial food web surrounding Lake Mývatn where midges are allochthonous inputs to multiple trophic levels. We formulated the model in terms of nitrogen (N) to provide a "common currency" among the inorganic, dead, and living pools. We chose N as our common currency because it is one the most limiting elements in arctic ecosystems (Chapin III et al. 1986, Manzoni et al. 2010), biological processes are intimately involved in its circulation through terrestrial systems (Bosatta and Ågren 1996), and it is a common tracer used in other food web studies (Liu et al. 2005, Zelenev et al. 2006, Manzoni and Porporato 2009).

We analyzed a hybrid community–ecosystem model as a system of ordinary differential equations (ODEs) combining classical consumer–resource dynamics (e.g., Rosenzweig and MacArthur 1963) with nutrient cycling via inorganic soil and detrital N pools (DeAngelis 1992, Loreau 2010). The model contains seven N pools: midges ($M$), inorganic soil N ($I$), detritus ($D$), plants ($P$), detritivorous arthropods ($V$), herbivorous arthropods ($H$), and predatory arthropods ($X$; Fig. 1). While the model does not explicitly include microbial pools, it does include microbially mediated processes such as decomposition and remineralization; this is equivalent to assuming that these processes are proportional to the substrate availability but not microbial biomass. We perturbed the model with pulsed inputs to the midge pool, which in turn directly subsidized the detritus and predatory arthropods; therefore, effects of the midge pulse on the other trophic levels arise through bottom-up and top-down processes propagating from predators and detritus. The model was formulated such that equilibria were locally stable (Hastings 2013; Appendix S1: Section S1 and Appendix S2: Fig. S1) in the absence of allochthonous pulses, which allowed us to track the temporal variation in bottom-up and top-down effects during and after the pulse as the system returned to equilibrium.

In the model, soil nutrients increase from a fixed external input rate and remineralization of detritus, while the detritus pool increases through losses from the living pools (i.e., non-consumptive mortality) and midges. The transfer of N to both the soil and detritus pools is assumed to occur with some inefficiency (the terms "1 – $l$" in Eq. 1), reflecting inefficient transfer of nutrients between trophic levels and facilitating the stability of the model in the absence of the midge pulse (Leroux and Loreau 2008, Loreau 2010). The living pools increase through N uptake from the inorganic pool or consumption from either the detritus or living pools (Fig. 1), an approach similar to models presented in Loreau (2010). Gains to the living pools are in terms of N, and therefore are not only due to the reproduction of individuals, but also to increases in individual N content (i.e., biomass).

Each living pool experiences density-dependent losses due to processes such as mortality, excretion, and shedding of tissue (e.g., leaves).

Plant uptake of N from the soil-nutrient pool, detritivore consumption of detritus, and herbivore consumption of plants are all modeled as type-II functional responses (Holling 1959), whereby uptake saturates with increasing resource availability. Predator consumption of herbivores, detritivores, and midges is modeled as a multispecies type-II functional response (Murdoch 1969), whereby consumption of each of the pools saturates with the total availability of all three pools. For both single and multispecies functional responses, the saturation is influenced by both the uptake or "attack" rate (the rate at which uptake increases when resources are sparse) and the "handling time" (the inverse maximum uptake rate when resources are abundant). For simplicity, we use the same predator handling time for detritivores and herbivores; however, we use a separate handling time for midges and explore how variation in this value affects the dynamics. The midge handling time likely varies depending on the size and composition of the midge subsidy; at Mývatn, the individuals within midge swarms vary in size.

Together, these assumptions translate into the following system of ODEs:

$$\frac{dI}{dt} = i_I + (1-l)\mu_D D - \frac{a_I I P}{1 + a_I h_I I} - \mu_I I$$

$$\frac{dD}{dt} = (1-l)\mu_M M + (1-l) \sum_{j \in \{P,V,H,X\}} \left(\mu_j + m_j j\right) j - \frac{a_D D V}{1 + a_D h_D D} - \mu_D D$$

$$\frac{dP}{dt} = \frac{a_I I P}{1 + a_I h_I I} - \frac{a_P P H}{1 + a_P h_P P} - (\mu_P + m_P P) P$$

$$\frac{dV}{dt} = \frac{a_D D V}{1 + a_D h_D D} - \frac{a_X V X}{1 + a_X h_X H + a_X h_X V + q a_X h_M M} - (\mu_V + m_V V) V$$

$$\frac{dH}{dt} = \frac{a_P P H}{1 + a_P h_P P} - \frac{a_X H X}{1 + a_X h_X H + a_X h_X V + q a_X h_M M} - (\mu_H + m_H H) H$$

$$\frac{dX}{dt} = \frac{(a_X V + a_X H + q a_X M) X}{1 + a_X h_X H + a_X h_X V + q a_X h_M M} - (\mu_X + m_X X) X$$

$$\frac{dM}{dt} = i_{M(t)} - \frac{q a_X M X}{1 + a_X h_X H + a_X h_X V + q a_X h_M M} - \mu_M M$$

$$(1)$$

with state variables and parameters defined in Table 1.

The input of midges to the system is characterized as a step-function

TABLE 1. Food web model parameter definitions.

| Pool | Description | Units | Baseline value |
|---|---|---|---|
| $I$ | inorganic soil nitrogen (N) | g N/m$^2$ | 250† |
| $D$ | detritus | g N/m$^2$ | 15† |
| $P$ | plants | g N/m$^2$ | 40† |
| $V$ | detritivores | g N/m$^2$ | 1† |
| $H$ | herbivores | g N/m$^2$ | 1† |
| $X$ | predators | g N/m$^2$ | 0.5† |
| $M$ | midges | g N/m$^2$ | NA |
| $i_I$ | inorganic nutrient input rate | g N·m$^{-2}$·d$^{-1}$ | 10‡ |
| $\mu_I$ | density-independent loss of soil nutrients | d$^{-1}$ | 0.01‡ |
| $\mu_D$ | density-independent loss of detritus | d$^{-1}$ | 0.1‡ |
| $\mu_P$ | density-independent loss of plants | d$^{-1}$ | 0.01‡ |
| $\mu_V$ | density-independent loss of detritivores | d$^{-1}$ | 0.1‡ |
| $\mu_H$ | density-independent loss of herbivores | d$^{-1}$ | 0.1‡ |
| $\mu_X$ | density-independent loss of predators | d$^{-1}$ | 0.1‡ |
| $\mu_M$ | density-independent loss of midges | d$^{-1}$ | 0.5‡ |
| $m_P$ | density-dependent loss of plants | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.024§ |
| $m_V$ | density-dependent loss of detritivores | m$^2$·g N$^{-1}$·d$^{-1}$ | 2.36§ |
| $m_H$ | density-dependent loss of herbivores | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.1‡ |
| $m_X$ | density-dependent loss of predators | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.1‡ |
| $l_x$ | proportion mortality of $x$ lost from system | dimensionless | 0.1‡ |
| $a_I$ | uptake rate of soil nutrients by plants | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.0078§ |
| $a_D$ | uptake rate of detritus by detritivores | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.032§ |
| $a_P$ | uptake rate of plants by herbivores | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.012§ |
| $a_X$ | uptake rate of detritivores, herbivores, and midges by predators | m$^2$·g N$^{-1}$·d$^{-1}$ | 0.125§ |
| $q$ | predator exploitation of midges | dimensionless | $8 \times 10^{-3}$ to 8‡ |
| $h_I$ | handling time of soil nutrients by plants | d | 0.51‡ |
| $h_D$ | handling time of detritus by detritivores | d | 2.1‡ |
| $h_P$ | handling time of plants by herbivores | d | 2.1‡ |
| $h_X$ | handling time of herbivores and detritivores by predators | d | 2.7‡ |
| $h_M$ | handling time of midges by predators | d | 1.3 to 5.3‡ |

*Notes:* Density-dependent and density-independent losses are the "natural" values (i.e., the values for those pools at equilibrium). The $x$ in $l_x$ represents all pools, as they have the same value.

†Value is based on empirical approximation from the literature.

‡Values on a comparable scale to the other parameters.

§Value was solved from the equilibrium of the ODEs. For more details, see the Parameter values subsection in the methods.

$$i_{M(t)} = \begin{pmatrix} b & \text{for } t_0 < t \le t_0 + w \\ 0 & \end{pmatrix} \qquad (2)$$

where $t_0$ is the time at which the pulse begins, $w$ is the width or duration of the pulse, and $b$ is the rate of midge input during the pulse. The total midge input over the duration of pulse equals $b \times w$. Once in the midge pool, the midge N either enters the detritus pool via decay of carcasses or the predator pool via consumption. "Predator exploitation" ($q$) is the predator attack rate on midges relative to that on herbivores and detritivores, and it partly controls the number of midges captured and consumed by predators. At Mývatn, various factors may affect how effectively arthropod predators can passively exploit midges, including the vegetation structure. Grasslands have more structure in which midges can become trapped, thereby increasing predators' abilities to exploit midges and decreasing the direct input into the detrital pool. Furthermore, increased plant structure favors web-building spiders with slower handling times,

whereas reduced plant structure favors ground-hunting spiders with much faster handling times.

*Parameter values*

While we present our model in the context of Mývatn to make the analysis more concrete, our objective is to use the model to provide broader insights into transient food web responses to pulses with multiple entry points. Nonetheless, to numerically explore the dynamics of the model, it was necessary to select parameter values. Rather than conducting an exhaustive exploration of the dynamics across the full parameter space, we defined a "baseline" parameter set partially informed by data from Mývatn or similar systems. We then explored the dynamics across a range of values for a select set of parameters that governed the intensity (and consequently, total magnitude) of midge pulse ($b$), and direct responses to the pulse (e.g., predator exploitation of

midges, $q$, and the predator handling time on midges, $h_M$).

To define the baseline parameters, we first specified equilibrium sizes of the N pools in the absence of midge subsidies based on empirical estimates. Pool sizes were based on biomass estimates (g N·m$^{-2}$·yr$^{-1}$) within a range of values from studies in similar habitats (midges from Dreyer et al. [2015]; soil and plants from Marion et al. [1982]; detritus from Shaver et al. [1992]; herbivores, detritivores, and predators from Hoekman et al. [2011] and Dreyer et al. [2012]). Next, we fixed values for parameters that could be intuitively related to the equilibrium pool sizes. For example, we selected the handling times for the type-II functional responses (e.g., $h_P$) such that the resource level at which the uptake reached one-half its maximum (i.e., the half-saturation value) occurred at the equilibrium density for that pool. The exception to this was the predator handling time ($h_X$), which was selected so that the half-saturation value was 50% of the combined equilibrium densities of the detritivores and herbivores; this allowed the predators to exploit the midge subsidy when all pools were at their equilibria. Other parameters were given arbitrary values based on comparable scales to the other parameters until enough were specified so that the remaining values could be determined by solving the system of equations set to their equilibria (with the midge pool set to 0; Table 1). This approach ensured that the relative equilibrium pool sizes resulting from the combinations of parameters were empirically plausible and ensured that the corresponding equilibria were locally stable (Appendix S1: Section S1 and Appendix S2: Fig. S1). Therefore, we had a clear baseline against which we could explore the transient dynamics of the system in response to resource pulses.

Although we focus our analysis on the baseline parameter set, to assess the generality of the results we also analyzed the model for alternative parameter sets for different combinations of herbivore/detritivore uptake rates (Appendix S2: Fig. S2) and inorganic nutrient input and outflow rates (Appendix S2: Figs. S3–S4). These combinations were selected based on how relevant they were to the main questions of our research. The qualitative dynamics for these alternative parameterizations were similar to the baseline set; therefore, all the results refer to the baseline parameter set unless noted otherwise.

*Analysis*

To explore the effects of midge pulse intensity and multitrophic entry points, we numerically solved the system of ODEs for different combinations of parameters that governed the total magnitude of the midge pulse ($b$, keeping pulse duration $w$ fixed) and direct responses to the pulse, such as predator exploitation ($q$) and the predator handling time on midges ($h_M$). For each run of the model, the pools were initialized at their equilibrium

values in the absence of midges, such that they would remain fixed through time in the absence of perturbations from the midge pulse. We ran the models for 500 time steps to ensure that they all returned to equilibrium (defined as being within 1% of the equilibrium pool size). We present the timescale in terms of days to help constrain the range of midge pulse durations we explored; specifically, we constrained the midge pulse duration ($w$) to 20 d, which is approximately twice the duration of an average single midge emergence at Mývatn. However, we note that the timescale is relative to the internal rates of the model, many of which are not well constrained. Therefore, the timescales in the model should be interpreted loosely.

We focused our analysis on the dynamics of herbivores and detritivores because neither of these two pools is directly influenced by midges but are indirectly affected through both top-down and bottom-up forces. The top-down effects of midges on herbivores and detritivores manifest through consumption by the predators and are identical on a per capita basis for the two pools (because they are modeled symmetrically). In contrast, the bottom-up effects differ because of their different trophic positions and proximity to the subsidy entry point: decaying midges directly enter the detritus pool and are then available to the detritivores, while the midge N must additionally enter the soil pool from the detritus and then be taken up by plants before becoming available to the herbivores. Therefore, detritivores receive an immediate benefit from allochthonous resources entering the detrital pool, whereas herbivores are several steps removed, leading to a slower response to midge pulses.

To measure the proximate mechanisms through which bottom-up and top-down fluxes affect target pools, we quantified the effect of the midge pulse on detritivores and herbivores as the difference between either the N gain due to consumption (bottom-up) or loss due to predation (top-down) in response to a midge pulse (both during and after the pulse) and the corresponding gain or loss given the equilibrium pool sizes in the absence of the pulse (i.e., in an unperturbed system). Specifically, the effect of midges on the bottom-up flux of N to detritivores at time $t$ was defined as

$$\text{BU}_V(t) = \frac{a_D D(t) V(t)}{1 + a_D h_D D(t)} - \frac{a_D D^* V^*}{1 + a_D h_D D^*} \quad (3)$$

where $D(t)$ and $V(t)$ are the pool sizes at time $t$ obtained from the numerical solution of the system of ODEs when perturbed with the midge pulse, while $D^*$ and $V^*$ are the equilibrium pool sizes in the absence of the midge pulse. This expression gives the difference between the bottom-up gain to the detritivore pool at a given point in time and what that gain would be in the absence of the midge pulse, per unit of N in the detritivore pool. The bottom-up effect of midges on the herbivores was defined analogously

$$\mathrm{BU}_H(t) = \frac{a_P P(t) H(t)}{1 + a_P h_P P(t)} - \frac{a_P P^* H^*}{1 + a_P h_P P^*} \qquad (4)$$

where $P(t)$ and $H(t)$ are the pool sizes at time $t$ obtained from the numerical solution of the system of ODEs when forced with the midge pulse, while $P^*$ and $H^*$ are the equilibrium pool sizes in the absence of the midge pulse. The effects of the midge pool manifest through the solution to the system of ODEs, and these effects can persist beyond the end of the midge pulse.

The effect of midges on top-down pressure on detritivores at time $t$ was defined as

$$\mathrm{TD}_V(t) = \frac{a_X V(t) X(t)}{1 + a_X h_X H(t) + a_X h_X V(t) + a_X h_M q M(t)} - \frac{a_X V^* X^*}{1 + a_X h_X H^* + a_X h_X V^*}$$
$$(5)$$

where $V(t)$, $H(t)$, $M(t)$, and $X(t)$ are the pool sizes at time $t$ obtained from the numerical solution of the system of ODEs when forced with the midge pulse, while $V^*$, $H^*$, and $X^*$ are the equilibrium pool sizes in the absence of the midge pulse. Analogous to the top-down effects (Eqs. 3 and 4), Eq. 5 gives the difference between the top-down loss from the detritivore pool due to predation at a given point in time and what that loss would be in the absence of the midge pulse, per unit of N in the detritivore pool. Because the per capita multispecies functional response was the same for both detritivores and herbivores, they experienced identical top-down effects per unit N, such that $\mathrm{TD}_V(t) = \mathrm{TD}_H(t) \equiv \mathrm{TD}(t)$.

In addition to top-down losses of N due to predation, the midge pulse also affects the loss of N from detritivore and herbivore pools through density-dependent mortality. On a per capita basis, the density-dependent mortality for a given pool directly follows changes in the size of the corresponding pool, and so does not provide much additional information about the factors driving the dynamics. This stands in contrast to the effects of the midge pulse on bottom-up and top-down processes, which involve the interactions between multiple pools and so drive the dynamics. Therefore, while it is worth noting that the total effect of the midge pulse includes its effects on density-dependent mortality, we focus our analysis of the impacts of midges on bottom-up and top-down processes.

Our metrics of top-down and bottom-up effects of midges are proximate, in the sense that their directionality (i.e., bottom vs. top) is defined with respect to the target pool. However, an alternative approach is to define the directionality relative to the entry point of the midges to the food web (i.e., low vs. high trophic levels). To explore this, we analyzed scenarios with different entry points for midges into the food web: (1) midges to detritus only, (2) midges to predators only, and (3) midges to both detritus and predators (see Appendix S1: Section S2 for corresponding modifications to Eq. 1). By both

manipulating the way in which midges enter the food web and quantifying fluxes to and from each pool, we were able to provide a comprehensive assessment of bottom-up and top-down effects. Furthermore, our scenarios parallel how bottom-up or top-down effects are studied empirically (e.g., Marczak and Richardson 2007, Hoekman et al. 2011, Dreyer et al. 2016), while our metrics based on proximate fluxes (i.e., $\mathrm{BU}_H$, $\mathrm{BU}_V$, and TD) capture mechanisms that are difficult to directly observe and so take advantage of the theoretical setting. We note that other metrics that have been developed for quantifying transient responses to pulses in theoretical (Neubert and Caswell 1997) and empirical (Yang et al. 2010) settings. We opted for our approach because it allowed us to separate transient responses of certain trophic levels to the pulse into bottom-up and top-down components.

The analyses above demonstrate how the transient responses of detritivore and herbivore pools to midge subsidies vary across different scenarios of midge entry to the food web. To provide a more comprehensive exploration of these processes, we also calculated the cumulative effect of midges on bottom-up and top-down processes over the entire period during and after a midge pulse until the return to equilibrium. We focused on the case where midges subsidize both the detrital and predator pools across different levels of cumulative midge input, the predator exploitation ($q$), and handling times on midges ($h_M$).

The effect of midges on bottom-up N gains to detritivores ($\mathrm{BU}_V(t)$) and herbivores ($BU_H(t)$) was nonnegative across the full range of explored parameters. Therefore, we defined the cumulative bottom-up effect of midges to detritivores as

$$\mathrm{BU}_{V,\mathrm{total}} = \int_{t_0}^{t_{\mathrm{end}}} \mathrm{BU}_V(t)\,dt \qquad (6)$$

where $t_0 = 0$ and $t_{\mathrm{end}} = 500$, by which point all pools were within 1% of their equilibrium abundance in the absence of midges. The total bottom-up effect of midges on herbivores was defined analogously.

We observed both positive and negative effects of the midge pulse of the strength of top-down pressure $[\mathrm{TD}_V(t)]$; thus, we defined the cumulative intensification of top-down pressure during and after a midge pulse

$$\mathrm{TD}_{\mathrm{intensification}} = \int_{t_0}^{t_{\mathrm{end}}} \min(0, \mathrm{TD}(t))\,dt \qquad (7)$$

and the cumulative alleviation as

$$\mathrm{TD}_{\mathrm{Alleviation}} = -\int_{t_0}^{t_{\mathrm{end}}} \max(0, \mathrm{TD}(t))\,dt. \qquad (8)$$

The net top-down effect of midges was therefore

$$\mathrm{TD}_{\mathrm{net}} = \mathrm{TD}_{\mathrm{intensification}} - \mathrm{TD}_{\mathrm{alleviation}}. \qquad (9)$$

All analyses were performed in R v4.0.0 (R Development Core Team 2020). Numerical solutions to ODEs

were obtained using the ode function from the deSolve package (Soetaert et al. 2010).

## Results

Our analysis was designed to illustrate how a resource pulse that simultaneously enters multiple trophic levels affects the transient dynamics of a recipient food web, with a focus on how the bottom-up and top-down consequences of resource pulses vary through time. We begin by presenting the transient dynamics of the model given some example parameter combinations to illustrate its key behaviors, followed by an exploration of the dynamics across a wider range of parameter values that influence the capacity of different predators to exploit the resource pulse (e.g., predator exploitation of the resource pulse and handling time). Rather than attempting to provide a comprehensive assessment of the model dynamics across the full parameter space, our analysis instead provides a more focused examination of the qualitative behaviors that can arise in a system with resource pulses to multiple trophic levels (see Appendix S2: Figs. S2–S4 for results of alternative parameterizations).

### Responses of lower and upper trophic levels to midge pulse

We first show the time series for the N content of each trophic level in response to a single resource pulse using the baseline parameter set (Fig. 2); the values are relative to the equilibrium (see Appendix S2: Fig. S5 for absolute values). An unrealistically large pulse (i.e., 1000 g N/m², 10–100× higher than empirical estimates in Dreyer et al. 2015) was used to better illustrate the qualitative behavior of the system under extreme conditions. All trophic levels increased in response to the pulse, followed by a gradual decline from their peaks towards their respective equilibria in the absence of elevated resources. However, the timing and relative magnitude of each peak's response varied depending on the trophic position of the recipient pool. For example, the detritus pool is directly subsidized by decay from the midge pool and therefore has a rapid response to the midge pulse. In contrast, for N from midges to enter the soil and plant pools, it must first be remineralized from the detritus pool into the inorganic N pool before then being taken up by the plants. This introduces lags to the responses of the soil and plant pools, which manifest as a delay in their peak responses relative to the detritus pool.

### Transient responses of detritivores and herbivores

There were qualitatively different responses of detritivores and herbivores that arose through changes in the pulse entry point of the midges (Fig. 3). When midges only entered via detritus (Fig. 3a), detritivore and herbivore pools increased during the midge pulse, showing a
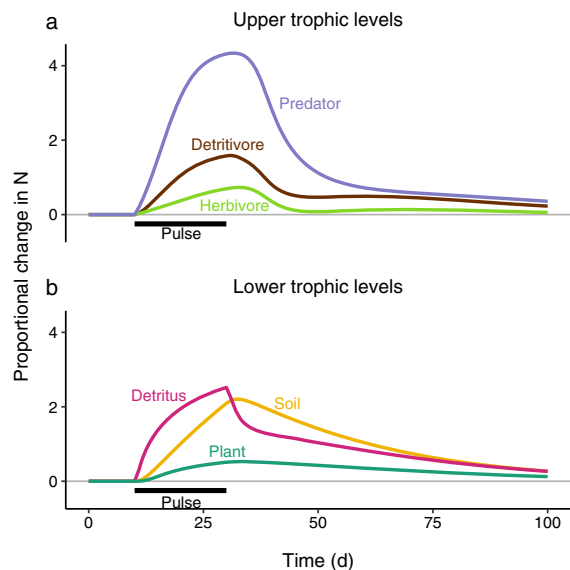
Fig. 2. Time series of proportional changes in N content among (a) upper trophic level (herbivore, detritivore, predator) and (b) lower trophic level (detritus, soil, plant) pools. Lines indicate the N content at time $t$ relative to that at time 0 (i.e., $(N_t - N_0)/N_0$). The lower black bar represents the duration of the midge N pulse. Parameter values are as in Table 1, with predator exploitation $q = 3$, pulse duration $w = 20$, and pulse rate $b = 50$. [Color figure can be viewed at wileyonlinelibrary.com]

gradual and monotonic decay toward their equilibrium pool sizes following the end of the midge pulse. This was accompanied by a modest increase in the abundance of predators, which was stimulated by the increased abundance of herbivores and detritivores. When midges only entered via predators (Fig. 3c), there was an increase in the abundance of herbivores and detritivores during the pulse followed by a steep decline immediately following the pulse to sub-equilibrium levels, followed by a gradual increase to equilibrium. This was accompanied by a steep increase in the size of the predator pool. The responses of herbivores and detritivores were nearly identical as the consumption of herbivores/detritivores by predators was identical on a per capita basis due to the use of the same uptake rates and handling times. When both predators and detritivores received the subsidy (Fig. 3b), the qualitative dynamics were generally similar to the case when only predators were the recipients. However, both the increase in herbivore/detritivore abundance during the pulse and the decline in abundance following the pulse were more dramatic in the presence of midge subsidies to both detritus and predators; this was especially true for detritivores.

To explore the mechanisms responsible for transient dynamics exhibited by herbivores and detritivores, we examined the proximate bottom-up and top-down effects of midges through time (Eqs. 3–5). Overall, the bottom-up effect of midges was greater for detritivores than for herbivores when midges entered the detrital

pool (Fig. 4a,b), which is expected given that herbivores were further removed from the entry point of the midges into the food web. For the baseline parameter set, the uptake rate of detritus by detritivores was higher than the uptake rate of plants by herbivores (Table 1), which also contributed to the larger bottom-up effect of midges on detritivores. However, even when switching the uptake rates for detritivores and herbivores, the bottom-up effect of the midge pulse was always greater for the

detritivores than for the herbivores (Appendix S2: Fig. S2). Therefore, their relative trophic positions with respect to the pulse entry point caused the difference in the bottom-up effects on these two pools. When predators were the only recipients of the pulse (Fig. 4c), the bottom-up effects were negligible, reflecting the limited contribution of N passing through predators to the detrital and soil N pools.

The per capita top-down effects of the midge pulse on detritivores and herbivores were identical (Fig. 4a–c), due to the predator attack rates and handling times on those pools being set to the same values. When midges only entered via the detrital pool, there was a modest increase in top-down pressure (Fig. 4a), due to the
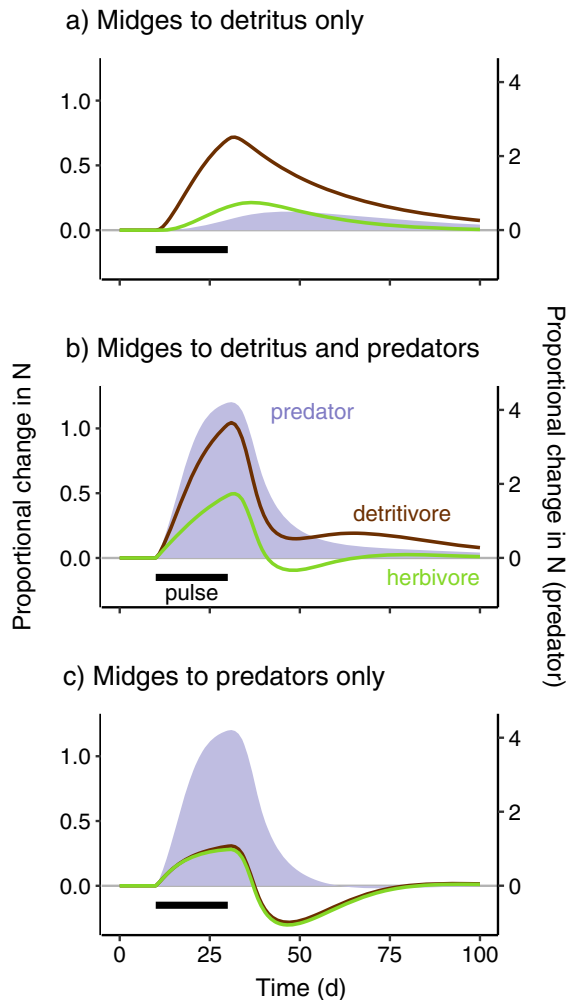


Fig. 3. Time series of proportional changes in N content for detritivore and herbivore pools (indicated by the left $y$-axis). This is shown for when (a) midges only enter the detritus pool, (b) midges enter both detritus and predator pools, and (c) midges only enter the predator pool. The blue-shaded regions represent the proportional change in N for predators, which is indicated by the right $y$-axis. Different $y$-axis scales are used to aid visualization of the transient dynamics of the herbivores and detritivores, which had a weaker response to the pulse than predators for the selected parameter values. The lower black bar represents the duration of the midge N pulse. Parameter values are as in Table 1, with predator exploitation $q = 3$, pulse duration $w = 20$, and pulse rate $b = 20$. [Color figure can be viewed at wileyonlinelibrary.com]
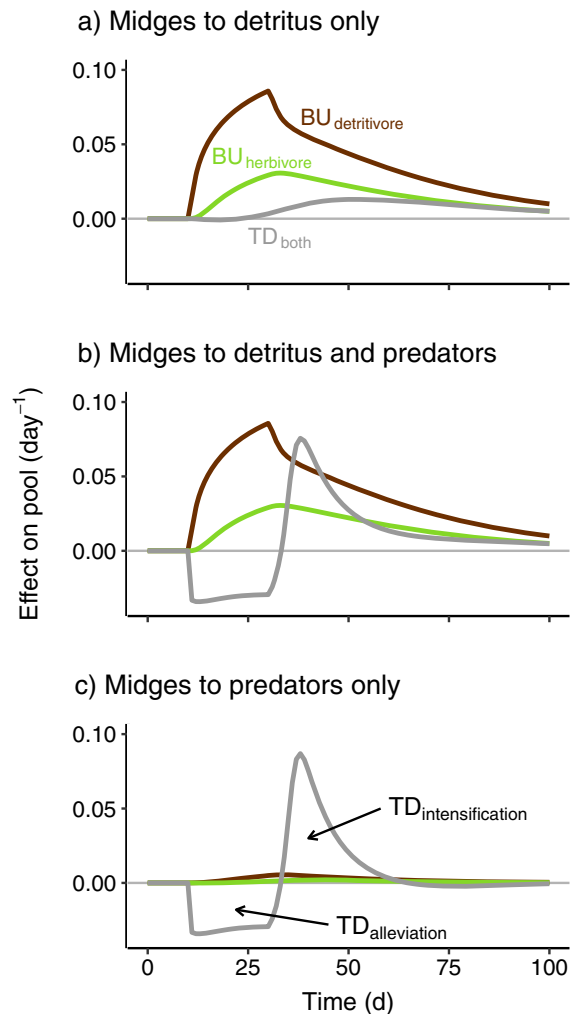


Fig. 4. Time series of the top-down (TD) and bottom-up (BU) effects on detritivore and herbivore pools. This is shown for when (a) midges only enter the detritus pool, (b) midges enter both detritus and predator pools, and (c) midges only enter the predator pool. The gray line indicates the top-down effects on both detritivore and herbivore pools, as they are identical in the model. Parameter values are as in Table 1, with predator exploitation $q = 3$, pulse duration $w = 20$, and pulse rate $b = 20$. [Color figure can be viewed at wileyonlinelibrary.com]

elevated predator abundance sustained by the increased herbivore and detritivore pools. In contrast, when midges entered via the predator pool (regardless of whether they also enter the detrital pool), there was a steep reduction in top-down pressure during the pulse followed by a steep increase after the pulse (Fig. 4b,c). The reduction in top-down pressure during the pulse occurred because predator consumption of all prey types saturated according to the multispecies functional response. This is an example of "apparent mutualism" between the midge pool and the herbivore/detritivore pools (Abrams and Matsuda 1996). Following the end of the midge pulse, the elevated predator pool size and the rapid depletion of the midge pool cause a steep increase in top-down pressure (Fig. 4b,c). This is an example of "apparent competition" between the midge pool and the herbivore/detritivore pools (Holt 1977). Therefore, when predators are able to exploit the midge pool, there is a serial pattern of alleviation (i.e., apparent mutualism) followed by intensification (i.e., apparent competition) of top-down pressure (Fig. 4c).

In addition to apparent mutualism and competition between midges and herbivores/detritivores, there is also potential for apparent mutualism and competition between herbivores and detritivores themselves that could change in response to the midge pulse. To explore this, we performed numerical experiments with midge pulses to both detritus and predators and then removed either herbivores or detritivores from the model (recalculating the equilibrium pool sizes for each case). This analysis shows that apparent mutualism between herbivores and detritivores predominates (Appendix S2: Figs. S6–S7).

### Cumulative responses of detritivores and herbivores

We show $BU_{V,\text{total}}$, $TD_{\text{alleviation}}$, $TD_{\text{intensification}}$, and $TD_{\text{net}}$ for the detritivores across a range of total midge inputs for different predator exploitations and handling times on midges (Fig. 5). The cases with subsidies going to either detritivores or predators (but not both) are shown in Appendix S2: Fig. S8a,c, and the qualitatively similar results for herbivores are shown in Appendix S2: Fig. S8b. Here, we focused on predator exploitation and handling time because they mediate the ability of predators to prey on the midge pulse, which in turn mediates their effects on detritivores. Furthermore, changes to predator exploitation represent a continuous analogue to inclusion or removal of the midge subsidy to predators, as we do for the "numerical experiments" in Figs. 3 and 4.

In general, $TD_{\text{intensification}}$ increased with total midge input until plateauing at high values (Fig. 5a,c,d). The exception was when predator exploitation was high and handling time was low (Fig. 5b), where $TD_{\text{intensification}}$ reached a peak at low midge inputs before declining towards relatively stable values (although with a slight increase at high midge inputs). The saturation of $TD_{\text{intensification}}$ at high midge inputs, whether approached monotonically or following a peak, is the result of the saturation of the multispecies functional response that limits the ability of the predator to exploit high midge inputs. The level of this saturation is determined by both the midge handling time and predator exploitation, with low predator exploitation and handling times yielding the largest $TD_{\text{intensification}}$ (Fig. 5a). It may seem counterintuitive that low predator exploitation yielded greater intensification of top-down effects at high midge inputs; however, this is because predator exploitation scales the "effective" size of the midge pool available to predators, which in turn contributes to the saturation of per capita predator consumption. This is made clear by the presence of the predator exploitation parameter $q$ in the denominator of the multispecies functional response.

When midge handling time was low (Fig. 5a,b), total alleviation of top-down effects ($TD_{\text{alleviation}}$) was low and varied non-monotonically with total midge input, with the exact pattern depending on predator exploitation. When handling time was high (Fig. 5c,d), $TD_{\text{alleviation}}$ was much higher and increased monotonically with total midge input. Across the range of total midge inputs and handling times, $TD_{\text{alleviation}}$ was slightly higher when predator exploitation was high than when it was low. The saturation of $TD_{\text{alleviation}}$ at high midge inputs occurred for the same reason as for $TD_{\text{intensification}}$: alleviation of top-down pressure was a direct result of the saturation of the multispecies functional response, and so could only increase over the range of midge inputs where the predator consumption was not completely saturated.

The net midge effect on top-down pressure ($TD_{\text{net}}$) was determined by the balance between $TD_{\text{intensification}}$ and $TD_{\text{alleviation}}$ (Eq. 9). Over the range of parameters examined here, the magnitudes of $TD_{\text{intensification}}$ and $TD_{\text{alleviation}}$ at high midge inputs were negatively associated across scenarios. Specifically, low handling time and predator exploitation yielded the greatest $TD_{\text{intensification}}$ and lowest $TD_{\text{alleviation}}$ (Fig. 5a), while the reverse was true for high handling time and predator exploitation (Fig. 5d). Consequently, the values of $TD_{\text{net}}$ varied more widely than either $TD_{\text{intensification}}$ and $TD_{\text{alleviation}}$, with $TD_{\text{net}}$ ranging from strongly positive (i.e., stronger top-down pressure in the presence of midges) to weakly negative (i.e., weaker top-down pressure in the presence of midges). The negative association between $TD_{\text{intensification}}$ and $TD_{\text{alleviation}}$ is a direct consequence of the saturation of the multispecies functional response, in which the basic mechanism for $TD_{\text{alleviation}}$ imposes a constraint on $TD_{\text{intensification}}$.

The total effect of midges on bottom-up pressure ($BU_{V,\text{total}}$) increased monotonically with the total midge input and did not vary substantially across exploitation or handling time; this is expected, since the bottom-up effect of midges was chiefly dictated by processes occurring at the lower trophic levels. The net effect of the midge pulse on both top-down and bottom-up pressure
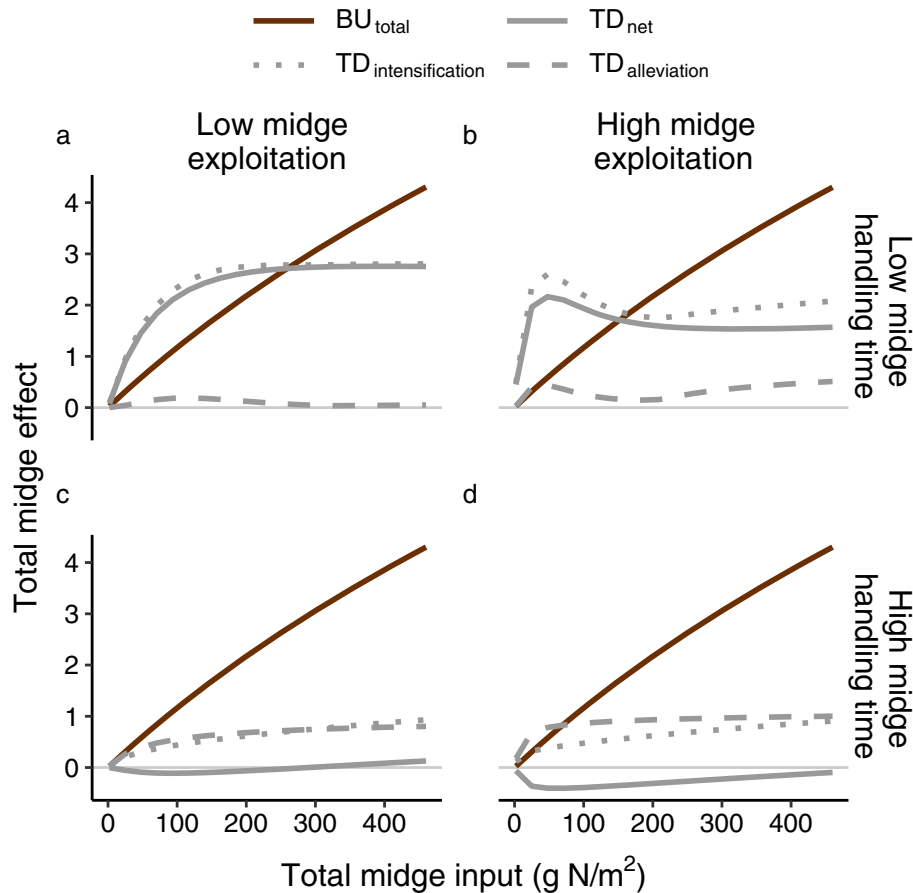
FIG. 5. Cumulative midge effect on total bottom-up control ($BU_{total}$), net top-down control ($TD_{net}$), top-down intensification, and top-down alleviation as a function of total midge inputs. The panels show different combinations of high and low predator exploitation and handling times on midges. Data are from detritivores; herbivores gave broadly similar responses to the cumulative midge effects (Appendix S2: Fig. S8b). Parameter values are as in Table 1, with low exploitation $q = 0.8$, high exploitation $q = 8$, low midge handling time $h_M = 1.3$, high midge handling time $h_M = 5.3$, pulse duration $w = 20$, and pulse rate $b$ ranging from 0.1 to 23 to produce different total midge inputs. [Color figure can be viewed at wileyonlinelibrary.com]

is determined by the balance between $BU_{V,total}$ and $TD_{net}$, with points of intersection (i.e., $BU_{V,total} = TD_{net}$) indicating no net effect of midges, excluding those arising from changes in density-dependent mortality. Because $BU_{V,total}$ was relatively stable across different scenarios, variation in the net midge effect was primarily determined by changes in $TD_{net}$. For low handling times (Fig. 5a,b), $TD_{net}$ exceeded $BU_{V,total}$ at low total midge inputs. However, the more rapid saturation of $TD_{net}$ with increasing total midge input relative to $BU_{V,total}$ caused them to intersect at intermediate midge inputs, above which $BU_{V,total}$ exceeded $TD_{net}$. This intersection point was affected by predator exploitation, with lower exploitation resulting in $BU_{V,total}$ exceeding $TD_{net}$ at relatively higher total midge inputs. Under high handling times (Fig. 5c,d), detritivore (and herbivore) growth was enhanced by indirect effects of the midge subsidies through both enhanced bottom-up and generally weakened top-down forces.

## DISCUSSION

We developed and analyzed a mathematical model of a soil–plant–arthropod food web to examine how allochthonous resource pulses affect transient top-down and bottom-up dynamics when entering multiple trophic levels. We found that all trophic levels increased in biomass during an allochthonous pulse, but the magnitude and timing of the peaks depended on the trophic position. Inorganic soil N, detritus, and plants were mainly affected by bottom-up processes, whereas intermediate trophic levels (detritivores and herbivores) were affected by a combination of top-down and bottom-up forces. We also found that midge subsidies could either alleviate or intensify top-down effects on intermediate trophic levels; the former resulting from saturation of the predators' ability to exploit the allochthonous resource while the latter resulting from elevated abundance of predators. The net cumulative top-down effect on herbivores and detritivores was determined by the tendency of the

multispecies functional response to saturate, with greater saturation leading to increased dominance of bottom-up effects. Our findings show how resource pulses to multiple trophic levels can influence transient food web dynamics, with bottom-up dominating top-down effects under most circumstances.

Our results illustrate that bottom-up and top-down responses to the midge pulses can alter detritivore and herbivore dynamics, with the relative balance of top-down and bottom-up effect being determined by proximity to the pulse entry point, pulse size, and ability of predatory arthropods to exploit it. Due to direct access to allochthonous N in the form of detritus, detritivores receive an immediate boost from subsidy inputs, buffering them against top-down effects from predators. In contrast, allochthonous inputs must go through the detritus, soil, and plant pools before herbivores are subsidized, leading to increased sensitivity to top-down pressures. However, our model shows that when pulse inputs are sufficiently high, the bottom-up pathways for detritivores and herbivores are enough to overcome top-down effects of predators, leading to a dominance of bottom-up forces.

We also show that predators' abilities to exploit pulsed resource subsidies can lead to both intensification and alleviation of top-down pressure on intermediate consumers, akin to apparent competition (Holt 1977) and apparent mutualism (Abrams and Matsuda 1996). When predators can exploit midges at a high rate, we found that both top-down intensification and alleviation were possible on intermediate tropic levels, with alleviation occurring during the pulse and intensification occurring after the end of the pulse. Such a shift from apparent mutualism to apparent competition was shown theoretically by Takimoto et al. (2002). Though their model only investigated top-down effects, they demonstrated a seasonal switch from predators utilizing prey subsidies early in the season to local prey late in the season, leading to stronger top-down effects on local prey when subsidies were absent. Several examples from natural systems have also observed this seasonal shift in top-down pressure on local prey following a resource pulse (Nakano et al. 1999, Sabo and Power 2002, Piovia-Scott et al. 2019). For example, Henschel et al. (2001) found that aquatic insect subsidies lead to short-term depression of top-down pressure from spiders on terrestrial leafhoppers due to diet shifts, followed by enhanced top-down pressure resulting from increased predator abundance. These top-down effects are likely enhanced by aggregative responses of large mobile generalist predators, which are commonly observed in studies of pulsed dynamics (Schmidt and Ostfeld 2008, Yang et al. 2010, Dreyer et al. 2016). It is important to note that previous theoretical studies have often included explicit prey switching or preference for allochthonous vs. autochthonous resources, which is absent from our model. However, the saturating functional response has a similar effect to these more explicit mechanisms in that per capita predation pressure on some focal population (e.g., herbivores) is reduced in the presence of alternative resources.

We used parameter values that were informed by the Mývatn system and selected to have reasonable equilibrium pool sizes in the absence of the midge subsidy. Under these conditions, bottom-up effects always dominated for the lower trophic levels (inorganic soil N, detritus, and plants) and often predominated for intermediate trophic levels (detritivores and herbivores), especially when the magnitude of the subsidy was large. Our model results are consistent with empirical assessments of the dynamics observed at Mývatn. For example, high-midge areas adjacent to Mývatn are generally productive grasslands with higher densities of arthropods compared to nearby heathlands with fewer midge subsidies (Dreyer et al. 2012, Hoekman et al. 2019). Moreover, adding midge carcasses to heathlands near Mývatn increased grass cover, plant biomass, detritivore and herbivore densities, and abundances of several predator groups (e.g., predaceous beetles and parasitoids) (Hoekman et al. 2011, Gratton et al. 2017). These results are also consistent with how pulsed resources influence food webs in other nutrient-poor ecosystems, which are generally controlled by bottom-up forces (Sanchez-Pinero and Polis 2000, Schwinning and Sala 2004, Stoessel et al. 2019).

### Conclusions

Our findings indicate that when an allochthonous resource pulse enters a recipient food web through multiple compartments as both live prey and carcasses, bottom-up effects prevail in most circumstances, particularly when the pulse magnitude is high. Although our model results hold across a range of parameter combinations, our food web is a simple caricature of natural systems. Food webs in nature have multiple predators, each with a distinct preference for herbivores, detritivores, or allochthonous prey. Thus, future work should evaluate transient bottom-up and top-down effects of pulsed resources for multiple predators with different prey preferences. Furthermore, as soil microbial activity likely influences cycling of N via resource subsidies (Yang 2004), incorporating soil microbes into future models would clarify their role in mediating these dynamics.

While research on bottom-up vs. top-down control in ecology has a long history of manipulating both basal resources and consumers simultaneously (Hillebrand 2002, Gruner et al. 2008), no empirical study has simultaneously manipulated allochthonous pulses entering the food web via multiple pathways (Allen and Wesner 2016). Empirical research could test our model results by manipulating a single resource pulse that enters the food web at multiple trophic levels and then monitoring the food web responses through time, especially at periods during the resource pulse and immediately after. Future research should also evaluate how pulse

magnitude might influence the net bottom-up vs. top-down effects on recipient food webs, as our model suggests that the magnitude of the pulse can amplify top-down control under certain conditions. Such empirical work will further improve our mechanistic understanding of the interrelationship between bottom-up and top-down dynamics across time and space (Leroux and Loreau 2015).

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