Omnivory does not preclude strong trophic cascades

Ashkaan K. Fahimipour[1,*], David A. Levin[2], and Kurt E. Anderson[3]

Abstract. Omnivory has been cited as an explanation for why trophic cascades are weak in many food webs, but empirical support for this prediction has been equivocal — compared to carnivores, documented indirect effects of top omnivore populations on primary producer biomass have ranged from beneficial, to non-existent, and negative. To gain intuition about the effects of omnivory on the strength of cascades, we analyzed models of fixed and flexible top omnivores, two foraging strategies that are supported by empirical observations. We identified regions of parameter space in which omnivores following a fixed foraging strategy non-intuitively generate larger cascades than predators that do not consume producers at all, but that are otherwise demographically identical: (*i*) high productivity relative to consumer mortality rates, and (*ii*) smaller discrepancies in producer versus consumer reward create conditions in which cascades are stronger with moderate omnivory. In contrast, flexible omnivores that attempt to optimize *per capita* growth rates during search never induce cascades that are stronger than the case of carnivores. Although we focus on simple models, the consistency of these general patterns together with prior empirical evidence suggests that omnivores should not be ruled out as agents of strong trophic cascades.

Introduction

Trophic cascades occur when predators indirectly effect change in biomass at lower trophic levels by directly reducing populations of intermediate consumers (Paine, 1980; Strong, 1992; Terborgh & Estes, 2013). A growing number of factors that control the strength of trophic cascades continue to surface from model-based and experimental studies, and their identification has improved our understanding of processes that dampen or enhance indirect effects in ecological networks, and ecosystem responses to disturbances (Pace et al., 1999; Shurin et al., 2002; Borer et al., 2005; Shurin et al., 2010; Heath et al., 2014; Piovia-Scott et al., 2017; Estes et al., 2011). Theories for trophic cascades have traditionally focused on the effects of top predators that do not interact directly with primary producers (Oksanen et al., 1981; Schmitz et al., 2000; Heath et al., 2014; Fahimipour et al., 2017). In many food webs however, omnivores that feed on both consumers and primary producers occupy top trophic levels (Arim & Marquet, 2004; Thompson et al., 2007). Intuitively, omnivory of this type has been predicted to disrupt cascades in most cases (Polis & Strong, 1996; Pace et al., 1999; Duffy et al., 2007; Kratina et al., 2012; Wootton, 2017).

[1] Biology & the Built Environment Center, University of Oregon, Eugene, OR, USA
[2] Dept. of Mathematics, University of Oregon, Eugene, OR, USA
[3] Dept. of Evolution, Ecology, & Organismal Biology, University of California, Riverside, CA, USA
E-mail addresses: *ashkaanf@uoregon.edu.

Documented instances of weak, dampened, and even reversed trophic cascades in food webs with omnivory (Flecker, 1996; Pringle & Hamazaki, 1998; Snyder & Wise, 2001; Finke & Denno, 2005; Bruno & O'Connor, 2005; Denno & Finke, 2006; Johnson et al., 2014; Visakorpi et al., 2015; Fahimipour & Anderson, 2015), compared to those typically induced by carnivores (Shurin et al., 2002), provide some support to the hypothesis that omnivory precludes strong trophic cascades. Still, empirical evidence to the contrary — strong trophic cascades that are generated by omnivores (Power et al., 1992; Borer et al., 2005; Okun et al., 2008; France, 2012) — implies that weak cascades may not be a necessary outcome of omnivory, and that the strength of cascades generated by omnivores may depend on other factors (Wootton, 2017). Despite this growing body of empirical work, the population- and community-level features that predict when omnivores occupying top trophic positions will generate strong or weak cascades remain unclear.

Here we analyze mathematical models describing trophic interactions between basal producers, intermediate consumers, and top omnivores to systematically evaluate the effects of omnivory on the strength of trophic cascades. We consider two types of empirically-observed foraging behaviors, namely *fixed* (Diehl & Feißel, 2000) and *flexible* (Fahimipour & Anderson, 2015) omnivory, and present a comparison between trophic cascades in these systems and traditional ones induced by analogous carnivores. We have chosen to study minimally detailed models to focus on coarse-grained system features that may point to potential future directions for experimental work as opposed to making predictions about the behavior of a particular ecosystem (Anderson et al., 2009). We draw two primary conclusions based on numerical and analytical methods: stronger trophic cascades with omnivory are possible in high productivity systems if omnivores forage according to a fixed strategy, whereas cascades are never stronger when omnivores forage flexibly.

Model Formulations

Models were analyzed with a focus on equilibrium outcomes to gain insight into how differences in predator foraging strategies (i.e., carnivory versus fixed or adaptive omnivory) influence long-term community structure as measured by the trophic cascade. We first considered differences in trophic cascades between carnivores in food chains and fixed omnivores that lack flexibility in their foraging strategies. We modeled the population dynamics of three species: (*i*) basal producers, that are eaten by (*ii*) intermediate consumers and (*iii*) top omnivorous predators (*omnivores* hereinafter) that in turn consume both producers and consumers (Diehl & Feißel, 2000). Analyses of similar three-node trophic modules have demonstrated how the coexistence of all species and community stability are sensitive to variation in system primary productivity and the strength of omnivory (parameters ρ and ω in eqs. 1 and 3 below; discussed extensively by McCann & Hastings, 1997; Diehl & Feißel, 2000, 2001; Gellner & McCann, 2011). For this reason, a primary goal of our analysis was

to elucidate how primary productivity and omnivory strength interact to influence trophic cascades in three species modules with and without true omnivory.

Two omnivore foraging strategies with empirical support were considered. We refer to the first as a *fixed* foraging strategy, indicating that foraging effort toward producers and consumers comprise a constant proportion of the omnivores' total foraging effort (McCann & Hastings, 1997; Diehl & Feißel, 2000). The second strategy, which we refer to as *flexible* foraging, indicates that the effort apportioned toward either producers or consumers can be represented as dynamical variables that depend on the relationships between resource availability, reward, and omnivore fitness (Kondoh, 2003).

Fixed foragers

We assume a linear (type I; Holling, 1959) functional response relating resource densities to *per capita* consumption rates, so that the dynamics of species' biomasses are represented by the system of equations

$$\frac{dr}{dt} = \rho r(1 - \frac{r}{k}) - \alpha rn - \omega\beta rp \tag{1a}$$

$$\frac{dn}{dt} = e_{r,n}\alpha rn - \mu_n n - \tilde{\omega}\beta np \tag{1b}$$

$$\frac{dp}{dt} = e_{r,p}\omega\beta rp + e_{n,p}\tilde{\omega}\beta np - \mu_p p, \tag{1c}$$

where r, n, and p are the biomasses of producers, prey, and omnivores.

Here, ρ and k are the producer productivity rate and carrying capacity, α is the consumer foraging rate, μ_i is the *per capita* mortality rate of species i, and $e_{i,j}$ is the resource i assimilation efficiency for consumer j. We assumed a total foraging rate β for omnivores, that is apportioned toward consumers proportionately to $\tilde{\omega}$, where $\tilde{\omega} = 1 - \omega$. We therefore interpret ω as a nondimensional parameter describing omnivory strength (McCann & Hastings, 1997); the system reduces to a food chain when $\omega = 0$. See Table 1 for a summary of all model parameters.

Parameter	Description	Units	Range or Value
ρ	producer productivity rate	time^{-1}	$\rho > 0$
k	producer carrying capacity	producer $\cdot$ area^{-1}	$k > 0$
α	consumer foraging rate	area $\cdot$ consumer^{-1} $\cdot$ time^{-1}	$\alpha > 0$
β	omnivore foraging rate	area $\cdot$ omnivore^{-1} $\cdot$ time^{-1}	$\beta > 0$
ω	fraction of omnivore foraging effort toward producers	dimensionless	$0 < \omega < 1$
$\tilde{\omega}$	fraction of omnivore foraging effort toward consumers	dimensionless	$1 - \omega$
$e_{i,j}$	conversion efficiency of resource i to consumer j	units of j $\cdot$ units of i^{-1}	$0 < e_{ij} < 1$
μ_i	mortality rate of species i	time^{-1}	$\mu_i > 0$
v	time scale of behavioral change	dimensionless	$v > 0$

TABLE 1. Parameter descriptions for the system of equations (1).

Flexible foragers

Equations (1) can be modified to include flexible foraging behavior by the omnivore, by substituting the omnivory strength parameter ω with the dynamical state variable Ω. Flexible foraging behavior was modeled using a replicator-like equation (Kondoh, 2003), which provides a reasonable representation of flexible omnivory in real food webs (Fahimipour & Anderson, 2015). The behavioral equation is

$$\frac{d\Omega}{dt} = v\Omega\left[\frac{\partial\gamma}{\partial\Omega} - \left(\Omega\frac{\partial\gamma}{\partial\Omega} + \tilde{\Omega}\frac{\partial\gamma}{\partial\tilde{\Omega}}\right)\right] \tag{2a}$$

where $\tilde{\Omega} = 1 - \Omega$, $\gamma = e_{r,p}\Omega\beta r + e_{n,p}\tilde{\Omega}\beta n$ is the flexible omnivore's instantaneous *per capita* biomass production rate, and the constant v is a nondimensional ratio between the time scales of foraging adaptation and omnivore population dynamics (Heckmann et al., 2012). Values of $v > 1$ represent behavioral changes that occur on faster time scales than omnivore generations. This behavioral model implies that omnivores gradually adjust their foraging strategy during search if behavioral changes yield a higher instantaneous *per capita* biomass production rate than the current diet.

Model nondimensionalizations and assumptions

The parameters in equations (1) and (2) were transformed into nondimensional parameters using scaled quantities, reducing the total number of model parameters to those with values having clear interpretations (Murray, 1993; Nisbet & Gurney, 2003). We use substitutions similar to Amarasekare (2007): $\hat{r} = r/k$, $\hat{n} = n/e_{r,n}k$, $\hat{p} = p/e_{r,p}k$, $\hat{\rho} = \rho/\mu_n$, $\hat{\alpha} = \alpha e_{r,n}k/\mu_n$, $\hat{\beta} = \beta e_{r,p}k/\mu_n$, $\hat{f} = e_{r,n}e_{n,p}/e_{r,p}$, $\hat{\delta} = \mu_p/\mu_n$, and $\tau = \mu_n t$. After substituting into eqs. (1) and (2), the hats were dropped for convenience giving the nondimensional system

$$\frac{dr}{d\tau} = F^{(1)}(r,n,p,\omega) = \rho r(1-r) - \alpha rn - \omega\beta rp \tag{3a}$$

$$\frac{dn}{d\tau} = F^{(2)}(r,n,p,\omega) = \alpha rn - n - \tilde{\omega}\beta np \tag{3b}$$

$$\frac{dp}{d\tau} = F^{(3)}(r,n,p,\omega) = \omega\beta rp + \tilde{\omega}\beta fnp - \delta p \tag{3c}$$

for fixed foragers, with

$$\frac{d\Omega}{d\tau} = F^{(4)}(r,n,p,\Omega) = v\beta\Omega(r - \Omega r - \tilde{\Omega}fn) \tag{4a}$$

representing flexible foraging behavior. Scaled resource, consumer, and omnivore biomasses are represented as $\boldsymbol{x} = (r,n,p)$. For fixed ω, the vector field which maps (r,n,p) to $(F^{(1)}(r,n,p,\omega), F^{(2)}(r,n,p,\omega), F^{(3)}(r,n,p,\omega))$ is denoted by $F_{O,\omega} : \mathbb{R}^3 \to \mathbb{R}^3$, and the coexistence equilibrium of the fixed foraging model eq. (3) is denoted by $\boldsymbol{x}_O^\star = (r_O^\star, n_O^\star, p_O^\star)$. We assume that the equilibrium is stable, satisfying

$$(r_O^\star, n_O^\star, p_O^\star) > 0 \qquad \text{(positivity, all species coexist)}, \tag{5a}$$

$$F_{O,\omega}(\boldsymbol{x}_O^\star) = 0 \qquad \text{(equilibrium)}, \tag{5b}$$

$$\max_{1\le i\le 3} \mathrm{Re}\lambda_i < 0 \qquad \text{(stability)}, \tag{5c}$$

where $\dot{\boldsymbol{x}} = F_{O,\omega}(\boldsymbol{x})$ describes the system of equations (3), and $\{\lambda_i\}_{i=1}^3$ are the eigenvalues of the Jacobian matrix $DF_{O,\omega}(\boldsymbol{x}_O^\star)$. These assumptions ensure a straightforward comparison of trophic cascades, which in the case of non-equilibrium conditions would depend on the time scales under consideration.

Eq. (3) can be extended to the flexible foraging scenario by replacing the fixed foraging parameter ω with a quantity satisfying (4). The system of equations is now four-dimensional and is defined by the vector field $F_F : \mathbb{R}^4 \to \mathbb{R}^4$ which maps (r, n, p, Ω) to $(F^{(1)}(r, n, p, \Omega), F^{(2)}(r, n, p, \Omega), F^{(3)}(r, n, p, \Omega), F^{(4)}(r, n, p, \Omega))$. We assume that the flexible model likewise has a coexistence equilibrium $\boldsymbol{x}_F^\star = (r_F^\star, n_F^\star, p_F^\star, \Omega_F^\star)$, so that $(\boldsymbol{x}_F^\star, \Omega^\star) > 0$, $F_F(\boldsymbol{x}_F^\star, \Omega^\star) = 0$, and all eigenvalues of $DF_F(\boldsymbol{x}_F^\star, \Omega^\star)$ have negative real parts. Finally, for the case of carnivores in a food chain we denote by $(r_C^\star, n_C^\star, p_C^\star)$ the stable and positive solution satisfying (5) when setting $\omega = 0$.

A comparison of trophic cascades

We quantified differences in trophic cascade strengths between systems with omnivorous (i.e., $\omega > 0$) and non-omnivorous (i.e., $\omega = 0$) top predators, and examined the dependencies of these differences on model parameters. We denote by $(r_\chi^\star, n_\chi^\star, 0)$ the non-positive equilibrium solution to (3) in the absence of predators, so that $F_O(r_\chi^\star, n_\chi^\star, 0) = 0$. A traditional measure of trophic cascade strength (Shurin et al., 2002; Borer et al., 2005) applied to omnivory systems at equilibrium is therefore $\log_2(r_O^\star/r_\chi^\star)$. Likewise, cascade strength in the analogous food chain can be calculated as $\log_2(r_C^\star/r_\chi^\star)$. The difference in trophic cascade strengths induced by a fixed omnivore and the predator in its analogous food chain, κ_O

$$\kappa_O := \log_2 \frac{r_O^\star}{r_\chi^\star} - \log_2 \frac{r_C^\star}{r_\chi^\star} = \log_2 \frac{r_O^\star}{r_C^\star}. \tag{6}$$

This measure κ_O of the relative cascade strength is similar to the "proportional response" measure of Heath et al. (2014), and equals 1 (or -1) if the trophic cascade induced by omnivores is twice as strong (or half the strength) as in the analogous food chain. Likewise, the difference in cascade strengths between flexible omnivory systems and food chains, $\kappa_F := \log_2 r_F^\star/r_C^\star$. Closed form equilibrium solutions for all variables in eqs. (3) and (4) are provided in Supplementary Table 1.

Results

Fixed omnivores can generate strong trophic cascades

In Figure 1 we summarize numerical results demonstrating the relationship between productivity ρ, omnivory strength ω, and the relative cascade strengths induced by fixed omnivores, κ_O. We observed four regions (marked by roman numerals) leading to qualitatively different outcomes: (i) only resources and consumers coexist at stable equilibrium, (ii) only resources and omnivores coexist at stable equilibrium, (iii) all species coexist at stable equilibrium and cascades are weaker with omnivory, and (iv) all species coexist at stable equilibrium and cascades are stronger with omnivory. Predictions of weak trophic cascades with omnivory (Pace et al., 1999; Shurin et al., 2010; Kratina et al., 2012; Wootton, 2017) held when primary productivity, ρ, was below a critical value (Fig. 1, orange region). However, we identified a critical transition in relative trophic cascade strengths depending on productivity, and we refer to this value as ρ_{crit} or the *critical productivity* for convenience (Fig. 1). A vertical black dashed line marks the critical productivity, which is the value of ρ at which $\kappa_O = 0$, given parametrically by $\rho_{\text{crit}} = \delta\alpha^2(f-1)/f[\alpha(\delta-\beta)+\beta f(\alpha-1)]$. When productivities are

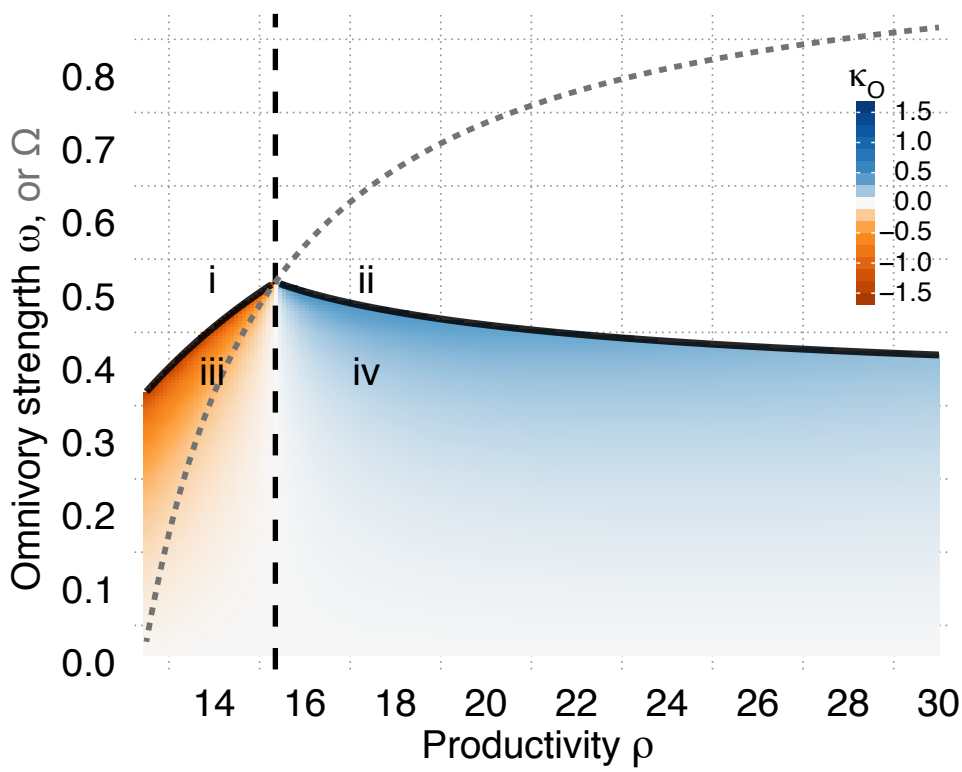

FIGURE 1. Summary of numerical solutions relating relative cascade strength, κ_O, scaled productivity ρ, and omnivory strength ω. Colors represent associated values of κ_O for combinations of ρ and ω, such that cool colors (blue) represent stronger cascades with omnivory, and warm colors (orange) represent weaker cascades with omnivory. Solid black curves mark extinction boundaries for either the omnivore or consumer species. See *Results* for complete description. Parameter values are $\alpha = 7.5$, $\beta = 5.5$, $f = 0.345$, $\delta = 2$, and $v = 1.05$.

above this value, cascades induced by omnivores are non-intuitively stronger compared to carnivores (Fig. 1, blue region). Note that the transition from weaker ($\kappa_O < 0$) to stronger ($\kappa_O > 0$) cascades with productivity does not depend on omnivory strength. Instead, omnivory strengths near the system's extinction boundaries attenuate the discrepency between cascade strengths, such that omnivory cascades are weakest when productivity is low and omnivory strength approaches values leading to omnivore exclusion (Fig. 1, region i), and strongest when productivity is high and omnivores have nearly excluded consumers (Fig. 1, region ii).

To explain the non-intuitive result of stronger cascades with fixed omnivory, we examined the relationship between system primary productivity and the optimal foraging effort that would lead to the highest *per capita* growth rate by omnivores at equilibrium, $\Omega_F^\star$ (Supplementary Table 1). The dotted grey curve in Fig. 1 illustrates $\Omega_F^\star$ as a function of ρ; the growth rate-maximizing strategy monotonically approaches pure herbivory with increasing productivity. Precisely at $\rho > \rho_{\text{crit}}$, the optimal strategy becomes unsustainable for fixed omnivores. Intuitively, this indicates that strong trophic cascades by omnivores emerge only when their foraging effort toward producers is suboptimal.

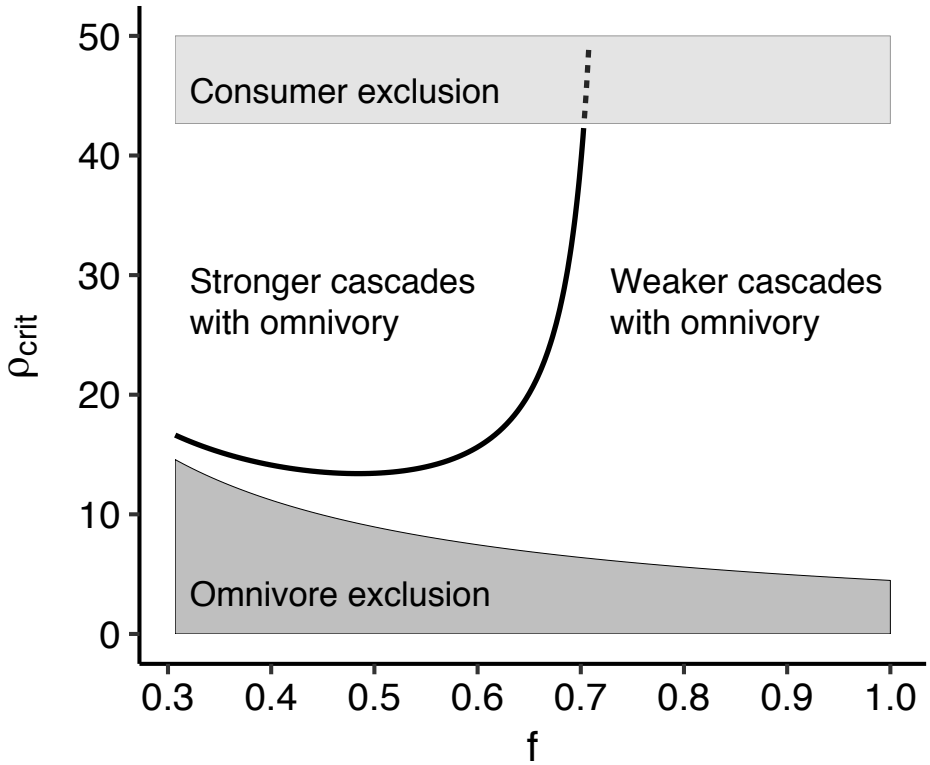

FIGURE 2. The relationship between critical productivity, ρ_{crit} and relative profitability, f (Table 1). The curve is solid if the critical productivity lies in the 3-species coexistence region, and dashed otherwise. The light and dark grey shaded regions mark the extinction of consumers and omnivores respectively. Parameter values are the same as in Fig. 1 with $\omega = 0.4$.

We next sought to determine whether the presence of a critical productivity value is sensitive to other model parameters. In Fig. 2 we show how ρ_{crit} (i.e., the location of the vertical dashed line in Figure 1 along the x-axis) depends on the ratio of resource profitabilities, f. Recall that larger f values represent systems in which consumers are much more profitable to omnivores than producers. For large enough profitability ratios, the curve of ρ_{crit} versus f enters a region in which coexistence between all species cannot be achieved (Fig. 2). Thus, for large enough f we would not expect to see strong cascades with omnivory, regardless of other population- or community-level properties. In Supplementary Fig. 1 we show that other model parameters do not similarly influence the presence of a switch from always-weaker to always-stronger trophic cascades with fixed omnivory.

Flexible omnivores never generate stronger trophic cascades

Unlike fixed omnivores, flexibly foraging omnivores can never induce cascades that are stronger than in the analogous food chain. We show analytically that at a positive equilibrium solution, $\kappa_F < 0$. At the interior equilibrium (Supplementary Table 1), if $\phi := -\alpha\delta + \delta f(\alpha - \rho) + \beta f(\rho - 1)$ then

$$p_F^\star = \frac{\phi}{f\beta^2}\,,$$
$$\Omega_F^\star = \frac{\alpha\delta + f\rho(\delta - \beta)}{-\phi}\,.$$

The ratio of flexible omnivory to linear chain trophic cascade strengths,

$$\kappa_F = \log_2 \frac{r_F^\star}{r_C^\star} = \log_2 \frac{\frac{\delta}{\beta}}{1 - \frac{\alpha\delta}{\beta f \rho}}\,.$$

As $p_F^\star > 0$ and evidently $f\beta^2 > 0$, we must have $\phi > 0$. Moreover, since $0 < \Omega_F^\star < 1$, we must also have $\delta f \rho > \beta f \rho - \alpha\delta$. That is,

$$\alpha\delta + f\rho(\delta - \beta) > 0\,. \tag{7}$$

Combining (7) with the solution $\Omega_F^\star$ (Supplementary Table 1) shows that for positive equilibria, $\kappa_F < 0$, since $\phi < 0$ cannot be true for a biological system. Thus, consistent with conceptual models of trophic cascades (Strong, 1992; Pace et al., 1999), cascades in systems with flexibly foraging top omnivores will be bounded in strength by those in their analogous food chains. Numerical results confirm these analytical expectations, and illustrate how increasing consumer reward (i.e., increasing f) attenuates this result but does not alter the qualitative relationship between κ_F and ρ (Fig. 3).

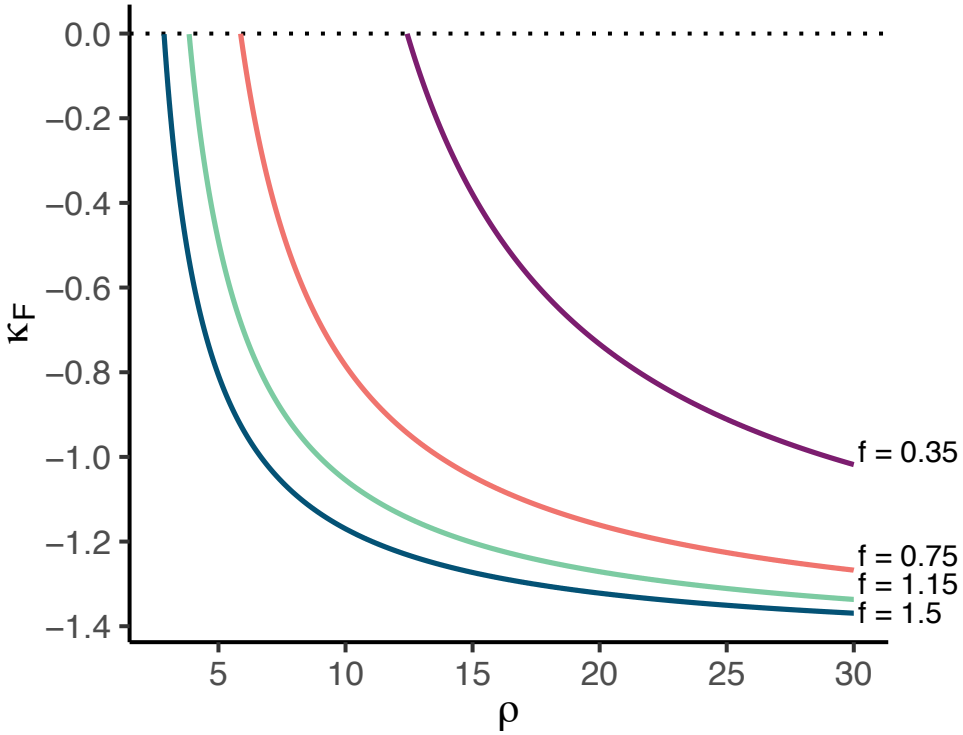

FIGURE 3. Numerical solutions relating relative cascade strength, κ_F, scaled productivity ρ, and scaled resource profitability f in the flexible model. Colors represent associated values of f in the margin. Parameter values are $\alpha = 7.5$, $\beta = 5.5$, $\delta = 2$, and $v = 1.05$.

Discussion

Intuition suggests that trophic cascade will not occur when top predators additionally feed on primary producers (Polis & Strong, 1996; Pace et al., 1999; Duffy et al., 2007; Shurin et al., 2010; Kratina et al., 2012; Wootton, 2017), but our results predict that strong cascades will emerge under a wider range of foraging types than previously appreciated. We identified many cases in which omnivores are indeed likely to generate weak cascades, although we have shown that this should not be a uniform expectation for omnivory in food webs. Particularly, in high productivity systems in which forging reward does not strongly differ between producers and consumers (Fig. 1; Fig. 2), omnivores were capable of generating stronger cascades than would be expected if they did not consume producers at all. This result provides at least one general explanation for the weaker (Finke & Denno, 2005; Denno & Finke, 2006), comparable or indistinguishable (Borer et al., 2005), and stronger (Okun et al., 2008; France, 2012) cascades that have now been observed with omnivorous top predators. It is not surprising that a more comprehensive catalogue of species foraging behaviors is needed to improve predictions of trophic cascades, but our model-based results indicate that this knowledge may be especially important when predators consume resources across trophic levels.

Comparisons of fixed and flexible models showed that omnivores were capable of generating strong cascades only when consuming an energetically suboptimal level of primary producers (Fig. 1). This leads to the question: how common is this type of fixed foraging in food webs? Empirical evidence for fixed foragers exists for groups as diverse as protists, arthropods, and mammals (Clark, 1982; Mooney & Tillberg, 2005; Diehl & Feißel, 2001). Fixed omnivory may also manifest in other ways, for example when organisms forage in a way that is suboptimal in terms of pure energetics but is otherwise required to maintain nutritional or stoichiometric balances (Berthoud & Seeley, 1999; Remonti et al., 2016; Zhang et al., 2018). Suboptimal foraging has also been observed in heavily disturbed or human-altered systems where consumer behaviors are not adapted to current resource conditions, or when changes in habitat structure alter the ability to efficiently locate preferred food sources (Walsh et al., 2006).

Allometric scaling relationships between species' energetic rates and body masses have helped identify biological constraints on the strengths of trophic cascades in food chains with carnivory (DeLong et al., 2015), but body mass may have additional implications for cascades that are generated by species facing complex foraging decisions. The prevalence of dynamical or adaptive foraging behaviors, like those represented by our flexible model, across the tree of life has shown some association with organismal brain sizes and body masses by proxy (Eisenberg & Wilson, 1978; Rooney et al., 2008). Body mass distributions may also influence cascades that are induced by species with size-mediated ontogenetic shifts from herbivory to carnivory (Pace et al., 1999), wherein average population-level foraging behaviors could be characterized as 'omnivory' and would largely reflect intraspecific size structures. Future empirical work and simulation-based analyses of more complex models will be key for uncovering additional relationships between species' body masses and trophic cascades in complex food webs, and to develop a coherent understanding of when foraging behavior drives deviations from predictions of cascades from food chain models. In many of these case, fixed omnivory could appear as an average population-level behavior and not necessarily at the level of the individual.

Figure 1 suggests an interesting analytical question for future study. Namely, multiple qualitative changes are observed precisely at the phase transition for strong omnivory cascades, $\kappa_O > 0$, which is indicated by the vertical dashed line $\rho = \rho_{crit}$. Also occurring at this point are the phase boundaries for species coexistence at stable equilibrium given by the curve separating regions (i) and (ii) from (iii) and (iv); and the dotted curve showing the omnivory strength for the optimal foraging strategy, $\Omega_F^\star$, as a function of ρ passes into a region that is unattainable by the fixed forager. It remains to understand why these three curves all intersect at a single point.

Examples from agroecosystems and disturbed natural habitats indicate that cascade theories can directly inform applied management problems and efforts to curb human alteration of ecosystems (Schmitz, 2006; Estes et al., 2011). Our comparative analyses together

with the ubiquity of omnivory in nature (Arim & Marquet, 2004; Kratina et al., 2012; Wootton, 2017) suggest that omnivores may contain promise for such applications of cascade theory. For instance, nutrient inputs to agricultural systems that lead to artificially enriched communities are exactly the conditions where we expect a potential for strong omnivorous cascades. If management goals include reducing the density of agricultural pests in enriched systems through integrated management strategies that manipulate top trophic levels, then, counterintuitively, top omnivores with certain features may warrant additional consideration (Agrawal et al., 1999). Achieving these outcomes in practice may prove challenging (Cortez & Abrams, 2016).

Conclusions

Omnivory has long been cited as a reason for why trophic cascades are less frequent or weaker than expected, although empirical data on the role of omnivory has been equivocal (Borer et al., 2005; Shurin et al., 2010; Kratina et al., 2012; Wootton, 2017). Our theory generally agrees with the prediction of omnivory in weakening cascades, but also demonstrates where these predictions are weak or even where they exhibit unexpected directions of change. Thus, these predictions generate a framework for future investigation that can focus expectations on when and where omnivory effects might occur in more complex ecosystems. At the least, our models help elucidate the limited support for an intuitive ecological hypothesis.

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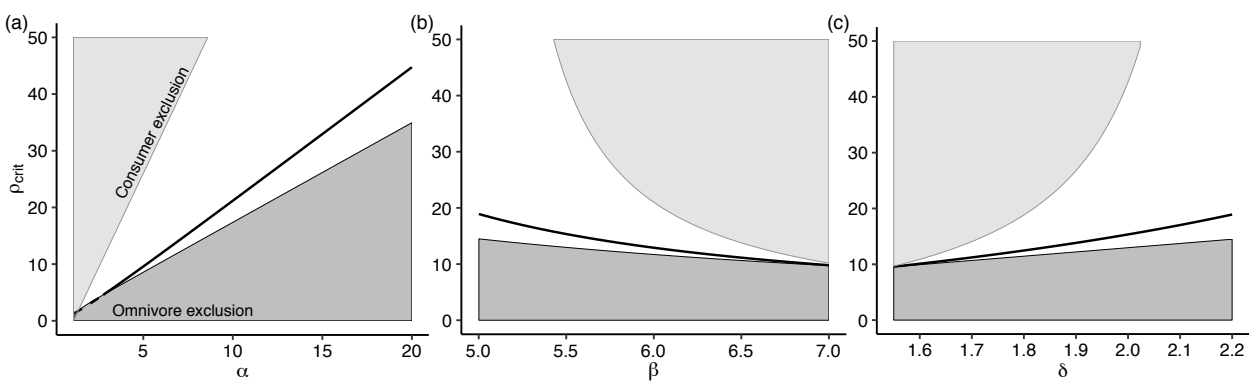
Supplementary Materials

Model	Variable	Solution
Food chain		
	$r_C^\star$	$1-\frac{\alpha\delta}{\beta f\rho}$
	$n_C^\star$	$\frac{\delta}{\beta f}$
	$p_C^\star$	$\frac{\beta f\rho(\alpha-1)-\delta\alpha^2}{f\rho\beta^2}$
Fixed omnivory		
	$r_O^\star$	$\frac{\beta f(-\rho\tilde{\omega}-\omega)+\alpha\delta}{\beta f(-\rho\tilde{\omega}-\alpha\omega)+\alpha\beta\omega}$
	$n_O^\star$	$\frac{\delta(\alpha\omega-\rho\omega+\rho)+\beta\omega(\rho(\omega-1)-\omega)}{\beta\tilde{\omega}(f\rho\tilde{\omega}+\alpha(f-1)\omega)}$
	$p_O^\star$	$-\frac{-\beta f\rho\tilde{\omega}-\delta\alpha^2+\alpha\beta[f(\rho-\rho\omega)+\omega]}{\tilde{\omega}\beta^2(\alpha\omega-f\rho\tilde{\omega}-\alpha f\omega)}$
Flexible omnivory		
	$r_F^\star$	$\frac{\delta}{\beta}$
	$n_F^\star$	$\frac{\delta}{\beta f}$
	$p_F^\star$	$\frac{-\alpha\delta+\delta f(\alpha-\rho)+\beta f(\rho-1)}{\beta^2 f}$
	$\Omega_F^\star$	$\frac{\alpha\delta+f\rho(\delta-\beta)}{\alpha\delta+f[\delta(\rho-\alpha)-\beta\rho+\beta]}$

Supplementary Table 1. Closed-form equilibrium solutions for all systems of equations. Variables and parameters in the *Variable* and *Solution* columns refer to the nondimensional scaled quantities in eqs. (3) and (4).



Supplementary Figure 1. The critical productivity point, ρ_{crit} as a function of (a) scaled consumer search rate, α, (b) scaled omnivore search rate, β, and (c) scaled omnivore mortality rate δ (Table 1). The curve is solid if the critical productivity lies in the 3-species coexistence region, and dashed otherwise. The light and dark grey shaded regions mark the extinction of consumers and omnivores respectively. The parameter values are the same as in Fig. 1 with $\omega = 0.4$.