

Omnivory does not preclude strong trophic cascades

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ABSTRACT. Omnivory has been cited as an explanation for why trophic cascades are weak in many ecosystems, but empirical support for this prediction is equivocal. Compared to predators that feed only on herbivores, top omnivores — species that feed on both herbivores and primary producers — have been observed generating cascades ranging from strong, to moderate, null, and negative. To gain intuition about the sensitivity of cascades to omnivory, we analyzed models describing systems with top omnivores that display either fixed or flexible diets, two foraging strategies that are supported by empirical observations. We identified regions of parameter space wherein omnivores following a fixed foraging strategy, with herbivores and producers comprising a constant proportion of the diet, non-intuitively generate stronger cascades than predators that are otherwise demographically identical: *(i)* high productivity relative to herbivore mortality, and *(ii)* small discrepancies in producer versus herbivore 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 predators. Although we focus on simple models, the consistency of these general patterns together with prior empirical evidence suggests that omnivores should not be uniformly ruled out as agents of strong trophic cascades.

1 Introduction

2 Trophic cascades occur when top predators indirectly effect change in primary producer
3 biomass by directly reducing populations of intermediate herbivores (Paine, 1980; Strong,
4 1992; Terborgh & Estes, 2013). A growing number of factors that control the strength of
5 trophic cascades continue to surface from model-based and experimental studies, and their
6 identification has improved our understanding of processes that dampen or enhance indirect
7 effects between species in ecological networks, and ecosystem responses to disturbance (Pace

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8 et al., 1999; Shurin et al., 2002; Borer et al., 2005; Shurin et al., 2010; Estes et al., 2011;
9 Heath et al., 2014; Piovia-Scott et al., 2017; Fahimipour et al., 2017). Theories for cascades
10 have traditionally focused on top-down effects in tritrophic food chain models comprising
11 predators that do not directly interact with primary producers (Oksanen et al., 1981; Schmitz
12 et al., 2000; Heath et al., 2014). In many communities however, omnivores that additionally
13 feed on producers occupy top trophic levels (Arim & Marquet, 2004; Thompson et al., 2007).
14 This potential for direct consumption of both producer and herbivore species has led to the
15 prediction, that omnivory should override indirect beneficial effects on producer biomass,
16 thereby dampening or disrupting cascades in most cases (Polis & Strong, 1996; Pace et al.,
17 1999; Bruno & O'Connor, 2005; Duffy et al., 2007; Kratina et al., 2012; Wootton, 2017).

18 Documented instances of weakened and even reversed trophic cascades in food webs
19 with omnivory (Flecker, 1996; Pringle & Hamazaki, 1998; Snyder & Wise, 2001; Finke &
20 Denno, 2005; Bruno & O'Connor, 2005; Denno & Finke, 2006; Johnson et al., 2014; Visakorpi
21 et al., 2015; Fahimipour & Anderson, 2015), compared to those typically induced by predators
22 (Shurin et al., 2002), are not uncommon and provide support to the intuitive hypothesis
23 that omnivory precludes strong trophic cascades. However, a large meta-analysis of 114
24 experimental predator and omnivore manipulations in terrestrial, freshwater, and marine
25 systems could not identify differences in the magnitudes of trophic cascades between the
26 two groups (Borer et al., 2005). Empirical evidence to the contrary — namely, examples
27 of stronger or comparable cascades that are generated by omnivores (Power, 1990; Power
28 et al., 1992; Okun et al., 2008; France, 2012) — implies that weak cascades may not be
29 a guaranteed outcome of omnivory in food webs. Despite a growing body of theoretical
30 and empirical work, an understanding of when omnivores occupying top trophic positions

31 will generate strong or weak cascading effects is lacking, and likely depends on multiple
32 population- or community-level factors (Wootton, 2017).

33 We analyzed mathematical models describing trophic interactions between basal pro-
34 ducers, intermediate herbivores, and top omnivores to systematically evaluate the effects of
35 omnivory on the strength of trophic cascades. We consider two types of empirically-observed
36 foraging behaviors, namely *fixed* (Diehl & Feiel, 2000) and *flexible* (Fahimipour & Anderson,
37 2015) omnivory (see *Model Formulations* for definitions), and present a comparison between
38 trophic cascades in these systems and traditional ones induced by analogous predators. We
39 have chosen to study minimally detailed models to focus on coarse-grained system features
40 that may point to potential future directions for experimental work, as opposed to making
41 predictions about the behavior of a particular ecosystem (Anderson et al., 2009). We draw
42 two primary conclusions based on numerical and analytical results: stronger trophic cas-
43 cades with omnivory are at least possible in high productivity systems if omnivores forage
44 according to a fixed strategy, whereas cascades are never stronger when omnivores forage
45 according to a flexible strategy.

46 **Model Formulations**

47 Models were analyzed with a focus on equilibrium outcomes to gain insight into how differ-
48 ences in the foraging strategies of species occupying top trophic levels (i.e., predators versus
49 fixed or adaptive omnivores) influence long-term community structure as measured by the
50 trophic cascade. We modeled the population dynamics of three species: (i) basal producers,
51 that are eaten by (ii) intermediate herbivores and (iii) top omnivores that consume both
52 producers and herbivores (Diehl & Feiel, 2000). Analyses of similar three-node trophic
53 modules have demonstrated how the coexistence of all species and community stability are

54 sensitive to variation in system primary productivity and the strength of omnivory (param-
55 eters ρ and ω in eqs. 1 and 3 below; discussed extensively by McCann & Hastings, 1997;
56 Diehl & Feiel, 2000, 2001; Gellner & McCann, 2011). For this reason, a primary goal of
57 our analysis was to elucidate how primary productivity and omnivory strength interact to
58 influence trophic cascades in three species modules with and without true omnivory.

59 Two omnivore foraging strategies with empirical support were considered. We refer to
60 the first as a *fixed* foraging strategy, indicating that foraging effort toward either producers
61 or herbivores comprise constant proportions of the *fixed omnivores'* total foraging effort
62 (McCann & Hastings, 1997; Diehl & Feiel, 2000). The second strategy, which we refer to
63 as *flexible* foraging, indicates that the foraging effort apportioned toward either producers
64 or herbivores by the *flexible omnivore* varies in time, and depends on the availability and
65 reward associated with each resource species (Kondoh, 2003).

66 *Fixed foragers*

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

$$(1a) \quad \frac{d\hat{r}}{dt} = \hat{\rho}\hat{r}\left(1 - \frac{\hat{r}}{\hat{k}}\right) - \hat{\alpha}\hat{r}\hat{n} - \omega\hat{\beta}\hat{r}\hat{p}$$

$$(1b) \quad \frac{d\hat{n}}{dt} = \hat{e}_{r,n}\hat{\alpha}\hat{r}\hat{n} - \hat{\mu}_n\hat{n} - \tilde{\omega}\hat{\beta}\hat{n}\hat{p}$$

$$(1c) \quad \frac{d\hat{p}}{dt} = \hat{e}_{r,p}\omega\hat{\beta}\hat{r}\hat{p} + \hat{e}_{n,p}\tilde{\omega}\hat{\beta}\hat{n}\hat{p} - \hat{\mu}_p\hat{p},$$

70 where hats over terms indicate that they have dimensions, and \hat{r} , \hat{n} , and \hat{p} are the biomasses
 71 of producers, herbivores, and omnivores.

72 Here, $\hat{\rho}$ and \hat{k} are the producer productivity rate and carrying capacity, $\hat{\alpha}$ is the her-
 73 bivore foraging rate, $\hat{\mu}_i$ is the *per capita* mortality rate of species i , and $\hat{e}_{i,j}$ is the resource
 74 i assimilation efficiency for consumer j . We assumed a total foraging rate $\hat{\beta}$ for omnivores,
 75 that is apportioned toward herbivores proportionately to $\tilde{\omega}$, where $\tilde{\omega} = 1 - \omega$. We therefore
 76 interpret ω as a nondimensional parameter describing omnivory strength (McCann & Hast-
 77 ings, 1997); the system reduces to a food chain when $\omega = 0$. See Table 1 for a summary of
 78 all model parameters.

79 *Flexible foragers*

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

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

Parameter	Description	Units	Range or Value
$\hat{\rho}$	producer productivity rate	time ⁻¹	$\hat{\rho} > 0$
\hat{k}	producer carrying capacity	producer · area ⁻¹	$\hat{k} > 0$
$\hat{\alpha}$	herbivore foraging rate	area · herbivore ⁻¹ · time ⁻¹	$\hat{\alpha} > 0$
$\hat{\beta}$	omnivore foraging rate	area · omnivore ⁻¹ · time ⁻¹	$\hat{\beta} > 0$
ω	fraction of omnivore foraging effort toward producers	dimensionless	$0 < \omega < 1$
$\tilde{\omega}$	fraction of omnivore foraging effort toward herbivores	dimensionless	$1 - \omega$
$\hat{e}_{i,j}$	conversion efficiency of resource i to consumer j	units of j · units of i ⁻¹	$0 < \hat{e}_{ij} < 1$
$\hat{\mu}_i$	mortality rate of species i	time ⁻¹	$\hat{\mu}_i > 0$
v	time scale of behavioral change	dimensionless	$v > 0$

TABLE 1. Parameter descriptions for equations (1) and (2).

85 where $\tilde{\Omega} = 1 - \Omega$, $\gamma = \hat{e}_{r,p}\Omega\hat{\beta}\hat{r} + \hat{e}_{n,p}\tilde{\Omega}\hat{\beta}\hat{n}$ is the flexible omnivore's instantaneous *per capita*
 86 biomass production rate, and the constant v is a nondimensional ratio between the time
 87 scales of foraging adaptation and omnivore population dynamics (Heckmann et al., 2012).
 88 Values of $v > 1$ represent behavioral changes that occur on faster time scales than omnivore
 89 generations. This behavioral model implies that omnivores gradually adjust their foraging
 90 strategy during search if behavioral changes yield a higher instantaneous *per capita* biomass
 91 production rate than the current diet (Kondoh, 2003).

92 *Model nondimensionalizations and assumptions*

93 The parameters in equations (1) and (2) were transformed into nondimensional parameters
 94 using scaled quantities, reducing the total number of model parameters to those with values
 95 having clear interpretations (Murray, 1993; Nisbet & Gurney, 2003). We use substitutions
 96 similar to Amarasekare (2006) and Amarasekare (2007): $r = \hat{r}/\hat{k}$, $n = \hat{n}/\hat{e}_{r,n}\hat{k}$, $p = \hat{p}/\hat{e}_{r,p}\hat{k}$,
 97 $\rho = \hat{\rho}/\hat{\mu}_n$, $\alpha = \hat{\alpha}\hat{e}_{r,n}\hat{k}/\hat{\mu}_n$, $\beta = \hat{\beta}\hat{e}_{r,p}\hat{k}/\hat{\mu}_n$, $f = \hat{e}_{r,n}\hat{e}_{n,p}/\hat{e}_{r,p}$, $\delta = \hat{\mu}_p/\hat{\mu}_n$, and $\tau = \hat{\mu}_n t$.
 98 Substituting into eqs. (1) and (2), we obtain the nondimensional system

$$(3a) \quad \frac{dr}{d\tau} = \rho r(1 - r) - \alpha r n - \omega \beta r p \equiv F_r(r, n, p)$$

$$(3b) \quad \frac{dn}{d\tau} = \alpha r n - n - \tilde{\omega} \beta n p \equiv F_n(r, n, p)$$

$$(3c) \quad \frac{dp}{d\tau} = \omega \beta r p + \tilde{\omega} \beta f n p - \delta p \equiv F_p(r, n, p)$$

99 for fixed omnivory, with

$$(4) \quad \frac{d\Omega}{d\tau} = v\beta\Omega(r - \Omega r - \tilde{\Omega}fn) \equiv F_\Omega(r, n, p, \Omega)$$

100 representing flexible foraging behavior. For the fixed model, scaled producer, herbivore, and
 101 omnivore biomasses are represented as $\mathbf{x} = [r, n, p]$. The vector field which maps $[r, n, p]$
 102 to $[F_r(r, n, p), F_n(r, n, p), F_p(r, n, p)]$ is denoted by $F_{\text{fixed}} : \mathbb{R}^3 \rightarrow \mathbb{R}^3$, and the coexistence
 103 equilibrium of the fixed foraging model eq. (3) is denoted by $\mathbf{x}_{\text{fixed}}^* = [r_{\text{fixed}}^*, n_{\text{fixed}}^*, p_{\text{fixed}}^*]$. We
 104 considered trophic cascades in systems with stable equilibria, satisfying

$$(5a) \quad [r_{\text{fixed}}^*, n_{\text{fixed}}^*, p_{\text{fixed}}^*] > 0 \quad \text{positivity, all species coexist,}$$

$$(5b) \quad F_{\text{fixed}}(\mathbf{x}_{\text{fixed}}^*) = 0 \quad \text{equilibrium,}$$

$$(5c) \quad \max_{1 \leq i \leq 3} \text{Re} \lambda_i < 0 \quad \text{stability,}$$

105 where $\dot{\mathbf{x}}_{\text{fixed}} = F_{\text{fixed}}(\mathbf{x}_{\text{fixed}})$ describes the system of equations (3), and λ_i are the eigenvalues
 106 of the Jacobian matrix evaluated at equilibrium $\mathbf{J}_{\text{fixed}} = DF_{\text{fixed}}(\mathbf{x}_{\text{fixed}}^*)$. These conditions
 107 ensure a straightforward comparison of trophic cascades, which in the case of nonstationary
 108 steady states would depend on the time scales under consideration (Borer et al., 2005).

109 Eq. (3) is extended to the case of flexible foraging by replacing the fixed forag-
 110 ing parameter ω with a quantity satisfying (4). The system of equations is now four-
 111 dimensional and is defined by the vector field $F_{\text{flexible}} : \mathbb{R}^4 \rightarrow \mathbb{R}^4$ which maps $[r, n, p, \Omega]$
 112 to $[F_r(r, n, p, \Omega), F_n(r, n, p, \Omega), F_p(r, n, p, \Omega), F_\Omega(r, n, p, \Omega)]$. We demand that the flexible
 113 model likewise has a coexistence equilibrium $\mathbf{x}_{\text{flexible}}^* = [r_{\text{flexible}}^*, n_{\text{flexible}}^*, p_{\text{flexible}}^*, \Omega_{\text{flexible}}^*]$, so
 114 that $\mathbf{x}_{\text{flexible}}^* > 0$, $F_{\text{flexible}}(\mathbf{x}_{\text{flexible}}^*) = 0$, and all eigenvalues of the system's Jacobian matrix
 115 $\mathbf{J}_{\text{flexible}} = DF_{\text{flexible}}(\mathbf{x}_{\text{flexible}}^*)$ have negative real parts. Finally, for the case of predators in

116 a food chain, that do not feed on primary producers, we denote by $[r_{\text{chain}}^*, n_{\text{chain}}^*, p_{\text{chain}}^*]$ the
117 stable and positive solution satisfying (5) when setting $\omega = 0$.

118 *A comparison of trophic cascades*

119 We quantified differences in trophic cascade strengths between systems with omnivores (i.e.,
120 $\omega > 0$) and predators (i.e., $\omega = 0$), and examined the dependencies of these differences on
121 model parameters. We denote by $[r_{\chi}^*, n_{\chi}^*, 0]$ the non-positive equilibrium solution to (3) in the
122 absence of predators, so that $F_{\text{fixed}}(r_{\chi}^*, n_{\chi}^*, 0) = 0$. A traditional measure of trophic cascade
123 strength (Shurin et al., 2002; Borer et al., 2005) applied to omnivory systems at equilibrium
124 is therefore $\log_2(r_{\text{fixed}}^*/r_{\chi}^*)$. Likewise, cascade strength in the analogous food chain can be
125 calculated as $\log_2(r_{\text{chain}}^*/r_{\chi}^*)$. The difference in trophic cascade strengths induced by a fixed
126 omnivore and the predator in its analogous food chain, κ_{fixed}

$$(6) \quad \kappa_{\text{fixed}} := \log_2 \frac{r_{\text{fixed}}^*}{r_{\chi}^*} - \log_2 \frac{r_{\text{chain}}^*}{r_{\chi}^*} = \log_2 \frac{r_{\text{fixed}}^*}{r_{\text{chain}}^*}.$$

127 This measure κ_{fixed} of the relative cascade strength is similar to the “proportional response”
128 measure of Heath et al. (2014), and equals 1 (or -1) if the trophic cascade induced by
129 omnivores is twice as strong (or half the strength) as in the analogous food chain. Like-
130 wise, the difference in cascade strengths between flexible omnivory systems and food chains,
131 $\kappa_{\text{flexible}} := \log_2 r_{\text{flexible}}^*/r_{\text{chain}}^*$. Closed form equilibrium solutions for all variables in eqs. (3)
132 and (4) are provided in Supplementary Table 1.

133 Results

134 *Fixed omnivores can generate strong trophic cascades*

135 We first considered the case of fixed omnivores that do not exhibit diet flexibility. In Figure
136 1 we summarize changes in the relative cascade strengths induced by fixed omnivores κ_{fixed}
137 (Fig. 1a), community dynamics, and species coexistence (Fig. 1b) as primary productivity
138 ρ and omnivory strength ω — two key determinants in the behavior of omnivory systems
139 (McCann & Hastings, 1997; Diehl & Feiel, 2001; Amarasekare, 2007; Gellner & McCann,
140 2011) — are varied while other parameters are held constant. Consistent with prior analyses
141 of three-species omnivory modules, increasing omnivory strength ω causes the system to
142 undergo a transcritical bifurcation (McCann & Hastings, 1997) resulting in extinction of
143 either omnivores at low productivities, or herbivores at high productivities (Fig. 1b; Diehl
144 & Feiel, 2001; Amarasekare, 2007). These occur when the determinant of the Jacobian
145 matrix vanishes, $\det \mathbf{J}_{\text{fixed}} = 0$, for a combination of ρ and ω , marking the presence of a zero
146 eigenvalue (Kuznetsov, 2013).

147 Within the stable coexistence region (Fig. 1b, green and blue regions), predictions of
148 weaker trophic cascades with omnivory (Pace et al., 1999; Shurin et al., 2010; Kratina et al.,
149 2012; Wootton, 2017) held when primary productivity, ρ , was below a threshold value (Fig.
150 1a, orange region). Productivities above this threshold however, yield omnivory cascades
151 that are non-intuitively stronger compared to predators (Fig. 1a, blue region). This critical
152 transition in relative trophic cascade strengths with increasing productivity occurs at a point
153 which we refer to as ρ_{crit} or the *critical productivity* for convenience (Fig. 1a). A vertical
154 dashed line marks the critical productivity, which is the value of ρ at which $\kappa_{\text{fixed}} = 0$,
155 given parametrically by $\rho_{\text{crit}} = \frac{\delta\alpha^2(f-1)}{f[\alpha(\delta-\beta) + \beta f(\alpha-1)]}$ (Supplementary Fig.

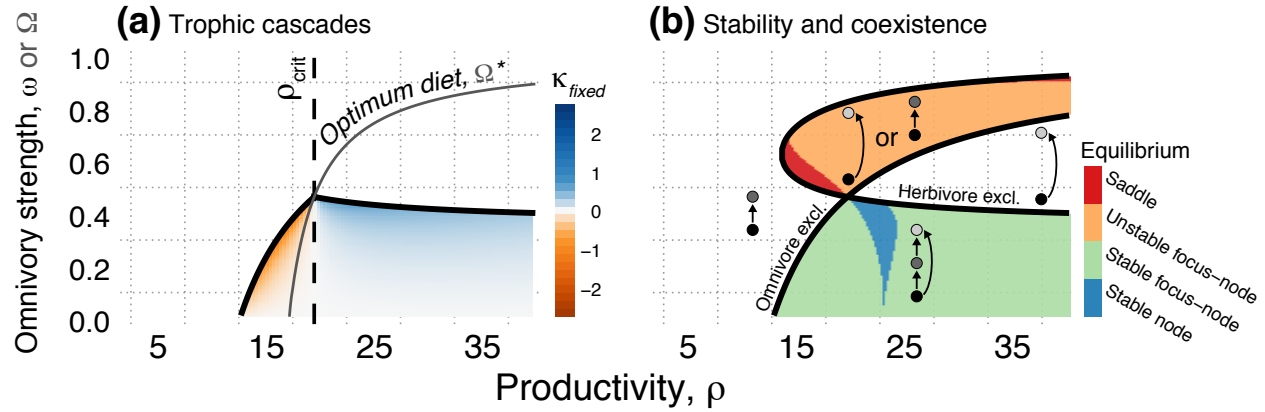


FIGURE 1. (a) Numerical summary of relationships between relative cascade strength κ_{fixed} , productivity ρ , and omnivory strength ω . Colors show κ_{fixed} values for combinations of ρ and ω within the three-species coexistence region. Blue represents stronger cascades with omnivory, orange represents weaker cascades with omnivory. Black curves mark extinction boundaries for either the omnivore or herbivore species (see panel b). The grey curve shows the equilibrium foraging strategy for the flexible omnivore, $\Omega_{flexible}^*$. A vertical dashed line marks the critical productivity ρ_{crit} . (b) Bifurcation curves identify stability boundaries separating steady states with different dynamics. Colors are different types of equilibria, determined by eigenvalues of the Jacobian matrix \mathbf{J}_{fixed} . Non-coexistence regions are labelled and identified by the inset networks of producers (black), herbivores (dark grey), and omnivores (light grey). Parameter values are $\alpha = 7.5$, $\beta = 5.5$, $f = 0.25$, $\delta = 2$, and $v = 1.05$.

156 1). Note that the transition from weaker ($\kappa_{fixed} < 0$) to stronger ($\kappa_{fixed} > 0$) cascades
 157 along a productivity gradient does not depend on omnivory strength. Instead, omnivory
 158 strengths near the extinction boundaries attenuate the discrepancy between cascades, such
 159 that omnivory cascades are weakest when productivity is low and ω approaches values leading
 160 to omnivore exclusion, and strongest when productivity is high and omnivores have nearly
 161 excluded herbivores (Fig. 1).

162 To explain the non-intuitive result of stronger cascades with fixed omnivory, we ex-
 163 amined the relationship between primary productivity and the optimal foraging effort that
 164 would lead to the highest *per capita* growth rate by omnivores at equilibrium, $\Omega_{flexible}^*$ (Sup-
 165 plementary Table 1). The grey curve in Fig. 1a illustrates $\Omega_{flexible}^*$ as a function of ρ ; the
 166 growth rate-maximizing strategy monotonically approaches pure herbivory as productiv-
 167 ity increases, recapitulating results that coexistence occurs over a wider range of omnivory

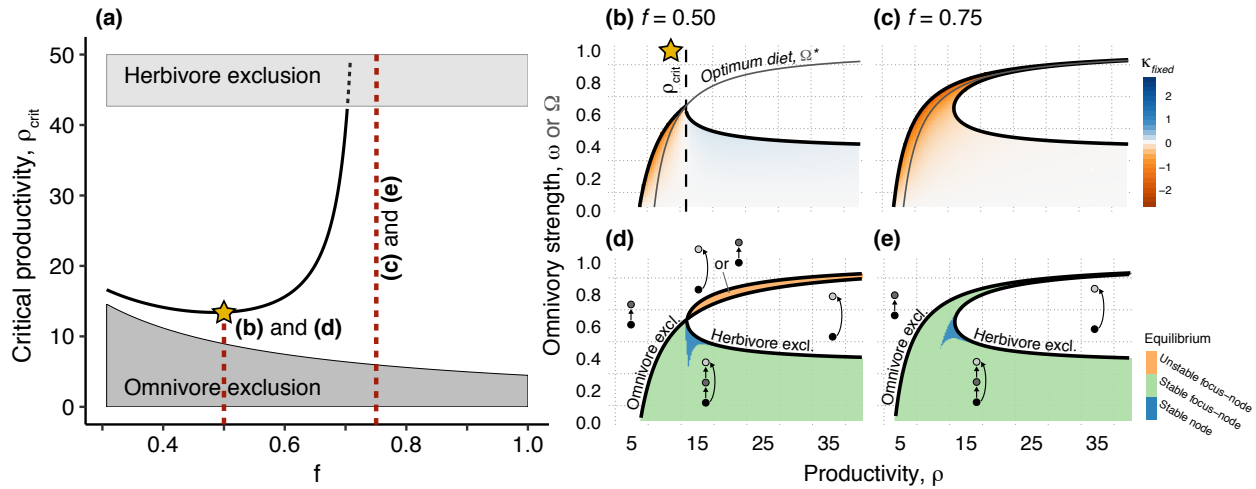


FIGURE 2. (a) Relationship between critical productivity ρ_{crit} and efficiencies f (Table 1). The curve is solid if the critical productivity lies in the coexistence region, and dashed otherwise. The light and dark grey shaded regions mark the extinction of herbivores and omnivores respectively. The left- and righthand red dashed lines correspond to panels b & d and c & e respectively. Parameter values are the same as in Fig. 1. (b & c) Relationships between relative cascade strength κ_{fixed} , productivity ρ , and omnivory strength ω . Colors show κ_{fixed} values within the three-species coexistence region. Blue represents stronger cascades with omnivory, orange represents weaker cascades with omnivory. Black curves mark extinction boundaries for either the omnivore or herbivore species (see panels d & e). The grey curve shows the equilibrium foraging strategy for the flexible omnivore, $\Omega_{flexible}^*$. A vertical dashed line marks the critical productivity ρ_{crit} . (d & e) Bifurcation curves identify stability boundaries separating steady states with different dynamics. Colors mark different types of equilibria. Non-coexistence regions are labelled and identified by the inset networks of producers (black), herbivores (dark grey), and omnivores (light gray).

168 strengths when omnivores forage flexibly (Křivan & Diehl, 2005). Precisely at $\rho > \rho_{crit}$,
 169 the fixed omnivore is no longer able to achieve the optimal foraging strategy (Fig. 1a).
 170 Intuitively, this indicates that strong trophic cascades are induced by omnivores when their
 171 foraging effort toward producers is guaranteed to be energetically suboptimal.

172 We next sought to determine whether the presence of a critical productivity, or a switch
 173 from weaker to stronger cascades with fixed omnivory, depends on other model parameters.
 174 In Fig. 2 we show that ρ_{crit} (i.e., the location of the vertical dashed line in Figure 1a
 175 along the x -axis) is sensitive to the conversion efficiency parameter, f . Recall that f is the
 176 product of the producer-to-herbivore conversion efficiency $\hat{e}_{r,n}$, and the ratio of herbivore-
 177 and producer-to-omnivore conversion efficiencies (i.e., omnivore rewards), $\hat{e}_{n,p}/\hat{e}_{r,p}$ (Table

178 1). Model-based and experimental studies have suggested that $\hat{e}_{r,n} > \hat{e}_{r,p}$ and $\hat{e}_{n,p} > \hat{e}_{r,p}$ are
179 realistic conditions for omnivores in nature (Diehl & Feiel, 2000; Křivan & Diehl, 2005).
180 Satisfying these conditions, we would generally expect small f values when herbivores are
181 only slightly more rewarding than producers to omnivores (for instance, if $\hat{e}_{n,p} = \hat{e}_{r,p} + \epsilon$
182 where ϵ is a small number), and large f values when rewards from eating herbivores are
183 much higher than for producers, $\hat{e}_{n,p} \gg \hat{e}_{r,p}$. For large enough values of f , the curve of
184 ρ_{crit} enters a non-coexistence region (Fig. 2a). Thus, the potential for strong omnivory
185 cascades is lost as f increases, regardless of other population- or community-level properties;
186 an example of when this happens is shown in Figs. 2c and 2e. We examine the sensitivity
187 of these results to other model parameters in Supplementary Fig. 1. Briefly, the critical
188 productivity shifts to the right (i.e., larger ρ_{crit} values lead to smaller parameter regions with
189 strong omnivory cascades) as α and δ increase, and shifts toward zero (i.e., smaller ρ_{crit}
190 values lead to an expansion of the parameter region with stronger omnivory cascades) as β
191 increases (Supplementary Fig. 1).

192 *Flexible omnivores never generate stronger trophic cascades*

193 Unlike fixed omnivores, flexibly foraging omnivores can never induce cascades that are
194 stronger than in the analogous food chain. We show analytically that at a positive
195 equilibrium solution, $\kappa_F < 0$. At the interior equilibrium (Supplementary Table 1), if
196 $\phi := -\alpha\delta + \delta f(\alpha - \rho) + \beta f(\rho - 1)$ then

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

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

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

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

$$(7) \quad \alpha\delta + f\rho(\delta - \beta) > 0.$$

200 Combining (7) with the solution Ω_F^* (Supplementary Table 1) shows that for positive equi-
201 libria, $\kappa_F < 0$, since $\phi < 0$ cannot be true for a biological system. Thus, consistent with
202 conceptual models of trophic cascades (Strong, 1992; Pace et al., 1999), cascades in systems
203 with flexibly foraging top omnivores are bounded in strength by those in their analogous
204 food chains. Numerical results confirm these analytical expectations, and illustrate how in-
205 creasing consumer reward ratios (i.e., increasing f) attenuates this result but does not alter
206 the qualitative relationship between κ_{flexible} and ρ (Fig. 3).

207 Discussion

208 Intuition suggests that trophic cascade will not occur when top predators additionally feed
209 on primary producers (Polis & Strong, 1996; Pace et al., 1999; Duffy et al., 2007; Shurin et
210 al., 2010; Kratina et al., 2012; Wootton, 2017), but our results predict that strong cascades
211 will emerge under a wider range of foraging types than previously expected. We identified
212 many cases in which omnivores are indeed likely to generate weak cascades, although we
213 have shown that this should not be a uniform expectation for omnivory. Particularly, in

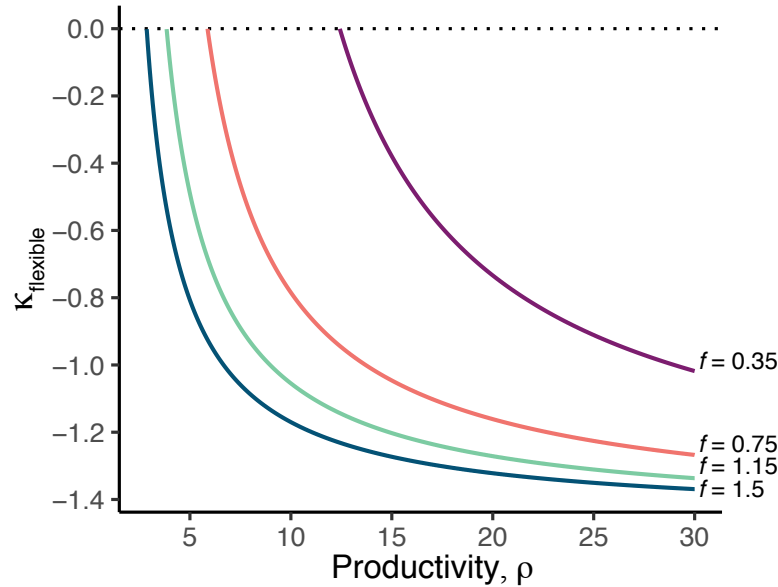


FIGURE 3. Numerical solutions relating relative cascade strength, κ_F , scaled productivity ρ , and scaled resource profitability f in the flexible model. Colors represent associated values of f in the margin. Parameter values are $\alpha = 7.5$, $\beta = 5.5$, $\delta = 2$, and $v = 1.05$.

214 high productivity systems in which foraging rewards do not strongly differ between producers
215 and herbivores (Fig. 1a; Fig. 2a), fixed omnivores are capable of generating stronger cascades
216 than would be expected if they did not consume producers at all. This is due to suboptimal
217 omnivore foraging, and the additional source of herbivore population losses in models of
218 fixed omnivory, in which the herbivore must compete with its own consumer for resources
219 (Diehl & Feiel, 2000). This result provides at least one general explanation for the weaker
220 (Finke & Denno, 2005; Denno & Finke, 2006), comparable or indistinguishable (Borer et al.,
221 2005), and stronger (Okun et al., 2008; France, 2012) cascades that have now been observed
222 with omnivorous top predators: they largely depend on primary productivity and the types
223 of omnivory. It is not surprising that a more comprehensive catalogue of foraging behaviors
224 will improve predictions of trophic cascades, but our model-based results indicate that this
225 knowledge may be especially important when species consume resources across trophic levels.

226 Comparisons of fixed and flexible models showed that omnivores were capable of gen-
227 erating strong cascades only when consuming an energetically suboptimal level of primary
228 producers could be guaranteed (Figs. 1a, 2b, and 2c). This leads to the question: how
229 common is this type of fixed foraging in food webs? Empirical evidence for approximately
230 fixed foraging exists for groups as diverse as protists, arthropods, and mammals (Clark,
231 1982; Mooney & Tillberg, 2005; Diehl & Feiel, 2001). Fixed omnivory may also manifest
232 in other ways, for example when organisms forage in a way that is suboptimal in terms of
233 pure energetics but is otherwise required to maintain nutritional or stoichiometric balances
234 (Berthoud & Seeley, 1999; Remonti et al., 2016; Zhang et al., 2018). Suboptimal foraging has
235 also been observed in heavily disturbed or human-altered systems where consumer behaviors
236 are not adapted to current resource conditions, or when changes in habitat structure alter
237 the ability to efficiently locate preferred food sources (Walsh et al., 2006).

238 Allometric scaling relationships between species' demographic rates and body masses
239 have helped identify biological constraints on the strengths of trophic cascades in food chains
240 with top predators (DeLong et al., 2015), but body mass may have additional implications
241 for cascades that are generated by species facing complex foraging decisions. The preva-
242 lence of dynamical or adaptive foraging behaviors, like those represented by our flexible
243 model, across the tree of life has shown associations with organismal brain sizes and body
244 masses by proxy (Eisenberg & Wilson, 1978; Rooney et al., 2008; Edmunds et al., 2016).
245 Body mass distributions may also influence cascades that are induced by species with size-
246 mediated ontogenetic shifts from herbivory to carnivory (Pace et al., 1999), wherein average
247 population-level foraging behaviors could be characterized as "omnivory" and would reflect
248 intraspecific size structures. Future empirical work and simulation-based analyses of more

249 complex models will be key for uncovering additional relationships between species' body
250 masses and trophic cascades in food webs, and to develop a coherent understanding of when
251 foraging behavior drives deviations from predictions of cascades from simple tritrophic food
252 chain models. In many of these case, omnivory could appear as an average population-level
253 behavior and not necessarily at the level of the individual.

254 Our analysis focuses on models characterized by type I functional responses that re-
255 late resource biomass to consumer growth. Alternate nonlinear functional responses (e.g.,
256 Holling type II; Holling, 1959) may modulate the effects of omnivory on trophic cascades.
257 Preliminary analyses show that closed-form equilibrium solutions similar to those in Sup-
258 plementary Table 1 can also be obtained for Type II functional responses. The predictive
259 power of these solutions in cases where the model shows oscillatory behavior remains an open
260 question. We conjecture that, for mild instabilities, the oscillatory behavior introduced by
261 saturating consumption would result in similar qualitative outcomes predicted by equilib-
262 rium values when cascades are measured as time-averaged quantities (Fox, 2007). However,
263 for larger-amplitude oscillations cascade strengths will likely depend strongly on the time-
264 scale over which they are measured, potentially yielding a mechanism for the observation
265 that cascade strengths are related to experimental duration (Borer et al., 2005). Models that
266 formally extend the concept of trophic cascades to cases of nonstationary equilibria will be
267 an important direction for future analyses.

268 Figure 1 suggests an interesting analytical question for future study. Namely, multi-
269 ple qualitative changes are observed precisely at the phase transition for strong omnivory
270 cascades, $\kappa_{\text{fixed}} > 0$, which is indicated by the vertical dashed line $\rho = \rho_{\text{crit}}$. Also occurring
271 at this point are the phase boundaries for species coexistence at stable equilibrium given by

272 the curves separating different non-coexistence regions (Fig. 1b); the grey curve showing the
273 optimal omnivory strength, $\Omega_{\text{flexible}}^*$, as a function of ρ passes into a region that is unattain-
274 able by the fixed forager (Fig. 1a); and two saddle-node bifurcation curves intersect (Fig.
275 1b). It remains to understand why these curves all intersect at a single point, and how this
276 relates to qualitative changes in trophic cascade strengths.

277 Examples from agroecosystems and disturbed natural habitats indicate that trophic
278 cascade theories can directly inform applied management problems and efforts to mitigate
279 human alteration of ecosystems (Schmitz, 2006; Estes et al., 2011). Our comparative analyses
280 together with the ubiquity of omnivory in nature (Arim & Marquet, 2004; Kratina et al.,
281 2012; Wootton, 2017) suggest that omnivores may contain promise for such applications of
282 cascade theory. For instance, nutrient inputs to agricultural systems that lead to artificially
283 enriched communities are exactly the conditions where we expect a potential for strong
284 omnivorous cascades. If management goals include reducing the density of agricultural pests
285 in enriched systems through integrated strategies that manipulate top trophic levels, then,
286 counterintuitively, top omnivores with certain features may warrant additional consideration
287 (Agrawal et al., 1999). Achieving these outcomes in practice may prove challenging (Cortez
288 & Abrams, 2016).

289 *Conclusions*

290 Omnivory has long been cited as a reason for why trophic cascades are less frequent or weaker
291 than expected, although empirical data on the role of omnivory has been equivocal (Borer
292 et al., 2005; Shurin et al., 2010; Kratina et al., 2012; Wootton, 2017). Our theory generally
293 agrees with the prediction of omnivory in weakening cascades, but also demonstrates where
294 these predictions are weak or even where they exhibit unexpected changes. Thus, these

295 predictions generate a framework for future investigation, that can focus expectations on
296 when and where omnivory effects might occur in more complex ecosystems. At the least,
297 our models help elucidate the mixed support for an intuitive ecological prediction.

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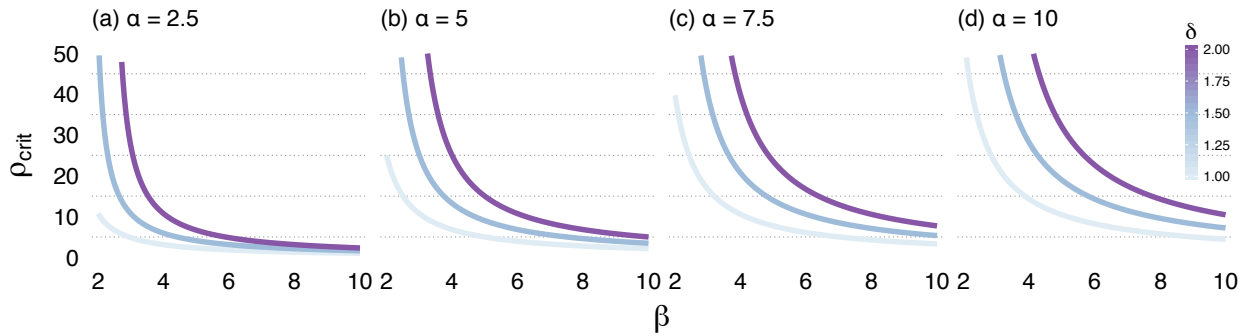
Acknowledgements

We thank two reviewers for comments. A.K.F was supported by a grant from the Alfred P. Sloan Foundation to the Biology & the Built Environment Center at the University of Oregon, and by the National Science Foundation (NSF) award #006741-002. K.E.A. was supported by NSF grant DEB #1553718.

Supplementary Materials

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

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 ρ_{crit} as a function of α (panels), β (x -axis), and δ (color scale). The parameter $f = 0.5$.