**Omnivory as a Dynamic Response to Changing Conditions**

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# Abstract

While ecology has long been interested in omnivory, much of the historical data has often been presented from a static viewpoint with researchers often looking at patterns in trophic position (a surrogate for omnivory) and the degree of omnivory within and across ecosystems.   Here, we briefly review this aspect of omnivory before arguing that omnivory is better considered a dynamic response to changing conditions (e.g., seasonality; ENSO) and that omnivory is highly context dependent. With this dynamic perspective in mind, we then synthesize existing omnivory theory to argue that there are two general categories of mechanisms promoting omnivorous responses by organisms, both of which enhance stability in the face of environmental variation. First, there are bottom-up driven conditions in which environmental conditions spatially or temporally alter the production of plants or animals in a manner that pushes predators to optimally forage more on lower level prey (**bottom-up omnivory**). Second, there are cases where environmental conditions (e.g., high productivity, small ecosystems) and organismal traits (e.g. high interaction strengths) can generate strong cascading predator influences that implicitly drive conditions that promote omnivory (**top-down omnivory**). We end by reviewing the recent literature on omnivory pointing out that there appears to be cases that fall into the two categories although that much further work is done.  This dynamic understanding of omnivory to changing conditions, importantly, allows us to begin to consider how global change will alter carbon transfer, stability and production in while food webs.

# A Brief History of Omnivory:

## Theory: Stable or unstable?

Historically, the theoretical battle lines of omnivory have revolved around whether omnivory is a stabilizing or destabilizing presence in real ecosystems.

* Theory: Pimm and others to Gellner and others – muting interactions
* Intraguild Predation – muting competitive exclusion
* Weak omnivory

## Empirical Data: Rare or Common and Where in the Food Web?

The early …… . Pimm argued that there was little evidence of omnivory but he intriguingly ignored interactions that were weak ….. More recently Thompson has found omnivory is rampant and appears to increase with trophic level such that higher trophic level organisms are more likely to display omnivory.

Maybe transition within this to argue that most of this work above assumes that omnivory is a static trait in a sense, and little considering how an organisms may alter its omnivory. Given the recent emphasis on changing condition empirical data on omnivory has increasingly begun to document changing amounts in omnivory across space and time (incorporate review by Kratina et al. 2012). Below, we now review and synthesize existing theory within this dynamic framework.

# Theory: Omnivory as a Dynamic Response

## Bottom-up Driven Omnivory and Stability

Review this? Maybe if nothing much on omnivory can touch on generalism in a stochastic world literature (can look at Kratina et al. 2012 for a review, Takimoto et al. 2002 for theory)

Stochastic and or periodic (e.g., seasonal)– model P-C-R with something like carrying capacity () being a function of time (or space). We allow top predator to consume or as a function of its relative density only (Tunney 2012 did something like this).  Look at how such variation drives changing omnivory under this rational model and ii) Compare CV (stability) of P-C-R dynamics with and without omnivory.

Predator feeds more relatively more omnivorously at time, , compared to time, , when:

# Top-down Driven Omnivory and Stability

Here, we do not consider temporal changes as much as changing conditions generally (e.g., two ecosystems with different productivity) to show that the same organism under the two conditions can act to feedback on the same to generate more or less omnivory.  Need to briefly review this as McCann 2001, Tunney et al. 2012; Ward et al. (2018), “the more food webs change the more they stay the same”; and others (look for this in literature)

# Empirical Responses to Changing Conditions

* review this broadly

Known examples from our lab and others

## Bottom-Up Examples

1. Budworm, links not strength here (Eveleigh et al. 2007), parasitoids in space (silviculture versus )
2. Bailey Marine seasonal example, fish eat more from lower basal/detrital connections in cold
3. Feral pig example, I need to dig up data from Gabe and but in space, shows evidence of pigs eating more omnivorously in areas where acorn production is high and less in places prone to strong insect pulses (wet)
4. Birds can eat insects or fruit as it varies in availability and still meet their nutritional and energy demands (i.e. high dietary flexibility can still meet their physiological needs; Marshall et al. 2015)
5. Trophic position of ghost crabs is higher on narrower beaches and reduces on wider beaches with increased consumption of clams vs. amphipods and mole crabs (Tewfik et al. 2016)
6. Eating young of other species during reproductive pulses might count, if eggs are considered lower trophic position? Adult fish can binge on eggs of other fish during reproductive pulses (dolly varden binge on salmon eggs, Armstrong et al. 2013; benthic whitefish eat cisco eggs in winter; Stockwell et al. 2014). There is also the other way….‘forced piscivory’ where cyprinids (that are usually planktivores) eat higher trophic position YOY perch in years the YOY perch have suppressed Daphnia (Vejrik et al. 2016).
7. In some cases resource waves might fit in here just to say that a consumer might be omnivorous for even longer than expected if they can move and resources that are ephemeral at any single location but long lasting across an entire landscape
8. Other examples?

## Top-Down Omnivory

1. Lake trout, lake size (Vander Zanden 1999 etc., McCann 2005), shape (Dolson), climate **across space** (Tunney); **across time** (Guzzo)  others
2. Stream webs: Emily (yearly); Marie (Seasonally)
3. Others?

## Top-down and Bottom-Up?

1. Floodplains could be both. Bottom up during wet and top down during late dry, when they are spatially restricted and maybe eventually suppress their prey (Welcomme, Junk, McMeans).
2. Physiological traits (enzyme activity, nutritional requirements) can dictate omnivory from ‘within’ the predator and might be both bottom up and top down (or it could go in its own section). Some fish for example can't eat plants at cold temperatures because they lack the gut microbe activity to digest cellulose, so they select for plants at warm and animals at cold (Vejkrikova et al. 2016). The same might be true for nutritional requirements where predators select prey from different trophic levels (that whole diet mixing literature). And gut size (or cold temps that slow digestion) might mean fish are 'gut limited' even when prey is really abundant (Fall and Fiksen 2019). Physiological traits (enzyme activity, gut size, nutritional requirements, etc.) might therefore be viewed to both: 1) allow a predator to take advantage of bottom up opportunities, like a gate keeper controlling access to low trophic level resources, and 2) generate omnivory to meet demands, more akin to top down because it’s not necessarily driven by prey density.

# Discussion

# Results

* Global Change –
* As a Rewiring response?

# Methods

Building on standard three species omnivory modules (McCann and Hastings, 1997) we have:

Where measures the predators preference scaling of its attack rate on the resource () versus the consumer (). We will examine two configurations one with a fixed (density independent) preference of , and a density dependent, behavioral preference modelled as:

# References

McCann, K.S., Hastings, A., 1997. Re-Evaluating the Omnivory-Stability Relationship in Food Webs. Proc. Biol. Sci. 264, 1249–1254. https://doi.org/10.1098/rspb.1997.0172