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SYNTHESIS & INTEGRATION

Stability and persistence of food webs with omnivory: Is there a general pattern?

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Citation: Kratina, P., R. M. LeCraw, T. Ingram, and B. R. Anholt. 2012. Stability and persistence of food webs with omnivory: Is there a general pattern? Ecosphere 3(6):50. http://dx.doi.org/10.1890/ES12-00121.1

Abstract. The relationship between omnivory and stability has been the subject of a longstanding debate in ecology. Early theory predicted that omnivory would decrease the probability of food webs being stable. While early empirical data appeared to support the prediction that omnivory should be rare, detailed study of food webs later revealed that omnivory is ubiquitous across ecosystems and taxa. Recent years have seen renewed interest in the omnivory-stability debate, and advances in mechanistic non-equilibrium models demonstrated that omnivory can both increase and decrease stability. Current efforts have therefore focused on identifying biological mechanisms that promote the persistence of food webs with omnivory. We synthesize recent evidence that omnivory often stabilizes food webs when it occurs as life-history omnivory, when prey experience reduced predation rates due to refuges or adaptive antipredator defences, and when omnivores interfere with each other or feed adaptively. Empirical research has lagged behind theory and there remains a shortage of studies directly measuring the stability of diverse natural communities that vary in the number and strength of omnivorous interactions. Early microcosm experiments indicated a narrow range of conditions for the persistence of simple omnivorous modules, while studies of omnivory embedded within larger natural networks have demonstrated its stabilizing effects. These new findings alter our view of food web dynamics and show that rather than looking for a simple and general omnivory-stability relationship, we should focus on identifying conditions under which omnivory is a stabilizing feature of more complex natural systems.

Key words: community dynamics; competition; food web models; intraguild predation; metacommunity; omnivory; species coexistence; stability and persistence; trait evolution.

Received 24 April 2012; accepted 16 May 2012; **published** 14 June 2012. Corresponding Editor: O. Schmitz.

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OVERVIEW

Omnivory is a feeding strategy in which a consumer feeds at multiple trophic levels (Pimm and Lawton 1978). Early theoretical work predicted that omnivory should be rare in nature, because adding omnivory to model food webs reduced their stability (Pimm and Lawton 1978, Pimm 1980, 1982). Empirical food web data initially supported the prediction that omnivory is rare (Cohen 1978, Pimm and Lawton 1978, Cohen et al. 1990), but suffered from bias due to low resolution and omission of weak interactions (Martinez 1991, Polis 1991). In the past few decades, it has become clear that omnivory is widespread, occurring in a wide range of taxa and across all types of ecosystems (Menge and Sutherland 1987, Walter 1987, Polis 1991, Diehl 1993, Ponsard and Arditi 2000, Scheu and Falca 2000, Arim and Marquet 2004). These observations led to new theoretical investigations showing that under certain conditions, omnivory is expected to persist and even to confer stability on otherwise unstable food webs. Stability may also be facilitated by features of the environment or of other species in the broader ecological network. Both theory and data therefore indicate that food webs with many omnivorous links can persist over long time periods.

Here, we synthesize our current understanding of the effect of omnivory on the stability and persistence of food webs. We begin by describing the special cases that are encompassed by the broad definition of omnivory, and discussing the prevalence of omnivory across ecosystems and taxa. We summarize the incongruity between early model predictions and subsequent observations in natural systems, and then critically evaluate more recent theoretical and empirical work that seeks to identify mechanisms explaining the patterns seen in nature. We discuss several major factors that have the potential to promote persistence of food webs with omnivory, and integrate our current state of understanding into a general framework. We conclude our synthesis by highlighting promising venues for future research, focusing on the potential effects of metacommunity dynamics and trait evolution on the relationship between omnivory and stability.

What Defines Omnivory?

In food web studies, omnivory is typically defined as feeding on more than one trophic level (Pimm and Lawton 1978, Pimm 1982, Pimm et al. 1991). This may include, but does not require, feeding on both plants and animals. For example, omnivorous birds and lizards can feed on both predatory spiders and the herbivorous insects that the spiders prey upon (Perfecto et al. 2004). The classic definition of omnivory derives from the trophic-dynamic model, in which energy and biomass flow through a series of discrete trophic levels: plant, herbivore, primary carnivore, and so on (Lindeman 1942). The existence of omnivory implies that not all species can be neatly assigned to a discrete trophic level, resulting in the recognition of fractional trophic levels, or trophic positions (Levine 1980, Williams and Martinez 2004). Under this view of food webs as tangled networks rather than stacked trophic levels, omnivory can be defined either as a qualitative feature of an organism (do all of its diet items have the same trophic level or not?) or as a continuous feature based on the variance in trophic positions of its resources (Levine 1980, Goldwasser and Roughgarden 1993, Williams and Martinez 2004).

Under any definition, omnivory emphasizes the ecological role of species within food webs. The level of omnivory, whether expressed as the proportion of omnivorous species or the average of a quantitative measure across all species, is a crucial determinant of food web architecture. More omnivory in a system increases the degree to which it departs from a simple trophic level structure, which may reduce the likelihood of strong direct or indirect interactions (trophic cascades) between trophic levels (Polis and Strong 1996, Bascompte et al. 2005). Omnivory is thus both an important characteristic of species and a key structural feature of the food webs in which they occur.

Varieties of omnivory

The broader definition of omnivory encompasses a number of important special cases. In many instances, it is convenient to study community modules—small networks consisting of only a few species—in isolation from the larger food webs in which they are embedded (Holt 1997). One such module has been the focus of much of the theoretical and experimental exploration on omnivory and stability: intraguild predation (IGP). In this module, an omnivore (the IG predator) feeds on an intermediate consumer (the IG prey), and also utilizes a resource of this consumer (Polis et al. 1989, Holt and Polis 1997). The intermediate consumer and its predator are therefore also involved in exploitative competition for the shared resource. Because it is analytically tractable, widespread in natural food webs (Rosenheim et al. 1995, Arim and Marquet 2004), and directly comparable to competition and predation modules that lack an omnivorous link, the IGP module has been a focal point of research on omnivory. Other forms of omnivory may include predators feeding at two or more trophic levels without a direct competition link with their prey. Black and grizzly bears, for example, feed on wild berries in terrestrial habitat and fish in aquatic habitat without competing with either prey type (Welch et al. 1997).

Another common type of omnivory, mutual predation, occurs when two predatory species reciprocally prey upon each other (Polis 1991, Woodward and Hildrew 2002, Montserrat et al. 2012). Omnivory can also take the form of cannibalism, when organisms eat conspecifics as well as prey from lower trophic levels (Fox 1975, Polis et al. 1989). Cannibalism is ubiquitous in many insects, fish, lizards and other taxa with stage or size-structured life history (e.g., Polis 1981, Elgar and Crespi 1992, Persson et al. 2000).

Arguably the most common form of omnivory occurs when organisms change the trophic level at which they feed over their lifetimes (Werner 1988, Polis et al. 1989, Mylius et al. 2001, Miller and Rudolf 2011). Life-history omnivory is common when organisms undergo substantial changes in size or body form over their lifetimes (Pimm and Rice 1987, Polis 1994, Polis and Strong 1996). Empirical data show that ontogenetic diet shifts are the norm rather than the exception in many families of holometabolic insects, fish, reptiles, amphibians, gape-limited invertebrates, and parasites with complex life cycles (Werner and Gilliam 1984). Differences in diet among life stages of the same individual are often greater than differences among distinct species (Polis 1984, Muñoz and Ojeda 1998), and recent estimates show that species with metamorphosis share less than 8% of their diet among ontogenetic stages (Rudolf and Lafferty 2011). The ubiquity of size and stage structure generates horizontal and vertical heterogeneity in food webs (reviewed in Persson 1999) and demonstrates difficulty with classification of species into discrete trophic levels (Oksanen 1991, Hairston and Hairston 1997).

While life-history omnivory involves individuals feeding at different trophic levels at different life stages, intraspecific variation among individuals at the same life stage can also result in omnivory at the species level. Genetic polymorphism or phenotypic plasticity may result in the coexistence of discrete morphs that feed at different trophic levels (e.g., Pfennig 1992). Omnivory can also result from spatially segregated conspecific individuals feeding on different trophic levels. For example, some parasitoids can feed on their hosts in cropland, but consume mostly nectar in natural ecosystems (Coll and Guershon 2002). Marine euphausids (*Euphauisia pacifica*) are largely herbivorous in rich coastal waters, but switch to carnivory in offshore waters where low productivity results in smaller phytoplankton (Parsons and LeBrasseur 1970).

The dynamic nature of omnivory

Topological representations of food webs imply that omnivory is a static property of certain species, but the presence and extent of omnivory can instead be a dynamic response to changing conditions. For instance, intraguild predation can be perceived as a transitional state between two distinct systems: a tri-trophic food chain (consisting of resource, intermediate consumer, and predator), and exploitative competition between the consumer and the predator (McCann and Hastings 1997). The transition between the food chain and competition modules occurs as the predator's feeding habit changes from eating mainly the consumer to eating mainly the resource. In this model, the degree of omnivory varies along a continuum and is determined by the parameter ω (ranging from 0 to 1). The degree of omnivory is highest when the predator feeds on the resource and the consumer in proportion to their availability ($\omega = 0.5$), and decreases as the system converges on a tri-trophic food chain ($\omega = 0$) or pure exploitative competition ($\omega = 1$). This useful representation was extended to recognize omnivory as the intermediate food web topology between any two of the three distinct systems: tri-trophic food chain, competition and polyphagy (Vandermeer 2006; Fig. 1). Emphasizing the dynamic nature of omnivory may provide insight in cases where the degree of omnivory changes due to life histories,

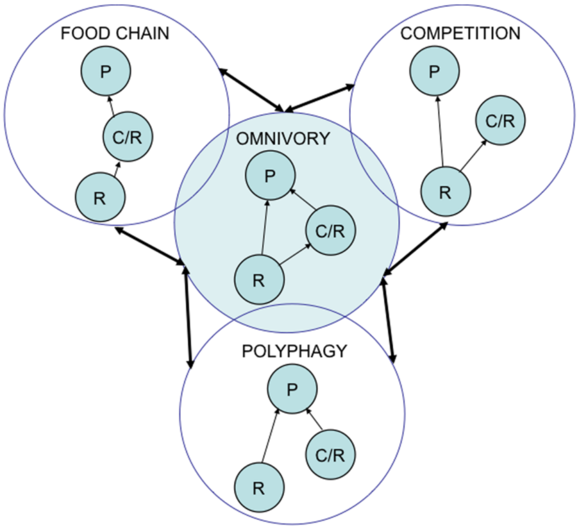

Fig. 1. Diagrammatic representation of omnivory—specifically the well-studied intraguild predation module—as a transitional state among different three-species modules: linear food chain, competition and polyphagy. Nodes describe the predator/omnivore (P), the consumer (C) and the resource (R). Thin arrows indicate the direction of energy flows from resources to higher trophic levels, and bold arrows show transitions among modules (modified from Vandermeer 2006 with permission from Elsevier).

evolution, or flexible foraging behavior of consumers.

INCIDENCE OF OMNIVORY

Distribution across taxa

Omnivory is taxonomically widespread. Hundreds of examples are known from insects (Coll and Guershon 2002, Buck et al. 2003), and other invertebrate taxa (Parsons and LeBrasseur 1970, Fagan 1997). In addition, members of many vertebrate groups are known to feed on multiple trophic levels (Vadas 1990, O'Donoghue et al. 1995, Cooper and Vitt 2002, Persson et al. 2007). More than half of lizard species live on a mixed herbaceous and animal diet (Cooper and Vitt 2002). Shifts in diet accompanying a gradual increase in body size during ontogeny often lead to life-history omnivory in fishes (Persson et al. 2007). In mammals, predatory lynx, coyotes and wolves often kill and consume each other when their preferred prey, herbivorous snowshoe hares and squirrels, are scarce (O'Donoghue et al. 1995). Herbivorous red squirrels and arctic ground squirrels also consume juvenile hares when they are available (O'Donoghue 1994). Examples of cannibalism and IGP among predatory raptors and owls are well documented (O'Donoghue et al. 1995). Omnivory is thus a frequent strategy in a functionally and phylogenetically diverse taxa.

Distribution across ecosystems and habitats

The accumulation of well-resolved food web data has made it apparent that omnivory is widespread in terrestrial, freshwater, marine, and soil ecosystems (Menge and Sutherland 1987, Walter 1987, Polis 1991, Diehl 1993, Goldwasser and Roughgarden 1993, Ponsard and Arditi 2000, Scheu and Falca 2000, Arim and Marquet 2004). Although omnivory is common in virtually all studied food webs, its prevalence varies among ecosystem types. Review of published food webs recently showed that the proportion of omnivorous species was highest in marine planktonic systems, lowest in streams, and intermediate in lake and terrestrial ecosystems (Dunne et al. 2004, Thompson et al. 2007). Omnivory was reported to be common in a detailed survey of 515 North American lakes (Sprules and Bowerman 1988). Analyses of 19 terrestrial and aquatic food webs categorized between 8% and 87% of taxa as omnivores, with omnivores comprising at least 50% of taxa in 14 of the webs (Dunne et al. 2004).

MAIN APPROACHES TO MEASURING THE OMNIVORY-STABILITY RELATIONSHIP

Stability is a complex, multifaceted property that generally measures either the ability of a food web to remain in approximately its present condition, or the time it takes to return to this condition after a perturbation (Grimm and Wissel 1997). Various metrics used to assess stability emphasize the occurrence of stable point equilibria, limit cycles, chaotic orbits, alternative stable states, or the robustness of food webs to species loss (McCann 2000, Dunne et al. 2004, Ives and Carpenter 2007). Early research used mainly the equilibrium approach and asked whether omnivory influences the probability of an equilibrium point to which all species will return after a small perturbation. Later, the focus shifted to include non-equilibrium criteria, acknowledging that communities are dynamic and asking how the presence of omnivory influences the probability that all species in a module will persist over long period of time. We will discuss both equilibrium and non-equilibrium approaches, and focus on measures of stability that emphasize the temporal constancy or persistence of food webs.

EARLY THEORETICAL PREDICTIONS

Equilibrium approach

Historically, the stability of model food webs was investigated by evaluating whether there existed an equilibrium point at which all species had positive densities, and whether any such equilibrium point was stable. Early matrix methods used simple, linear Lotka-Volterra models, and defined local (neighborhood) stability as the tendency for all species to return to their equilibrium densities following a small perturbation (Pimm and Lawton 1977, 1978, Pimm and Rice 1987). This approach is similar to the early theory that suggested a destabilizing effect of food web complexity, which led to a longstanding debate in ecology that parallels the omnivory-stability debate (May 1972, 1973). As applied to omnivory, this analysis showed that increasing the number of omnivorous links rapidly increased the percentage of unstable model food webs composed of strongly interacting species (Pimm and Lawton 1978). Life-history omnivory, where different life stages of species feed at different trophic levels, was also found to reduce food web stability, although to a lesser extent (Pimm and Rice 1987). Overall, early modeling attempts using the equilibrium approach consistently predicted that omnivory should destabilize food webs and therefore be rare in nature.

Much of the early theory that examined local stability of Lotka-Volterra models has focused on simple IGP modules. The double threat of competition and predation from the omnivore (IG predator) can have substantial negative demographic effects on the IG prey (Holt and Polis 1997). One general prediction of these models is that coexistence is only possible if the IG prey is a superior competitor for the shared resources, and only at intermediate levels of system productivity (Holt and Polis 1997, Diehl and Feissel 2000).

Non-equilibrium approach

Later studies acknowledged that ecological systems may not have stable equilibrium points, and investigated alternative metrics of stability. In particular, persistence is often a better measure of the type of stability ecologists are interested in, and can be applied under both equilibrium and non-equilibrium conditions. Persistence means that the minimal densities of all species in the focal food web are bounded away from zero, and that they can therefore coexist for a long period of time (Hutson and Law 1985). Law and Blackford (1992) measured persistence in four-species Lotka-Volterra model food webs containing omnivory, and showed different outcomes than local stability analysis. Specifically, some food webs that would be considered unstable by local stability analysis were shown to be persistent. Another work explored the resistance of food webs to further extinction following species loss, and found that omnivory appeared to have a stabilizing effect (Borrvall et al. 2000). In this four-species Lotka-Volterra model, omnivory increased the resistance of the system to the loss of a herbivore. In general, however, increasing the number of omnivorous links reduced the parameter space in which model food webs persisted (Law and Blackford 1992, Fussmann and Heber 2002).

Non-equilibrium models have shown that omnivory can confer stability on food webs when the omnivorous interactions are weak to intermediate (McCann and Hastings 1997). In contrast, a three-species Lotka-Volterra model predicted that the presence of omnivory would initiate chaotic dynamics (Tanabe and Namba 2005) due to an increase in overall consumption rate resulting from the addition of a feeding link. However, this destabilizing effect is sensitive to the assumption of strong species interactions. While non-equilibrium analyses of stability have revealed that strong omnivory is detrimental to stability, weak to moderate strength of omnivorous interactions can confer food web stability.

Experimental Tests of Early Predictions

Microcosm experiments allow precise manipulation of simple multigenerational communities, and thus frequently provide the first tests of theoretical predictions (Desharnais 2005). Dynamics of simple three- and four-species microcosms, especially intraguild predation modules, have been measured to test whether and how omnivory alters stability and persistence. Persistence, measured as low population fluctuations and high population size, was assessed in food web modules with or without omnivory (Lawler and Morin 1993). Bacteria and a bacteriovorous ciliate *Colpidium striatum* (hereafter *Colpidium*) were incubated either with the IG predator *Blepharisma americanum* (hereafter *Blepharisma*), or with one of the pure predators *Amoeba proteus* and *Actinosphaerium eichhornii*. The results of this experiment, and of similar experiments with other omnivorous and predatory protists (Morin and Lawler 1996), showed no effect of omnivory on IG prey. However, the population dynamics of the omnivore were always more stable than the dynamics of the pure predators.

Other experiments have investigated the conditions for coexistence across a productivity gradient. For example, a microcosm system composed of IG predator *Blepharisma* feeding on IG prey *Tetrahymena pyriformis* (hereafter *Tetrahymena*) and basal resources (mixed bacteria), was investigated at five different levels of enrichment over 144 days (Diehl and Feissel 2000). Consistent with theory, all three species were able to coexist only at an intermediate level of productivity. The IG prey competitively excluded the IG predator at the lowest nutrient levels and the IG predator excluded the IG prey with increasing enrichment. Unpredicted extinction of the IG predator at the highest nutrient level may have been caused by transient dynamics and inability of IG predator to recover from low population densities (Diehl and Feissel 2000). Similarly, the coexistence of an IG predator with an IG prey was possible only at an intermediate level of productivity in a system containing *Blepharisma*, *Colpidium*, and bacteria (Morin 1999). The IG prey *Colpidium* was a superior competitor for shared resources in these microcosms. A more complex four-species food web, consisting of *Blepharisma* feeding on both resources (mixed bacteria) and two IG prey (bacterivorous ciliates *Tetrahymena* and *Colpidium*), was investigated across an enrichment gradient (Liess and Diehl 2006). A strong destabilizing effect of the IG predator was demonstrated in this study. In contrast to outcomes of simple three-species models (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001) and previous experimental work (Morin 1999, Diehl and Feissel 2000, 2001) coexistence of the IG predator with the IG prey was not achieved. Both *Tetrahymena* and *Colpidium* went extinct or persisted at very low densities in the presence of *Blepharisma* across all enrichment levels.

In summary, controlled laboratory food webs modules generally confirmed the early predictions and showed that coexistence of an omnivore, consumer and basal resource is restricted to very specific conditions. However, none of these experiments directly manipulated the strength of the omnivorous interactions, so the predicted stabilizing effect of weak omnivory could not be tested directly. Potentially stabilizing effects have been demonstrated for the population dynamics of the omnivore but not of the consumer.

While microcosm studies make up the majority of the experimental examinations, larger-scale experiments also provide evidence for effects of omnivory on stability. One of the few direct experimental tests of food web stability as a function of an increasing degree of omnivory was conducted using natural arthropod assemblages (Fagan 1997). In this case, stability was defined as the capacity of the community to recover from a perturbation. Experimental plots were established with omnivorous wolf spiders (*Pardosa mackenziana* and *Pardosa wyuta*), a non-omnivorous damselbug (*Nabis alternatus uniformis*), or a mix of all three species. As a disturbance, the plots were then exposed to two levels of an aphicide that strongly reduced densities of the aphid *Macrosiphum valeriani*, an important prey item of *Nabis*. The responses of the fourteen most abundant arthropod species in the plots were measured, and it was found that a high degree of omnivory did stabilize the community dynamics after perturbation (Fagan 1997). In contrast, manipulating omnivory at the predator level resulted in increased temporal variability of herbivore populations in a sub-tidal marine food web (Long et al. 2011).

What Features Stabilize Omnivorous Interactions?

Many of the early theoretical studies and some microcosm experiments suggested that omnivory should rarely be a stabilizing feature in food webs, making it a challenge to explain the ubiquity of omnivory in natural systems. Explanations for this discrepancy are beginning to emerge from later studies that incorporate more realistic biological parameters. Theoretical and experimental work has begun to reveal ecological mechanisms through which omnivory can persist and even stabilize food webs.

Theoretical studies using a non-equilibrium dynamic approach and increased biological realism brought more evidence for the stabilizing role of omnivory. The extension of models beyond simple Lotka-Volterra models allows the incorporation of non-linear functional responses and other realistic assumptions. Weak omnivory has been shown to stabilize three-species systems that would otherwise show chaos, transient chaos, and limit cycles (McCann and Hastings 1997). A stable equilibrium point remained in the food web with omnivory, but the system became less persistent as the strength of omnivory increased (McCann and Hastings 1997). Another model examining trade-offs between predatory and competitive ability also supported the key role of weak interaction strengths (HilleRisLambers and Dieckmann 2003). Here, the coexistence was most likely at intermediate level of trade-offs, when attack rates were low enough to allow persistence of consumers but still provided energy intake to support a viable population of omnivores (HilleRisLambers and Dieckmann 2003). The development of a novel framework that combines the classic community matrix approach (e.g., Pimm and Lawton 1978) with more recent modular analysis (e.g., McCann and Hastings 1997), further confirmed that the stabilizing role of omnivory strongly depends on the strength of trophic interactions (Gellner and McCann 2012). While strong omnivory is always destabilizing, weak to intermediate omnivorous interaction strengths confer substantial stability to food webs in most cases (Gellner and McCann 2012).

Omnivory can alter the system dynamics, depending on which transitional state between the food web modules it represents (Vandermeer 2006; Fig. 1). Analysis of the transition from a tritrophic food chain to exploitative competition corroborated the stabilizing effect of weak omnivory (McCann and Hastings 1997). However, a numerical search over the parameter space resulted in sets of parameter values that show also examples of decreased food web stability (Vandermeer 2006). Similarly, another study that measured susceptibility to perturbation (in this case, the per capita death rate at a focal trophic level) found that omnivory can both increase and decrease stability (Ispolatov and Doebeli 2011). The direction of the effect depended on the position of the omnivorous link and/or perturbation relative to the top predators. A qualitatively similar outcome has been indicated for different stability measures, in models using non-linear functional response, and in food webs that have more complex architecture (Ispolatov and Doebeli 2011). In sum, new theory shows a wider range of conditions for which omnivory is a stabilizing force, but suggests that we may not always be able to assess stability using only the architecture of studied food webs.

A number of stabilizing factors have recently been recognized by ecologists, and these may help to explain how omnivory persists and stabilizes natural systems (Fig. 2). We have grouped these mechanisms into five main categories: habitat complexity (including prey refuges), antipredator phenotypes of prey, adaptive feeding behavior of omnivores, life-history omnivory and interference between omnivores. Furthermore, consumers and resources outside of the focal food web module can also explain stability of modules that would not persist in isolation.

Prey refuges and habitat complexity

Ecological mechanisms that weaken the interaction strength between predators and prey generally stabilize food webs (May 1973, McCann et al. 1998). Spatial and temporal refugia allowing prey to avoid omnivores have been proposed as potentially stabilizing factors. For example, a set of dynamic models based on a benthic food web concluded that the parameter space where omnivory can persist was extended when refugia from omnivores were present (HilleRisLambers et al. 2006). This led to de-

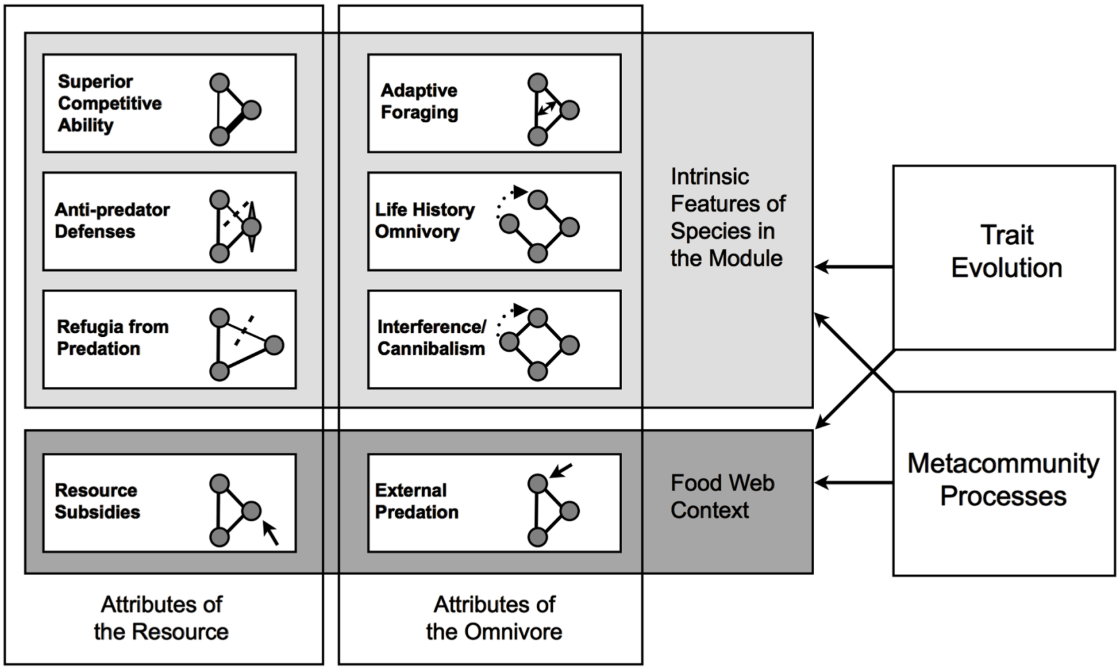

Fig. 2. Summary of the major factors that enhance the stability and long-term persistence of food webs with omnivory. We represent omnivory as an intraguild predation module, and loosely group stabilizing factors into those more directly affecting the omnivore or the consumer, and those more associated with features of the organisms in the module or with the surrounding food web. Each of these mechanisms can be influenced by trait evolution or dispersal processes, and potentially modeled on a landscape scale using an evolutionary metacommunity framework.

creased interaction strengths in the food web and extended the range of productivity along which all species could persist.

Structural habitat complexity can reduce encounter or capture rates between an omnivore and its prey. Habitat structure has been experimentally shown to provide refuges for IG prey and substantially weaken trophic interactions between IG prey and IG predator (Persson and Eklöv 1995). Predators may also induce shifts in habitat use by conspecific juveniles, which in turn alters competitive interaction between the IG prey and juvenile predator (Persson and Eklöv 1995). The effect of refugia weakening trophic interactions has been documented from numerous systems (e.g., Warfe and Barmuta 2004, Finke and Denno 2006) and confirmed in a meta-analysis (Janssen et al. 2007). Although the short-term studies reviewed in Janssen et al. (2007) are often difficult to extrapolate to long-term dynamics (Briggs and Borer 2005), the reduction in the species' interaction strengths suggests the importance of spatial heterogeneity for persistence of omnivorous systems.

Experimental evidence for the stabilizing effect of spatial heterogeneity was also shown in a microcosm experiment (Liess and Diehl 2006). The absence of wheat seeds (a potential refuge from predation) in the microcosm increased the omnivore's (*Blepharisma*) encounter and attack rates with ciliates and bacteria and prevented coexistence (Liess and Diehl 2006). In contrast, the reduction of the omnivore's attack rate as a result of spatial heterogeneity in previous experiments (Morin 1999, Diehl and Feissel 2000, 2001) might have facilitated the persistence of the IG prey. Such results support the conclusion that spatial refuges can positively affect persistence of food webs with omnivory in natural ecosystems (HilleRisLambers et al. 2006).

Refugia from predation can be temporal as well as spatial. The presence of temporal prey refugia promoted coexistence in a model of two competing parasitoids including a superior resource competitor, and an IG predator (Amarasekare 2007*a*). A model testing the theory of temporal refugia due to differing cold tolerance of the two species explained the conflict between lab experiments, in which the IG prey is excluded within one generation, and field observations in which the two parasitoids have coexisted for decades. Adding a time period in which the IG prey was free of the IG predator allowed coexistence of the two species (Amarasekare 2007*a*).

Antipredator defence by prey

Many species induce changes in their morphology, behavior, and life history in response to cues from natural enemies. Such inducible defenses are widespread across a wide variety of taxa, and often reduce per capita predation rates (Harvell 1990, Tollrian and Harvell 1999). Both theoretical studies and recent microcosm experiments support the hypothesis that inducible prey defences act as stabilizing forces in simple food webs with omnivory.

The seminal theoretical study of intraguild predation suggested that antipredator behavior in prey could stabilize IGP systems (Holt and Polis 1997, see also Kimbrell et al. 2007). In 3-species models, inducible defences did, in fact, increase the range of conditions under which IG predators and IG prey could coexist. This outcome was confined to intermediate levels of enrichment; IG prey species were still driven extinct at high levels of productivity (Urbani and Ramos-Jiliberto 2010). The stability of omnivorous food webs including inducible defences in prey has been shown to either increase or decrease with resource enrichment (Abrams and Fung 2010*b*). Inducible defences increased the parameter space allowing intraguild prey to persist or even increase in density at high levels of productivity (Abrams and Fung 2010*b*). However, the predictions of these models may be modified by the temporal scale of the adaptive response considered. Specifically, inducible defences that have considerable time-lags between the onset of predation and induction or relaxation of defences can destabilize simple predator-prey models (Underwood 1999, Luttbeg and Schmitz 2000, Miner et al. 2005; but see Abrams 1992).

Empirical studies provide some evidence that inducible antipredator defences increase the persistence of IG prey. In a microcosm experiment that varied the levels of inducible defences in the IG prey, the more plastic prey species with greater ability to induce defensive morphology were able to persist significantly longer in the presence of the IG predator (Kratina et al. 2010). Given the short timescale of the response in this model system, increased persistence likely resulted from weakening the interaction strengths between IG prey and IG predator.

Prey defences may evolve over extended exposure to an omnivore instead of being induced by short-term exposure. A mesocosm experiment including an IG predator (prickly sculpin, *Cottus asper*), and prey (threespine stickleback, *Gasterosteus aculeatus*), showed that prey that had coevolved with the IG predator were more heavily armoured and less vulnerable to predation (Ingram et al. 2012). This suggests that IG prey persistence may be enhanced by defences that result from evolutionary response to an IG predator as well as from from phenotypic plasticity. While the effect of inducible defences may vary due to resource enrichment, time-lags or costs to defence traits, there is general support for the prediction that prey defences contribute to greater persistence of food webs with omnivory.

Adaptive feeding behavior of omnivores

Another biologically realistic factor that may promote stability in food web models with omnivory is adaptive foraging (Holt and Polis 1997). The omnivore may modify its diet based on the profitability and abundance of its two resources, either by switching prey or by adjusting the proportion of each in a mixed diet. A potential outcome is that if either the resource or consumer becomes temporarily depleted, it will suffer reduced exploitation by the omnivore, allowing it to recover and stabilizing the system. A series of theoretical explorations has shown that adaptive omnivory can have a positive effect on the permanence of a tri-trophic system, although the magnitude of the stabilizing effect depends on the details of the foraging model (Křivan 2000, Křivan and Schmitz 2003, Křivan and Diehl 2005, Abrams and Fung 2010*a*).

Křivan (2000) showed that the coexistence occurred across a substantially wider region of parameter space when an omnivore adaptively switched between feeding on the resource and on the consumer in response to their densities. Subsequent work showed that coexistence was also facilitated when the omnivore adaptively changed the proportion of each prey in its diet, although this result was weaker and restricted to certain conditions (Křivan and Diehl 2005). In particular, this effect only increased the persistence of the omnivore when it would otherwise be excluded due to competition, and may not by itself explain the persistence of consumers or the prevalence of omnivory in natural communities. Another model with optimal foraging allowed the coexistence of omnivore and consumer over a wider range of degrees of omnivory (ω parameter in Vandermeer 2006) than models without prey switching (Faria and Costa 2009). Finally, Abrams and Fung (2010*a*) demonstrated that all three species can coexist across a wide range of productivities if the omnivore exhibits adaptive prey choice and cannot persist on basal resource alone, or if its functional response to the basal resource is substantially less linear than that of the prey (Abrams and Fung 2010*a*). These results add to a growing number of conditions under which omnivores can persist and even maintain high density at high levels of resource productivity (Abrams and Fung 2010*a*).

Life-history omnivory

Early theory examining the local stability of equilibria predicted that inclusion of a diet shift in the life history of an omnivore would weaken its destabilizing effect on food webs (Pimm and Rice 1987). Food webs with trophic links introduced as life-history omnivory remained less stable than those with no omnivorous links, but the destabilizing effect was less pronounced than in food webs with standard omnivory (Pimm and Rice 1987). Analyses of a model that incorporated a size refuge for the IG prey, or a predatory life stage incapable of IGP, confirmed predictions about coexistence limited to intermediate levels of resource productivity (Mylius et al. 2001).

Subsequent size-structured models have incorporated more detail into the life histories of omnivores and their prey. The presence of life-history omnivory decreased the probability of coexistence for the IG prey and IG predator under the assumption that adult IG predators can be sustained on basal resources alone (van de Wolfshaar et al. 2006). The lack of stable coexistence resulted from a positive feedback between food-dependent growth and size-dependent foraging. In contrast, increasing coexistence of IG predator and IG prey over a wide range of productivity gradient was demonstrated when adult predators exclusively consume IG prey, reducing competition between juvenile predators and IG prey (Hin et al. 2011). Alternatively, predators may be excluded if they compete strongly with IG prey as juveniles, which reduces their predation rates on IG prey as adults (Hin et al. 2011).

Mutual predation between the IG prey and IG predator is a common phenomenon in size-structured food webs (Polis et al. 1989, Wissinger 1992, Woodward and Hildrew 2002). Experimental work shows that resident stage-structured IG prey can become invulnerable to invasions by IG predators in productive environments when they reach high densities and their adults feed on vulnerable stages (e.g., larvae) of IG predator (Montserrat et al. 2012). Resident stage-structured IG predators also cannot be invaded by IG prey in food webs with mutual predation and high levels of productivity (Montserrat et al. 2008). Persistence of these systems in nature is likely conferred by spatial segregation of IG prey and predator brought about by habitat complexity (Montserrat et al. 2012).

Enrichment of the basal resource may cause frequent transitions between alternative states with or without the omnivore, under the assumption of discrete shifts between the juvenile and adult diet of the omnivore. Further analyses showed that coexistence and stability are possible under specific conditions; for example, if the IG prey is a superior competitor for resources and there is low mortality rate of adult IG predators (Abrams 2011). A model including a time-delay for a maturation period of the IG predator also found stability only at a narrow range of maturation period and at low predator mortality rates (Yamaguchi et al. 2007). Overall, theory shows that life-history omnivory *can* stabilize food webs, but that feedbacks between the growth of the juvenile IG predator and their foraging ability on the IG prey restrict this effect to specific conditions. Empirical tests of these dynamic model predictions are still extremely scarce and open an important avenue for future research.

Interference among omnivores

There is evidence that predators both alter their foraging behavior in the presence of other predators, and engage in intraspecific interference (Hassell 1978, Skalski and Gilliam 2001, Kratina et al. 2009). Interference among omnivores is often generated by aggressive behavior or cannibalism by larger individuals (Crowley and Martin 1989, Polis et al. 1989, Arim and Marquet 2004, Crumrine 2005) and is expected to be more common in actively searching than in sit-and-wait predators (Delclos and Rudolf 2011). This density-dependent process can result in reduction of the per capita interaction strength between omnivore and consumer and dampen strong population cycles across a productivity gradient.

Addition of predator interference to an unstructured IGP model enhanced the upper limit of resource productivity where IG prey persists, but only under the assumption of strong fitness cost to the IG predator (Amarasekare 2008). In contrast, the persistence is reduced when predator gains a net per capita benefit from interference. Analyses of a stage-structured model with intraspecific interference predicted a wider range of productivity allowing stable coexistence than an unstructured IGP model (Amarasekare 2008).

Size-structured cannibalism and asymmetrical competitive and behavioral interactions result in a trophic structure with different dynamic properties than unstructured systems (Persson et al. 2000, Claessen et al. 2004, Rudolf 2006, 2007*b*). Although the interactions between cannibalistic mortality and time delays in simple models can have a destabilizing effect, cannibalism can stabilize predator-prey cycles generated by different density-dependent mechanisms (Claessen et al. 2004). A recent model of the stage-structured cannibalistic omnivore showed increased stability and species coexistence even if the IG predator was a superior competitor for the basal resources (Rudolf 2007*a*). When predation by the IG predator targets members of its own species (density-dependent cannibalism) in addition to the IG prey, it introduces a degree of self-regulation that counters its competitive and predatory advantage over the IG prey (Rudolf 2007*a*). Lower temporal variability and increased persistence of omnivores that feed on conspecifics (cannibals) has been supported by microcosm experiments (Holyoak and Sachdev 1998). Behavioral interference among cannibals and smaller conspecifics in the IG predator has also been shown to enhance food web stability (Rudolf 2007*b*).

In a system with size-structured IG prey, large cannibals of prey and top predators displayed different behaviors when exposed to conspecifics versus to each other and direct behavioral interference resulted in mortality risk reduction for smaller IG prey (Crumrine and Crowley 2003, Rudolf and Armstrong 2008). It has been also shown that IG prey can distinguish between conspecific cannibals and heterospecific predators and alter their behavior specifically to the threat (Rudolf and Armstrong 2008). These changes in trophic interactions likely alter food web dynamics, however, stability effects of intraspecific interference remain to be tested in long-term multigenerational experiments.

BROADER FOOD WEB CONTEXT

Most of the studies reviewed above examined the effects of omnivory on persistence and stability of three or four interacting species. In nature, however, such modules are embedded in far more complex communities, which may influence the dynamics within the module. An omnivory module may be affected by shared top predators, additional resource subsidies to consumers (IG prey), and neighboring modules including other omnivory modules. These interactions with the surrounding food web can influence the stability of omnivorous interactions.

Theory shows that the presence of a shared top predator can stabilize the dynamics of a food web involving intraguild predation. In the case where the IG predator is a superior competitor for the basal resource, it is typically expected to exclude the IG prey (Polis and Holt 1992). However, if the shared top predator feeds preferentially on the IG predator (relative to the IG prey), it can stabilize the food web by preventing the exclusion of the IG prey (Hall 2011). Another model found that addition of a top predator feeding on the IG predator created highly unstable dynamics (Namba et al. 2008). However, in this model the IG prey was more efficient at consuming the basal resource. Adding a fourth species to the model that consumed only the IG prey greatly stabilized the food web dynamics (Namba et al. 2008). These two studies show generally, that the presence of a top predator in the system can stabilize otherwise unstable dynamics, provided it feeds preferentially on the more efficient competitor for the basal resource. This stabilizing effect is supported by a whole lake invasion study in which the IG prey (roach, *Rutilus rutilus*) could only establish in the presence of an additional predator (pike, *Esox lucius*) feeding preferentially on the IG predator (perch, *Perca fluviatilis*; Persson et al. 2007).

Another way in which species external to an omnivory module can confer stability is if the IG prey is subsidized by additional resources that are not shared with the IG predator. Theoretical work has shown that the availability of non-shared resources often allows the IG prey to persist even if it is the inferior competitor for the shared resource (Daugherty et al. 2007, Holt and Huxel 2007). If the alternative resources are spatially or temporally segregated from the shared resources, the subsidy may act in concert with refugia from predation. Resource subsidy appears to play a role in the persistence of threespine stickleback in the presence of their IG predator, as stickleback have evolved preferences and morphology to feed more on zooplankton when they are sympatric with benthic sculpin (Ingram et al. 2012).

Surrounding modules in the community can stabilize the otherwise unstable omnivorous module in which the IG predator is a better competitor for resources than the IG prey. In an extensive analysis of fish feeding modules from a Caribbean food web, the proportion of modules predicted to be intrinsically stable due to the competitive superiority of IG prey was higher than expected by chance (Kondoh 2008). Omnivorous modules that were intrinsically unstable were still present in the community, but were surrounded by stable modules that benefited the IG prey more often than expected by chance. This suggests that the broader food web context of unstable modules enabled their long-term persistence (Kondoh 2008). Another study examined the persistence of different module types in isolation, their influence on persistence of the whole community, and the prevalence of those module types in real communities. While the omnivory modules were less persistent than tri-trophic food chains in isolation, having a greater proportion of omnivory modules in the community conferred the greatest benefit to the persistence of the whole community (Stouffer and Bascompte 2010). A survey of the representation of modules in real food webs found that omnivory modules do tend to be over-represented in relation to other modules, suggesting that they are an important stabilizing feature of many natural systems (Stouffer and Bascompte 2010).

Conclusions

In classical representations of food webs, each organism is slotted into a distinct trophic level, and derives all its energy from the trophic level immediately below its own (Elton 1927, Lindeman 1942). However, as many consumers select resources based on availability, size or nutritional quality rather than trophic level per se (Diehl 1993, Woodward and Hildrew 2002), species' diets can include plant matter as well as herbivorous and carnivorous prey (Polis et al. 1989, Polis 1991). Omnivory thus increases the connectance or complexity of a food web, which is predicted to decrease the stability of randomly assembled communities (May 1973). Indeed, early mathematical analyses and some laboratory experiments with three or four species exhibited limited coexistence and lower stability when omnivory was added (Pimm and Lawton 1978, Pimm 1982). Contrasting empirical results showing that omnivory is widespread in nature stimulated further theoretical and experimental explorations.

New theoretical advances, supported by the early empirical work, have demonstrated that omnivory in natural food webs can be stabilized by a diverse set of processes that weaken the strength of the omnivorous interactions (e.g., Amarasekare 2007*a*, Daugherty et al. 2007, Janssen et al. 2007, Kondoh 2008, Namba et al. 2008, Gellner and McCann 2012, Ingram et al. 2012). We identified a number of broad categories of conditions under which omnivory can be stabilizing. The presence of prey refugia or adaptive antipredator defence can reduce the vulnerability of consumers to omnivores and prevent their exclusion. Adaptive feeding behavior by omnivores can reduce predation pressure on depleted consumer populations and allow them to recover. Changes over the life-history of the omnivore, including cannibalism and other forms of interference can also serve to reduce the strength of omnivory. Finally, even if omnivorous interactions are not intrinsically stable, they may be stabilized by interactions with species in the broader food web.

The presence and effectiveness of these factors depend upon the identity and characteristics of species in the omnivory module and in the broader ecological network. The diversity and traits of species found locally may be influenced both by interactions with a surrounding metacommunity and evolutionary processes that alter species interactions. Evolutionary dynamics and metacommunity processes have the potential to modify both internal stabilizing mechanisms for omnivory modules such as prey switching and prey refugia and external interactions with the rest of the food web (Fig. 2). Combining all of these components to understand the role of omnivory in stabilizing food webs within evolving metacommunities is the next step toward resolving the omnivory-stability debate.

Future Directions

A few theoretical studies have already begun to explore the relationship of omnivory and stability in metacommunities. It has been suggested that in a landscape of connected patches, omnivory is not only possible, but necessary for the stability of the metacommunity as a whole (Pillai et al. 2011). Furthermore, differential dispersal strategies of omnivores and their prey are likely to play a key role in modulating the system stability (Amarasekare 2006, 2007*b*). As many of the stabilizing mechanisms discussed in this study can be directly incorporated in the metacommunity model, evaluating how the conditions for stability apply at this larger spatio-temporal scale will be an important element of new research.

From the recent attempt to understand omnivory in the unifying metacommunity framework (Pillai et al. 2011), new questions for empirical study arise. Micro- or mesocosm experiments can be used to test the theoretical prediction that both within patch and between patch omnivory and generalist feeding are necessary to support complex metacommunities. Experimental mesocosms and observational studies can be used to test the asymmetrical effect of dispersal strategies of omnivores and consumers on the long-term dynamics of both groups. Comparing these effects of dispersal on stability among food webs that vary in the prevalence and strength of omnivory is another important empirical avenue that could elucidate the relationship between the omnivory-stability link and dispersal within metacommunities.

In addition to incorporating the spatial dimension of a metacommunity context, theory and experiments are beginning to take an evolutionary perspective on the relationship between omnivory and stability. Evolutionary assembly models simulate the emergence of complex food webs through speciation and trait evolution (Caldarelli et al. 1998). One size-structured evolutionary assembly model predicted that variation in the strength of foraging trade-offs could result in an emergent positive relationship between the level of omnivory and the rate of species turnover (Ingram et al. 2009). A possible explanation is that because species interactions are stronger in the food webs with strong trade-offs and low omnivory, new species are less able to establish (Case 1990). Concurrent with the development of theory that includes evolutionary processes, empirical work is beginning to address how evolution in the shorter term can modify the strengths of omnivorous interactions (Ingram et al. 2012). A key question will be whether adaptive evolution within a species has a general tendency to increase or decrease the stability of omnivorous interactions in which it is involved.

Theoretical and empirical studies of omnivory in small food web modules have shown several conditions under which omnivory can have a stabilizing influence. While inconsistencies and unanswered questions remain in studies of isolated modules, they have helped to account for the disconnect between early theory and data. The next major step forward will come as this knowledge is applied in the context of larger communities subject to change due to trait evolution and species interactions across space. New empirical studies and understanding the role that omnivory plays in the structure and stability of natural evolutionary metacommunities will be an essential part of a more predictive theory of omnivory.

ACKNOWLEDGMENTS

This research was funded by the Canada Research Chairs Program to B.R.A. and the Natural Sciences and Engineering Research Council (NSERC) of Canada to P.K., R.M.L, T.I. and B.R.A.

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