UC Davis

UC Davis Previously Published Works

Title

Temporal Variation in Trophic Cascades

Permalink

<https://escholarship.org/uc/item/5p6796tc>

Journal

Annual Review of Ecology, Evolution, and Systematics, 48(1)

ISSN

1543-592X

Authors

Piovia-Scott, J
Yang, LH
Wright, AN

Publication Date

2017-11-02

DOI

10.1146/annurev-ecolsys-121415-032246

Peer reviewed

Title: Temporal variation in trophic cascades

Authors: Jonah Piovia-Scott^{1*}, Louie H. Yang², Amber N. Wright³

¹ School of Biological Sciences, Washington State University, Vancouver; jonah.piovia-scott@wsu.edu

² Department of Entomology and Nematology, University of California, Davis; lhyang@ucdavis.edu

³ Department of Biology, University of Hawaii, Manoa; anwright@hawaii.edu

* corresponding author: 14204 NE Salmon Creek Ave, Vancouver, WA 98686.

Running title: Trophic cascades in time

Keywords: food web, community, predator, indirect effect, species interactions, global environmental change

Abstract

The trophic cascade has emerged as a key paradigm in ecology. While ecologists have made progress in understanding spatial variation in the strength of trophic cascades, temporal variation remains relatively unexplored. Our review suggests that strong trophic cascades are often transient, appearing when ecological conditions support high consumer abundance and rapidly growing, highly edible prey. Persistent top-down control is expected to decay over time in the absence of external drivers, as strong top-down control favors the emergence of better-defended resources. Temporal shifts in cascade strength – including those driven by contemporary global change – can either stabilize or destabilize ecological communities. We suggest that a more temporally explicit approach can improve our ability to explain the drivers of trophic cascades and predict the impact of changing cascade strength on community dynamics.

1. Introduction

The trophic cascade has emerged as a key paradigm in community ecology (Terborgh & Estes 2010). This paradigm holds that consumer limitation of lower trophic levels (also known as top-down control) plays an important role in determining community composition and ecosystem function. In the last few decades, ecologists have made great progress in understanding spatial variation in the strength of trophic cascades (Menge 1995, Paine 1980, Polis et al. 1997, Power et al. 1996, Shurin et al. 2002, 2006; Strong 1992). However, temporal variation in the strength of trophic cascades remains relatively unexplored. This is an important knowledge gap, as changes in the strength of trophic cascades over time have been associated with dramatic shifts in community structure and function (Folke et al. 2004). In addition, a more temporally-explicit approach to trophic cascades promises to improve our understanding of the underlying drivers of top-down control and enhance our ability to predict how food webs respond to perturbations on multiple time scales. We suggest that the nature of temporal variation in trophic cascades will have important implications for evaluating the role of predators and pathogens in community dynamics, and will inform our understanding of how species interactions mediate the effects of environmental change on ecological communities.

2. What is a trophic cascade, and why does trophic cascade strength vary?

2.1 Definitions and historical context

We define a trophic cascade as an indirect species interaction that originates with a consumer and spreads downward through more than one linked consumer-resource interactions in a food web. This definition is consistent with Paine's original formulation of the concept, in which "destabilizations at the highest trophic level induce structural changes which cascade through the community, transmitted by a chain of strongly interacting links" (Paine 1980). This definition also adheres closely to that recently proposed by Ripple et al. (2016), although we have generalized their definition to include all consumers, rather than just predators, as parasites and pathogens can also trigger strong trophic cascades (Lafferty et al. 2008, Preston et al. 2016). The simplest trophic cascades involve three species (Figure 1), but indirect effects that are transmitted through longer chains of sequential consumer-resource interactions are also considered trophic cascades. Importantly, this definition includes interaction pathways that are mediated by either density or traits (such as behaviors) of the transmitting consumer(s) (Abrams 1995, Werner & Peacor 2003). Consistent with previous surveys of indirect effects (Menge 1995, Wootton 1994), we adhere to a broad definition that characterizes any indirect effect fitting the configuration and definition described above as a trophic cascade.

The 'Green World Hypothesis' (Hairston et al. 1960) formalized ideas about top-down control extending across multiple trophic levels and the term trophic cascade was later coined to describe these effects (Paine 1980). In subsequent decades, robust empirical evidence for trophic cascades began to accumulate in a range of ecosystems, most notably subtidal nearshore marine environments (Estes & Palmisano 1974), rivers (Power et al. 1985), and

temperate lakes (Carpenter & Kitchell 1993). Eventually, formal meta-analytic methods began to be applied to evaluate the frequency and importance of trophic cascades (Brett & Goldman 1996, Halaj & Wise 2001, Schmitz et al. 2000). These advances facilitated a shift in emphasis from qualitative inquiries (e.g., Are trophic cascades common or uncommon?) to quantitative inquiries (e.g., What drives variation in the strength of trophic cascades?) (e.g., Borer et al. 2005; Shurin et al. 2002, 2006). While the expectation that the strength of trophic cascades will vary in both space and time was articulated more than 20 years ago (e.g., Hunter & Price 1992, Power 1992, Schoenly & Cohen 1991), synthetic studies conducted to date have focused on variation in space, both within and among systems (e.g., Shurin et al. 2002, 2006). The current review seeks to expand the scope of exploration into varying trophic cascade strength – whereas previous inquiries have examined where we should expect to see strong trophic cascades, we ask when we should expect to see strong trophic cascades.

2.2 Mechanisms underlying variation in cascade strength

Variation in trophic cascade strength can be caused by differences in the characteristics of consumers, resources, and the broader ecological context surrounding the focal interactions. Most of the specific mechanisms underlying variation in trophic cascade strength were first proposed in conceptual papers (e.g., Paine 1980, Polis 1999, Polis & Strong 1996, Strong 1992), but in recent years meta-analyses have brought synthetic data to bear on these hypotheses (Borer et al. 2005, Shurin et al. 2002).

Properties of consumers and resources that can affect cascade strength include the following:

1. Consumer traits: size, mobility, metabolic efficiency, territoriality, and degree of omnivory (Borer et al. 2005, Estes 1995, McCauley et al. 2012, Paine 1988, Polis 1999, Strong 1992, Yodzis & Innes 1992).
2. Resource traits: growth rate, reproductive capacity, defensive investment, and nutrient content (Coley et al. 1985, Power 1992, Shurin et al. 2006, Shurin & Seabloom 2005).
3. Characteristics of particular consumer-resource interactions: resource quality (including both stoichiometric differences and effectiveness of anti-consumer defenses), abundance ratio, and body-size ratio (Borer et al. 2005, Heath et al. 2014, McCann et al. 1998, Shurin et al. 2006, Shurin & Seabloom 2005, Yodzis & Innes 1992).

Aspects of the ecological context that are thought to influence trophic cascade strength include the following:

1. Spatial heterogeneity or spatial extent of habitat (Borer et al. 2005, McCann et al. 2005, Paine 1988, Polis & Strong 1996).
2. The complexity of the food web in which the trophic cascade is embedded (Duffy 2002, Duffy et al. 2007, Finke & Denno 2004, Halaj & Wise 2001, Pimm 1982, Polis & Strong 1996, Strong 1992).
3. Spatial resource subsidies, which can alter trophic cascades by increasing or stabilizing consumer abundance (Leroux & Loreau 2008, Polis et al. 1997) or by causing shifts in consumer diet or behavior (Fahimipour & Anderson 2015, Takimoto et al. 2009).

4. Control of populations and traits by the abiotic environment (e.g., Menge & Sutherland 1987, Paine 1980, Polis 1999).

Reviews and meta-analyses of empirical studies of spatial variation in trophic cascade strength have provided support for many of the mechanisms described above. For example, Borer et al. (2005) found evidence suggesting that the metabolic efficiency of herbivores is associated with cascade strength, and Shurin et al. (2002, 2006) argued that the high growth rate, small size, and nutritional quality of autotrophs are key drivers of strong cascades in aquatic ecosystems. These studies highlight the critical importance of primary consumers in determining cascade strength – many studies show strong predator control of herbivores, but relatively weaker herbivore control of primary producers (e.g., McQueen & Post 1988).

2.3 Measuring temporal variation in the strength of trophic cascades

A trophic cascade can be detected and measured when a perturbation to the initiating consumer has a direct effect on a transmitting consumer, which in turn has a direct effect on a lower-level, receiving resource (Figure 1; Abrams 1995, Abrams et al. 1996). This is usually achieved in ecological field studies by comparing areas with and without the initiating consumer (Ripple et al. 2016), an approach that yields a quantitative measure of trophic cascade strength based on responses by the lower-level resource. Following this approach, previous synthetic studies have used the log response ratio (a measure of effect size) for the

lower-level resource as a measure of trophic cascade strength (e.g., Borer et al. 2005, Schmitz et al. 2000, Shurin et al. 2002).

Strong evidence for temporal variation in trophic cascades is provided when measurements of trophic cascade strength taken during different time periods in the same system yield ecologically relevant differences. Thus, each system serves as its own 'control', which avoids confounding spatial and temporal variation in cascade strength. Importantly, measurements of trophic cascade strength taken from the same system during different time periods should be based on studies of similar duration, as most measures of ecological effects, including trophic cascades, are inherently time dependent (Berlow et al. 1999, Novak & Wootton 2010). Finally, measurements taken during different time periods should be collected in such a way that diminishes the role of temporal autocorrelation, or carryover effects, in determining measured cascade strength.

Temporal variation in the strength of trophic cascades can occur when the component direct effects vary in time (Figure 1b). When temporal variation in the effects of sequential consumer-resource interactions align in a way that allows these interactions to be linked by the transmitting consumer, trophic cascades can be strong. When this alignment does not occur, cascading effects of initiating consumers on recipient resources are expected to be weak (Figure 1b). It is important to note that while the temporal alignment of effects that allows strong trophic cascades can be associated with synchronous variation in the strength of adjacent consumer-resource interactions, such synchrony is not required – time lags could

allow non-synchronous episodes of strong direct consumer-resource interactions to be linked. This perspective on temporal variation in trophic cascade strength is consistent with previous explorations of indirect effects in food webs, which have noted that they are likely to be more variable in time than direct effects due to an increase in the probability of “broken” links at any given point in time (Schoener 1993).

3. What drives temporal variation in cascade strength?

Here we review the empirical literature on temporal variation in cascade strength, with a focus on key drivers of this variation. First, we consider abiotic drivers, which include cycles (e.g., diel cycles, seasons), interannual variation, and episodic disturbance events (e.g., storms, floods, fire). Second, we consider biotic drivers, including endogenous changes in community membership (e.g., succession), species abundances (e.g., consumer-resource cycles), and traits of species in the community (e.g., induced defenses, ontogenetic shifts). Finally, we consider changes in the strength of “novel” trophic cascades driven by introduced (exotic) consumers; we consider these cascades to be novel because such a cascade does not exist prior to the introduction of the initiating consumer.

3.1 Abiotic drivers

In many cases, it may be useful to examine short-term variation in a trophic cascade in order to understand when key interactions are occurring, even though the impacts of these effects

manifest over much longer time scales. For example, diel vertical migrations in planktonic food webs, in which visually orienting zooplanktivores cause their zooplankton prey to migrate to deeper water during the day (with cascading effects on phytoplankton), produce diel variation in the strength of cascading top down effects on lower trophic levels (e.g., Bollens et al. 2010, Dini & Carpenter 1991). Diel variation in trophic cascades is known from other systems as well. In an experimental stream, Katano et al. (2013) evaluated the specific effects of several nocturnally and diurnally feeding fish species on a trophic cascade involving fish, benthic invertebrates and algae. They concluded that the diurnal benthic species had a stronger cascading effect than the nocturnal species, perhaps due to higher prey detection efficiency. Finally, in an experimental study specifically examining the effects of diel variation in predation on trophic cascades, Kalka et al. (2008) showed that night-active bats have a larger effect on arthropod densities and herbivory in understory plants than day-active birds, resulting in diel variation in the strength of the cascading effects of aerial vertebrate predators on plants. This experiment was able to disentangle the strength of bat- versus bird-initiated trophic cascades using night- and day-specific whole plant exclosures, illuminating previously unexamined differences in the diurnal versus nocturnal components of a trophic cascade.

Lunar variation can also affect resource-consumer interactions, potentially altering the strength of trophic cascades. Both predators and prey can use lunar variation in coordinated ways. For example, kangaroo rats become less nocturnal and more crepuscular on full moon nights, reducing their vulnerability to nocturnal predators, but increasing their vulnerability to diurnal shrikes (Daly et al. 1992). Similarly, Penteriani et al. (2013) observed that rabbits moved less on

full moon nights, when they are more vulnerable to predators; predatory lynx activity patterns responded to those of their rabbit prey, while activity patterns of mesopredatory foxes (which are predators of rabbits, but are preyed upon by lynx) appear to strike a balance between prey availability and lynx avoidance. In a meta-analysis of 59 nocturnal mammal species (mostly herbivores and omnivores), visually-orienting taxa tended to be more active in moonlight, while species that emphasized other senses became less active (Prugh & Golden 2014). These examples suggest that lunar variation could also affect the strength of trophic cascades on short timescales.

Seasonal variation in trophic cascades can result from changes in the abiotic conditions that constrain and shape species interactions. For example, Norrdahl et al. (2002) observed evidence of a trophic cascade using exclosure experiments that limited predation on voles. Predator exclosure allowed dramatic increases in vole densities, which showed the potential for strong cascading effects on plants when the voles were at high densities. However, the strength of this trophic cascade was strongly limited by severe winter mortality of the voles at their peak, which limited the indirect effects of the predator exclosure on vegetation in the following growing season. Similarly, Rogers et al. (2012) found that the bird-mediated cascading effects of brown tree snakes on spiders varied seasonally. Such seasonal drivers of temporal variation in trophic cascades can involve multiple mechanisms. For example, in an experimental study manipulating the densities of herbivorous and predatory fish, Haavisto and Jormalainen (2014) observed strong seasonal variation in the strength of a trophic cascade affecting algae,

mediated by the interacting effects of seasonally synchronized reproduction in an important grazing species and induced resistance in a foundational alga species.

Year-to-year variation in the relative phenological timing of interacting species could also potentially affect the strength of seasonal trophic cascades. For example, mismatches in the seasonal timing of raptors, passerine birds, herbivorous lepidopterans, and budburst has reduced the strength of top-down control in The Netherlands (Both et al. 2009). Similarly, extreme weather-driven shifts in the arrival of migratory warblers relative to budburst and peak insect abundance were associated with variation in measurements of plant damage in an oak savanna (Wood & Pidgeon 2015). In an experimental study manipulating the developmental stage of larval dragonflies, Rudolf and Rasmussen (2013) observed that large and medium dragonfly nymphs showed stronger cascading effects on plant biomass and net primary productivity than small dragonflies of the same species, suggesting that shifts in phenology and development can drive shifts in the strength of trophic cascades. In a lake system, interannual variation in temperature affected the strength of a trophic cascade by creating phenological mismatches between the departure and arrival of migratory fish and periods of rapid phyto- and zooplankton growth (Brodersen et al. 2011). In general, year-to-year variation in phenological mis-matches between consumers and resources have the potential to alter the nature and magnitude of trophic interactions (Yang & Rudolf 2010), and thus drive temporal variation in the strength of trophic cascades.

Interannual variation in climatic conditions provide some of the most rigorously-documented examples of changes in cascade strength over time. For example, the persistence and mobility of an entomopathogenic nematode predator was increased in wet years characteristic of El Niño-Southern Oscillation events, leading to strong top-down control of ghost moths, with positive effects on bush lupine plants (Preisser & Strong 2004). Similarly, a whole-tree bird exclosure study on cottonwood trees conducted over two years in Utah found evidence of a significant trophic cascade only under particularly wet and productive conditions (Bridgeland et al. 2010). In the wolf-moose-balsam fir cascade on Isle Royale, the strength of the cascade is strongest in high-snowfall years because wolves have higher capture efficiency when moose are encumbered by deep snow (Post et al. 1999); top-down control is weakened in this system when North Atlantic Oscillation forcing causes lower snowfall years. In a grassland ecosystem, cascading effects of spiders on grasshopper herbivores and herbaceous plants were strongest in warmer years, possibly due to changes in herbivore foraging activity (Barton et al. 2009). In addition to the general climatic variation described in the previous examples, interannual variation in the magnitude of seasonal disturbances such as floods, drought, and fire can also cause changes in the strength and direction of trophic cascades over time. In the Eel River, strong cascading effects of predators on algae were observed in years with scouring winter floods – as the community recovered from scouring, predators limited herbivory, and large blooms of filamentous algae occurred (Power et al. 2008). In years without scouring floods, large numbers of heavily-armored caddisfly larvae survived through the winter rainy season and became the dominant herbivore; these grazers resist predation by fish and odonates, eliminating predator-driven cascades. (Power et al. 2008, Wootton et al. 1996).

Episodic disturbance events can affect the strength of trophic cascades via multiple mechanisms. The most dramatic effects occur when a disturbance directly reduces consumer population density, or even drives local extinction of consumers, changing community composition. Such losses would weaken or remove a trophic cascade, which could re-establish and strengthen over time as consumer numbers rebound or consumers re-colonize from elsewhere. For example, anoxic winterkill in a midwestern US lake extirpated largemouth bass, causing a shift from a 4-level to a 3-level trophic cascade (Mittelbach et al. 1995). In the absence of largemouth bass, the lake became dominated by zooplanktivorous fish, reducing the abundance of large *Daphnia* species and water clarity (due to increasing density of phytoplankton). Experimental reintroduction of bass caused the lake to return to pre-winterkill conditions. Disturbances often have direct effects on lower trophic levels as well, and how these lower levels respond can lead to varying strength in cascades over time. For example, on Bahamian islands the cascading effects of lizard predators on plants increased after hurricanes: there were large increases in herbivory on islands without lizard predators following hurricanes, but these differences were less pronounced on islands with lizards (Spiller et al. 2016, Spiller & Schoener 2007). Hypothesized mechanisms include decreased compensation by invertebrate predators in the absence of lizard predators (because invertebrate predators are more vulnerable to hurricane disturbance than lizards), and increased susceptibility of new leaves on plants damaged by hurricanes. Disturbance can also affect cascade strength indirectly by modifying habitat in ways that affect antipredator behavior and foraging patterns of prey (Doherty et al. 2015). In longleaf pine savannahs, fire reduces habitat cover for deer. When

predators are excluded from these open, frequently-disturbed habitats, deer use them more. This change in habitat use causes a shift in which plants are under greater top-down control: deer shift from eating fire-impeding and low-quality woody forage to eating higher quality forage plants in open areas (Cherry et al. 2016).

3.2 Biotic drivers

Changes in the abundance of consumers and resources due to population dynamics can alter the strength of trophic cascades. For example, the well-described population cycles in Canadian lynx and snowshoe hare (e.g., Krebs et al. 1995, 2001a), have also been linked with changes in biomass of forage shrubs, including small birch and willow twigs (Krebs et al. 2001b). These patterns are consistent with a trophic cascade, where temporal variation in the strength of the trophic cascade results from cyclic changes in the abundance of initiating consumers and transmitting consumers. Importantly, however, it remains unclear whether temporal variation in this trophic cascade could play a key role in driving the cyclic population dynamics themselves (Krebs et al. 2001a,b), potentially through reductions in forage quality, or lagged overcompensatory growth responses of the shrubs to herbivory (Krebs et al. 2001a). By comparison, in the case of the southern pine beetle, top-down control by a predaceous clerid beetle does seem capable of driving population cycles (Reeve & Turchin 2002, Turchin et al. 1999). The cyclic reduction in southern pine beetle densities is of a sufficient magnitude to reduce the number of trees killed (Reeve & Turchin 2002), thus driving temporal variation in a trophic cascade.

Endogenous changes in community composition can directly affect the consumers and resources involved in a trophic cascade. Such changes in community composition may commonly occur as a result of succession, wherein a community could shift from a state in which a given trophic cascade is strong to one in which it is weaker or nonexistent (Power et al. 1996). Classic examples of trophic cascades in early successional old-field communities (e.g., Moran & Hurd 1998, Schmitz 1998) are dependent on a vegetation community which is profoundly changed over successional time. Changes in community composition are also predicted to arise as a result of top-down processes themselves if the relative abundance of different resource species changes as a result of differential consumption of relatively edible versus inedible species (Borer et al. 2005, Holt et al. 1994, Leibold 1989, Leibold et al. 1997). Such directional changes in community composition would generally be expected to weaken the strength of trophic cascades over time, as resources or transmitting consumers become increasingly inedible (Power et al. 1996), although consumers may evolve counter-adaptations that reinvigorate top-down processes (Ehrlich & Raven 1964).

Variation in the strength of trophic cascades would also be expected to result from changes in the traits of species (due to ontogenetic shifts, phenotypic plasticity, or adaptive evolution), even without changes in community membership. For example, ontogenetic changes can reduce top-down control by consumers (Werner & Gilliam 1984). In addition, a straightforward extension of the theoretical expectations based on species turnover discussed above (e.g., Leibold 1989, Leibold et al. 1997) can be applied to examples involving trait changes within

species. Phenotypic plasticity in edibility (i.e., induced defenses) would be expected to weaken the strength of trophic cascades. For example, a trophic cascade linking carnivorous zooplankton, herbivorous zooplankton and algae in experimental microcosms was stronger with an uninducible herbivorous rotifer than with a similar rotifer species that induces defensive spines (van der Stap et al. 2007), consistent with the idea that inducible defenses per se weaken trophic cascades. Similarly, adaptive evolution can also drive similar shifts in cascade strength. For example, a mesocosm experiment by Ingram et al (2012) showed that the cascading effects of sculpin on benthic invertebrates tended to be reduced when sticklebacks (the transmitting consumer) were from populations that had evolved defensive adaptations to sculpin predation. Thus, available studies suggest that adaptive changes in resource traits that weaken direct effects of consumers on resources are also likely to weaken the overall trophic cascade.

3.3 Species Introductions and Novel Cascades

Novel consumer introductions (i.e., biological invasions) provide some particularly strong examples of temporal variation in trophic cascades. These introductions can have unexpected consequences in communities because they involve the creation of novel (i.e., “no-analog”, Williams & Jackson 2007) species assemblages which lack a shared ecological and evolutionary history. Introduced predators and pathogens often have particularly dramatic effects on lower trophic levels, and there is substantial evidence that strong novel cascades can be triggered by introduced predators (Kurle et al. 2008, O’Dowd et al. 2003, Rogers et al. 2012, Townsend

2003) and pathogens (Holdo et al. 2009, Lessios 1988, Schultz et al. 2016, Sumption & Flowerdew 1985). However, similar to the population dynamics of introduced species, there is some evidence that cascades driven by introduced consumers can show an initial “lag” phase (sensu Sakai et al. 2001), during which cascade strength is relatively weak, and an attenuation phase during which strong cascades weaken as the community responds and adapts to the novel situation. For example, yellow crazy ants invaded Christmas Island (in the northeast Indian Ocean) in the early 20th century (O’Dowd et al. 2003). This introduced omnivore persisted at low densities for many decades, with little impact on island food webs. At the end of the 20th century, supercolonies began to form and ant densities increased greatly, initiating cascading effects on plant recruitment and litter breakdown via interactions with red land crabs and honeydew-producing scale insects. However, there is some evidence that the densities and impacts of these ants may have declined (Abbott 2005, Cooling & Hoffmann 2015), which could lead to an attenuation of cascading effects. A pronounced lag phase in the emergence of a novel cascade also occurred in Flathead Lake, where introduced lake trout had cascading effects on zooplankton and phytoplankton, but only after an introduced shrimp facilitated an expansion of the lake trout population 80 years after their initial introduction (Ellis et al. 2011). Attenuation of a strong novel cascade also appears to have occurred in the Caribbean Sea, where the invasion of an unknown pathogen caused massive regional die-offs in a common urchin, leading to algal overgrowth of coral reefs. Three decades after their initial decline urchin populations have begun to recover, with subsequent declines in algal cover in certain areas (Lessios 2016). Finally, the initial introduction of canine parvovirus on Isle Royale severely reduced the wolf population (in combination with food stress), with cascading effects on

balsam fir via moose (Peterson et al. 2014). In subsequent decades the strength of this pathogen-initiated cascade has varied with the prevalence of the virus. In the examples described above, the mechanisms for declines in trophic cascade strength over time are not clear. While strong top-down control is likely to favor the emergence of less susceptible resources (section 3.2), evolution may also favor traits in the introduced consumers that reduce their impact, as occurred with the evolution of attenuated virulence in introduced myxoma virus in Australian rabbits (Kerr 2012).

3.4 Summary of the empirical literature

Our findings are generally consistent with the idea that strong trophic cascades are often transient phenomena, even when they have long-lasting impacts on ecosystems. Importantly, transient shifts in cascade strength can be rapid, especially when they involve changes in traits. The ephemeral nature of many strong cascades may be due in part to the fact that persistent top-down control should select for better defended resources, eroding the strength of trophic cascades over time (section 3.2). Cascades can be re-invigorated when conditions shift in a way that favors rapidly-growing resources rather than better-defended resources (e.g., in early successional communities). In other words, apparent competition (i.e, the success of a better-defended resource at the expense of a less well-defended resource in the presence of a consumer) should drive ecological and evolutionary changes that diminish trophic cascades, but trade-offs between growth and defense (Coley et al. 1985) can allow cascades to be amplified when conditions shift. This pattern of variation in cascade strength is common in systems that

feature seasonal “resets”, and can occur after disturbance as well (section 3.1). Disturbance can also amplify cascade strength by limiting food-web complexity. Reduced complexity limits the potential for compensatory effects of alternate consumers to reduce trophic cascade strength (e.g., Spiller & Schoener 2007). In addition, a lack of species diversity and genetic diversity can constrain the emergence of better-defended resources by limiting the rate of ecological selection (*sensu* Vellend 2010) and natural selection, respectively. Finally, strong cascades driven by high consumer abundance are often the result of ephemeral phenomena, such as peaks in consumer-resource cycles; similar phenomena may result from bottom-up effects of resource pulses, but we could find no empirical examples of this. The general pattern of transient episodes of strong trophic cascades punctuating periods of weaker cascade strength appears to be recapitulated in “novel” cascades involving introduced consumers, which often become very strong (sometimes after an initial lag phase) but can attenuate over time.

Examples in the literature (e.g., Table 1) suggest that changes in both ecological context and the characteristics of consumers and resources are associated with temporal variation in trophic cascade strength. For abiotic drivers, changes in trophic cascade strength are often the result of alterations in ecological context. Changes in context often lead to changes in consumer or resource traits, highlighting the fact that these categories are often interdependent. For example, Preisser et al. (2004) suggested that changing soil moisture increases the cascading effect of entomopathogenic nematodes on plants because a change in soil moisture (context) increases the mobility of the nematodes (a key trait determining their ability to find new moth prey). In the case of biotic drivers, most of the variation in trophic cascade strength is

generated by variation in traits or abundance of constituent species driven from within the system. Similarly, the strong trophic cascades triggered by introduced consumers, and their subsequent attenuation (when it occurs), are often the result of variation in the interaction between the introduced consumer and the transmitting consumer (i.e., changes in the characteristics of this direct interaction drives the overall strength of the cascade). Finally, while there is ample evidence that changes in characteristics of the initiating consumer (e.g., abundance, capture rate) influence cascade strength, there are also examples of trophic cascade strength being influenced by lower trophic levels (e.g., Power et al. 2008), underscoring the notion that resource characteristics can drive variation in cascading effects of consumers.

Our review of empirical evidence focused on manipulative and natural experiments. Not surprisingly, certain types of studies were much more common than others. For example, experiments in which consumer manipulations were repeated in multiple growing seasons (e.g., Barton et al. 2009, Power et al. 2008) or sustained over many years (e.g., Spiller et al. 2016, Spiller & Schoener 2007) provided the majority of robust examples of variation in cascade strength. These types of studies often included a close examination of the responses at each level of a cascade that provided insights into the mechanisms driving shifts in cascade strength that were not evident in simple calculations of effect size (Figure 2). Interestingly, we found few studies that conducted short-term manipulations during specified time periods, such as Kalka et al.'s (2008) comparison of the effects of daytime predator exclusions vs. nighttime predator exclusions. An exciting new generation of experimental studies focusing on phenology and ontogeny is underway, in which the seasonal timing of consumer-resource interactions is

manipulated, but relatively few studies adopting this type of design have been published to date. Finally, our review is notably short on examples from systems where temporal variation in trophic cascades is probably quite common. For example, agricultural systems in which natural enemies represent important controls on herbivores of crop plants (e.g., Liere et al. 2015), and open-ocean marine systems, where experimental studies of trophic cascades are rare. In the latter case, correlational techniques involving data sets collected over large spatial and temporal scales may help elucidate variation in the strength of trophic cascades (e.g., Baum & Worm 2009, Casini et al. 2009, Daskalov et al. 2007, Frank et al. 2005).

4. What are the implications of temporal variation in trophic cascade strength for community stability?

We found cases in which temporal variation in trophic cascade strength can have both stabilizing and destabilizing impacts on communities. For example, an increase in trophic cascade strength following perturbation may hasten the return of a system to its previous state (e.g., Spiller et al. 2016). In addition, periodic shifts in cascade strength associated with cyclical consumer-resource dynamics are likely to be stabilizing (e.g., Krebs et al. 2001a). More generally, shifts in trophic cascade strength can accompany dampened dynamics of lower trophic levels (e.g., if consumers prevent population irruptions of lower trophic levels), enhancing stability. However, the historical focus on the stabilizing effects of consumers may reflect the fact that consumer-induced transitions to alternate states can occur relatively quickly, whereas situations in which trophic cascades are associated with stability are, by definition, more likely to persist and be observable. For example, episodic pathogen-urchin-

macroalgae cascades stabilize macroalgal communities in temperate marine ecosystems, but strong cascading effects of an introduced urchin pathogen facilitated a dramatic shift from a coral-dominated state to what appears to be a macroalgae-dominated alternate stable state (Feehan & Scheibling 2014). Furthermore, a meta-analysis of empirical trophic cascade studies found that predators tend to increase temporal variance in herbivore abundance (Halpern et al. 2005), an effect which can cascade to primary producers in some cases (e.g., Fox 2007), suggesting that the dynamics of lower trophic levels may be destabilized, rather than dampened, by higher-level consumers. Indeed, episodes of strong cascading effects associated with introduced consumers (section 3.3) or alterations in effective food chain length (examples in Filbee-Dexter & Scheibling 2014) often destabilize communities. Thus, our review highlights the notion that trophic cascades can be both stabilizing and destabilizing in ecological communities.

5. How will contemporary global change affect trophic cascades?

Global change is likely to alter the strength of trophic cascades via multiple pathways. These range from direct effects on individual physiology to regional-scale range shifts and subsequent changes in community composition (e.g., Post 2013). As reviewed in section 3.1, seasonal and interannual climate variation, phenological shifts, and episodic disturbances affect trophic cascades, and these factors will be strongly affected by climate change. Similarly, species introductions associated with globalization and urbanization are also likely to continue, resulting in creation of additional novel cascades (section 3.3). Here we briefly review

additional mechanisms by which global changes may influence cascade strength, focusing on increasing temperature, ocean acidification, nutrient addition, and the loss of top predators. While many of these mechanisms are plausible, changes in trophic cascade strength due specifically to global change will need to be demonstrated through long-term studies of food webs in nature.

There is a vast literature on the effects of temperature on properties of consumers and resources such as individual physiology, metabolism, development, and activity. These effects can, in theory, lead to changes in cascade strength if consumers and resources respond differently to warming (Both et al. 2009, Dell et al. 2014, Gilbert et al. 2014, Parmesan & Yohe 2003). For example aquatic mesocosms and small-scale terrestrial manipulations have found stronger cascades under warming treatments which may be due to increased activity by herbivores (Barton et al. 2009, Kratina et al. 2012, Shurin et al. 2012), although this may not always be the case (e.g., Kishi et al. 2005). However, while the general observation that interacting species are responding to differently to ongoing climate change appears to be robust (Parmesan 2007; Thackeray et al. 2010, 2016), specific examples showing how these differences lead to changing trophic cascade strength in nature are scarce (Section 3.1).

Ocean acidification could affect cascade strength by directly reducing abundance of calcifying grazers or producers (Wootton et al. 2008), and indirectly via increasing susceptibility of prey and/or decreasing predator efficiency – if shells serve as anti-predator defenses, then weakening of shells due to acidification would increase prey susceptibility (Amaral et al. 2012),

potentially allowing stronger top-down control. However, there is also increasing evidence that changes in pH directly affect performance (e.g. reaction times, antipredator behavior) of fish (e.g., Allan et al. 2013, Dixon et al. 2010) and invertebrates (Jellison et al. 2016). Asymmetries in these effects on multiple trophic levels could result in changes in cascade strength, but as with changing temperatures, generating predictive insight into these asymmetries and consequent changes in trophic cascade strength has been challenging.

Eutrophication can potentially increase the strength of trophic cascades because more productive systems can support greater abundances of consumers (Oksanen et al. 1981). However, meta-analyses have found little evidence that fertilization increases cascade strength (Borer et al. 2005, Micheli 1999). This may occur because of trade-offs between competition and defense traits, with predator-resistant forms dominating at high productivity (Leibold 1996, Power et al. 1996), or because other changes associated with eutrophication (e.g., decreasing oxygen and visibility in aquatic systems) may reduce the effects of predators.

Reductions, extirpations, and extinctions of top predators have occurred in many systems due to anthropogenic effects, and such losses have the potential to dramatically change food webs through altered trophic cascades (Baum & Worm 2009, Duffy 2003, Estes et al. 2011, Myers & Worm 2003, Ripple et al. 2014). For example, declines of piscivorous predators due to overharvesting has resulted in a shift from a 4-level to a 3-level cascade in the Baltic Sea (Daskalov et al. 2007), and similar reductions in functional food chain length may continue as a result of “fishing down” food webs (sensu Pauly et al. 1998). Elimination of the classic sea otter,

urchin, kelp cascade has been linked to shifting foraging behavior by orcas (Estes et al. 1998), possibly due to anthropogenic effects on alternative prey (Springer et al. 2003). Concerns about the ecosystem consequences of defaunation of top predators has become worrisome enough to lead some to argue for restoring top down control by facilitating the recovery of apex predators, including measures such as introductions of functionally-equivalent predators (Svenning et al. 2015), but these efforts face significant challenges (Stier et al. 2016).

6. Conclusion

Our review suggests that temporal variation in trophic cascade strength is widespread, but rigorously documented in relatively few cases. To some extent, this is likely due to the paucity of long-term data sets from consumer manipulation studies that extend across two or more lower trophic levels; it may also result from a focus on studying time periods in which trophic cascades are strong. However, as we move beyond simply documenting the importance of trophic cascades, it is critical to focus more attention on the question of when trophic cascades are pronounced and why they are strong during those periods. Our review shows that trophic interactions are often concentrated in time, and that strong trophic cascades observed over long time periods may actually be the result of episodes of strong cascades intermingled with periods during which the constituent species have little effect on one another. In many cases, it may be useful to examine how variation in the strength of trophic cascades on shorter component timescales contributes to the overall trophic cascade. For example, understanding the diurnal versus nocturnal components of trophic cascades or separating the seasonal

components of a trophic cascade could provide additional insight into how changes in environmental conditions will alter the strength and influence of trophic cascades.

We found that strong cascades often occur during periods where resource growth and susceptibility to consumption are maximized, including periods following disturbance, seasonal “resets”, and invasions of introduced consumers. However, these cascades often decrease in strength over time as both ecological selection (*sensu* Vellend 2010) and natural/evolutionary selection favor traits that reduce susceptibility to consumers throughout the food web. Our review shows that consumers can be potent stabilizers of the dynamics of lower trophic levels, enhancing community persistence and decreasing variation in ecosystem function – a key component in maintaining the architecture of many communities. However, consumers can also be agents of rapid change in ecosystems whose effects may be difficult to reverse. In a rapidly-changing world, it is increasingly important to determine when (and where) consumers maintain desirable attributes of extant ecosystems, and when (and where) they facilitate dramatic ecological shifts.

Summary Points

1. Strong trophic cascades are often transient phenomena.
2. Strong trophic cascades are likely after disturbance or seasonal resets.
3. Strong trophic cascades are expected to weaken and become more episodic over time in the absence of external perturbation.

4. While temporal shifts in trophic cascade strength can destabilize communities, these shifts can also be potent stabilizing mechanisms.
5. Changes in the strength of trophic cascades are likely to play a key role in determining ecological responses to rapid, contemporary environmental change

Future Issues

1. Is the attenuation of unperturbed trophic cascades over time a general phenomenon? If so, what are the primary causes of this attenuation?
2. What is the role of eco-evolutionary dynamics in driving variation in cascade strength?
3. How does temporal variation in resource inputs drive temporal variation in trophic cascades?
4. Under what conditions does a change in the strength of trophic cascades enhance community stability in the face of perturbation? When does the opposite occur?
5. Which climatic components (e.g., seasons, decadal-scale drivers, extreme events) account for the most temporal variation in cascade strength?

Acknowledgements

We thank David Spiller, Justin Bastow, Kyle Edwards, Daniel Preston, Evan Preisser, Mark Novak, Jonathan Shurin, Thomas Schoener, and Mary Power for providing helpful feedback on

the manuscript. Funding for research related to this manuscript was provided by a grant from the National Science Foundation (DEB-11968).

Literature cited

- Abbott KL. 2005. Supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes*, on an oceanic island: Forager activity patterns, density and biomass. *Insectes Soc.* 52(3):266–73
- Abrams PA. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *The American Naturalist.* 146(1):112–34
- Abrams PA, Menge BA, Mittelbach GG, Spiller DA, Yodzis P. 1996. The role of indirect effects in food webs. In *Food Webs: Integration of Pattern and Dynamics*, eds. GA Polis, KO Winemiller, pp. 371–95. Chapman and Hall
- Allan BJM, Domenici P, McCormick MI, Watson S-A, Munday PL. 2013. Elevated CO₂ affects predator-prey interactions through altered performance. *PLoS ONE.* 8(3):e58520
- Amaral V, Cabral H, Bishop M. 2012. Effects of estuarine acidification on predator–prey interactions. *Marine Ecology Progress Series.* 445:117–27
- Barton BT, Beckerman AP, Schmitz OJ. 2009. Climate warming strengthens indirect interactions in an old-field food web. *Ecology.* 90(9):2346–51
- Baum JK, Worm B. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology.* 78(4):699–714
- Berlow EL, Navarrete SA, Briggs CJ, Power ME, Menge BA. 1999. Quantifying variation in the strengths of species interactions. *Ecology.* 80(7):2206–24
- Bollens SM, Rollwagen-Bollens G, Quenette JA, Bochdansky AB. 2010. Cascading migrations and implications for vertical fluxes in pelagic ecosystems. *J. Plankton Res.* 349–55
- Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, et al. 2005. What determines the strength of a trophic cascade? *Ecology.* 86(2):528–37

- Both C, Van Asch M, Bijlsma RG, Van Den Burg AB, Visser ME. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*. 78(1):73–83
- Brett MT, Goldman CR. 1996. A meta-analysis of the freshwater trophic cascade. *PNAS*. 93(15):7723–26
- Bridgeland WT, Beier P, Kolb T, Whitham TG. 2010. A conditional trophic cascade: birds benefit faster growing trees with strong links between predators and plants. *Ecology*. 91(1):73–84
- Brodersen J, Nicolle A, Nilsson PA, Skov C, Brönmark C, Hansson L-A. 2011. Interplay between temperature, fish partial migration and trophic dynamics. *Oikos*. 120(12):1838–46
- Carpenter SR, Kitchell JF. 1993. *The Trophic Cascade in Lakes*. Cambridge University Press
- Casini M, Hjelm J, Molinero J-C, Lövgren J, Cardinale M, et al. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *PNAS*. 106(1):197–202
- Cherry MJ, Warren RJ, Mike Conner L. 2016. Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. *Forest Ecology and Management*. 368:133–39
- Coley PD, Bryant JP, F. Stuart Chapin III. 1985. Resource availability and plant antiherbivore defense. *Science*. 230:895–900
- Cooling M, Hoffmann BD. 2015. Here today, gone tomorrow: declines and local extinctions of invasive ant populations in the absence of intervention. *Biol Invasions*. 17(12):3351–57
- Daly M, Behrends PR, Wilson MI, Jacobs LF. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour*. 44(1):1–9
- Daskalov GM, Grishin AN, Rodionov S, Mihneva V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *PNAS*. 104(25):10518–23
- Dell AI, Pawar S, Savage VM. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *J Anim Ecol*. 83(1):70–84

- Dini ML, Carpenter SR. 1991. The effect of whole-lake fish community manipulations on *Daphnia* migratory behavior. *Limnol. Oceanogr.* 36(2):370–77
- Dixon DL, Munday PL, Jones GP. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters.* 13(1):68–75
- Doherty TS, Dickman CR, Nimmo DG, Ritchie EG. 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation.* 190:60–68
- Duffy JE. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos.* 99(2):201–19
- Duffy JE. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters.* 6(8):680–687
- Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters.* 10(6):522–38
- Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution.* 18(4):586–608
- Ellis BK, Stanford JA, Goodman D, Stafford CP, Gustafson DL, et al. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. *PNAS.* 108(3):1070–75
- Estes JA. 1995. Top-level carnivores and ecosystem effects: questions and approaches. In *Linking Species and Ecosystems*, eds. CG Jones, JH Lawton, pp. 151–59. New York: Chapman and Hall
- Estes JA, Palmisano JF. 1974. Sea otters: Their role in structuring nearshore communities. *Science.* 185(4156):1058–60
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, et al. 2011. Trophic downgrading of planet earth. *Science.* 333(6040):301–6
- Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science.* 282(5388):473–76
- Fahimipour AK, Anderson KE. 2015. Colonisation rate and adaptive foraging control the emergence of trophic cascades. *Ecol Lett.* 18(8):826–33

- Feehan CJ, Scheibling RE. 2014. Effects of sea urchin disease on coastal marine ecosystems. *Mar Biol.* 161(7):1467–85
- Filbee-Dexter K, Scheibling RE. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series.* 495:1–25
- Finke DL, Denno RF. 2004. Predator diversity dampens trophic cascades. *Nature.* 429(6990):407–10
- Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, et al. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics.* 35:557–81
- Fox JW. 2007. The dynamics of top-down and bottom-up effects in food webs of varying prey diversity, composition, and productivity. *Oikos.* 116(2):189–200
- Frank KT, Petrie B, Choi JS, Leggett WC. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science.* 308(5728):1621–23
- Gilbert B, Tunney TD, McCann KS, DeLong JP, Vasseur DA, et al. 2014. A bioenergetic framework for the temperature dependence of trophic interactions. *Ecol Lett.* 17(8):902–14
- Haavisto F, Jormalainen V. 2014. Seasonality elicits herbivores' escape from trophic control and favors induced resistance in a temperate macroalga. *Ecology.* 95(11):3035–45
- Hairston NG, Smith FE, Slobodkin LB. 1960. Community structure, population control, and competition. *The American Naturalist.* 94(879):421–25
- Halaj J, Wise DH. 2001. Terrestrial trophic cascades: how much do they trickle? *The American Naturalist.* 157(3):262–81
- Halpern BS, Borer ET, Seabloom EW, Shurin JB. 2005. Predator effects on herbivore and plant stability. *Ecology Letters.* 8(2):189–94
- Heath MR, Speirs DC, Steele JH. 2014. Understanding patterns and processes in models of trophic cascades. *Ecol Lett.* 17(1):101–14

- Holdo RM, Sinclair ARE, Dobson AP, Metzger KL, Bolker BM, et al. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLOS Biology*. 7(9):e1000210
- Holt RD, Grover H, Tilman D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*. 144(5):
- Hunter MD, Price PW. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*. 73(3):724–32
- Ingram T, Svanbäck R, Kraft NJB, Kratina P, Southcott L, Schluter D. 2012. Intraguild predation drives evolutionary niche shift in threespine stickleback. *Evolution*. 66(6):1819–32
- Jellison BM, Ninokawa AT, Hill TM, Sanford E, Gaylord B. 2016. Ocean acidification alters the response of intertidal snails to a key sea star predator. *Proc. R. Soc. B*. 283(1833):20160890
- Kalka MB, Smith AR, Kalko EKV. 2008. Bats limit arthropods and herbivory in a tropical forest. *Science*. 320(5872):71
- Katano O, Natsumeda T, Suguro N. 2013. Diurnal bottom feeding of predator fish strengthens trophic cascades to benthic algae in experimental flow-through pools. *Ecol. Res*. 28(5):907–18
- Kerr PJ. 2012. Myxomatosis in Australia and Europe: a model for emerging infectious diseases. *Antiviral Research*. 93(3):387–415
- Kishi D, Murakami M, Nakano S, Maekawa K. 2005. Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology*. 50(8):1315–22
- Kratina P, Greig HS, Thompson PL, Carvalho-Pereira TSA, Shurin JB. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*. 93(6):1421–30
- Krebs CJ, Boonstra R, Boutin S, Sinclair ARE. 2001a. What drives the 10-year cycle of snowshoe hares? *BioScience*. 51(1):25–35
- Krebs CJ, Boutin S, Boonstra R, Sinclair ARE, Smith JNM, et al. 1995. Impact of food and predation on the snowshoe hare cycle. *Science*. 269(5227):

- Krebs CJ, Dale MRT, Nams VO, Sinclair ARE, O'Donoghue M. 2001b. Shrubs. In *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*, eds. CJ Krebs, S Boutin, R Boonstra, pp. 92–115. Oxford University Press
- Kurle CM, Croll DA, Tershy BR. 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. *PNAS*. 105(10):3800–3804
- Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, et al. 2008. Parasites in food webs: the ultimate missing links. *Ecology Letters*. 11(6):533–46
- Leibold MA. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist*. 134:922–49
- Leibold MA. 1996. A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *The American Naturalist*. 147(5):784–812
- Leibold MA, Chase JM, Shurin JB, Downing AL. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics*. 28:467–94
- Leroux SJ, Loreau M. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters*. 11(11):1147–56
- Lessios HA. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics*. 19(1):371–93
- Lessios HA. 2016. The great *Diadema antillarum* die-off: 30 years later. *Annual Review of Marine Science*. 8(1):267–83
- Liere H, Kim TN, Werling BP, Meehan TD, Landis DA, Gratton C. 2015. Trophic cascades in agricultural landscapes: indirect effects of landscape composition on crop yield. *Ecological Applications*. 25(3):652–61

- McCann KS, Hastings A, Strong DR. 1998. Trophic cascades and trophic trickles in pelagic food webs. *Proceedings of the Royal Society of London B: Biological Sciences*. 265(1392):205–9
- McCann KS, Rasmussen JB, Umbanhowar J. 2005. The dynamics of spatially coupled food webs. *Ecology Letters*. 8(5):513–23
- McCauley DJ, Young HS, Dunbar RB, Estes JA, Semmens BX, Micheli F. 2012. Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications*. 22(6):1711–17
- McQueen DJ, Post JR. 1988. Cascading trophic interactions: uncoupling at the zooplankton-phytoplankton link. *Hydrobiologia*. 159(3):277–96
- Menge BA. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*. 65(1):21–74
- Menge BA, Sutherland JP. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*. 130(5):730–57
- Micheli F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science*. 285(5432):1396–98
- Mittelbach G, Turner A, Hall D, Rettig J, Osenberg C. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology*. 76(8):2347–60
- Moran MD, Hurd LE. 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia*. 113(1):126–32
- Myers RA, Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*. 423(6937):280–83
- Norrdahl K, Klemola T, Korpimäki E, Koivula M. 2002. Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos*. 99(3):419–30

- Novak M, Wootton JT. 2010. Using experimental indices to quantify the strength of species interactions. *Oikos*. 119(7):1057–63
- O’Dowd DJ, Green PT, Lake PS. 2003. Invasional “meltdown” on an oceanic island. *Ecology Letters*. 6(9):812–17
- Oksanen L, Fretwell SD, Arruda J, Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist*. 118:240–61
- Paine RT. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*. 49(3):667–85
- Paine RT. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology*. 69(6):1648–54
- Parmesan C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*. 13(9):1860–72
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 421(6918):37–42
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998. Fishing down marine food webs. *Science*. 279(5352):860–63
- Penteriani V, Kuparinen A, del Mar Delgado M, Palomares F, Vicente Lopez-Bao J, et al. 2013. Responses of a top and a meso predator and their prey to moon phases. *Oecologia*. 173(3):753–66
- Peterson RO, Vucetich JA, Bump JM, Smith DW. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and Systematics*. 45(1):325–45
- Pimm S. 1982. *Food Webs*. University of Chicago Press
- Polis GA. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*. 86(1):3–15

- Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*. 28:289–316
- Polis GA, Strong DR. 1996. Food web complexity and community dynamics. *The American Naturalist*. 147(5):813–46
- Post E. 2013. *Ecology of Climate Change : The Importance of Biotic Interactions*. Princeton, US: Princeton University Press
- Post E, Peterson RO, Stenseth NC, McLaren BE. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature*. 401(6756):905–7
- Power ME. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology*. 73(3):733–46
- Power ME, Matthews WJ, Stewart AJ. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology*. 66(5):1448–56
- Power ME, Parker MS, Dietrich WE. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs*. 78(2):263–82
- Power ME, Parker MS, Wootton JT. 1996. Disturbance and food chain length in rivers. In *Food Webs: Integration of Patterns & Dynamics*, eds. GA Polis, KO Winemiller. Chapman and Hall
- Preisser EL, Strong DR. 2004. Climate affects predator control of an herbivore outbreak. *The American Naturalist*. 163(5):754–62
- Preston DL, Mischler JA, Townsend AR, Johnson PTJ. 2016. Disease ecology meets ecosystem science. *Ecosystems*. 19(4):737–48
- Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J Anim Ecol*. 83(2):504–14

- Reeve J, Turchin P. 2002. Evidence for predator-prey cycles in a bark beetle. In *Population Cycles: The Case for Trophic Interactions*, ed. A Berryman. Oxford University Press
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science*. 343(6167):1241484
- Ripple WJ, Estes JA, Schmitz OJ, Constant V, Kaylor MJ, et al. 2016. What is a trophic cascade? *Trends in Ecology & Evolution*. 31(11):842–49
- Rogers H, Hille Ris Lambers J, Miller R, Tewksbury JJ. 2012. “Natural experiment” demonstrates top-down control of spiders by birds on a landscape level. *PLoS ONE*. 7(9):e43446
- Rudolf VHW, Rasmussen NL. 2013. Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology*. 94(5):1046–56
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, et al. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics*. 32(1):305–32
- Schmitz OJ. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist*. 151(4):327–42
- Schmitz OJ, Hambäck PA, Beckerman AP. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist*. 155(2):141–53
- Schoener TW. 1993. On the relative importance of direct versus indirect effects in ecological communities. In *Mutualism and Community Organization: Behavioral, Theoretical and Food Web Approaches*, eds. H Kawanabe, JE Cohen, K Iwasaki. Oxford University Press
- Schoenly K, Cohen JE. 1991. Temporal variation in food web structure: 16 empirical cases. *Ecological Monographs*. 61(3):267–98
- Schultz JA, Cloutier RN, Côté IM. 2016. Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ*. 4:e1980

- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*. 5(6):785–91
- Shurin JB, Clasen JL, Greig HS, Kratina P, Thompson PL. 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*. 367(1605):3008–17
- Shurin JB, Gruner DS, Hillebrand H. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society of London B: Biological Sciences*. 273(1582):1–9
- Shurin JB, Seabloom EW. 2005. The strength of trophic cascades across ecosystems: predictions from allometry and energetics. *Journal of Animal Ecology*. 74(6):1029–38
- Spiller DA, Schoener TW. 2007. Alteration of island food-web dynamics following major disturbance by hurricanes. *Ecology*. 88(1):37–41
- Spiller DA, Schoener TW, Piovato-Scott J. 2016. Predators suppress herbivore outbreaks and enhance plant recovery following hurricanes. *Ecology*. 97(10):2540–46
- Stier AC, Samhouri JF, Novak M, Marshall KN, Ward EJ, et al. 2016. Ecosystem context and historical contingency in apex predator recoveries. *Science Advances*. 2(5):e1501769
- Strong DR. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*. 73(3):747–54
- Sumption KJ, Flowerdew JR. 1985. The ecological effects of the decline in rabbits (*Oryctolagus cuniculus* L.) due to myxomatosis. *Mammal Review*. 15(4):151–86
- Svenning J-C, Pedersen PBM, Donlan CJ, Ejrnæs R, Faurby S, et al. 2015. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *PNAS*. 201502556
- Takimoto G, Iwata T, Murakami M. 2009. Timescale hierarchy determines the indirect effects of fluctuating subsidy inputs on in situ resources. *The American Naturalist*. 173(2):200–211

- Terborgh J, Estes JA, eds. 2010. *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press
- Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature*. 535(7611):241–45
- Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*. 16(12):3304–13
- Townsend CR. 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology*. 17(1):38–47
- Turchin P, Taylor AD, Reeve JD. 1999. Dynamical role of predators in population cycles of a forest insect: An experimental test. *Science*. 285(5430):1068–71
- van der Stap I, Vos M, Verschoor AM, Helmsing NR, Mooij WM. 2007. Induced defenses in herbivores and plants differentially modulate a trophic cascade. *Ecology*. 88(10):2474–81
- Vellend M. 2010. Conceptual synthesis in community ecology. *The Quarterly Review of Biology*. 85(2):183–206
- Werner EE, Gilliam and JF. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*. 15(1):393–425
- Werner EE, Peacor SD. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*. 84(5):1083–1100
- Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*. 5(9):475–82
- Wood EM, Pidgeon AM. 2015. Extreme variations in spring temperature affect ecosystem regulating services provided by birds during migration. *Ecosphere*. 6(11):216–216

- Wootton JT. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*. 25(1):443–66
- Wootton JT, Parker MS, Power ME. 1996. Effects of disturbance on river food webs. *Science*. 273(5281):1558–61
- Wootton JT, Pfister CA, Forester JD. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *PNAS*. 105(48):18848–53
- Yang LH, Rudolf VHW. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*. 13(1):1–10
- Yodzis P, Innes S. 1992. Body size and consumer-resource dynamics. *The American Naturalist*. 139(6):1151–75

Definitions

Direct interaction; direct effect: an interaction between two species with no interceding species; the effect of one species on another resulting from a direct interaction.

Indirect interaction; indirect effect: an interaction between two species with one or more interceding species (involving two or more adjacent links in an interaction chain); the effect of one species on another resulting from an indirect interaction.

Trophic cascade: an indirect species interaction that originates with a consumer and spreads downward through more than one linked consumer-resource interaction in a food web.

Initiating consumer: the species that originates or initiates a trophic cascade.

Transmitting consumer: a species that transmits a trophic cascade from higher-level consumers to lower-level resources.

Receiving resource: The lower-level resource species used to measure the strength of a trophic cascade; in other words, the species being indirectly affected by the initiating consumer.

Annotated References

Borer et al. 2005: Meta-analysis examining factors contributing to variation in trophic cascade strength.

Paine 1980: Introduces the term trophic cascade.

Polis 1999: Conceptual synthesis exploring why trophic cascades are expected to be rare and variable.

Ripple et al 2016: Clarifies and defines the term trophic cascade.

Shurin et al. 2006: Mechanistic perspective on differences in cascade strength between ecosystems.

Strong 1992: Outlines many of the factors driving variation in the strength of trophic cascades.

Figure Captions

Figure 1: A temporally-explicit perspective on trophic cascades. a) a typical trophic cascade in which the solid arrows depict negative direct effects of consumers and the dashed arrow depicts a positive indirect effect of the initiating consumer on the resource; terminology follows that of Abrams et al. (1996). b) temporal variation in the strength of a trophic cascade: at T1 a strong direct effect of the initiating consumer on the transmitting consumer is not transmitted to the resource (attenuation), at T2 a strong direct effect of the transmitting consumer on the resource is not modulated by the initiating consumer (reduction in functionally significant food chain length), at T3 a strong trophic cascade is generated when the two constituent direct effects are linked in time.

Figure 2: Evaluating the mechanisms underlying temporal shifts in trophic cascade strength. Cascade strength is usually characterized using standard effect size metrics (e.g., log response ratio), but these metrics can obscure patterns related to the mechanisms underlying shifts in cascade strength. This point is illustrated using data from a study showing how hurricanes influence changes in the cascading effect of lizards on a common plant (Spiller et al. 2016). In this study, data on herbivore and plant abundance were collected from islands with and without lizards, and log responses ratios were used to quantify lizard effects on herbivores and plants. Hurricane Floyd hit the study area after the 1999 data were collected, whereas the 2000 and 2001 data were collected after the hurricane. Lizard effects on herbivorous moths were generally strong, and increased between 1999 and 2001 (panels a and b). Despite the strong

effects of lizards on moths in 2000, the cascading effects of lizards on plants were weak (attenuation), as plant abundance was severely reduced on all islands by the hurricane (panels c and d). In 2001, the effects of lizards on moths cascade strongly to plants, as plants exhibit rapid growth on lizard islands after the hurricane and moths effectively constrain plant recovery on islands without lizards.

Table 1: Key examples of temporal variation in trophic cascade strength.

Ecosystem	Taxa	Drivers of variation in cascade strength	Key references
Isle Royale National Park	Virus – wolf – moose – tree	Severe winter, genetic rescue	(Peterson et al. 2014)
Bahamian islands	Lizard – herbivorous arthropods – plant	Hurricanes	(Spiller & Schoener 2007; Spiller et al. 2016)
Eel River	Fish – aquatic insects – macroalga	Seasonal floods	(Power et al. 2008)
Boreal forest	Lynx – hare – shrubs	Predator-prey cycles	(Krebs et al. 2001)

Figure 1

a

b

Figure 2