

# Temporal Variation in Trophic Cascades

Jonah Piovia-Scott,<sup>1</sup> Louie H. Yang,<sup>2</sup>  
and Amber N. Wright<sup>3</sup>

<sup>1</sup>School of Biological Sciences, Washington State University, Vancouver, Washington;  
email: jonah.piovia-scott@wsu.edu

<sup>2</sup>Department of Entomology and Nematology, University of California, Davis, California;  
email: lhyang@ucdavis.edu

<sup>3</sup>Department of Biology, University of Hawaii, Manoa, Hawaii; email: anwright@hawaii.edu

Annu. Rev. Ecol. Evol. Syst. 2017. 48:281–300

First published online as a Review in Advance on  
August 25, 2017

The *Annual Review of Ecology, Evolution, and  
Systematics* is online at [ecolsys.annualreviews.org](http://ecolsys.annualreviews.org)

<https://doi.org/10.1146/annurev-ecolsys-121415-032246>

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## Keywords

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

## Abstract

The trophic cascade has emerged as a key paradigm in ecology. Although 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.



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**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

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

## 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 timescales. 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.

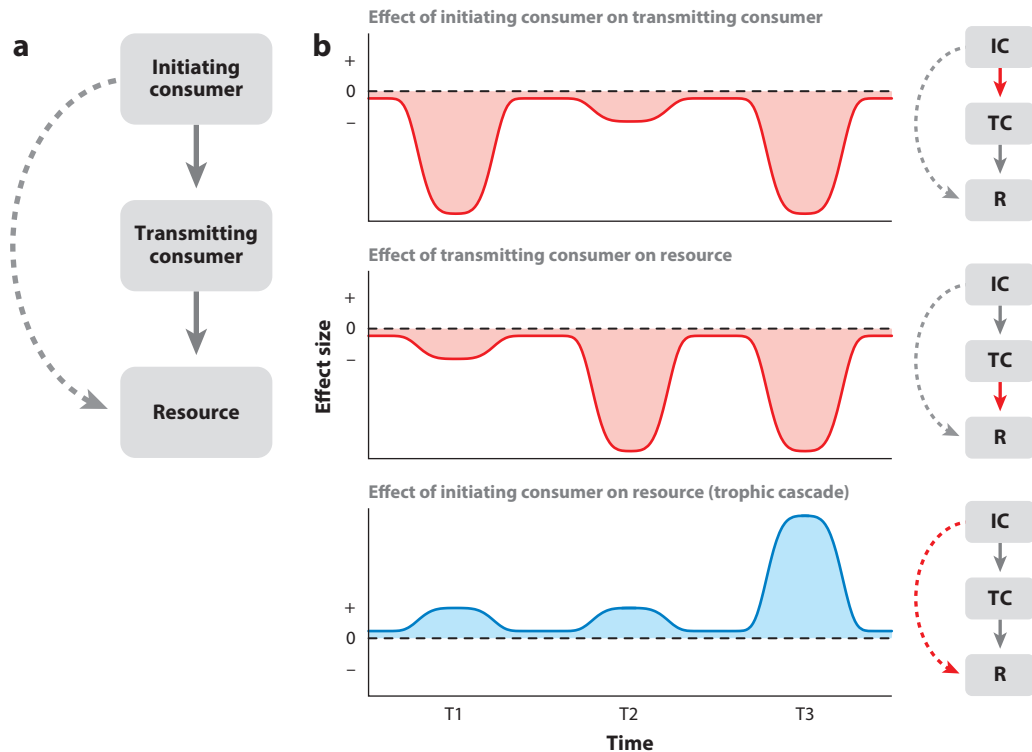
## 2. WHAT IS A TROPHIC CASCADE AND WHY DOES TROPHIC CASCADE STRENGTH VARY?

### 2.1. Definitions and Historical Context

We define a trophic cascade as an indirect species interaction (see the sidebar titled Direct and Indirect Interactions and Effects) that originates with a consumer and spreads downward through more than one linked consumer–resource interaction 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, p. 674). 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 (an initiating consumer, a transmitting consumer, and a receiving resource; **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.

### DIRECT AND INDIRECT INTERACTIONS AND EFFECTS

Direct interactions are interactions between two species with no interceding species. These result in direct effects, which are the effects of one species on another resulting from a direct interaction. Indirect interactions are interactions between two species with one or more interceding species (i.e., involving two or more adjacent links in an interaction chain) and result in indirect effects of one species on another.



**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), and at T3 a strong trophic cascade is generated when the two constituent direct effects are linked in time. Red arrows indicate which effect is depicted in the adjacent plot. Abbreviations: IC, initiating consumer; R, resource; TC, transmitting consumer.

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). Although 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). This review seeks to expand the scope of exploration into temporally varying trophic cascade strength—whereas previous inquiries have examined *where* we

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

**Receiving resource:** the lower-level resource used to measure the strength of a trophic cascade (i.e., the species being indirectly affected by the initiating consumer)

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 articles (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 & Seabloom 2005, Shurin et al. 2006, 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 although 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 nonsynchronous 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 owing 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 (e.g., year-to-year differences in seasonal phenology), 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 to understand when key interactions are occurring, even though the impacts of these effects manifest over much longer timescales. 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 owing 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 greater 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 consumer–resource 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 move less on full moon nights, when they are more vulnerable to predators; predatory lynx activity patterns responded to those of their rabbit prey, whereas 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, whereas species that emphasized other senses became less active (Prugh & Golden 2014). These examples suggest that lunar variation could 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 & 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 have 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 & 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 phytoplankton and zooplankton growth (Brodersen

et al. 2011). In general, year-to-year variation in phenological mismatches between consumers and resources has 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 provides 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, Michigan, 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 owing 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, California, 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 caddis fly larvae survived through the winter rainy season and became the dominant herbivore; these grazers resisted 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, thereby changing community composition. Such losses would weaken or remove a trophic cascade, which could reestablish and strengthen over time as consumer numbers rebound or consumers recolonize from elsewhere. For example, anoxic winter-kill in a Midwestern US lake extirpated largemouth bass, causing a shift from a four-level to a three-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-winter-kill conditions. Disturbances often have direct effects on lower trophic levels as well, and how these lower levels respond can lead to varying cascade strengths over time. For example, in The Bahamas, the cascading effects of lizard predators on plants increased after hurricanes: Large increases in herbivory on islands without lizard predators were seen 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 the biomass of forage shrubs, including small birch and willow twigs (Krebs et al. 2001b). These patterns are consistent with a trophic cascade, in which 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 pine forests in the southern United States, 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 that 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 counteradaptations that reinvigorate top-down processes (Ehrlich & Raven 1964).

Variation in the strength of trophic cascades may also 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. 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 traits that weaken the 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; see Williams & Jackson 2007) species assemblages that lack a shared ecological and evolutionary history. Introduced predators and pathogens often have particularly dramatic effects on lower trophic levels, and substantial evidence shows 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, some evidence shows that, similar to the population dynamics of introduced species, 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 twentieth 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 twentieth 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, some evidence shows 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, Montana, 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, Michigan, 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. Although 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

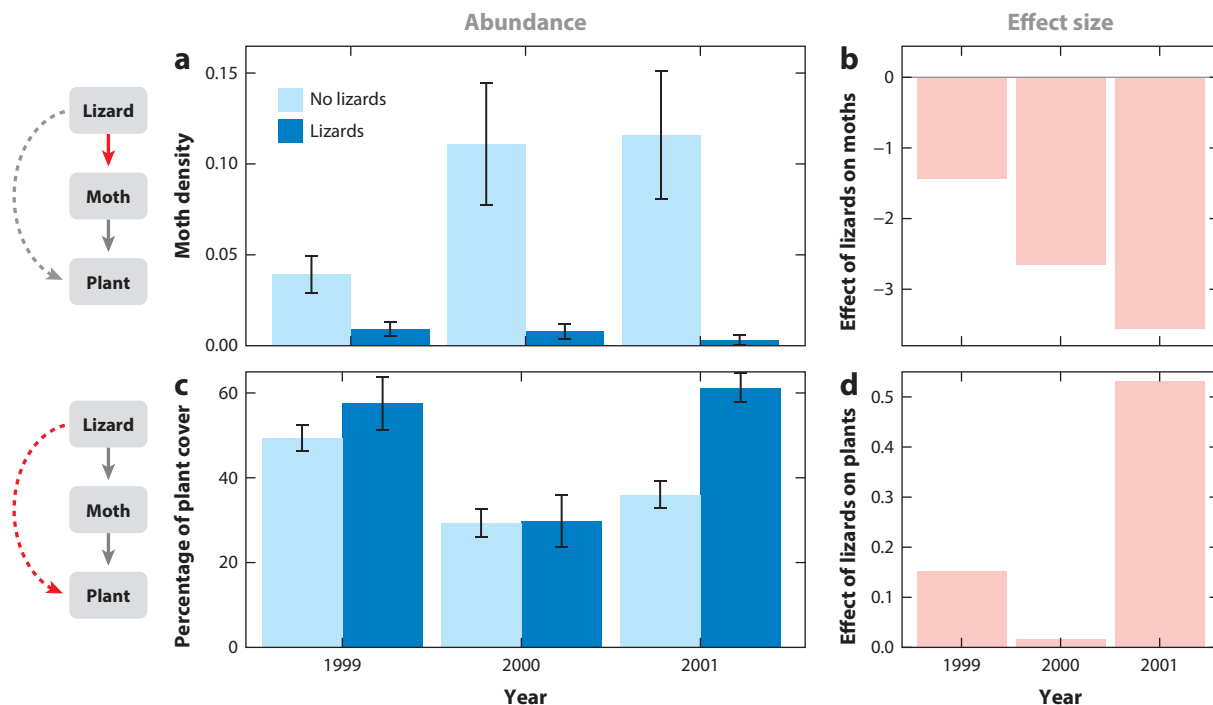
Our findings are generally consistent with the idea that strong trophic cascades are often transient phenomena, even when they have long-lasting impacts on ecosystems. Importantly, transient shifts in cascade strength can be rapid, especially when they involve changes in traits. The ephemeral nature 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 reinvigorated 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 (Yang et al. 2008, 2010). 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 & Strong (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 drive the overall strength of the cascade). Finally, although ample evidence demonstrates that changes in characteristics of the initiating consumer (e.g., abundance, capture rate) influence cascade strength, other examples show trophic cascade strength being influenced by lower trophic levels (e.g.,

**Table 1** Key examples of temporal variation in trophic cascade strength

Ecosystem	Taxa	Drivers of variation in cascade strength	Key reference(s)
Isle Royale National Park, Michigan	Virus–wolf–moose–trees	Severe winter, genetic rescue	Peterson et al. 2014
The Bahamas	Lizards–herbivorous arthropods–plants	Hurricanes	Spiller & Schoener 2007, Spiller et al. 2016
Eel River, California	Fish–aquatic insects–macroalgae	Seasonal floods	Power et al. 2008
Boreal forest, Canada	Lynx–hare–shrubs	Predator–prey cycles	Krebs et al. 2001a



**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. The 1999 data were collected before Hurricane Floyd hit the study area, whereas the 2000 and 2001 data were collected after the hurricane. (*a,b*) Lizard effects on herbivorous moths were generally strong and increased between 1999 and 2001. (*c,d*) 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. In 2001, the effects of lizards on moths cascade strongly to plants, as plants exhibit rapid growth on islands with lizards after the hurricane and moths effectively constrain plant recovery on islands without lizards.

Power et al. 2008), underscoring the notion that resource characteristics can also 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 & Schoener 2007, Spiller et al. 2016) 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 and colleagues' (2008) comparison of the effects of daytime predator exclusions versus 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 in which temporal variation in trophic cascades is probably quite common. Examples include 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, in which 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 historic 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 that 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 (for examples, see 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 the creation of additional novel cascades (Section 3.3). In this section, 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. Although 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.

A vast literature has been written 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 that 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, although the general observation that interacting species are responding 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 directly by 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 antipredator defenses, then weakening of shells owing to acidification would increase prey susceptibility (Amaral et al. 2012), potentially allowing stronger top-down control. However, increasing evidence has been found 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 owing 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 have resulted in a shift from a four-level to a three-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), which is possibly owing to anthropogenic effects on alternative prey (Springer et al. 2003). Concerns about the ecosystem consequences of defaunation of top predators have 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. CONCLUSIONS

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 in which 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 evolutionary (i.e., natural) 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 profound change in ecosystems whose effects may be difficult to reverse. In a rapidly changing world, it is increasingly important to determine when consumers maintain desirable attributes of extant ecosystems and when they facilitate dramatic ecological shifts.

### SUMMARY POINTS

1. Strong trophic cascades are often transient phenomena.
2. Strong trophic cascades likely occur 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. Although 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?

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

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 grants from the National Science Foundation (DEB-1119688 and DEB-1253101) to L.H.Y.

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Meta-analysis examining factors contributing to variation in trophic cascade strength.

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trophic cascade.

Conceptual synthesis  
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Clarifies and defines the term trophic cascade.

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Mechanistic perspective on differences in cascade strength between ecosystems.

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

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