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The consequences of mass mortality events for the structure and dynamics of biological communities

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Mass mortality events (MMEs) are rapidly occurring, substantial population losses that transpire within a short time interval relative to the generation time of the affected organism. Previous work has established that MMEs appear to be increasing in frequency and magnitude; however, currently, there is little understanding of the consequences of MMEs for biological communities. Here, we use theory and empirical data from observed MMEs to understand how MMEs impact the structure and dynamics of communities. To do so, we build upon existing resource pulse and trophic cascade theory to show that MMEs both share similarities and diverge from these ecological phenomena, producing distinct short- and long-term impacts by jointly altering the effects of species interactions across trophic levels and providing an influx of resources from decaying biomass. Second, we investigate how the magnitude of MMEs, trophic level of the impacted species, overall food web structure and ecosystem type may mediate the resulting ecological response. Third, we compare the understanding gained by our models to existing observational data on MMEs. Our synthesis, offers an empirical path forward for understanding MMEs through experimentation and improved observational data collection. While complex, resolving the consequences of MMEs should be a high research priority due to their role in determining how ecological systems respond to environmental change driven by rare events.

Keywords: catastrophes, defaunation, die offs, extreme events, rare demographic events, resource pulse

Introduction

Understanding how global environmental change may affect the structure and dynamics of biological communities is a pressing, yet challenging task. Extreme environmental conditions such as heat waves and precipitation events are on the rise, which can directly and indirectly impact key demographic rates of organisms (Buckley and Huey 2016). As such, extreme environmental events can strongly affect ecological dynamics (Huston 1979, Gutschick and BassiriRad 2003, Bailey and Pol 2016, Batt et al. 2017, Ummenhofer and Meehl 2017). Mass mortality events (MMEs; also called population die-offs), defined here as demographic catastrophes that can simultaneously affect all life stages and rapidly remove a

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substantial proportion of a population over a short period of time relative to the generation time of the organism, can occur as a direct consequence of extreme environmental events (Hoffmann and Parsons 1991, Scheffer et al. 2001, Gutschick and BassiriRad 2003, Hastings 2004, Siepielski and Benkman 2007, Haney et al. 2015, Fey et al. 2019). For example, the recent death of more than 200 000 saiga antelope *Saiga tatarica tatarica* within three weeks represented a 62% decline of their global population and was preceded by a period of unusually high relative humidity and high temperatures (Kock et al. 2018). While within a continuum of mortality event magnitudes, MMEs are a regular feature that many populations contend with (Anderson et al. 2017). In many animal populations, the frequency and magnitude of MMEs has been increasing over the past several decades (Fey et al. 2015).

MMEs have already been integrated into theoretical and empirical population ecology and the population-level consequences of catastrophic population losses are relatively well understood in a single-species context (Lande 1993). Indeed, MMEs may be the single most important demographic event affecting population persistence (Mangel and Tier 1994, Anderson et al. 2017). By contrast, the community and ecosystem-level effects of MMEs, beyond those related to the population that underwent the die-off, have received less attention and are poorly understood (Peterson et al. 2003, Langangen et al. 2017). Given the critical role of species interactions across trophic levels for shaping community structure and dynamics (Hunter and Price 1992), we anticipate that MMEs have consequential short- and long-term community-level effects, despite their rarity.

However, due to the difficulty associated with being in the right place and the right time to study them, understanding how MMEs affect ecological dynamics presents numerous challenges (Weatherhead 1986, Gutschick and BassiriRad 2003, Yang et al. 2010, Fey et al. 2015). First, their rarity and unpredictability limits the total extent (e.g. number of unique events) and the quality (e.g. the temporal window) of the existing observational data. Secondly, logistical challenges have limited the extent of empirical manipulations of MMEs (although (Lashley et al. 2017, Tomberlin et al. 2017)), thus little mechanistic insight exists to disentangle the impacts of direct versus indirect effects of MMEs. Finally, no singular theoretical framework exists to make predictions and motivate targeted data collection efforts for resolving the community-level consequences of MMEs. Our goal here is to make progress towards resolving these issues.

Understanding MME mechanics from existing theory

Existing ecological theory that might be perceived as a foundation to understand the ecological consequences of MMEs has emphasized either the indirect trophic impacts associated with declines or loss of top predators via trophic cascade theory (Paine 1980, Carpenter 1988, Ripple et al. 2016) or the direct impacts of sudden resource pulses via resource pulse theory (Polis et al. 1997, Smith and Baco 2003, Gratton et al. 2008, Holt 2008, Yang et al. 2008). While trophic cascade and resource pulse theory outline limiting cases of how MMEs may impact communities, we wanted to explicitly investigate if community dynamics following MMEs lead to dynamics that are best understood as the coupled outcome of these two concurrent processes.

To illustrate, first consider what occurs during a 'typical' MME involving a top predator. In a three-species food chain, when the top predator – a trophic level disproportionately susceptible to environmental perturbations (Estes et al. 2011) and one where MMEs are frequently occurring (Fey et al. 2015) – undergoes an MME, this event can weaken or remove top–down control (Paine 1980, Ripple et al. 2016), thus releasing the intermediate trophic level (i.e. herbivores) from predation and subsequently reducing primary production (Pace et al. 1999, Estes et al. 2011, Ripple et al. 2016). However, MMEs may also increase primary production by providing an influx of limiting nutrients to primary producers due to elevated detrital biomass (i.e. carrion) resulting from top predator mortality (Yang et al. 2008, 2010, Bump et al. 2009b). Similarly, in the event of an herbivore MME, dead herbivore biomass may directly fuel primary production concurrent with the release of basal resources from herbivory. In such cases, MMEs have the potential to rapidly and radically re-structure food web dynamics by causing the interactions between upper and basal trophic levels to switch from top–down control to one driven, in part, by a bottom–up resource pulse. As such, considering MMEs as either only a resource pulse or a removal of individuals can be insufficient for establishing an understanding of community-level consequences of MMEs (Holt 2008, Yang et al. 2008, Levi et al. 2015), particularly in instances where dead biomass produces a strong resource pulse effect.

Overview and approach for exploring the dynamics of MMEs

Because MMEs have similarities with both trophic removals (i.e. a large population die-off occurs but the dead biomass immediately is lost from the system) and resources pulses (i.e. influxes of resources occur due to biotic or abiotic processes that may or may not be associated with MMEs), and because these are familiar scenarios that provide a good baseline for comparison, we unify these theoretical frameworks to intuit the community-level consequences of MMEs. We first assess what community-level properties may arise from concurrent trophic removals and resource pulses. To do so, we use a theoretical framework based on simple three-species trophic chains represented as systems of differential equations, and investigate the behavior of these communities post-MME. Rather than rely on mathematical models to exhaustive resolve the conditions for how and when MMEs may differ from other trophic removals and resource pulses, we utilize our models to provide a heuristic for exploring differences between perturbation types. Thus, the following approach ought to be considered as a simple formalization of verbal models based on first principles, aimed at shedding light onto the consequences of MMEs in a tractable fashion. Our initial analysis using relatively simple food chain modules with high magnitude MMEs with strong effects on basal resources is deliberate to identify and illustrate the ways in which MMEs may differ from other scenarios.

We explore the dynamics of MMEs using three-species trophic chains for simplicity and tractability, which includes a top predator that consumes an herbivore, which in turn grazes upon a basal resource (Fig. 1a). To illustrate the impacts of MMEs and establish how they resemble and differ from other scenarios, we compare the transient dynamics and equilibria of three tri-trophic food chain models under different types of perturbations of equal magnitude: 1) a 'predator removal' event, where a top predator die-off occurs, yet the dead biomass ensuing from the die-off is immediately extirpated from the system (i.e. mimicking a typical predator removal experiment; Fig. 1b), 2) a 'resource pulse', where a discrete allochtonous influx of resources that impacts the growth of the basal resource occurs (Fig. 1c) and 3) an 'MME', where a predator population suffers a die-off, and produces a pulse of dead biomass that influences the growth of the basal resource (Fig. 1d).

By comparing these scenarios, we isolate the key differences across the different perturbations while holding all other features identical. In all scenarios, a resource (*R*) with intrinsic growth rate (*r*) and carrying capacity (*K*) is consumed by an herbivore (*H*). The herbivore exhibits a type II functional response determined by its attack rate (*a*) and handling time (*h*). Herbivore abundance is determined by the balance between the impacts of consuming resources based on conversion efficiency (*e*), a mortality rate (*m*) that is expressed as being density-dependent on a per capita basis (Edwards and Yool 2000), and loss due to consumption by predators (*P*). The predator's consumption of herbivores is likewise a type II functional response determined by a

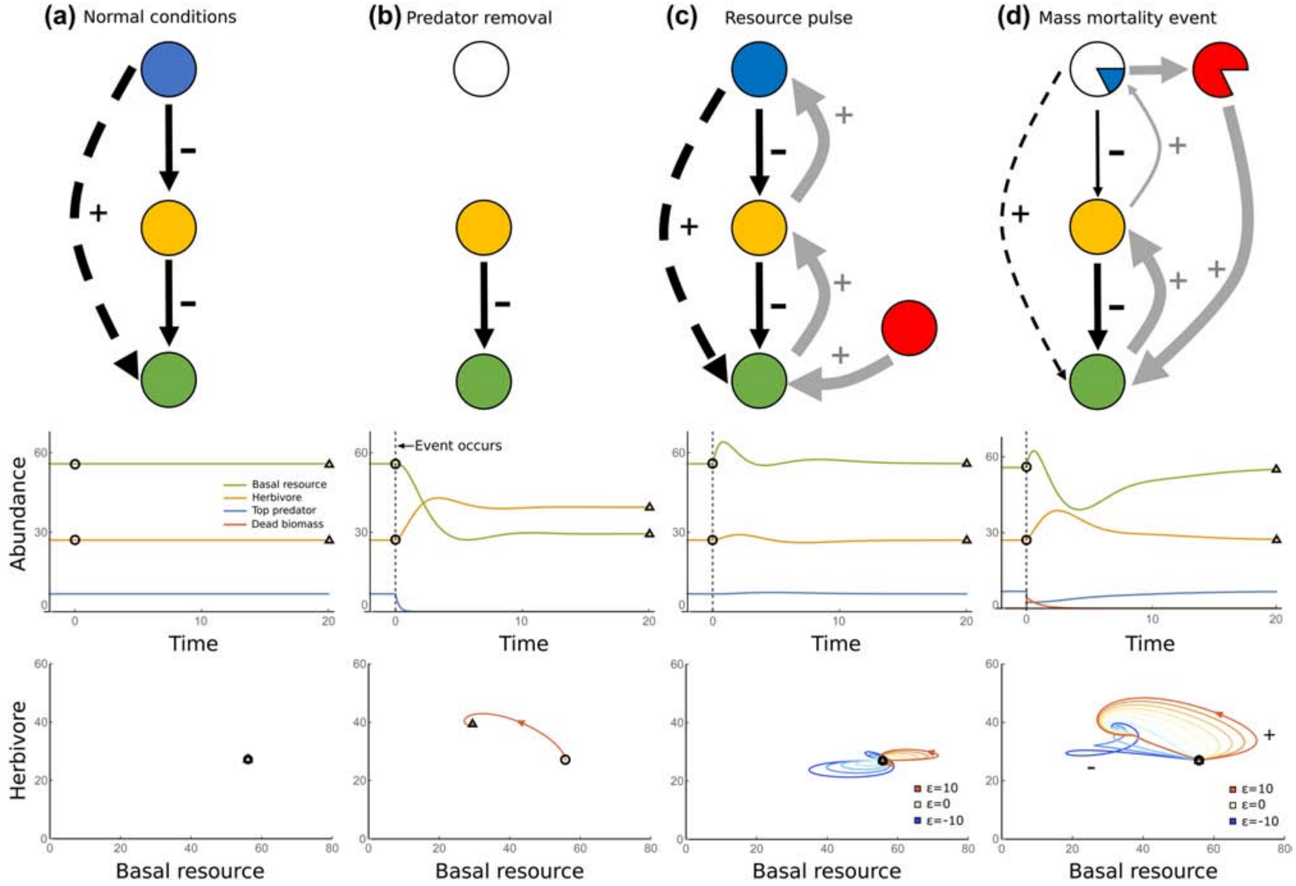

Figure 1. Top row. Conceptual representations of species interactions between a predator (blue), herbivore (orange) and basal resource (green; black solid arrows show direct effects; dashed arrows show indirect effects); and the flow of materials (gray arrows) from a resource pulse (red) during (a) normal, undisturbed conditions, (b) predator removal scenarios, (c) resource pulses, and (d) MMEs. Middle row: (a–d) general transient dynamics and equilibria for each scenario. Bottom row. Phase plane dynamics for the associated models with black circles marking pre-disturbance conditions, black triangles marking post-disturbance conditions at equilibrium and arrows indicating the direction of movement in phase plane during the transient phase. See Supplementary material Appendix 1 for parameter values.

predator attack rate (a_2) and predator handling time (h_2). The change in predator abundance over time depends on consuming herbivores with conversion efficiency (e_2) and, for simplicity, the losses due to density-independent mortality rate on a per capita basis (d). This assumption is warranted as species in higher trophic levels typically occur in lower abundances, and are thus expected to experience weaker density-dependence (Damuth 1981, Riede et al. 2011).

General model

Based on the aforementioned assumptions, we use the model:

$$\begin{aligned} \frac{dR}{dt} &= rR\left(1-\frac{R}{K}\right)-\frac{aRH}{1+ahR}+\varepsilon\gamma(t) \\ \frac{dH}{dt} &= \frac{eaRH}{1+ahR}-mH^2-\frac{a_2HP}{1+a_2h_2H} \\ \frac{dP}{dt} &= \frac{e_2a_2HP}{1+a_2h_2H}-d(t)P \end{aligned} \tag{1}$$

where γ defines the magnitude of a resource pulse, and ε describes how much of an impact the pulse has on the growth of the basal resource, such that there is no impact on resource growth when $\varepsilon = 0$, the resource pulse has a positive effect on resource growth when $\varepsilon > 0$, and the opposite is true when $\varepsilon < 0$.

Scenario 1. No event

Where no event occurs, both the death rate, d, and the magnitude of the resource pulse, γ, are constants through time and equal to the baseline death rate d_{base}, and $\gamma = 0$, respectively. Here, we assume that the flux of dead predator biomass produced is small enough that it does not have an appreciable impact on resource growth, or that it is essentially lost from the system.

Scenario 2. Predator removal

When a predator removal occurs, the predator death rate (d) is a function of time such that the death rate increases many times (M) relative to the baseline death rate (d_{base}) after a critical time (t_{crit}):

$$d(t)=\begin{cases} d_{\text{base}} & ,t<t_{\text{crit}} \\ M\,d_{\text{base}} & ,t\geq t_{\text{crit}} \end{cases} \tag{2}$$

Importantly, in this scenario the removed predator biomass is lost from the system without directly impacting the resource such that γ remains constant and equal to 0.

Scenario 3. Resource pulse

We modified previous work that modeled a resource pulse as an additive effect on the basal species growth rate (Holt 2008), by incorporating a decay rate that simulates decomposition (Swift et al. 1979). In this scenario, the resource pulse of magnitude γ occurs from an influx outside the system after a critical time (t_{crit}), then decays exponentially as,

$$\gamma(t)=\begin{cases} 0 & ,t<t_{\text{crit}} \\ S_0\mathrm{e}^{-\Theta(t-t_{\text{crit}})} & ,t\geq t_{\text{crit}} \end{cases} \tag{3}$$

where S_0 controls the magnitude of the pulse at $t = t_{\text{crit}}$, and Θ determines how fast the pulse disappears from the environment. Importantly, d is a constant through time and equal to d_{base}.

Scenario 4. MMEs

Similar to predator removals, the predator death rate (d) is a function of time that increases M times with the onset of the MME (i.e. $t \geq t_{\text{crit}}$, Eq. 2*), then decreases after some small amount of time, τ, such that:

$$d(t)=\begin{cases} d_{\text{base}} & ,t<t_{\text{crit}} \\ M\,d_{\text{base}} & ,t_{\text{crit}}\leq t<t_{\text{crit}}+\tau \\ d_{\text{base}} & t_{\text{crit}}+\tau\leq t \end{cases} \tag{4}$$

During the MME, yet unlike the above scenarios, the dead biomass does not immediately leave the system, and generates a resource pulse that directly impacts the growth of the basal resource at a rate $\varepsilon\gamma(t)$, where $\gamma(t)$ is as in Eq. 3, but where S_0 is a function of the dead predator biomass. This assumption is agnostic as to what the mechanism is for converting dead biomass into resource biomass, and ultimately, growth; however, assuming that dead biomass impacts either maximum growth rate, r, or carrying capacity, K, directly can produce qualitatively similar behaviors (Supplementary material Appendix 6 Fig. A2). The dead predator biomass (P_{dead}) is in turn equal to the product of the total predator biomass at time t_{crit}, the death rate at time t_{crit}, and the total amount of time the MME lasts for, τ, as: $P_{\text{dead}} = M\ d_{\text{base}}P(t_{\text{crit}})\tau$, provided values of τ are small. Then, by dividing both sides of the equation by $P(t_{\text{crit}})$, it is possible to calculate the fraction of the initial population that died, f_{dead}, as: $f_{\text{dead}} = M\ d_{\text{base}}\tau$. Then, it is possible to write S_0 as a function of the death rates during an MME ($S_0 = M\ d_{\text{base}}P(t_{\text{crit}})\tau$), if we know for how long the MME lasted, or as a function of the proportion of the population that was removed ($S_0 = P(t_{\text{crit}})f_{\text{dead}}$). While dynamically equivalent, we do the latter in this paper. The impact of γ on the basal resource can be positive ($\varepsilon > 0$) or negative ($\varepsilon < 0$). Potential negative impacts, for example, could occur due to toxicity or light-limitation where the carrion blocks sunlight necessary for primary production (Tomberlin et al. 2017).

Generalities and comparisons across models for extreme die-off events

Overall, MME transient dynamics (Fig. 1d) differ from that of normal conditions (when no perturbation is present, Fig. 1a), predator removals (Fig. 1b) and resource pulses

(Fig. 1c) whenever die-offs completely extirpate predator populations. Only when the impact of the dead biomass produced by MMEs on the resource is weak (low ε), do MME and predator removals behave similarly in their initial stages (Fig. 1b, d). For instance, the tell-tale sign of an MME, which occurs when the dead biomass produced by the MME has a positive impact on resource growth (e.g. a fertilization effect by carcasses contributing key limiting resources, as (in Bump et al. 2009a)) and leads to an increase in resource abundance at first (Fig. 1d, start to '+' sign), is absent in predator removal scenarios. Additionally, when the dead predator abundance has a negative impact on resource growth (e.g. a toxicity or a light-limitation impact), resource abundance initially strongly decreases with minimal impact on herbivore abundance (Fig. 1d, start to '–' sign), followed by an increase in herbivore abundance with little impact to resources.

While MMEs and resource pulses have in common that basal resource abundance initially increases, because the predator is still suppressing the herbivore during a resource pulse, the transients and equilibria are qualitatively different (Fig. 1c–d). The magnitude of the initial increase in basal resource is constrained in MMEs by the interplay between how much dead biomass is generated during the MME and the eventual surge in top–down control of basal resources by herbivores, while it is more dependent on the magnitude of the pulse in resource pulses.

The equilibrium conditions of MMEs can also differ from resource pulse and predator removal scenarios (Fig. 1 triangles). Not surprisingly, the equilibria resulting from predator removals, where a trophic level is indefinitely removed, are different from those experienced during a resource pulse, where following a perturbation the systems returns to its prior conditions (Fig. 1b–c). By contrast, the equilibrium conditions associated with MMEs can be of three kinds. The first occurs whenever the dead biomass has a positive impact on the basal resource ($\varepsilon > 0$) or whenever the impact is negative but small ($\varepsilon < 0$) and a 100% predator removal occurs (Fig. 2d). In both cases, as in a predator removal scenario, herbivore populations experience a positive increase in abundance while the basal resource experiences a reduced equilibrium (Fig. 2e, red). Importantly, unless the predator is completely extirpated, MME equilibria will resemble those of the resource pulse scenario (Fig. 1d). A third (not shown) MME equilibrium also exists, when the dead predator biomass has a strong negative impact on the resource growth ($\varepsilon \ll 0$). In such conditions, this depression of resource abundance from reduced growth, combined with the increased grazing pressure from a rebounding herbivore population jointly contribute to resource extirpation, leading to the subsequent extirpation of the herbivore.

General community level impacts following MMEs

The above model comparison suggests the potential for sudden and large magnitude die-offs to produce community-level

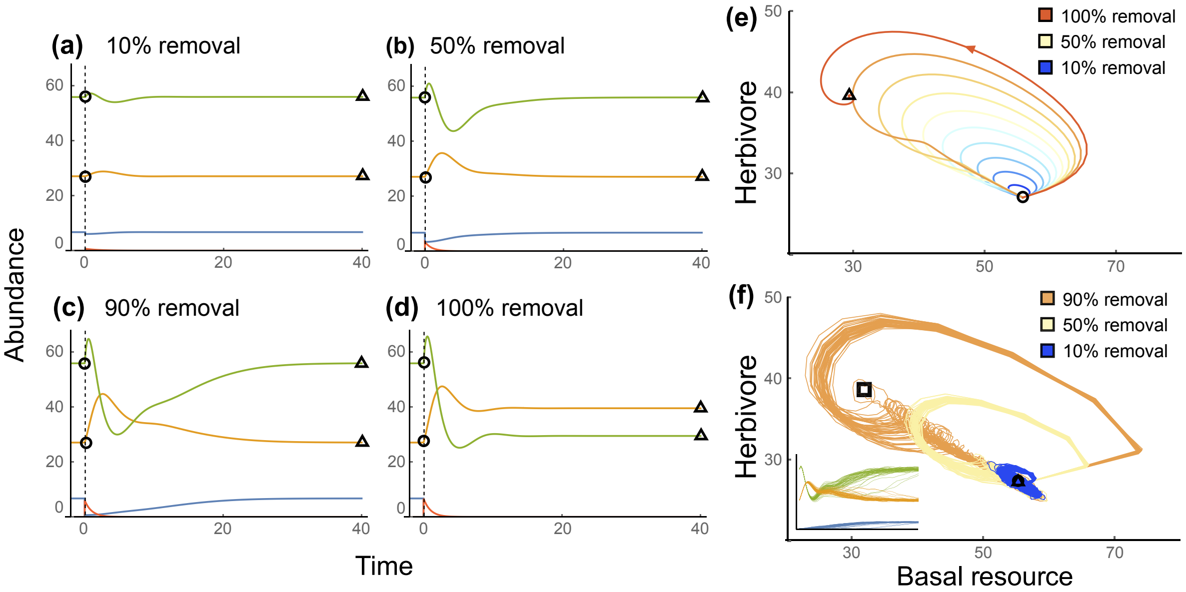

Figure 2. The impact of MME magnitude and demographic stochasticity on food web dynamics. (a) Three-species chain dynamics after 10% predator removal during the MME, (b) 50% removal, (c) 90% removal, and (d) 100% removal. (a–d) Color coding, symbols, as well as initial conditions and equilibria are as indicated in Fig. 1. (e) Phase plane dynamics post MME for 10% removal percentage increments. (f) Same as in (e) but for three removal conditions (10, 50 and 90%) for the stochastic differential equation (SDE) version of the model in Eq. 1 and 4. Notice the tendency of the system to remain near the equilibrium for 100% extinction (black square) even for low levels of stochasticity. Inset: SDE dynamics for 100 runs of the model and 90% removal for comparison with (c). See Supplementary material Appendices 1, 3 and 4 for information on simulation conditions. Quantitative differences between (e) and (f) are due to differences in the numerical methods used to simulate ODEs and SDEs, and not to meaningful differences between the two.

impacts that differ from that other well-studied environmental perturbations. We now focus on establishing baseline expectations for such community-level impacts. To do so, we evaluate how the magnitude of MMEs impact communities, how demographic stochasticity may affect these impacts, and whether the trophic position at which MMEs may occur can lead to different outcomes, as well as how food web complexity and ecosystem type may mediate these responses.

MME magnitude

MMEs describe a continuum of high magnitude mortality, ranging from substantial mortality to complete local extirpations (Fey et al. 2015). To understand how MME magnitude affects community structure and dynamics, we explored the response of the MME model (Scenario 4, above) for different magnitudes of predator population percent losses ranging from 10% to 100% in 10% increments (details in Supplementary material Appendix 2). We find that systems where partial MMEs occurred (e.g. MMEs with less than 100% population-level extirpations) will eventually return to their original equilibrium conditions (Fig. 2a–c, e); however, the larger the magnitude of the MME, the longer the transients (Fig. 2e). These results are robust under different assumptions about how fast the resource pulse disappears (θ) and impact the resource pulse has on the growth of the basal resource (ε) (Supplementary material Appendix 2 Fig. A1).

When allowing for demographic stochasticity to occur (details in Supplementary material Appendix 3), the magnitude of the MME makes it more likely for the target population to go extinct, which can make the community qualitatively change state, from a three-species system to a two-species system (Fig. 2f). Indeed, when MME magnitude is near 90%, stochastic phase plane dynamics are on par with those for deterministic 100% magnitude MMEs (Fig. 2f, orange), nearing predator extinction even for small levels of stochasticity.

MME magnitude at different trophic levels

While top predators appear to experience more MMEs (Fey et al. 2015), such events can occur at all trophic levels, including herbivores (Carpenter 1988, Subalusky et al. 2017) and basal resources (Kurz et al. 2008). We examined the community response of the MME model, following herbivore MMEs of varying magnitude. For an herbivore MME, our model predicts an initial, dramatic spike in the abundance of the basal resource following the herbivore mortality event (Fig. 3). This response is fueled by the basal resource simultaneously experiencing release from herbivory as well as a pulse of resources resulting from the dead herbivore biomass. Meanwhile, predator abundance temporally decreases from reduced prey levels (Fig. 3a–c, e bottom) unless the intermediate consumer is completely extirpated. In this extreme case, the top predator is also extirpated and the system reaches a new equilibrium where only resources remain at their carrying capacity (Fig. 3d–e). Thus, the trophic level impacted during an MME may differentially affect both short- and potentially long-term community dynamics.

Trophic complexity and the response of communities to MMEs

Working beyond simple tri-trophic food chains, we offer expectations about how MMEs may propagate through all major food web modules, which are the building blocks

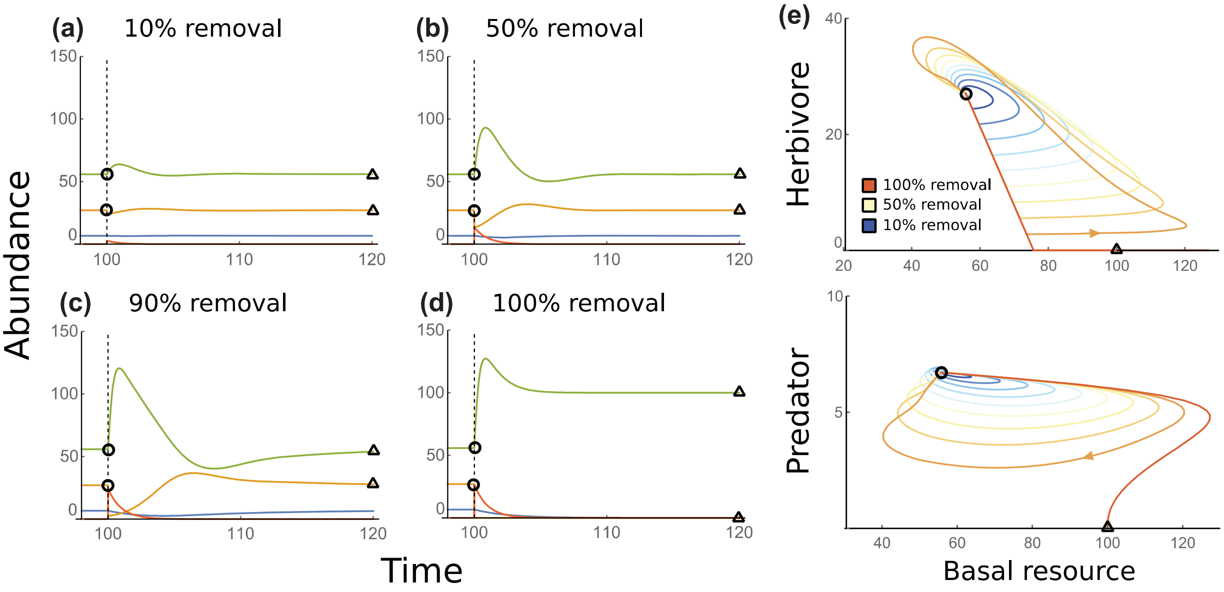

Figure 3. The impact of an herbivore MMEs across trophic levels. (a–d) MMEs of increasing magnitudes as in Fig. 2 but with the herbivore being the trophic level experiencing the MME. (e) Top: phase plane dynamics as in Fig. 2. Bottom: same as top figure but with the abundance of the top predator against the basal resource. Color coding, symbols for initial conditions and equilibria as in Fig. 1. See Supplementary material Appendix 1 for parameter values.

of larger, more complex food webs (McCann et al. 1998, McCann 2011). These are: the omnivory module, where a direct feeding interaction exist between the basal resources and top predators (Fig. 4a, Supplementary material Appendix 4), the diamond module, where there are two herbivores, and hence, two paths from basal resources to top predators (Fig. 4c, Supplementary material Appendix 4), the intra-guild predation module, which is a diamond food web with an additional predation link between the two intermediate predators (Fig. 4e, Supplementary material Appendix 4), and the four species trophic chain module to enable generalizations regarding odd versus even number length food webs (Fig. 4g, Supplementary material Appendix 4). In these instances, we compare these responses to our base model presented in Fig. 2.

Our models suggest that food webs with higher amounts of omnivory may exhibit more pronounced initial increases in basal resource abundances following MMEs, as evidenced by more horizontal transient dynamics when plotted in the consumer–resource phase plane (Fig. 4b relative to Fig. 2e). This is a consequence of basal resources benefiting following a top predator removal to a greater extent when substantial direct trophic interactions take place between top level consumers and basal resources: the basal resource is both fertilized by

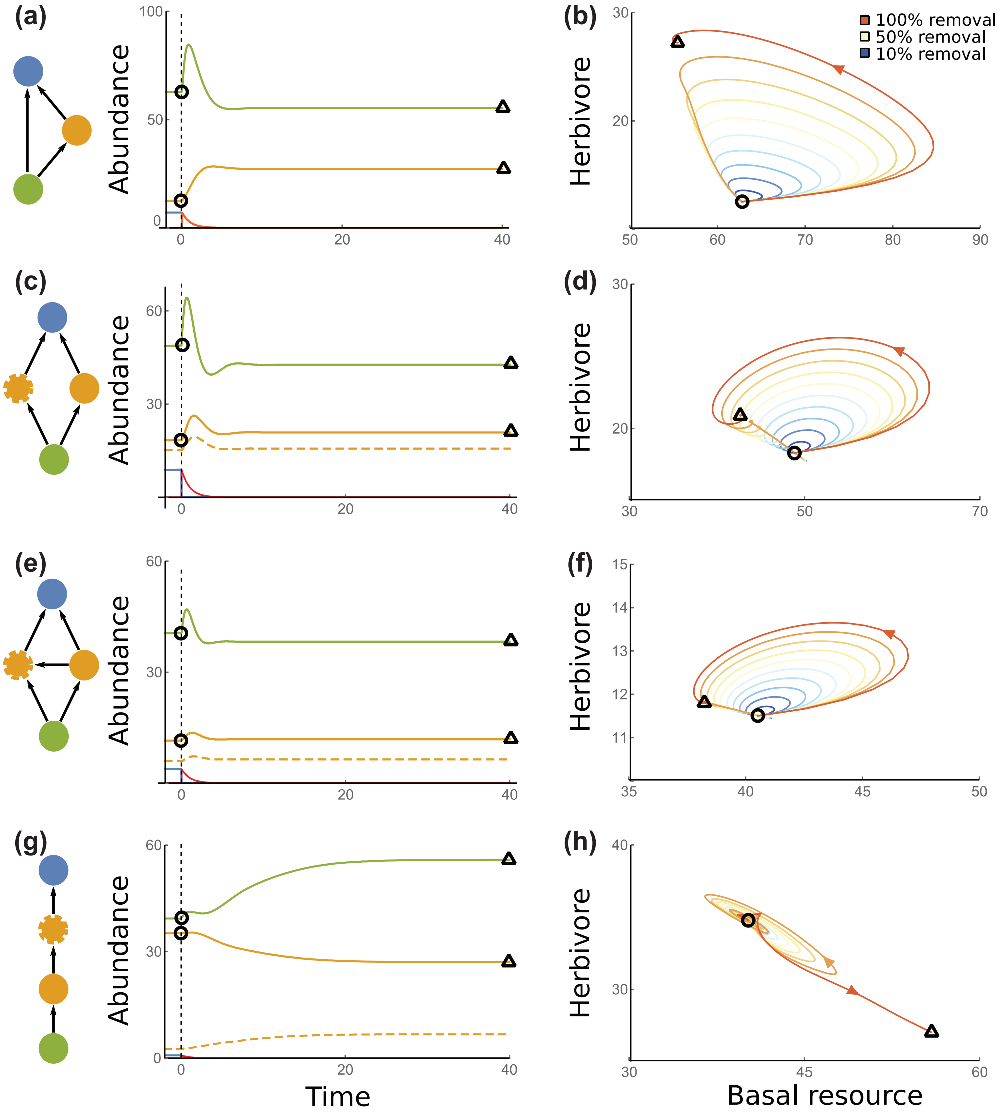

Figure 4. Food web modules and the impact of MMEs. Food web module is indicated to the left by circles (trophic levels) connected by arrows (feeding interactions), where the direction of the arrow indicates the direction of the flow of energy. (a) Omnivory module transient dynamics for 100% MME. (b) Phase plane dynamics for the omnivory module with color coding as before. (c) Diamond module and (d) phase plane dynamics. Second herbivore dynamics indicated by dashed line as well as dash border in diagram. (e) Intra-guild predation module and phase plane dynamics (f). Intra-guild predator indicated by dashed line and border. (g) Four-species chain and phase plane dynamics (h). Color coding, symbols, as well as initial conditions and equilibria as indicated in Fig. 1. See Suplemantary material Appendices 1, 2 and 4 for details on specific assumptions and parameter values.

dead biomass and released from predation by the top predator. These results hold generally across other modules as well (Fig. 4c–f), although the magnitude of the response seems to decay with increased number of trophic links (Fig. 4a–f). The latter may suggest that larger, more complex food webs might be less volatile in their response to MMEs, although further investigation is needed.

The number of trophic levels present in a food web, however, may lead to different responses due to even-odd effects (Hairston et al. 1960, May 2001), as the herbivore and the basal resource abundances now respond in opposite directions (Fig. 4g–h). Here, the basal resource initially increases whilst herbivore abundance decreases, and in the event of a complete top predator extirpation, achieves an equilibrium that is opposite from the one achieved during tri-trophic predator extirpations (e.g. higher resource and lower herbivore equilibrium abundance, Fig. 4g–h).

MMEs across different ecosystems

Because community dynamics strongly depend on fundamental ecological processes (e.g. mortality rates, conversion efficiencies), and these are well known to vary across terrestrial and aquatic ecosystems (Shurin et al. 2006), it is important to understand how the impacts of MMEs on community dynamics might vary across ecosystems. To this end, we parameterized our model by imposing differences in values for those parameters that are known to differ between terrestrial and aquatic ecosystems. We assumed larger maximum per capita population growth rates for the basal resource and increased conversion efficiencies in aquatic, relative to terrestrial ecosystems (Shurin et al. 2006). With these contrasting values imposed, our model suggests the potential for stronger oscillatory behavior in aquatic ecosystems following the MME, compared to terrestrial ecosystems (Fig. 5). The increased efficiency of aquatic herbivores in converting basal resources into offspring, combined with the faster turnover rate of basal resources, jointly contribute to a more rapid numeric response across aquatic food chains after the onset of an MME, which leads to more sustained oscillations and transient dynamics. The latter suggests that in the presence of additional stochasticity, aquatic systems may be consistently more vulnerable to local extirpations.

Other potential differences in how MMEs impact systems may occur via loss rates of dead biomass, which may even differ within a given ecosystem type. For example, MMEs involving pelagic aquatic and marine taxa can rapidly sink into benthic regions (Smith and Baco 2003). In such cases, the resulting community dynamics in pelagic ecosystems may more closely be approximated by trophic removals because the nutrient are not readily incorporated back into the system, while the resulting community dynamics in the recipient benthic ecosystems may more closely behave like resource pulse dynamics. On the other hand, ecosystems where dead biomass

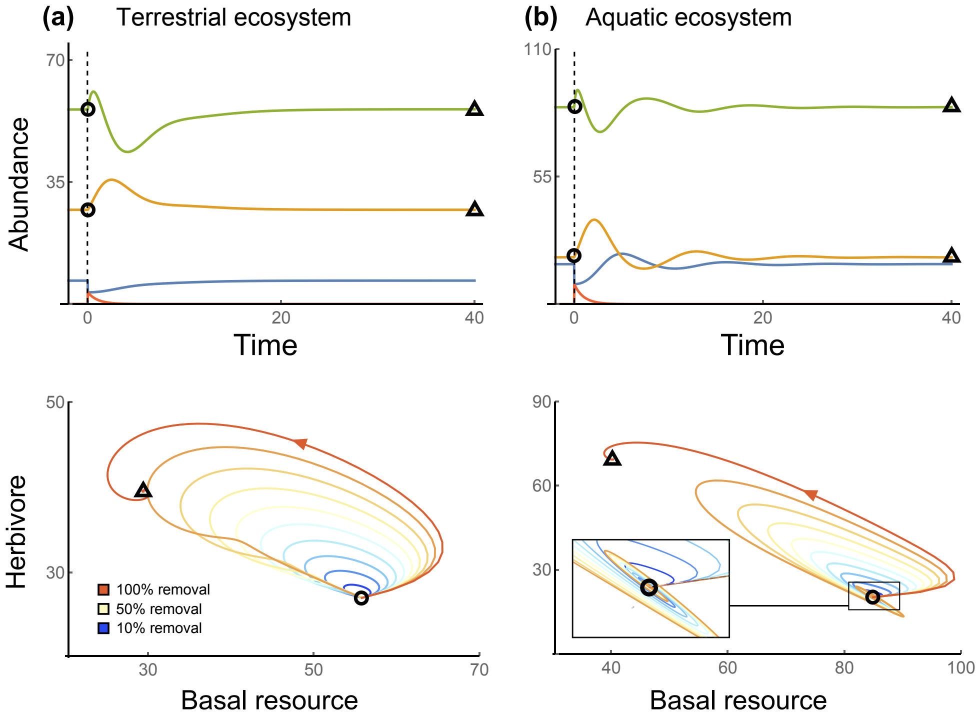

Figure 5. The impact of ecosystem type on post-MME dynamics. (a) Top: dynamics of the parameterization of the model assigned to a terrestrial ecosystem for 50% removal. Bottom: phase plane dynamics of the terrestrial ecosystem, model parameterization and color coding as before. (b) As in (a) but for a parameterization assigned to an aquatic system, this is, $r_{aq} = 2r_{te} = 4$, and conversion efficiencies are 0.1 larger in aquatic ecosystems (Shurin et al. 2006).

may last for longer durations (e.g. lakes and ponds, colder environments), may be subject to stronger post-MME effects and longer transients (Supplementary material Appendix 2 Fig. A1). The duration of such transients will also be mediated by the decay rates of the internal composition (i.e. tissue type, fat or protein content) of individuals in the impacted animal populations (Subalusky et al. 2017). Additionally, inverted biomass pyramids traditionally associated with aquatic ecosystems (Shurin et al. 2006) or systems receiving ecological subsidies (Trebilco et al. 2013) should yield a greater resource pulse after MMEs involving predator die-offs than predator MMEs in terrestrial ecosystems, due to higher standing predator biomass before the onset of the MME. For this same reason, herbivore MMEs should generally produce more of a resource pulse than predator MMEs within terrestrial ecosystems.

The above theoretical predictions are, by design, not exhaustive, and their simplicity is intended to characterize general expectations of MMEs. However, by investigating potential scenarios for the community-level effects of MMEs based on their magnitude, trophic level, food web topology, and ecosystem type, these results provide empiricists with some testable hypotheses. Future theoretical explorations of MME dynamics should be guided by patterns of data, which as we subsequently explore, are equally nascent.

Observational evidence of MME expectations

To investigate whether some of our theoretical expectations for MMEs occur in wild populations, we reviewed and extracted community-level observational data from a recent review of MMEs (Fey et al. 2015). This database identified 727 published MMEs from 460 studies and 2407 animal populations. We included an additional 53 studies using a literature search (performed November 2017, using Google Scholar) to include papers referencing Fey et al. (2015). We screened the resulting 513 papers to determine if they presented information on the community-level consequences of MMEs. From this exercise, we identified 31 published studies (Supplementary material Appendix 1 Table A1), of which 29 were observational and two were experimental. The majority of the observational studies ($n = 23$) involved MMEs affecting fish predators; four studies involved herbivorous or omnivorous aquatic invertebrates (mussel, urchin and clams); two involved herbivorous or omnivorous mammals. Below we use these empirical data collected to: 1) highlight generalities of this survey; 2) extract available time-series to construct phase-plane diagrams to qualitatively compare those with our theoretical models; and 3) highlight future research directions suggested by mismatches between our model dynamics and observed MME dynamics (Supplementary material Appendix 5 for details).

Confronting model dynamics with empirical patterns

We find general agreement between our model and reported community-level responses following MMEs. First, these observational data show support for the need to consider the resource pulse produced by decaying biomass following an MME. The vast majority of studies reported an appreciable pulse of nutrients following MMEs (Table 1, Supplementary material Appendix 5 Table A2). However, in response to predator MMEs, observed increases in basal resources were only reported in 60% of studies (Table 1). In these instances, it is difficult to determine whether the changes were driven by potential positive versus negative effects of resource pulses (Fig. 1d), by odd versus even trophic level effects (Fig. 4g), or by the original cause of the MME. Studies reporting the response of basal resources to herbivore MMEs were rarer, yet all reported an increase in basal resource abundance (Table 1). For example, Carpenter (1988) showed that after a sea urchin MME, algae biomass increased sharply alongside a 50% decrease in the amount of algal biomass removed by herbivores. Similarly, Daskin et al. (2016) showed that large herbivore die-offs in Africa have led to woodland expansion, changing the abundance and community composition of dominant plants.

The vast majority of studies reported an increase in herbivore abundances following a predator MME (Table 1), which was also consistent with model expectations for a predator MME. The single study that reported a decline in herbivore abundances was from a system with four distinct trophic levels, where the die-off of the top predator may have temporally increased the intermediate predator (Rask et al. 1996). This example supports the importance of food web topology in mediating the community response to MMEs and is consistent with our expectations in response to a four-trophic level system (e.g. Fig. 4g).

Confronting model predictions with observational MME time series data

Three studies, all from fish MMEs, presented time-series data that was sufficient to graphically visualize MME dynamics (Vanni et al. 1990, Nagdali and Gupta 2002, Mátyás et al. 2004). We extracted data from these studies using Image J ver. 1.50i (Schneider 2012) and then constructed phase-plane plots to qualitatively compare them to the dynamics predicted by our models (Fig. 6). We reported data for the duration of the MME as defined by the authors of each study. If the reported MME started mid-year, we included available data for the months preceding the MME; if the event started at the beginning of a year, we included the observations from the year preceding the event. The error inserted from such a procedure should in all cases be much smaller than the reported measurement error (DeLong et al. 2016).

Although not specifically incorporated into our models, all studies suggested that some limiting nutrients increased following the MME– increasing NO_3^- (Nagdali and Gupta 2002), soluble P and NO_3^- (Vanni et al. 1990), total and soluble reactive P (Mátyás et al. 2004); however, the three studies showed various degrees of an initial fertilization effect, including no initial increase in resource abundance (Fig. 6a), a short-term positive impact on resource abundance

Table 1. The predicted responses of different trophic levels following predator MMEs. MME prediction indicates a pattern that should exist following an MME. Necessary conditions indicate the theoretical conditions required to generate the given prediction. Observational support indicates the percentage of empirical studies supporting the model predictions. See also Supplementary material Appendix 1 Table A1 for more details.

MME predictions	Necessary conditions	Observational support
Decaying biomass should elevate nutrients above background as dead biomass creates a resource pulse	any MMEs	90% ($n = 10$ qualifying studies)
Basal resource population abundance increases above background levels	for top predator MME when $\varepsilon > 0$, initial stages	60% ($n = 10$ qualifying studies)
	for herbivore MME when $\varepsilon > 0$, initial stages	100% ($n = 3$ qualifying studies)
Herbivore abundance increases	when $\varepsilon > 0$, initial and middle stages	90% ($n = 10$ studies, ε not specified)
Herbivore abundance decreases	only when $\varepsilon <<< 0$, later stages, otherwise never	10% ($n = 10$ studies, ε not specified)

(Fig. 6b), and a prolonged, temporary increase (Fig. 6c). In the foremost case (Fig. 6a), if there was a fertilization effect for resources, the sampling regime of the study was presumably insufficient to detect it, or such an effect negatively affected resource growth rates. In this instance, the system reverted back to typical conditions three months post-MME, suggesting that the effects of MMEs can occur briefly, particularly when top predators, here mosquitofish, have rapid generation times. The latter two examples (Fig. 6b–c) are consistent with the initial effects suggested by our MME model (Fig. 1d). In all three instances (Fig. 6a–c), the post-MME trajectory, where all three communities exhibit an eventual increase in consumer abundance and a decrease in resource abundance, is also consistent with model predictions for tri-trophic food chains (Fig. 1d, 2).

Opportunities for future research

While there is agreement between our model results (cf. Fig. 1–5) and the available observational reports of MMEs (Table 1, Fig. 6, Supplementary material Appendix 5 Table A2), the existing mismatches between theory and empirical data provide an opportunity to highlight several key directions for future research. First, our findings indicate that MMEs that lead to a large resource pulse available for basal resources substantially differ from MMEs where decaying biomass is not integrated into the existing food web. As such, determining the joint community and ecosystem characteristics that contribute to the magnitude, the persistence, and the impact of the primary production of the resources generated from decaying biomass pulse should be a high priority for resolving how MMEs in different ecosystems may unfold.

Second, the extent to which community level changes are due to materials and nutrients released from decaying predator biomass (γ as represented in Eq. 3) or due to internal processes, is unclear. All reported observational accounts of nutrient pulses following MMEs involved fish, which, in addition to being comprised of limiting nutrients, exhibit patterns of N and P excretion that differ from that of other trophic levels (Verant et al. 2007) and ecosystems. Thus, loss of fish in a system can change internal nutrient cycling independent of the recourse pulse provided by decaying biomass. Similar patterns would also be expected for terrestrial consumers that cycle limiting nutrients that affect primary producers. As such, future research should prioritize capturing the altered stoichiometric dynamics that result from the restructuring of food webs following MMEs (Nagdali and Gupta 2002).

Additionally, observational accounts of MMEs often reported sustained community-level impacts within individual trophic levels (52% of top predator MMEs and 100% and herbivore MMEs). For example, a flood-induced mammal MME altered competitive dynamics among desert rodents and resulted in major changes in the relative abundance and

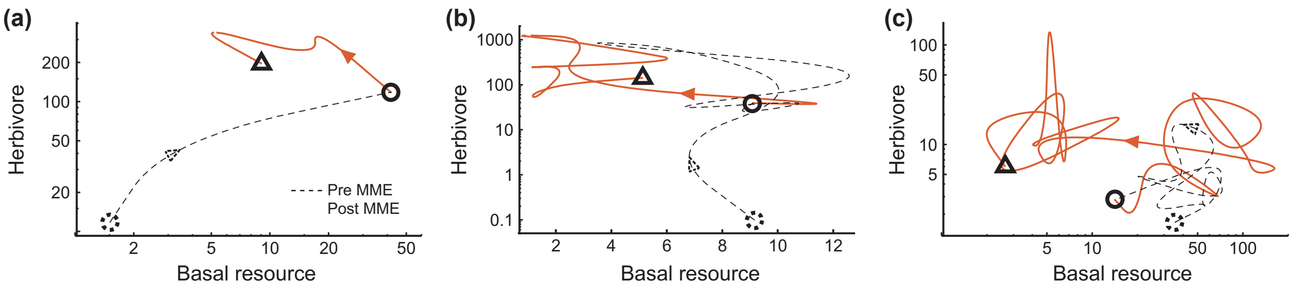

Figure 6. Transient dynamics of MMEs in nature. Phase plane dynamics are of abundances of zooplankton herbivores and their phytoplankton basal resources as reported from fish MMEs described by (a) (Nagdali and Gupta 2002) (b) (Vanni et al. 1990) and (c) (Mátyás et al. 2004). Dotted circles represent the start of the time series, solid circles represent the onset of the MME, and solid triangles represent the end of the time series. Dashed black lines indicate pre-MME dynamics and orange solid lines represent post-MME dynamics.

composition of rodent communities (Thibault and Brown 2008). Additionally, multiple studies of fish MMEs reported changes in the richness and relative abundances of the remaining fish assemblage, as well as the community composition of their resources (Supplementary material Appendix 5 Table A2). In one extreme case, a fish MME likely produced a state change, transitioning the basal resource community from phytoplankton dominated to macrophyte dominated (Perkins and Underwood 2002). MMEs can thus radically re-structure community composition, food web structure, and even ecosystem functioning. In addition to changes in community composition, fish MMEs also resulted in changes in the traits and performance of surviving individuals. For example, a study found that surviving fish after an MME had elevated growth rates (Rask et al. 1996), two other studies (Vanni et al. 1990, Jørgensen and Bernardi 1997) reported that after a fish MME, zooplankton, especially *Daphnia*, increased in size. These later results could reflect that action of natural selection or plastic responses to MMEs. Together, these results point to sweeping effects of MMEs and the need for more theoretical and empirical research that focuses on within trophic level and population genetic consequences of MMEs for both ecological and evolutionary dynamics.

Developing a thorough understanding of how MMEs impacts communities also requires an increased emphasis on data from experimental MMEs. While most MME studies have been observational, two recent studies (Novais et al. 2015, Lashley et al. 2017) experimentally investigated the indirect effects of MMEs. Unlike the majority of the above examples of MMEs in the wild, these studies involved intermediate consumers. Lashley et al. (2017) conducted an experimental MME involving wild boars *Sus scrofa* to understand how increasing dead biomass (e.g. larger magnitude MMEs, Fig. 2) may impact the surviving community members. They observed that increased hog carrion biomass lead to an increase in necrophagous consumers, especially invertebrates, as well as their predators, revealing escalating indirect effects. Similarly, Novais et al. (2015) conducted an experimental MME of clams by introducing five treatments levels (densities, mimicking large magnitude events) of an invasive clam *Corbicula fluminea* that is known to experience MMEs in response to extreme climatic events. They observed changes in abundance, biomass and richness of the terrestrial invertebrate community, demonstrating carryover effects. Both studies reveal the importance of major resource pulses triggered by MMEs, and the importance of considering the detritus-based responses to MMEs.

Concluding remarks

The challenge of understanding the community-level consequences of rare catastrophic events such as MMEs requires integrating observational, experimental and theoretical approaches, and the attention of scientists from different subfields of biology, especially ecologists and evolutionary biologists. This is not an insurmountable challenge, and many opportunities exist for making timely progress. The ideas advanced here were developed to complement and motivate improvements in existing data collection, and as such, focused primarily on understanding the response of MMEs. However, as data collection advances, we hope this will spur models more attuned to the complexities of the natural world that will more accurately capture the nuances of ecological communities and how they respond to extreme events.

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Supplementary material (available online as Appendix oik-06515 at <www.oikosjournal.org/appendix/oik-06515>). Appendix 1–6.