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Climate-driven animal mass mortality events: is there a role for scavengers?

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Summary

Animal mass mortality events (MMEs) will increase with weather and climate extremes. MMEs can add significant stress to ecosystems through extraordinary nutrient pulses or contribute to potential disease transmission risks. Given their efficient removal of carrion biomass from landscapes, we argue here for the potential of scavenger guilds to be a key nature-based solution to mitigating MME effects. However, we caution that scavenger guilds alone will not be a silver bullet. It is critical for further research to identify how the composition of scavenger guilds and the magnitude of MMEs will determine when scavengers will buffer the impacts of such events on ecosystems and when intervention might be required. Some MMEs are too large for scavengers to remove efficiently, and there is a risk of MMEs subsidizing pest species, altering nutrient cycling or leading to disease spread. Prioritizing native scavenger taxa in conservation management policies may help to boost ecosystem resilience through preserving their key ecological services. This should be part of a multi-pronged approach to MME mitigation that combines scavenger conservation with practices such as carcass dispersal or removal when exceeding a threshold quantity. Policymakers are urged to identify such thresholds and to recognize both the insects and the vertebrate scavengers that could act as allies for mitigating the emerging problem of climate-driven MMEs.

An emerging global problem of mass mortalities

Mass mortality events (MMEs) involve the rare, sudden death of large numbers of animals (Fey et al. 2015). They affect all age groups in a population and so differ from natural events such as seasonal migration (Subalusky et al. 2017) or mass emergence events (Yang 2004), and they are increasingly attributed to extreme climate- and weather-related phenomena (Seneviratne et al. 2021) such as droughts, floods or wildfires and cause mortality via heat stress, asphyxiation, disease or starvation (Fey et al. 2015). In our view, MMEs represent an emerging but overlooked problem that extends beyond species conservation into ecosystem functioning, and our aim in this paper is to highlight the potential of scavenger guilds to be a key nature-based solution to mitigating the effects of MMEs.

In the last decade, many MMEs have occurred across a global range of biomes and animal taxa (Fig. 1), and the proximate causes of death are mostly linked to climate and weather extremes (Table 1). MMEs range in magnitude from a few hundred elephants in Botswana (Wang et al. 2021) or reindeer in Norway (Hansen et al. 2014) through to many millions of mussels in the English Channel (Seuront et al. 2019) and perhaps billions of mammals and birds following Australia's catastrophic megafires in 2019/2020 (Dickman et al. 2020). The resulting quantities of carcass biomass through MMEs are therefore staggering (e.g., 700 million tonnes in a single event; Fey et al. 2015). As the magnitude of climate variability worsens and extreme weather events increase in frequency and intensity (Field et al. 2012, Seneviratne et al. 2021), the world will probably witness more frequent and severe MMEs (Fey et al. 2015, Lamberti et al. 2020).

MMEs can affect ecosystem equilibria through rapid and large shifts in numbers of the affected species, but they also cause changes to species interactions and energy flows through food webs (Fey et al. 2019, Lamberti et al. 2020). In nature, background inputs of carrion are continuously provided by countless species of animals across a large body-size spectrum that die from natural causes such as predation and disease (Barton et al. 2019a). Regular inputs of animal carcasses are important for maintaining the ecological and evolutionary processes that enhance biodiversity (DeVault et al. 2003, Barton et al. 2013, Benbow et al. 2019), and they contribute to the dynamics of ecosystem productivity, structure and function through, for example, scavenging by well-adapted species (Wilson & Wolkovich 2011, Subalusky et al. 2017, Barton et al. 2019a). But MMEs are a risk to ecological equilibria and human well-being where such

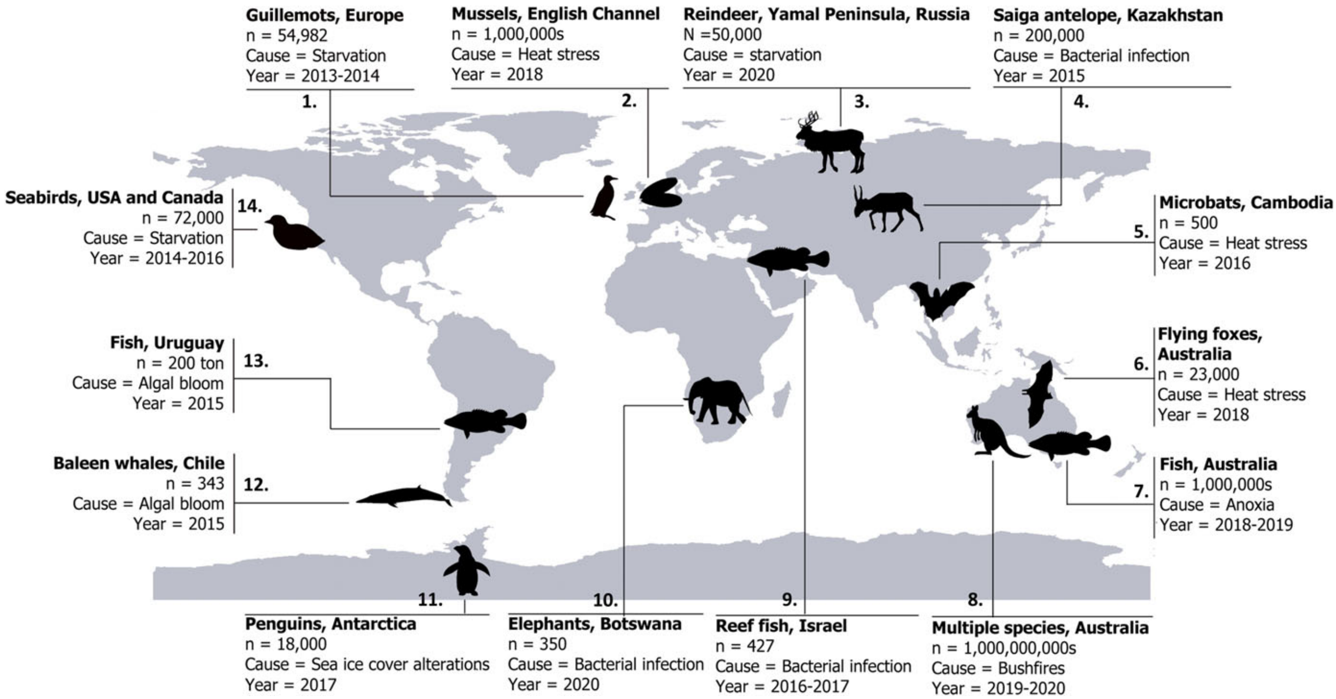

Fig. 1. Selected animal mass mortality events (MMEs) showcasing links to extremes in weather that have occurred across multiple biomes and animal taxa, involving hundreds to billions of individuals over periods of days to weeks. Examples are numbered 1–14 with details provided in Table 1.

events are not the result of millennia of evolution and adaptation (Oro et al. 2013, Fey et al. 2015, 2019, Lamberti et al. 2020) and where scavenging food webs have become severely altered due to landscape modification or direct persecution by humans (Pain et al. 2003, Ogada et al. 2016, Sebastian-Gonzalez et al. 2020). For example, increasing occurrences of MMEs could lead to nutrient pollution in soils or waterways, subsidies of pest species populations or promote disease transmission among wildlife. Among the most frequently threatened scavengers, vultures and top predators are functionally dominant species that are able to rapidly consume large amounts of carrion in some ecosystems (Supplementary Table S1, available online). Accordingly, their removal from those ecosystems could result in dysfunctional scavenger guilds and lead to longer carcass persistence in landscapes (Cunningham et al. 2018, Hill et al. 2018). This has also been demonstrated in Asia and Africa, where vultures have undergone significant declines (Pain et al. 2003, Sebastian-Gonzalez et al. 2020). An overlooked but ubiquitous group of scavengers is made up of blowflies (Calliphoridae), which can also contribute significantly to carrion removal (Barton & Evans 2017, Lashley et al. 2018). The absence of dominant scavenger groups may lead to altered pathways of nutrient flow or elevated risks of disease transmission to wildlife, livestock or people (Ogada et al. 2012, O'Bryan et al. 2020, Sanderson & Alexander 2020, Barbier 2021, Bloom et al. 2021). Thus, conserving scavenger communities should be considered as part of the solution to mitigating the effects of MMEs on both ecosystems and human well-being.

Native scavenger guilds as a nature-based solution to mitigating MMEs

Although scavengers cannot prevent MMEs from occurring, they can help buffer ecosystems against the impacts of MMEs on species interactions and nutrient flows through their consumption and dispersal of carrion biomass. A diverse range of scavenger species contribute to carcass consumption and removal from landscapes (Mateo-Tomás et al. 2017, Anderson et al. 2019, Sebastian-Gonzalez et al. 2020). Vertebrate scavengers include a range of mammalian, bird and reptile taxa (DeVault et al. 2003, Mateo-Tomás et al. 2015, Selva et al. 2019), as well as invertebrates such as flies, beetles and ants (Anderson et al. 2019, Barton & Bump 2019). These different taxa combine to form scavenging guilds that are unique to different biogeographical regions, land uses and habitat types (Anderson et al. 2019, Beasley et al. 2019, Sebastian-Gonzalez et al. 2019, Selva et al. 2019). Where data are available for carrion consumption, they show that removal of carcasses can be up to 100% for some scavenger species and groups (Table S1). However, consumption rates are still poorly understood for many taxa and locations, and increasing knowledge in this regard is critical to improving our understanding of the extent to which scavengers can assist with MME mitigation. Consumption capacity (as quantities per unit time or proportions of carcasses visited or biomass consumed) is particularly well known for keystone and native scavengers such as vultures, which dominate carcass consumption in many ecosystems across Asia, Africa and Europe (e.g., Mateo-Tomás et al. 2017, Gutierrez-Canovas et al. 2020, Buechley et al. 2022). Large native predators such as eagles, lions, wolves and bears are also able to rapidly consume large quantities of carrion in some African, European and North American ecosystems (Wilmers et al. 2003, Mateo-Tomás et al. 2017). The contributions of many less dominant species, including 'meso-scavengers' such as foxes, corvids and suids, may also be important in some contexts (Beasley et al. 2019, O'Bryan et al. 2019).

Despite the impressive quantity of carrion that many scavengers can consume (Table S1) in a few hours or days (e.g., >15 kg/day for *Gyps* vultures in Mediterranean and African ecosystems; Mateo-Tomás et al. 2017), there could be a threshold

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Table 1. Details of example mass mortality events (MMEs) as illustrated in Fig. 1 and grouped by cause of death and link to climate change.

Example number	Taxa	Proximate cause of death	Link to climate change	Number/ quantity	Year	Location	Source	Supporting literature
10	African elephant (*Loxodonta africana*)	Toxicosis due to cyanobacteria	Opportunistic pathogens already present in the environment or animal population can trigger MMEs when subjected to certain weather conditions, which weaken the host's immune system and promote bacterial proliferation	350	2020	Botswana	Wang et al. (2021)	Robinson et al. (2019), O'Bryan et al. (2020), Young et al. (2020)
9	Reef fish (multiple genera)	Bacterial infection (*Streptoccoccus iniae*)		427	2016–2017	Israel	Genin et al. (2020)	
4	Saiga antelope (*Cornu antelopis*)	Bacterial septicaemia (*Pasteurella multocida*)		200	2015	Kazakhstan	Kock et al. (2018)	
12	Baleen whale (*Balaenoptera borealis*)	Algal bloom	HABs are increasing in frequency due to climate change. Observed trends in HABs are attributed partly to the effects of ocean warming, marine heatwaves, oxygen loss, eutrophication and pollution	343	2015	Chile	Haussermann et al. (2017)	Paerl and Paul (2012), Ho et al. (2019), Gobler (2020)
13	Fish (multiple genera)			200 tons	2015	Uruguay	Reguera and Bresnan (2015)	
2	Mussels (*Mytilus edulis*)	Heat stress	Heatwaves are occurring more frequently and more intensely due to climate change. Animal physiological constraints are pushed to the limit by sudden temperature shocks such as heatwaves.	Millions	2018	English Channel	Seuront et al. (2019)	Ratnayake et al. (2019), Goss et al. (2020), Schwingshackl et al. (2021)
5	Microbats (*Chaerephon plicatus*, *Taphozous theobaldi*)			500+	2016	Cambodia	Pruvot et al. (2019)	
6	Flying foxes (*Pteropus* spp.)			72,175	2019–2020	Australia	Mo et al. (2021)	
11	Adélie penguin (*Pygoscelis adeliae*)	Sea ice cover loss	Ice cover (extent and duration) is affected by rising temperatures, changes in precipitation and freed icebergs	18,000	2017	Antarctica	Ropert-Coudert et al. (2018)	Smith and Barber (2007), Tamura et al. (2012)
8	Multiple vertebrate classes	Wildfires	Climate change increases the frequency and intensity of heatwaves, which create ideal conditions for large-scale wildfires	Billions	2019–2020	Australia	Dickman et al. (2020)	Mazdiyasni and AghaKouchak (2015), Williams et al. (2019), Goss et al. (2020)
7	Fish (multiple genera)	Anoxia due to drought conditions	Heatwaves and droughts create anoxic conditions that trigger fish kills	Millions	2018–2019	Australia	Normile (2019), Jackson and Head (2020)	Ratnayake et al. (2019), Schwingshackl et al. (2021)
3	Reindeer (*Rangifer tarandus*)	Starvation	Rain on snow leads to thick ice preventing foraging and grazing	50,000	2020	Yamal Peninsula, Russia	Siberian Times (2021)	Hansen et al. (2014), Forbes et al. (2016)
1	Common guillemot (*Uria aalge*)		Severe high-wind conditions contribute to the death of seabirds as they cannot feed as often as they need to	54,982	2013–2014	Spain, France	Louzao et al. (2019)	Roberts et al. (2019), Till et al. (2019)
14	Cassin's auklet (*Ptychoramphus aleuticus*) Common guillemot (*U. aalge*)		Increases in water temperature affect lower trophic levels such as prey fish and plankton. Marine heatwaves can also promote HABs, which further impact food webs	72,000	2014–2016	USA, Canada	Jones et al. (2018), Piatt et al. (2020)	

HAB = harmful algal bloom.

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over which scavengers will be overwhelmed and cannot assist with the rapid consumption and dispersal of carrion resulting from MMEs without further affecting ecosystem integrity (Oro et al. 2013). In these instances, additional intervention (e.g., disposing of carcasses via burial, burning or composting) may be required to reduce the impacts of MMEs on altered species interactions, pest species, nutrient pollution or disease risk. It is important to recognize this limitation, but research is needed to develop our knowledge regarding the ecological functions of scavenger guilds in different ecosystems and their capacity to consume very large and irregular influxes of carrion biomass, as well as other ecological and evolutionary consequences of such consumption (e.g., population and community alterations; Oro et al. 2013).

Dominant scavenger species play an important role in the rapid consumption of large quantities of carrion across ecosystems (Mateo-Tomás et al. 2017, Buechley et al. 2022), but it is the combined effect of the entire scavenger guild that often results in the complete recycling of carcass biomass and will be important to their response to MMEs. Research has identified behavioural plasticity among social vultures (black vultures, *Coragyps atratus*) that resulted in higher consumption rates when presented with larger carrion inputs (Baruzzi et al. 2022). Furthermore, the rapid development times and voracious appetite of blowflies (Calliphoridae; Barton et al. 2019b) suggest that they also have the capacity to rapidly colonize and consume excess carrion biomass (Lashley et al. 2018). Yet scavenger guilds may also include pest or invasive species that opportunistically consume carrion, such as wasps (*Vespula germanica*) or pigs (*Sus scrofa*) in southeast Australia (Spencer et al. 2021), or rats (*Rattus* sp.) and dogs (*Canis familiaris*) where vultures (*Gyps* sp.) have been extirpated in Southeast Asia (Pain et al. 2003). These pest species have been shown to alter species interactions at carcasses or change disease transmission risk, respectively. Thus, although scavenger guilds are a part of the solution to mitigating MMEs through the rapid consumption and dispersal of carrion, consideration must be given to those vertebrate and invertebrate scavengers that are able to maintain ecosystem resilience after climate-driven MMEs.

How can scavengers be incorporated into climate change mitigation strategies?

The UNEP Adaptation Gap Report 2020 (United Nations Environment Programme 2021) stresses the importance of identifying ecosystem-based solutions to mitigating the effects of climate change on people and nature. This should extend to the conservation and management of scavengers and scavenging food webs in order to boost ecosystem resilience to shocks and pressures stemming from MMEs. We suggest that this can be achieved in three ways: (1) improving knowledge of the roles of different vertebrate and invertebrate scavengers as providers of nutrient cycling services across ecosystems; (2) the protection and conservation of extant scavenger species known to be dominant carrion consumers and the reintroduction of locally extinct ones; and (3) planning mitigation actions to assist scavenger communities that are not able to deal with MMEs, particularly in vulnerable ecosystems already experiencing multiple threatening processes (Tulloch et al. 2016).

Globally, there is also a need for greater awareness of MMEs and their link to extreme weather and climate events, as well as raised awareness of scavengers as ecosystem service providers (Mateo-Tomás et al. 2017, Olea et al. 2019). Such knowledge should be integrated into international policies and agreements dealing with climate change, but also with the conservation and management of biodiversity in general and of scavengers in particular (Mateo-Tomas & Olea 2018). For example, the action plan for vultures in Africa and Europe (Botha et al. 2017) highlights the potential impacts of climate change on these species but does not mention vultures as potential key actors for resilient ecosystems through rapid carcass consumption over large areas (Ogada et al. 2012, Mateo-Tomás et al. 2017).

At regional and local scales, conservation management plans should include concrete actions for handling MMEs, acknowledging the key role that scavengers could play as providers of both supporting and regulating ecosystem services in this regard. Assessments of the status and health of ecosystems for adaptation to global change should include the assessment of scavenger biodiversity and the identification of dominant scavenger species, their conservation status and their contribution to carcass removal.

We also emphasize that species conservation is biased towards vertebrates (Clark & May 2002), but equal emphasis on both vertebrate and invertebrate scavenger guilds (Olea et al. 2019) should be promoted in conservation policy to encourage resilience to perturbations resulting from MMEs.

In light of the recently started United Nations Decade on Ecosystem Restoration (www.decadeonrestoration.org), conservation actions should also consider reintroductions of previously extirpated scavengers that clearly play a major role in carrion consumption and removal from landscapes. Scavengers should be part of a multi-pronged approach to MME mitigation that combines their conservation with practices such as carcass dispersal or removal when exceeding a threshold quantity. Scavengers may not be a silver bullet to solve all problems associated with MMEs, but it is important to recognize that they are one of the few nature-based solutions available to mitigate the effects of mass mortalities on ecosystems and human well-being.

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Ethical standards. None.

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