Not All Mass Mortality Events are Equal

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Abstract

Mass Mortality Events (MMEs) are defined as novel events involving many individuals dying in a relatively short period of time. In recent years, there has been an increased interest in MMEs due to their perceived increase in frequency. Current definitions are subjective and categorize mortalities varying in magnitude and frequency together. Within this manuscript, Multiple Mortality Events is a newly proposed term to involve multiple individuals dying but not overcoming ecosystem resistance and/or resilience sufficiently to elicit any long-term impact. The concept of “novelty” within MME definitions is dubious thus preventing defined parameters of such events. To address this issue, population dynamics of the species involved within the event, specifically the background death rate weighted against the number of individuals involved in the mortality and adjusted for background and experienced carrion biomasses are incorporated as parameters. This approach provides a numeric value for interpretation of novelty that can then be applied to mathematical models to predict various ecosystem outcomes. For example, this approach can be used in pulse models to identify pulse abruptness or be incorporated into new mathematical frameworks. Within, a modified logistic growth model has been developed to predict population outcomes of necrophagous ectotherms which can be used for further modeling in disease dynamics, conservation, and more.

Keywords

Mass Mortality Events, Multiple Mortality Events, Population Dynamics, Scavenger, Resource Pulse

Refined Approach to Defining Mass Mortality Events

In recent years, alarming numbers of organisms that typically do not exhibit large die-offs as part of their natural history have been exhibiting dramatic mortality events which can be linked directly or indirectly to human actions (1). Many organisms dying rapidly can be a unique pulse event that simultaneously removes biomass from living food chains (2) and increases resource availability for saprophagous species (3). These large die-offs introduce a large flux of nutrients into an ecosystem as the carrion decomposes (4). On a larger scale, unprecedented die-offs for a given taxon can alter evolutionary trajectory and ecology of that species (5).

Abnormal mortality of many individuals within a population of a given species in a short temporal window at a given location have been coined “Mass Mortality Events (MMEs)” (6–12). The primary criterion for an event to be considered an MME is its novelty, so much so that such occurrences have been noted as ecological “black-swan events” (13). While definitions vary slightly, none provide criteria beyond “novel” or “large” die-offs. In instances where definitions dissect out criteria for novelty, they tend to be subjective or possibly arbitrary and do not account for the large natural variation in population dynamics of the species in question. For example, one definition offers ~ 25% of a population dying within a given year as a threshold (14) with no justification as to why this threshold was selected. Regardless, when applying this definition, ‘large’ die-offs that are inherently part of the species biology would be categorized as an MME. For example, white-footed mice (*Peromyscus leucopus*) can have over 90% of the population die annually (15), which would be categorized as an MME under this definition despite majority of these mortalities being due to natural processes such as predation. Secondly, the current and largely ambiguous definitions of MMEs do not differentiate the magnitude of mortality events, inhibiting the ability to predict the perturbation effects of the die-off throughout the ecosystem. For example, die-offs that differ in orders of magnitude are lumped together under the MME umbrella, even though the ecological consequences are likely to be vastly different. For instance, the deaths of 323 reindeer, *Rangifer tarandus* (L.) due to a lightning strike (16, 17) was categorized as an MME as was the death of 200,000 saiga antelope, *Saiga tatarica*, (G.) due to a pathogen over a two-week period (18). The ecological consequences of these two events are undoubtedly different due to various factors, such as the biomass of deceased animals, the rate of which the populations died, location, and secondary effects (i.e., pathogen spread) to name a few; however, the current MME concept does not explicitly address these differences. Conflation of vastly different mortality events may be due to the lack of other terminology accounting for nuance. We suggest that mortality events involving multiple individuals that do not meet the vague criteria for “novelty” be called *Multiple Mortality Events*, where ecological change is expected to occur, but ecosystem resistance and or resilience will allow for this change to be non-existent or relatively short-lived in comparison to Mass Mortality Events. Below we propose criteria for defining novelty in a quantified manner to allow for quantitative reasoning for determinations of “novelty” within a population.

Accounting for unique characteristics of individual ecosystems in addition to the life-histories and evolution of the species in question when predicting ecosystem impact following pulse events have been proposed in the past [21 and citations within]. However, proposals accounting for these unique characteristics within pulse ecology rely heavily on nutrient flow, which may be difficult to ascertain during an ongoing mortality event and do not provide any clarification to the definition of an MME as related to novelty. *We suggest accounting for the population death rate of the* *effected population when considering if a mortality event is novel enough to be considered a true Mass Mortality Event. This approach allows for further application in prediction of population outcomes of carrion-consuming ectotherms utilizing the remains resulting from mortality events.*

Categorization of disturbance events has aided in understanding the nuance in the nature and resulting outcomes of resource pulses. In fact, reoccurring disturbance events generating ecological memory (adaptations of communities to respond faster to an event due to past events or ecological states) within an ecosystem, allowing for high ecosystem resistance is well established (20). Below, we make the argument that the magnitude of the impact of a carrion induced pulse event on the population dynamics of those animals consuming such resources consider the number of individuals involved in the mortality event as well as individual carrion's biomass be compared to what we consider to be the "background death," and average biomass of those contributing to the overall carrion biomass within an ecosystem in regards to the previous year. In fact, generating an average annual death rate by incorporating data from multiple previous years is recommended so as to capture the natural variation in life-history (as in cases where death rate of a population varies greatly across years) of the target populations.

Subjective Categorization of Mass Mortality Events Lacks Quantification.

We propose criteria based on population metrics such as the estimated death rate as a means to describe mortality events (i.e., mass mortality or multiple mortality) to be; 1) less-subjective (i.e., quantified), 2) account for recent ecosystem conditions (i.e., temperature within thermal accumulation modeling) (21), and 3) allow for comparison of the mortality event to historical death rates of the population in question.

Quantifying Mortality Magnitude- A Comparative Example

The death of 323 reindeer accounted for one-third of the deaths for the given population during the previous year (16, 17), while the death of over 200,000 saiga antelope for its population was 6.25X greater than the total deaths estimated to occur the previous year (18). In these examples, the proportional values are still reflective of raw mortality counts. Specifically, the saiga mortality event was a greater magnitude even when accounting for population metrics, suggesting a larger impact on the population and subsequent ecosystem. However, raw counts are not comparable between populations. For example, if the reindeer population had a mortality of 200,000 (mortality rate equivalent to that of the saiga), the event would account for 200X more deaths than estimated for the previous year. This discrepancy highlights the importance of looking past raw mortality metrics to infer impact. More specifically for this example, 200,000 saiga deaths do not have the same impact on the saiga population as 200,000 reindeer deaths on the reindeer population.

Biotic and Abiotic Factors Influences Expected Carrion Biomass in Ecosystems

The number of individuals dying is not the only factor influencing decomposition in an ecosystem. Increased competition, predation pressure, etc. as well as abiotic conditions such as extreme temperatures and seasonal disturbances contribute to population death rates (21). If considered from a biomass perspective and their associated influx of nutrients into an ecosystem, the reindeer and saiga mortality events are vastly different. Reindeer carrion from the mortality comprised approximately ~9,690 kg (assuming average body mass was ~30 kg (22)), and saiga carrion biomass encompassed ~4,600,000 kg (assuming the average biomass of an individual is ~23 kg as reported in (23)). It is indisputable that both events and the decomposition processes that followed would impact an ecosystem; however, the severity of the impact would vary due to the difference in carrion biomass, distribution, and how much carrion biomass the ecosystem can recycle through available scavengers.

Ecosystem Norms and Mortality Impact

Like other pulse occurrences, variation in the magnitude of mortality events is expected to uniquely impact different ecosystems. Of course, the response of an ecosystem to large influxes of nutrients would be ecosystem specific (24), and in some instances, large mortalities are apart of population's natural life histories, predictable, and part of ecosystem dynamics (4). In ecosystems where pulse events are annual or semiannual, ecological memory allows for the system to more efficiently recycle nutrients in comparison to systems that do not traditionally face such pulses (25). For example, adult mayflies (Ephemeroptera) die *en masse* (e.g., 3,000,000 kgs during a single mating season, (26)) after reproduction and are a predictable food resource for many consumers (27, 28). Similarly, salmon (*Oncorhynchus* spp.) introduce numerous micronutrients into the surrounding environment during/after mass die-off following spawning events, which are integral to ecosystem function (29) and also generate ecological memory within their respective ecosystems (20). In fact, historical consistency in occurrence of such events impact the evolution and life-history strategies of consumers of such resources leading to more efficient assimilation of these nutrients into the ecosystem. Under these parameters such events have been coined as reoccurring pulses (25) and inherently do not align with the generally accepted requirement of novelty in MME definitions. Unfortunately, despite mayfly and salmon events being reoccurring pulse events, they have previously been lumped within the MMEs category (27). In our proposed definitions that distinguish mass and multiple mortality events, massive, seasonal mortality of mayflies and salmon would be subcategorized as multiple mortality events. More specifically, since ecosystems that include reoccurring mass die-offs annually are typically resilient to these events, they are poor comparisons with mass mortality events which are generally expected to result in punctual ecological change.

Carrion biomass plays an important role in decomposition (30) and influences the diversity of animals consuming such resources (31, 32). Young, relatively small individuals that die decompose at different rates than adult and/or relatively large individuals despite being conspecifics (30). In populations such as mule deer (*Odocoileus hemionus*) where mortality is higher in younger individuals (33), death rate is influenced more by individuals of smaller biomass, thus the overall carrion biomass one may expect to enter the ecosystem is less than if only adult mortalities were accounted for. The biomass of the individuals that die should be considered when attempting to assess or predict the ecological consequences of MMEs. Thus, we include biomass as an important factor in the Mortality Impact (Mi) and act as resource pulse magnitude to understand pulse abruptness (as described in (19)).

Differentiating Multiple and Mass Mortality Events

As described above, when considering if a mortality event is historically unique for an ecosystem, one must consider the carrion ecology and impacted populations life history within an ecosystem. To evaluate if a mortality event is unique, we developed the *Mortality Impact (Mi)*; an index of the background death rate (based on the death rate of a given population regardless of cause of death) and carrion biomass to the death counts and biomass of the event in question [I]. This index can lead to a better understanding of the increase in carrion availability for scavengers and can be adopted into population growth models to predict population trajectories of saprophagous species within the associated ecosystem. Below, we present a case for the development of the Mi and its value to ecological research related to multiple and mass mortality events. In its current state, there is not enough empirical data to determine what Mi value should definitively separate Mass and Multiple Mortality Events, but this should be a target of future research. Till then, the Mi value can be used as a tool of quantitative reasoning (as done with concepts such as the p-value) and to infer pulse abruptness [VI] till this determination is made.

Quantifying Magnitude from Multiple Mortality Events

Here we outline how novelty may be defined by the magnitude of the pulse event in relation to carrion biomass. Consider the number of individuals that died in a given habitat the previous year (D), and their average biomass (D_M) in relation to the number of individuals impacted by a multiple mortality (nMM) and their average biomass (nMM_M), and you get a proportional number (Mi), as follows:

$$\frac{nMM\,(nMM_M)}{D\,(D_M)} = Mi \qquad [I]$$

Where Mi values (<<<1) are less likely to be novel in the environment, where Mi values (≥1) are likely to be a unique event for the given ecosystem.

In populations where young (and relatively smaller), and older (relatively larger) individuals make up D, the average biomass can be accounted for by separating the two groups. The same can be said for individuals impacted by the multiple mortality event (nMM). Numerical subscripts denote different sub populations. The modified model may be as follows:

$$\frac{(nMM_1\,(nMM_{1M})) + (nMM_2\,(nMM_{2M}))}{(D_1\,(D_{1M})) + (D_2\,(D_{2M}))} = Mi \qquad [II]$$

Where the Mi values follow the same rules outlined in [I].

In cases where "D" is unknown but is documented for a greater area (i.e., the data are known for a county, but not for a particular forest patch within the county in which the mortality event took place), the death rate (d), and predicted number of individuals residing in a given patch (p), can determine the predicted number of carrion introduced to the patch (Dp) using the following equations:

Death Rate (d)

$$\frac{D}{N} = d \qquad [III]$$

Number of Individuals in a Patch (p)

$$\frac{N}{\text{Total area population resides}} \times \text{Area of mortality} = p \qquad [IV]$$

The Predicted Number of Individuals that Died in a Given Patch the Previous Year

$$d \times p = Dp \qquad [V]$$

The predicted Dp can replace known death for the previous year (D) with the assumptions that the (1) population is homogeneously distributed, and (2) the death rate is consistent across the landscape.

Uncovering the Natural Mortality in Populations

Determining the death rate of a population may be exceptionally difficult to ascertain in certain circumstances. While the solution mentioned above does provide some aid, it draws on assumptions (such as habitat heterogeneity) which are largely not true in most populations. Researchers have been attempting to estimate natural mortality (defined in this paper as population death rate) through predictive modeling (34) and have generated computer models with this goal (see (35)). In populations that do not have a defined death rate for the local or greater area, these generated models are sufficient in standing in to "Dp" noted above.

Carrion Induced Pulse Abruptness

Modifying the equation for pulse abruptness as defined in (19), using mortality magnitude "Mi" to account for magnitude and duration of the event "t" to predict the abruptness of a pulse event "A"

$$\frac{Mi}{t} = A \qquad [VI]$$

Where pulse abruptness provides insight into the degree that ecosystem resistance and resilience is challenged.

Modeling Effects of Mass Mortality Events on Ecosystems

Due to the rise in reports of MMEs, there is ongoing discussion of how scavengers hinder or exacerbate secondary effects of large carrion biomass (such as pathogen spread) (36), highlighting the need to understanding population growth for purposes of conservation and understanding overall ecological outcomes. Scavenger communities (e.g., microbial and invertebrate) often rely on carrion as a portion or all of their diet (37, 38), the logistic growth model can be used as a basis to predict population growth of carrion feeders after a mortality event, assuming carrion resources are incorporated in the population's carrying capacity. To account for the increased abundance of food resources from a mortality event for these scavengers, the Mi can be used as an exponential function of carrying capacity, where an Mi > 0 will increase carrying capacity, and those values Mi ≤ 0 will have negligible effects. However, biomass alone is not the only factor in the decomposition process to consider. For example, carrion with higher surface area to volume ratios decompose at a faster rate, and therefore smaller carrion decomposes faster per gram than larger carrion (30). Therefore, decomposition rate can be calculated using a validated model and taxon specific coefficients (as defined by (30, 39)) incorporated into the logistic growth model. This surface area to volume ratio can be determined for the average biomass of an individual and then multiplied by carrion number introduced during the mortality event. Additionally, like the Mi, if there are two distinctly different biomasses impacted by the mortality event, the equation can be modified to account for each sub-biomass represented in the event.

Time as a parameter in the logistic growth model allows for prediction of the population dynamics per a given time point. Many organisms of importance that utilize carrion resources are invertebrates (40, 41) and microbes (24, 42, 43), where temperature is an important factor in development time of individuals (44). Therefore, accumulated degree day models (ADD) are used to determine the amount of time for an organism to meet a life stage in both necrophagous insects (45), and microbial communities (46) at carrion based on environmental temperature. The ADD of climatic conditions can therefore be compared to the developmental ADD needed to complete a life cycle. By using a proportion, this allows for the consideration of multivoltine generations, assuming offspring may be subsequently utilizing the carrion resources left from their parent.

Predicting Scavenger Populations from Multiple Mortality Events

The logistic growth model is a classic method in determining population growth at a given time in relation to carrying capacity (K). Several models have been adapted from the logistic growth model to better suit the population in question. The following model utilizes the logistic growth model as its backbone and introduces factors that impact ectothermic organisms that rely on carrion resources for reproduction (such as insects and microbial communities).

$$N = rN_0 \left(1 - \frac{N_0}{K(e^{Mi})}\right) x \left(\frac{b \text{ x } m^a}{m \text{ x } 0.997}\right) x \quad D_m \quad x \quad t_{ADD} \qquad [VI]$$

Where r is the intrinsic rate of increase. N_0 is the initial scavenger population prior to the event. e^{Mi} is added in the logistic growth model, where Mi values lift carrying capacity (K) exponentially as the value gets larger (becomes more novel). Surface area to volume ratio plays a large role in the rate of decomposition of carrion resources, and is calculated using this equation [27], where "m" is the average biomass of an individual, while "a" and "b" are predetermined coefficients previously determined for mammals [27], and birds [33]; where a= 0.701 and 0.67, and b=9.88 and 8.11 respectively [27, 33]. To incorporate the overall biomass, this equation is multiplied by the number of individuals impacted by the multiple mortality event (D_m). Time is denoted as t_{ADD} where Accumulated Degree Days are utilized to compare development to environmental temperatures (t_{ADD}= (Environmental ADD/ADD to complete life cycle). Together this provides the number of individuals from the carrion involved in the mortality event (N).

It is important to distinguish what the model proposed above is and is not. This model can be used to predict temporary changes in scavenger populations after a mortality event and quantify the relative novelty of an event, not to determine what is or is not ecologically important. A mortality event of 300 individual reindeer was determined to have long-term ecosystem effects (17) despite the Mi value being a relatively small numeric value suggesting a [relatively] low level of impact. Therefore, multiple mortality events as proposed can still have meaningful ecological consequences despite not meeting the requirement of novelty to be considered true MMEs per our definition. Even so, the proposed model is useful for both multiple and mass mortality events, where the overall impact of a mortality event is a function of the current ecosystem dynamics in light of these resource pulses.

Broad Applications of the Model

Since carrion is a resource for multiple taxa ranging from microbes (43), to invertebrates (40), the broader applications of predicting population dynamics of these taxa are numerous. For example, bacteria and fungi have been determined to drive many ecosystem processes such as nutrient recycling (24), plant diversity (47), symbiotic and commensal interactions (48), as well as pathogen spread (49). Therefore, understanding microbial proliferation through this model will aid with predicting these downstream ecological impacts, including impact of entomopathogens, that which can limit necrophagous arthropod survival (50). This model can be used to understand implications of other taxa as well. For example, necrophagous arthropods create bottom-up effects in food webs by serving as pollinators and prey items (51) in addition to serving as vectors. A single blow fly for example can pick up 9696 *Escherichia coli* cells on average within 30 seconds of contact with a surface (52). Therefore, this model can serve as a first step in predicting pathogen spread associated with mortality events.

Predicting insect population dynamics using models such as logistic growth has been useful for control methods of pest species (53) and can also be used to infer density dependent changes in resource preference as well. For example, an increase in competition due to high population densities among blow flies may lead to an increase in the number of cases of myiasis, a parasitic behavior where colonization of living organisms occurs (54). These examples highlight just a few of the ways this model can be used to help predict the ecological impacts of multiple and mass mortality events.

Limitations of the Model Regarding Vertebrate Scavengers

Unlike microbial or arthropod decomposers, vertebrate scavengers in most instances do not rely solely on carcasses for reproduction. Additionally, a majority of vertebrate scavengers are facultative, with vultures and condors being the only taxon to rely on carrion as a primary food source (55). Even when obligate scavengers were the primary consumers at sites of up to ~30 remains, vertebrate scavenging activity only persisted for five days after placement (56). Therefore, this model is unlikely to accurately predict vertebrate scavenger population dynamics. However, relatively short-term changes in the distribution and foraging behavior of individuals within a population can occur due to competition and predation pressures (57). For example, following the previously discussed reindeer mortality of 300 individuals, local raptor population densities increased and rodent populations were significantly reduced as a consequence (17). Secondary impacts of vertebrate scavengers should not go unnoticed either, as vertebrate scavengers had top-down effects on plant communities at the decomposition site following a mortality event (58).

An example using the reintroduction of *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) on the Deer in Big Pine Key, Florida

Key Deer (*Odocoileus virginianus clavium*) are endemic to the Florida Keys (59). During summer 2016, the primary screwworm, *C. hominivorax*, was accidentally reintroduced to the area, resulting in relatively high mortality of the deer (60). Due to the economic impact and eradication efforts of the primary screwworm in the USA and the documented population dynamics of Key deer, this mortality event can be used to validate our model.

It was documented that 44 deaths (~50% of total deaths) the previous year were due to vehicle impacts (61). This led to the conclusion that approximately 88 deaths occurred the previous year. The average adult weight for females and males are 32 and 36 kg respectively (62). Additionally, 135 individuals (mostly adult males) died from screwworm infestation (60), losing about 15% of their population due to the screwworm (63). With this information and the equation developed [I], we calculate the Mi value to be 1.62. In addition, we can utilize the known average male biomass, and number of individuals impacted by the multiple mortality in equation [VI].

The intrinsic rate of increase (r) for the primary screwworm is 0.98 (64), with carrying capacity for 1 km^2 to be 800 adults (65). Since Big Pine Key is 25.22 km^2 (60), the carrying capacity of this habitat is ~20,176 individuals. While it was unknown how many screwworms were reintroduced into the area, it was likely a small number, as Big Pine Key wildlife are monitored, and an outbreak would likely be detected early. For this reason, we artificially impose that 100 screwworm adults were initially introduced. In addition, development studies have not yet included the primary screwworm, so it will be assumed that one generation ($t_{ADD} = 1$) had occurred.

By utilizing this information and the equation [VI], we predict ~44,858 screwworm adults were produced from this event. In their surveillance program it was estimated that ~32,800 flies had emerged (66), and in response 188 million sterile flies/ km^2 were released over the following months, leading to the successful re-eradication of the primary screwworm in 2017 (60). The need for multiple releases was potentially a side effect of underestimation of initial population sizes. Thus, utilizing this proposed model may provide a more accurate method for predicting production of screwworm from events similar to that on the Deer in Pine Key, Florida to allow for efficient and quicker eradication efforts in future outbreaks.

Difficulties in Studying Mass Mortality Events

With increased interest in MMEs, there has been a push from researchers to better understand their ecological impacts. Empirical studies have been difficult as these events are typically unpredictable. Other studies have generated artificial mortality events to study ecosystem effects and have determined shifts in food web dynamics (67), as well as a localized impact of vertebrate scavengers (56), and a large increase of necrophagous insect biomass (3). Artificial mortality events add carrion biomass from another ecosystem (such as the placement of domestic swine in a forest to study decomposition) and with it introduce unique microbiomes that may influence decomposition. However, generating artificial MMEs has its own limitations, such as introducing carrion resources from animals that did not interact with the ecosystem or community prior to its death, and lacks a disturbance event that traditionally supersedes an MME (such as severe weather seen in (16, 17)). With current research attempting to predict the detection of mortality events (as in (68)), there are opportunities to begin research on MMEs as they occur. Utilization of models, such as the one outlined in this paper and others predicting ecological outcomes of these events

(See (2)) can provide pathways for hypothesis-driven research following less predictable (except in some instances, such as human induced mortalities) natural mortality events.

Concluding Remarks and Further Questions

Carrion systems are useful tools in understanding population, community, and large-scale ecosystem questions (24). While the framework proposed works to bridge gaps and subjectiveness in the current definition of MMEs, it presents its own set of limitations and questions that should be addressed as research surrounding MMEs continues. For example, spatiotemporal placement of remains can vary depending on the cause of a particular event (i.e., pathogens, extreme weather conditions, environmental toxicity) and has been of increasing interest in the field of carrion ecology. How does the variation in time of death and where an individual dies influence broader ecosystem dynamics? Does a mortality of 100 deer that died 10 m from the next equate to the same impact as if they died 70 m apart? Additionally, the proposed definition does not include the cause of mortality. Conditions surrounding an individual's death (such as succumbing to disease) and ecological context influence the decomposition process ((69) and citations within). Therefore, if a mortality event caused by a pathogen kills 75 individuals, and 15 individuals die from lack of starvation, is the ecosystem dynamics different than if all 100 individuals died of the same cause? Future work should determine the ecosystem impacts at various Mi values and its utility in population modeling via artificial and natural mortality events. While this model is intended for events that happen in a relatively short period of time (e.g., within one year), validation and further research can lead to modifications that can include multiyear events such as epidemics. We believe our quantitative approach to defining MMEs and their potential ecological effects will help ecologists and others to better understand the ecological importance of multiple and mass mortality events and further the discussion on how to meaningfully categorize and study these events.

Acknowledgements

The authors would like to thank the several professionals and graduate students who provided constructive feedback. Specifically, to those in the F.L.I.E.S. Facility in the Department of Entomology at Texas A&M University, as well as Drs. Kirk Winemiller, James Beasley, Thomas Chappell, and Oswald Schmitz. This manuscript also benefited greatly from the thoughtful commentary of multiple anonymous reviewers.

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