Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events

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Mass mortality events (MMEs) are rapidly occurring catastrophic demographic events that punctuate background mortality levels. Individual MMEs are staggering in their observed magnitude: removing more than 90% of a population, resulting in the death of more than a billion individuals, or producing 700 million tons of dead biomass in a single event. Despite extensive documentation of individual MMEs, we have no understanding of the major features characterizing the occurrence and magnitude of MMEs, their causes, or trends through time. Thus, no framework exists for contextualizing MMEs in the wake of ongoing global and regional perturbations to natural systems. Here we present an analysis of 727 published MMEs from across the globe, affecting 2,407 animal populations. We show that the magnitude of MMEs has been intensifying for birds, fishes, and marine invertebrates; invariant for mammals; and decreasing for reptiles and amphibians. These shifts in magnitude proved robust when we accounted for an increase in the occurrence of MMEs since 1940. However, it remains unclear whether the increase in the occurrence of MMEs represents a true pattern or simply a perceived increase. Regardless, the increase in MMEs appears to be associated with a rise in disease emergence, biotoxicity, and events produced by multiple interacting stressors, yet temporal trends in MME causes varied among taxa and may be associated with increased detectability. In addition, MMEs with the largest magnitudes were those that resulted from multiple stressors, starvation, and disease. These results advance our understanding of rare demographic processes and their relationship to global and regional perturbations to natural systems.

catastrophes | defaunation | death | rare demographic events

Death is a ubiquitous demographic process central to understanding ecological and evolutionary dynamics. Resource limitation, stochastic events, exceeding physiological thresholds, senescence, and interactions with predators, pathogens, or parasitoids generate death on daily, seasonal, and annual timescales. Although all organisms eventually die, the timing and magnitude of deaths within populations varies greatly. In contrast to mortality that affects one specific age or stage class, mass mortality events (MMEs) represent demographic catastrophes that can simultaneously affect all life stages (1) and can rapidly remove a substantial proportion of a population over a short period of time relative to the generation time of the organism (2, 3). These events are part of the continuum between background mortality levels, population extirpations (4), and species-level extinctions, such as the five Phanerozoic mass extinctions and the ongoing sixth mass extinction (5).

MMEs of varying spatial and temporal scales affect biological communities in the present day and are frequently a natural phenomenon (6, 7). For example, background mortality levels of sea stars are occasionally punctuated with MMEs driven by outbreaks of wasting syndrome (6), which have led to considerable and rapid population losses in species such as *Pisaster ochraceus* along both coasts of North America (6). MMEs such as these may trigger local extinction vortices by depressing populations to levels at which loss of genetic diversity, demographic stochasticity, or Allee effects can drive populations to extinction (1). Population loss through MMEs can alter the structure of food webs by abruptly generating resource pulses or losses, removing predators or competitors (8), or disturbing mutualist networks (9). Such events can reshape the ecological and evolutionary trajectories of life on Earth (10, 11). In addition, MMEs can generate large economic costs as well as disrupt ecosystem services such as pollination (12). Human populations have also experienced MMEs, often in response to extreme weather events or geologic disasters such as the 2004 Indian Ocean Tsunami, which resulted in an estimated 260,000 deaths (13).

Despite the importance of MMEs as a demographic process with considerable repercussions, no quantitative analysis has identified the features characterizing contemporary MMEs across animal taxa. Indeed, individual MMEs are rarely placed into a broader context (14). This lack of synthesis, commonly associated with the study of infrequent events across academic disciplines (15), presently precludes uncovering mechanisms underlying MMEs and contextualizing the importance of MMEs relative to background mortality levels. In addition, because MMEs can be associated with climatic events (16) and because the severity of extreme weather-related events such as heat waves, heavy precipitation, and droughts is expected to increase in the future as a result of climate change (17, 18), it is especially important to establish a quantitative framework to understand and gauge future MMEs.

Significance

Mass mortality events (MMEs), the rapid, catastrophic die-off of organisms, are an example of a rare event affecting natural populations. Individual reports of MMEs clearly demonstrate their ecological and evolutionary importance, yet our understanding of the general features characterizing such events is limited. Here, we conducted the first, to our knowledge, quantitative analysis of MMEs across the animal kingdom, and as such, we were able to explore novel patterns, trends, and features associated with MMEs. Our analysis uncovered the surprising finding that there have been recent shifts in the magnitudes of MMEs and their associated causes. Our database allows the recommendation of improvements for data collection in ways that will enhance our understanding of how MMEs relate to ongoing perturbations to ecosystems.

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As such, we synthesized existing information on MMEs to examine both the temporal patterns in the occurrence and magnitudes of MMEs among animal taxa and the causes of MMEs. To accomplish this, we assembled a database of 727 published animal MMEs affecting 2,407 populations of amphibian, bird, fish, invertebrate, mammal, and reptile species from throughout the world (Dataset S1).

Results and Discussion

Reports of MMEs have been increasing through time for all taxa (Fig. 1). However, contemporaneous heightened scientific awareness of MMEs coupled with an overall increase in total scientific productivity (Fig. 1 and *SI Appendix*, Fig. S1) could generate a perceived increase. This putative publication bias is a well-known phenomenon when dealing with rare events occurring in time series data, akin to the challenge of distinguishing ongoing epidemics from "epidemics of discovery" (19). Notably, however, more than half of the variation (mean = 54.5%; range = 15–84%) in changes in the occurrence of MMEs through time was not explained by increases in publication output alone (*SI Appendix*, Fig. S2). MMEs were only sporadically reported during the late nineteenth century and early part of the 1900s; since the 1940s, however, MMEs have been documented consistently for birds, fishes, mammals, and marine invertebrates on all continents and in all major biomes. Overall, fishes were the largest contributor of reported MMEs, accounting for 56% of all documented MMEs (Fig. 1). Our analysis also captures a sharp increase in the occurrence of amphibian and reptile MMEs beginning in the 1970s, coincident with the growing awareness of global amphibian declines (20), and more recently, declines in reptiles (21). The recent declines in the occurrence of MMEs since 2000 for all groups but reptiles (Fig. 1) are likely a result of reporting delays between when events occur and when they are reported in the literature (*SI Appendix*, Fig. S3), and statistically accounting for these delays reduces the extent of recent declines in MME occurrence (*SI Appendix*, Fig. S4). Such delays may increase in length as ecologists continue to use older datasets.

Our analysis reveals that the magnitudes of MMEs are changing through time, as measured by the number of animals that died during each event (Fig. 2). Interestingly, changes in the magnitude of MMEs are variable among animal taxa: magnitude increases for birds, marine invertebrates, and fishes; remains invariant for mammals; and decreases for amphibians and reptiles, despite substantial variation around these patterns (Fig. 2). With the exception of reptiles and amphibians, in which a slight quadratic trend in the magnitude of MMEs is present, a nonparametric local regression of these data reveals comparable trends (*SI Appendix*, Fig. S5). These trends in the number of individuals killed per MME likely do not result from a publication bias, as the observed trends for all taxa proved robust when the dataset was reanalyzed by resampling to account for increased MME reporting through time (*SI Appendix*, Fig. S6) (22). We note that the temporal patterns of reptile and marine invertebrate MMEs should be interpreted with caution because of their comparatively low sample size. Overall, taxon, cause, and year explained the largest amounts of variance in the magnitude of MMEs (21.0%, 7.4%, and 4.9%, respectively; multiple linear regression: $F_{21,770} = 18.3$; $P < 0.001$).

The positive trends in MME magnitude for fishes, birds, and marine invertebrates also runs counter to the tendency for scientists to report the largest, most obvious events, whereas less-obvious events are typically increasingly reported when scientific awareness and allocated effort escalate (23). As such, the average increases in MME magnitude for birds, fishes, and marine invertebrates, which on average tended to increase by 0.22, 0.33, and 0.60 orders of magnitude per decade, respectively, are surprising, given the increased MME reporting through time (Fig. 1).

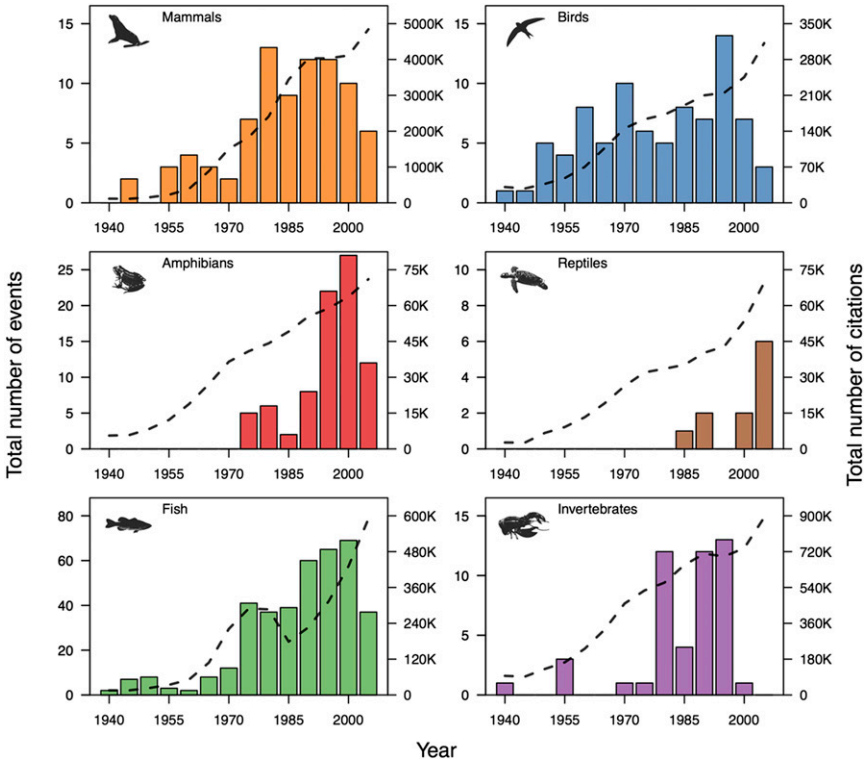

Fig. 1. Occurrences of animal MMEs and taxon-specific publication trends through time. Colored bars indicate the number of events during a 5-y interval (e.g., 1940 stands for the 1940–1944 period), and dashed lines show trends in the total number of papers published each year for each taxon. For all taxa, the increase in the number of MMEs is coincident with an increase in the number of publications (*SI Appendix*, Fig. S1).

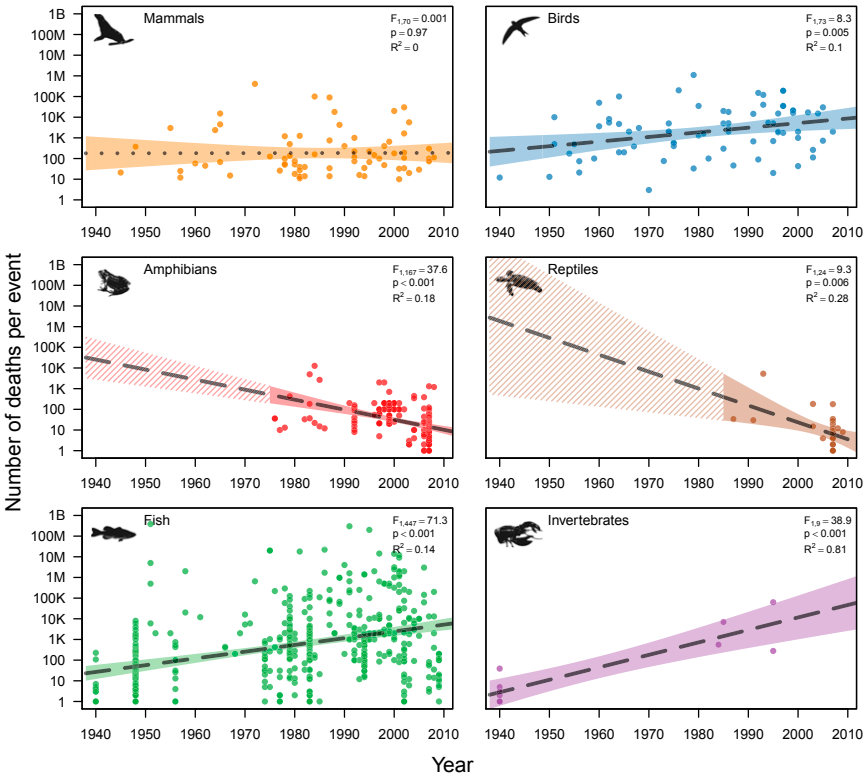

Fig. 2. Magnitude of animal MMEs through time. Each point is a single MME (n = 727 total events). Dashed lines represent statistically significant slopes, shading demarcates slope 95% confidence intervals, and hatched shading indicates extrapolation of regressions before the first reported MME.

Although the proportion of the animal population removed during an MME remains the most widespread approach for defining an MME (2, 3, 14), only 9.6% of published MMEs reported information on how MMEs affect population sizes (*SI Appendix*, Fig. S7). This lack of data limits our ability to resolve temporal patterns in the population-level consequences of MMEs. However, the available data suggest that reported MMEs frequently remove a substantial proportion of animal populations, including up to 100% of the population (*SI Appendix*, Fig. S7). Because we have no reason to suspect that population sizes for these taxa have consistently been increasing through time, the positive trends in MME magnitude documented in numbers of individuals for fishes, birds, and marine invertebrates likely indicate an increase in the proportion of the population being removed.

The differences in MME magnitude among animal taxa may also highlight an important relationship between MMEs and population demographics. Among vertebrate taxa, amphibians, reptiles, and mammals contain the largest proportion of species that are threatened, according to the International Union for Conservation of Nature (IUCN) Red List, and birds and fishes contain proportionally fewer threatened species (24). Thus, one possibility is that the tendency for MME magnitude among certain taxa to increase and then decrease over time may reflect an overall recent decrease in the size of their extant populations (Fig. 2 and *SI Appendix*, Fig. S5). Intriguingly, the recent patterns of amphibian and reptile MME magnitude (*SI Appendix*, Fig. S5) support this hypothesis; however, the comparatively small sample sizes for these taxa and lack of population-specific data suggest caution is warranted in this interpretation. One extreme example of this mechanism is the 1983 sea urchin *Diadema antillarum* MME, which was likely caused by a waterborne pathogen that removed an estimated 99% of all *Diadema* from the Caribbean. Such a large-scale event precludes the occurrence of similarly large die-offs in the near future (25) and may be a precursor to local and regional defaunation (26, 27).

Across all animal taxa, causes of MMEs were most often associated with disease (Fig. 3; 26.3%) and were attributed to viral (44.5%), bacterial (18.3%), and fungal infections (12.2%). Human perturbation was the second most common cause of MMEs, accounting for 19.3% of total MMEs, mainly from point source environmental contamination (42.5%). Biotoxicity was the third leading cause of MMEs (15.6%), primarily resulting from toxin-producing cyanobacteria and dinoflagellates that dominate marine and freshwater harmful algal blooms. Processes directly influenced by climate (weather, thermal stress, oxygen stress, starvation) also contributed to the occurrence of MMEs and accounted, collectively, for 24.7% of known cases.

The causes of MMEs also exhibit shifts through time, but importantly, the causes of MMEs do not change uniformly through time for all taxa. Overall, infectious disease, biotoxicity, and multiple stressors were the most rapidly intensifying causes of MMEs, increasing from 0–33%, 5–18%, and 0–8% of reported MMEs from the 1940s to the 2000s, respectively (Fig. 3). One explanation for these observed shifts is that technological improvements have enabled increased detection of disease and biotoxicity, which rely heavily on laboratory-based methods for detection (28). As such, increased efforts in disease and biotoxicity research could also produce such a pattern. However, if heightened awareness were responsible for these patterns, we would expect to see a positive relationship between the number of publications including disease and biotoxicity as keywords and the proportion of MMEs attributed to these causes. Analysis of this relationship shows that although scientific attention to these topical areas has increased, these increases are rarely coincident with the proportion of MMEs attributable to a particular cause for a particular period (*SI Appendix*, Fig. S8). Thus, although we suspect that heightened awareness of these issues has increased, both disease and biotoxicity likely remain important causes of MMEs that have changed through time.

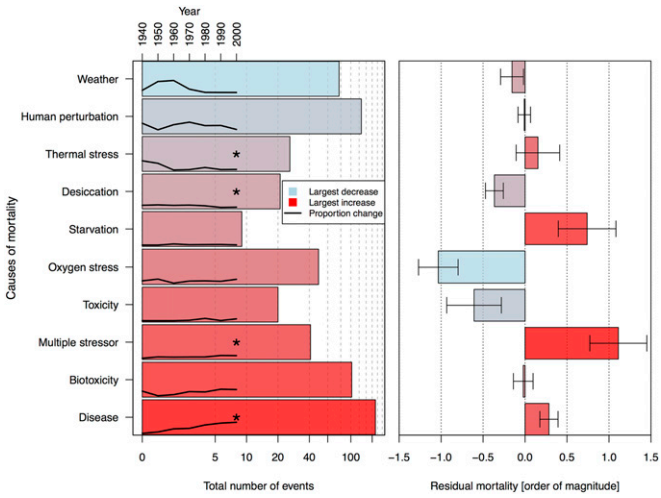

Fig. 3. Causes of MMEs and associated variation in the magnitude of events for different causes. (*Left*) Bars quantify the total number of mortality events for a given cause, and lines within the bars indicate the relative change in the occurrence of each cause from 1940 to 2009. *Significant temporal trends. (*Right*) Variation in the magnitude of mass mortality across causal categories after taking into account taxon-specific temporal trends. Shown are the residuals (mean ± 1 SE) from an ANCOVA model, including taxa and year; that is, a model that describes the expected mortality magnitude without taking into account the causes. Causes with larger magnitudes of death than the average will have positive residuals (e.g., starvation), whereas causes with smaller magnitude than the average will have negative residuals (e.g., O_2 stress).

However, not all taxa exhibited uniform increases in MMEs attributed to disease and biotoxicity (Fig. 4; ANOVA year × cause × taxa; $F_{45,210} = 1.47$; $P = 0.038$). Whereas fishes have had consistent proportions of MMEs attributed to disease and biotoxicity, birds have only recently seen an increase in the frequency of MMEs attributed to these causes. Moreover, fishes and birds exhibited sustained instances of MMEs caused by direct human perturbations, but mammal MMEs only included such causes in the last three decades (Fig. 4). Therefore, the observed shifts in MME causes might not be driven entirely by reporting or by a detectability bias, yet the varied emphasis put forth by the scientific community on these topics complicates this interpretation (*SI Appendix*, Fig. S8). Nevertheless, it remains possible that both infectious disease and biotoxicity caused by toxic algal blooms, which are commonly associated with recent land-use alterations and climate variability (29, 30), may increasingly cause MMEs, rather than simply being chronic and ongoing perturbations to natural systems.

In addition, recent shifts in MME causes may result from underlying patterns in the occurrence of MMEs within certain taxa. For example, amphibians and reptile MMEs are overwhelmingly associated with bacterial, fungal, and viral infections (Fig. 4), and reports of amphibian and reptilian MMEs sharply increased during the past several decades (Fig. 1), thus increasing the proportion of all MMEs attributed to disease.

Similarly, the overall relative occurrence of thermal stress as a casual factor of MMEs has been declining through time for birds, fishes, and marine invertebrates (Fig. 4). A closer examination of the patterns associated with thermal stress reveals that this trend resulted from reductions in the occurrence of cold thermal stress events (*SI Appendix*, Fig. S9), whereas events related to hot thermal stress, although infrequent ($n = 6$ events), have only appeared since the 1980s. The decrease in MMEs attributed to cold thermal stress may relate to the concurrent reductions in the severity of winter temperatures (18), and it is likely that trends toward increases in summer temperatures may result in an increased occurrence of hot thermal stress events in the future (31). Such trends in thermal stress events raise an important consideration regarding the underlying mechanisms of MMEs driven by environmental forces. MMEs arising from changes in the abiotic environment either may arise from large changes in environmental conditions (e.g., temperature or toxin concentration) or, alternatively, may arise from smaller environmental changes that have a disproportionately large negative fitness effect if biological thresholds are reached (32, 33). Thus, both incremental and episodic environmental change may contribute to the recent increased occurrence of MMEs (Fig. 1).

Interestingly, the causes of MMEs also varied in their associated magnitudes. After taking into account variation among taxa in the temporal trends in MME magnitudes (Fig. 2), we found that multiple stressors, starvation, and disease were associated with the largest MME magnitudes, whereas oxygen stress, toxicity, and desiccation were associated with the smallest MME magnitudes (Fig. 3). Identifying the factors generating variation in MME magnitude is important because it may improve predictions of MME magnitudes, assuming the current trends in MME causes persist. However, it is possible for MME causes to shift independent of trends in MME magnitudes. Mammals exhibited no directional changes in MME magnitude through time (Fig. 2), yet the occurrence of mammal MMEs caused by desiccation decreased through time (Fig. 4) and resulted in the overall decrease in desiccation-related MMEs across taxa (Fig. 3).

Overall, the interpretation of patterns related to MME causes or taxa should be considered in the context of sources of bias that may be present. The high proportion of MMEs reported in North America and Europe (*SI Appendix*, Fig. S10) reflects a reporting bias toward areas containing high human densities and areas where ecologists often conduct fieldwork (4, 34). Moreover, certain causes of MMEs are likely underrepresented in the publication records as a result of being difficult to detect (29). For example, causes of mortality affecting aquatic taxa are likely underreported because dead organisms can sink out of sight (7) or occur in the open ocean. In addition, losses of highly gregarious organisms or organisms that dominate biological communities in terms of relative abundance may be reported more often relative to losses of rare organisms, for which losses may even go undetected. Finally, the geographic location of MMEs likely determines whether it is encountered, and thus reported; for example, higher temperatures in tropical ecosystems can accelerate decomposition rates, shortening the window within which MMEs can be observed.

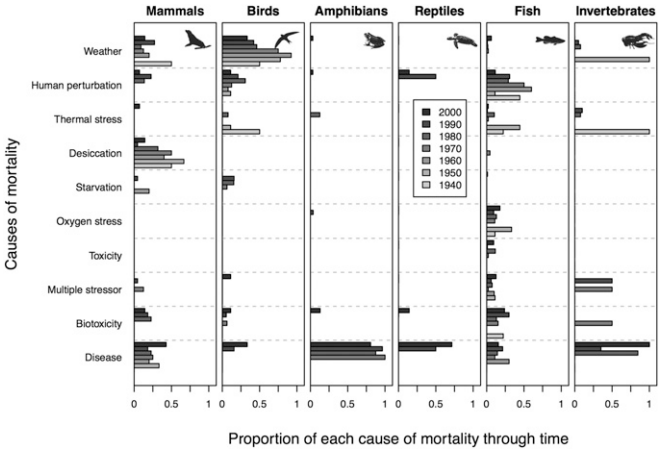

Fig. 4. Relative frequency of each cause of mortality for each taxon through time. Bars indicate the relative frequency of an MME cause for particular taxa for each decade. Decades are defined by their start year (e.g., 1940 represents the period 1940–1949).

In conclusion, our analysis of published animal MMEs indicates that the magnitude of MMEs has been undergoing taxon-specific shifts and that MMEs associated with multiple stressors and disease, which are associated with the largest MME magnitudes, are increasing in frequency. However, it is difficult at this time to determine how much of this increase reflects improved detection capabilities and a greater emphasis on these research topics. Determining whether or not the upswing in the occurrence of MMEs is a real phenomenon or simply a result of increased awareness remains a critical challenge that needs to be addressed. Such results, combined with lack of studies measuring MMEs using population-level data, highlights the need for an improved program for monitoring MMEs. Beyond data standardization, we encourage increased coordination of data collection networks such as citizen scientist contributions, state and federal agencies, and academic scientists. At this time, the vast majority of MMEs are presented in newspapers (7) and do not find their way into the primary literature. Ultimately, enhancing the study of MMEs will enable an appropriate integration of rare demographic processes into established ecological and evolutionary theory. Although MMEs are a natural occurrence, as we continue to proceed through an era of dramatic changes to Earth's physical (17, 18) and biological systems (5, 29), a heightened awareness and robust detection network (6, 29) may be warranted.

Materials and Methods

Literature Search. We reviewed the primary literature by searching the ISI Web of Knowledge database (The Thompson Corporation) for authors self-identifying and reporting MMEs using a keyword search for one or combinations of the following terms: mass mortalit*, die off*, die-off*, mass death*, kill*, mass kill*, or unusual mortality event, combined with a search term to select for the following organisms: birds (bird*, avian), fish (fish*), mammals (mammal*), invertebrate (marine invert* OR terrestrial invert* OR freshwater invert*), reptiles (lizard* OR snake* OR turtle* OR reptile* OR crocodile* OR alligator* OR caiman*), or amphibians (frog* OR toad* OR salamander* OR newt* OR caecilian* OR treefrog* OR amphibian*). As a second step, we examined the Introduction, Discussion, and References Cited sections of all relevant papers identified through our Web of Knowledge search to identify additional studies for inclusion. We did not include terrestrial invertebrates or freshwater invertebrates as taxa in our database because of the low number of studies that met our inclusion criteria ($n = 0$ and $n = 1$ studies, respectively). We finished conducting our search during September 2012, and as such, our database includes studies published through that time.

We included studies satisfying the following a priori criteria: mortality events must have occurred in a wild population, the mortality event must not be the result of an experiment, and each entry must be a unique event. Although we attempted to be as comprehensive as possible, we recognize that our retention criteria excluded some MMEs. In particular, coral reef MMEs in the form of catastrophic bleaching event die offs (25) were not included in our analysis, as whole-colony die-offs are often reported, instead of individual-level deaths. In addition, we excluded studies in which the authors indicated that the observed population declines might be a result of emigration as well as events based on paleontologic findings. Our final database yielded 727 MMEs.

For each event, we extracted data on the event start and end date, geographic location, event habitat, number of organisms that died, species identities of the organisms that died, cause of the event, and percentage of the population removed during the event, when available. We integrated qualitative information that existed for MME magnitude by making conservative estimates for such data (e.g., reporting "thousands of individuals died" as 2,000 individuals).

After all information had been entered into the database, two authors independently examined the specific cause of MME reported by the authors of the original paper and assigned it to one of 10 previously agreed on general categories associated with MMEs (biotoxicity, desiccation, direct human perturbation, disease, multiple stressors, oxygen stress, starvation, thermal stress, toxicity, or weather). The multiple stressors category consisted either of events described as being caused by two or more stressor categories or by two independent stressors within the same category (*SI Appendix*, Fig. S11). Events caused by multiple stressors on average consisted of events with 2.32 ± 0.60 (mean $\pm$ 1 SD) contributing factors, with biotoxicity combined with oxygen stress and toxicity combined with oxygen stress being the two most common combinations of contributing stressors (*SI Appendix*, Fig. S11). It is possible that this category is underrepresented, as events listed as having a singular cause may have had additional interacting stressors not reported. For example, because oxygen solubility decreases at high temperatures, oxygen stress and thermal stress are often coupled in aquatic ecosystems. When the cause did not fit into one of these existing categories, the cause was listed as "other." For instances in which we disagreed on the appropriate category of cause ($n = 22$ of 727), we discussed the paper together to reach a consensus.

Statistical Analyses. To compare temporal trends in the occurrence of MMEs for a given taxon relative to the number of publications per taxon, we recorded the number of citations in Web of Knowledge every year that contained the name of each taxon (singular and plural) as a keyword in the topic field (e.g., bird*). For the purpose of our study, we considered squamates, turtles, crocodilians, and tuatara as belonging to the taxon reptiles, and cartilaginous, ray-finned, lobe-finned, and jawless fish as belonging to the taxon fishes. As the number of reported MMEs each year is relatively small, we summed our data over 5-y periods for analyses of both the number of MMEs and the number of citations. Because temporal trends for both metrics were exponential, we $\log_{10}$-transformed the data, and therefore assessed the linear trend in order of magnitude and the difference between the number of MMEs and the number of publications with an analysis of covariance (ANCOVA) (*SI Appendix*, Fig. S1). We used the normalized change in order of magnitude (by subtracting the mean and dividing by the SD in each metric) as the response variable, year as a linear variable, and type of record (MME or publication record) as the covariate. To detect nonlinear trends in the magnitude of mortality over time, we used a local regression (LOESS), which fits simple linear regressions on each point of the explanatory variable (i.e., time). The difference from classical models is that only a subsample of the data can be used to calculate the local regression, and the data points are weighted such that the more distant data are down-weighted. In this particular case, we used all of the data available, and a standard tricubic weighting proportional to $[1 - (distance/maxdistance)^3]^3$, with *maxdistance* being 1.5 times the actual maximal distance (e.g., 70 y with data from 1940 to 2010) (35).

We calculated the order of magnitude of MME size as the $\log_{10}$ of the conservative estimate of mortality (described earlier). To account for a potential bias linked to uneven publication record, we randomly resampled the dataset 10,000 times, using the same number of events per decade (22). For each taxon, we counted the number of events per decade and resampled, with replacement, within each decade and for each taxon, a number of events equal to the median number of events per decade and taxon. Within each resampling, we computed the linear regression of the magnitude of events ($\log_{10}$-transformed conservative estimate of individual death) over time.

To determine temporal trends in the relative occurrence of MME causes, we computed the proportion of MMEs in each causal category within each decade and assessed change over time with linear regression. A small fraction of records did not determine a cause ($n = 61$ studies) or were categorized as "other" ($n = 11$ studies), and these were not included in this and subsequent analyses related to the causes of MMEs.

The lag between the occurrence of an MME and its publication was calculated as the difference in years between the year of publication and the year of the event, and the trend over time was assessed with linear regression. When an MME spanned more than 1 y, the starting year of the event was used to assess the lag ($n = 4$ studies). We used a conservative approach to estimate the extent of MMEs that have occurred but have not yet been published. We first created an empirical distribution of the lag between the year of MMEs and the year of their eventual publication. As the actual lag distribution is skewed on the basis of the fact that many events between 1990 and 2014 have likely not been published (*SI Appendix*, Fig. S3), we only used the data between 1940 and 1990. From this distribution of lag time between MME occurrence and publication, we estimated the proportion of MMEs that have been published within 2-, 5-, 10-, 15-, 20-, 25-, and 30-y intervals. With these estimated proportions, we could adjust the number of reported MMEs as if all MMEs had been published. For the expected number of citations in 2005–2009 (the most recent 5-y period of interest), we used a lag of 2 y to generate a conservative measure, as using a lag of 0 y would show a dramatic increase of predicted events.

To estimate differences in order of magnitude of mortality among causes, we first performed an ANCOVA of the $\log_{10}$-transformed number of deaths over time within each taxon. We then computed an analysis of variance with the residuals of the ANCOVA model as the response variable and the cause of death as the explanatory variable to determine whether certain causes led to MMEs of significantly greater or lower mortality than the average expected mortality based on the ANCOVA model. Finally, we estimated the proportion of variance in order of magnitude of MME explained by each variable with a multiple regression (using least square estimation) with the $\log_{10}$-transformed mortality rate as response variable and the cause of death and the interaction between year and taxa as explanatory variables. All analyses were performed with R (R Development Core Team), and effects were considered significant at $\alpha = 0.05$.

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