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Evolution caused by extreme events

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Extreme events can be a major driver of evolutionary change over geological and contemporary timescales. Outstanding examples are evolutionary diversification following mass extinctions caused by extreme volcanism or asteroid impact. The evolution of organisms in contemporary time is typically viewed as a gradual and incremental process that results from genetic change, environmental perturbation or both. However, contemporary environments occasionally experience strong perturbations such as heat waves, floods, hurricanes, droughts and pest outbreaks. These extreme events set up strong selection pressures on organisms, and are small-scale analogues of the dramatic changes documented in the fossil record. Because extreme events are rare, almost by definition, they are difficult to study. So far most attention has been given to their ecological rather than to their evolutionary consequences. We review several case studies of contemporary evolution in response to two types of extreme environmental perturbations, episodic (pulse) or prolonged (press). Evolution is most likely to occur when extreme events alter community composition. We encourage investigators to be prepared for evolutionary change in response to rare events during long-term field studies.

This article is part of the themed issue 'Behavioural, ecological and evolutionary responses to extreme climatic events'.

1. Introduction

The history of life on Earth has been a series of evolutionary expansions of biological diversity that were repeatedly reversed by minor or major geophysical disturbances [1]. Perturbations originated either endogenously within the Earth (e.g. volcanoes) or exogenously from without (e.g. impacts of extra-terrestrial bodies). Through direct and indirect (climatic) effects, these catastrophic events decimated communities often non-randomly, with the result that diversity renewal began from compositionally altered communities and took new evolutionary directions [2].

Today human activities are causing increases in atmospheric CO_2 and global temperatures at a rate unprecedented in recent geological history, with concomitant shifts in rainfall patterns and species distributions. Climate change, increased CO_2 and its direct physiological effects, and deoxygenation of subsurface water masses in the oceans are tightly linked in the Earth system and influence populations of organisms simultaneously and synergistically.

According to the Inter-Governmental Panel on Climate Change (IPCC), the probability of extreme climatic events associated with global warming is also increasing [3–4]. This has alerted ecologists to the likelihood of more frequent or more severe disturbances to ecological communities caused by droughts, storms, exceptional rainfall, heat waves, fires and abrupt changes in ocean circulation [3,5–8]. Indeed on a small and local scale this has been quantified, following droughts [9] and floods [10].

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The purpose of this article is to consider how extreme contemporary events are responsible for evolutionary change as well as ecological change [11,12]. We begin by discussing the scale and scope of extreme events. We then review the role of physiology, and studies of isolated fish populations, birds on islands, plant populations and plant–animal interactions, before returning to the really long-term context of geological history. Contemporary evolution in response to extreme events has rarely been studied simply because such events themselves are rare. Understanding contemporary evolution will be improved by a combination of short-term perturbation experiments and long-term studies that opportunistically take advantage of rare events.

2. Scope and scale

Our survey of contemporary evolution is concentrated on, but not restricted to, climate and the effect of extreme events on evolution. The scope is set by the way we treat the words extreme and event. Extreme events are close to, at or beyond the limits of the normal range of phenomena experienced by organisms, and are rare almost by definition. A high temperature recorded only twice a century is both extreme and rare. On the other hand, the highest summer temperature and the lowest winter temperature are extremes within a year, but may not be exceptional in any 1 year when compared with long-term maxima and minima. So it is important to place ‘extreme’ in temporal context [13].

We distinguish between a process and an event. A process is continuous through time whereas an event is an occurrence. Speciation is a process, whereas mutation is an event. A rise in temperature is a process whereas a maximum temperature is a single occurrence. Bender *et al*. [14] made a similar distinction in describing natural or experimental perturbations to the environment as either discrete (pulse) or prolonged (press). The distinction between process and event, prolonged or discrete, is blurred when an unusual event (e.g. 1982–1983 El Niño) lasts for an appreciably long time (nine months) [15]. This is another example of the importance of temporal scale and context of the event.

Climate modellers predict that the frequency of climatic extremes will increase as the Earth warms. And, as mean temperature rises, the maxima may become even more extreme, possibly more frequent [3,9,16] and hence less rare. Wherever we can make the distinction we will focus on the extremes and not on the mean, the variance or the process of gradual change and trends: several other articles in this issue attend to those.

It is natural to focus on physical phenomena as extreme events. However, biological events may also be extreme, and these can have climatic or other causes as well as evolutionary consequences. For example, colonization by an invading or immigrating species results in new interactions among members of a food web, potentially leading to new selection pressures and evolutionary change in some of the residents as well as the immigrants [17]. A second example is evolution that is set in motion by extinction. Mass extinctions at the end of the Permian due to exceptionally prolonged and extensive volcanism, and additional extinctions at the end of the Cretaceous, gave rise to strong evolutionary responses of the survivors, with major new clades arising and proliferating [2]. Extreme events themselves did not cause evolution—they set up the conditions that promoted evolution. Evolution facilitated by extinction of some species may be an undetected factor in modern communities subject to changing climate.

Extreme events in time may be coupled with extremes in space. For example, organisms encounter limits to their physiological tolerance to water, heat or chemical environment when they enter new environments at or beyond their normal geographical borders, and are then subject to strong selection [18]. One example is the entry into freshwater of marine-adapted fish, such as sticklebacks [19]. Another is the reverse: invasion of the marine environment by freshwater organisms [20]. A third example is the entry into arid terrestrial environments by organisms adapted to mesic conditions. This must have happened many times in the history of arthropods, reptiles [21], plants [22] and other taxa. Environmental conditions at the margins of geographical distributions are likely to be extreme—that is often why those locations are margins. Diurnal, seasonal or annual fluctuations in limiting factors in such environments put strong evolutionary pressures on organisms that live at the boundaries [23,24]. Those pressures are expected to increase in the future at some boundaries and relax at others.

How organisms respond to extreme environmental conditions depends in part on their behaviour, prior exposure to extremes, how phenotypically plastic they are, the degree to which they are genetically variable in fitness-related traits, and demographic factors such as lifespan and dispersal (gene flow) [25], as well as the magnitude of deviations from average environmental conditions and on how long these conditions persist relative to the lifespan of organisms. The rate and duration of environmental change in extreme conditions may be more important than the magnitude of change in determining whether the outcome is extinction, a shift in geographical distribution or local evolution and persistence [20,26–28].

We make the traditional distinction between an environmental event and the response of a population. Ecologists, especially those concerned with ecophysiological [11] or ecosystem-level [29] effects of unusual weather on plants, combine events and responses in a single definition of extreme events. This has the advantage of avoiding the many cases of normal responses to unusual events. Moreover, operational definitions are invaluable for comparative purposes. Our task is to identify or anticipate any evolutionary response to an extreme event. For this the general conception as outlined above is more useful than a precise definition. In the future extreme events might be defined as those with magnitudes outside the 95th percentiles of long-term measurements.

3. Evolution of physiology

The ecological and evolutionary impacts of extreme abiotic events are often mediated through an organism’s behaviour and physiology [30,31]. Behavioural evasion is often a mobile organism’s first line of defence against environmental extremes [32], but physiology helps transduce environmental variation—extreme or not—into performance and fitness. Behaviour and physiology are thus key filters and buffers of environmental challenges.

Extreme events can affect physiological performance by depleting environmental resources, altering physiological rates, inducing stress, elevating mortality or even reshuffling community composition (§6). In so doing, they can alter selective agents as well as the genetic composition of populations.

If associated mortality randomly reduces standing genetic variation, the extreme event will retard future adaptive evolution; but if mortality is selective, the event may enhance future tolerance [31,33,34].

Most field studies documenting rapid evolutionary shifts in physiology involve responses to gradual and sustained environmental change (e.g. climate warming), and so the involvement of extreme events is unclear. Still, standing genetic variation for physiological tolerance traits is evident from numerous laboratory studies, implying that evolutionary responses to extreme events in nature are possible. For example, laboratory (and mesocosm) selection experiments, which force organisms to experience a sudden and permanent change in environmental conditions, result in rapid physiological shifts [35]: such protocols mimic perturbations that are acute and permanent (e.g. island uplifts, §4, or myxoma virus, §7). Similarly, artificial selection experiments, which subject experimental lines to an extreme temperature every generation, also typically lead to increased heat tolerance [36]; however, these protocols are poor mimics of most natural extremes, which are rare and episodic [33]. Consequently, such protocols prevent reversion of the genetic constitution of experimental lines towards the pre-extreme state [34]. Most importantly, both types of experimental evolution eliminate any option for behavioural evasion and also generally eliminate involvement of other selective agents (e.g. predators). Not surprisingly, the evolved phenotypes do have enhanced tolerance but often would never survive in nature [37]. Experimental evolution thus demonstrates that extreme-driven shifts in physiology are feasible, but more realistic experimental designs are needed.

Field translocation studies also suggest that standing genetic variation can be sufficient to permit a selective physiological response to an extreme event. When lizards were forcibly introduced onto a hot Caribbean island, survival was highest in individuals that ran relatively quickly at high temperature [38]. Similarly, when marine stickleback fish were transferred to (relatively cold) freshwater ponds, their cold tolerance evolved within 3 years [39].

Potential physiological impacts of extreme events have recently been explored with evolutionary models. One was motivated by high mortality that intertidal limpets suffered on days with high air temperatures, high solar radiation plus low wind speeds [33]: a statistical model ('environmental bootstrap') generated a time series with long periods of benign conditions, punctuated with rare clusters of extreme events. Next, heat-transfer models mapped environmental variations onto body temperature and onto risk of heat stress, which were used as input values for an allelic evolutionary model. Simulations suggested that rare heat events will lead to the evolution of upper lethal temperatures in limpets that are 5–7°C above the average annual maximum temperature: this 'thermal safety margin' in fact approximates that observed for limpets.

A quantitative genetic model and an extension recently explored impacts of extreme temperatures on overall thermal sensitivity, not just extreme heat tolerance [31,34]: rare extreme events (even only one every 20 years) shifted the shape and position of thermal performance curves, especially when extreme events cause death or persistent injury, or when behavioural evasion and acclimation were blocked. This model correctly predicted a shallow latitudinal gradient in heat tolerance of *Drosophila* from eastern Australia, even though mean temperature varies substantially with latitude.

Mass mortality following extreme events is commonly reported and will deplete genetic variation (perhaps selectively), but documented genetic shifts following such events are rare. An extreme heat wave in Europe in spring 2011 caused frequencies of chromosome inversions of *Drosophila subobscura* to shift transiently to summer-like frequencies, implying survivors were relatively heat tolerant [40]. Similarly, an algal bloom along the California coast in 2011 was implicated in causing mass mortality and genetic shifts in abalone (*Haliotis rufescens*) [41].

An ideal design for a study of the evolutionary effects of extreme events might adopt a factorial controlled experiment. One would monitor physiological sensitivity, behaviour, demography and the genetic underpinnings thereof, in replicate populations, only some of which would experience the extreme event. One would monitor all populations before, during and after an extreme event, and ideally then replicate the entire 'experiment' with another set of populations during an independent extreme episode. Such an ideal study could be approximated by intentionally collecting tissues at intervals in sites where extreme events are likely to occur (and in protected sites nearby): if an event occurs, then 'forensic genomics' could quantify genetic and likely physiological impacts [41]. Alternatively, studies that have been repeatedly sampling populations for unrelated reasons can take advantage of an extreme event [40,42]. They would be most useful if genetically informed.

4. Fish in a new environment

Our first example of evolution of a population in contemporary time provides a link with geophysical perturbations in the past (§8) and exemplifies evolution in response to a press perturbation. The largest earthquake ever recorded in North America occurred on 27 March 1964. It uplifted islands in Prince William Sound and the Gulf of Alaska by as much as 3.4 m, thereby creating freshwater ponds from marine habitat. Sticklebacks (*Gasterosteus aculeatus*) colonized many of these ponds from the marine environment. Their subsequent evolution was documented by a detailed genomic study of several populations from samples collected in 2005 and 2011, i.e. 25–50 generations after the ponds were colonized. In this short time, the sticklebacks had diverged phenotypically and genetically [43]. The environmental perturbation lasted a day; the response took less than 50 years.

Genetic reconstruction confirmed that the freshwater populations were derived several times from the marine population and not from previously existing freshwater populations on Middleton and Montague islands [43]. Six new populations on Middleton Island rapidly diverged from each other, and even more from a nearby marine population, independently and in parallel. This happened despite recurring gene exchange between freshwater populations, and between them and the marine population, as indicated by some discordant phenotypic and genetic variation. A repeated reduction in lateral plate number was accompanied by shifts in traits used in foraging, defence and swimming. Because all the traits have a known genetic basis [44,45], the response to a new environment was genetic and not solely phenotypic. These traits have been well studied and the changes are in accord with what is known about adaptation to the freshwater environment [46,47].

The rapidity and magnitude of the changes are striking. F_{st} analysis showed that freshwater populations established after 1964 have diverged from marine ancestors nearly as much as have older post-glacial freshwater populations on the mainland that were formed 13 thousand years ago [43]. The new findings suggest that most evolution occurs rapidly in a new habitat. This example can be considered a prolonged *process* over a few decades, or a pulsed *event* on the scale of millennia [14]. Proponents of punctuated equilibria in the fossil record make a similar claim of rapid early evolution followed by stasis [48].

5. Demography of birds

Demographic studies are a powerful and direct way to investigate evolution, but need to be long term to have a chance of assessing evolutionary consequences of extreme environmental events [13]. Those events are pulsed perturbations that punctuate long periods of comparative stability or gradual environmental change [8].

The first, opportunistic, and short-term study was carried out by Bumpus [49] after an exceptional ice- and snow-storm hit Providence, Rhode Island in February 1898. Bumpus collected 136 specimens of the introduced house sparrow (*Passer domesticus*) that he found on the ground, and measured 72 that survived and 64 that died. Surviving males were relatively large, while surviving females were of intermediate size. Together with more recent studies of swallows [50], the study suggests natural selection had occurred in response to an extreme climatic event. However, both expose the difficulties of interpreting survival patterns from samples taken at the same or different times [51,52]. Longitudinal studies are needed to infer the role of selection, inheritance of selected traits and *trans*-generational evolutionary responses.

Two types of extreme climatic events occurred during a 40-year study of Darwin's ground finches (*Geospiza* spp.) on the small Galápagos island of Daphne Major (1973–2012): an abundance of rain and two sequential years of drought. The first was an extremely intense and prolonged El Niño event in 1982–1983 resulting in 1.3 m of rain falling on the island. It was the most severe event of the century, and possibly the most extreme in 400 years according to coral core data [53]. The abundant rain caused a change in composition of the vegetation, which became dominated by plants that produce small and soft seeds. The change had a selective effect on medium ground finch (*Geospiza fortis*) survival during a drought in 1985 when only 4 mm of rain fell and food became scarce: birds with small and pointed beaks had a selective advantage. The second extreme event was a 2-year drought (2003–2004). *Geospiza fortis* with large beaks were outcompeted by *G. magnirostris*, the large ground finch, for a dwindling supply of large seeds [54].

Evolution occurred in response to natural selection each time because morphological traits are highly heritable [54,55]. Notably two variants of a gene (*HMGA2*) with major effects on beak size changed in frequency in the expected direction as a result of natural selection in 2004–2005 [56]. Less predictable are the effects of environmental extremes on evolution [57]. There is an element of chance in what constitutes the food environment at any one time, and when major perturbations occur; hence evolution is partly stochastic. An extreme event can have mild or strong effects depending on the state of the environment when it occurs. For example in 2003, when seeds were abundant at the beginning of a drought, selection on beak size did not occur despite high finch mortality. Natural selection occurred only in 2004, the second year of a prolonged drought and food scarcity. Similarly, selection did not occur in the only other 2-year drought (1988–1989) because seeds were produced abundantly in the preceding (El Niño) year, 1987 [15].

Combinations of extreme events [5,7], and not just the single events themselves, may be unusually potent factors by permitting or causing evolution. Two unrelated and improbable events with long-term consequences occurred on Daphne Major Island in the 1980s [15]. First, a single hybrid male ground finch (*G. fortis* × *G. scandens*) immigrated in 1981. It produced offspring by breeding with *G. fortis*. The drought of 2003–2004 reduced this new lineage to two individuals, a brother and a sister, who bred with each other in 2005 and in subsequent years. The next two generations were entirely endogamous, hence the lineage was behaving as an incipient species. Second, two female and three male *G. magnirostris* immigrated to Daphne in 1982 and established a breeding population at the end of the year. Both colonizations are remarkable because none are known to have occurred elsewhere in the archipelago since the end of the nineteenth century when collectors for museums visited all islands in the archipelago and documented the distributions of finch species. Almost certainly an important factor in the success of both colonizations was the unusually favourable ecological conditions caused by the exceptionally prolonged El Niño event in 1982–1983.

The two colonization events were not initially connected. Twenty years later a connection was made when *G. magnirostris* determined the fate of the hybrid lineage by competitively eliminating most of the large members of the *G. fortis* population during the drought of 2003–2004 [54]. The hybrid lineage is ecologically similar to *G. fortis*. Without the El Niño event and the population of *G. magnirostris* that it fostered, the hybrid lineage may not have been able to persist beyond 2004. Rare and extreme events need not be exactly coincident to have profound and long-lasting effects, and the consequences may emerge after a long delay, as these examples illustrate [15].

They also illustrate another principle of general significance: a population that evolves as a result of a press perturbation does not necessarily evolve back to its original state. *G. fortis* remained small on average after 2005 because the composition of the finch community had changed. The agents of change—*G. magnirostris* and the hybrid lineage—rapidly increased in numbers after the drought.

6. Evolutionary responses of plant populations

In many plant species, populations across the species range exhibit the signature of past adaptation to climate. For these species, a critical question is whether local populations will be able to evolve fast enough *in situ* to survive extreme events, track rapid climate change and thus avoid extinction [58,59]. This question is particularly important for long-lived species such as forest trees, which are likely to experience rare extreme events combined with rapid climate change over decades within individual lifetimes. Relevant data are scarce. Even less is known about how increasing atmospheric CO_2 interacts with climate change to affect plant performance and evolutionary potential in nature. A few studies have used historical data and/or resurrection studies of banked seeds to demonstrate rapid evolutionary response to extreme events or the press of climate warming on decadal scales [42]. However, whether this rate of adaptation is sufficient to allow evolutionary rescue remains an open question.

One of the best examples of plant evolutionary response to an extreme climatic event comes from a resurrection study of the annual field mustard *Brassica rapa* [42,60]. The investigators collected a large sample of seeds from two California populations in 1997, after several wet years, and again in 2004 after several years of severe spring drought. They then grew population samples of genotypes collected in 1997 and in 2004 together in a common garden. The 2004 genotypes flowered significantly earlier in the common garden than the 1997 genotypes. Experimental water manipulations showed that early drought onset strongly selected for earlier flowering, evidence that the observed evolutionary change was adaptive.

These *B. rapa* populations also display a genomic signature of temporal drought adaptation [42]. A genome-wide scan for F_{st} outlier-loci found 855 genes with significant temporal differentiation in allele frequencies between the 1997 and 2004 samples. Many had annotations suggesting involvement in flowering time and drought response. However, only 11 genes exhibited parallel shifts in allele frequencies in both populations. Thus, rapid adaptation to drought in the two populations appears to have occurred along largely independent trajectories.

Extreme climate events may also result in strong selection episodes in longer-lived plants such as trees. For example, a severe heat wave and drought in 2003 resulted in selective mortality of Douglas fir trees (*Pseudotsuga menziesii*) in a common garden experiment in France [61]. Surviving trees had higher stem wood density, ring density and latewood density than did trees that died, probably because these traits conferred drought-resistant hydraulic properties [61]. If these traits are heritable then strong selection by this extreme event could have produced rapid evolutionary response. Long-term monitoring of forestry provenance trials, where tree genotypes originating from multiple populations are grown in common gardens in multiple sites, could provide an excellent opportunity to investigate the genetic basis of selective mortality in response to extreme climate events [62].

Long-term studies have demonstrated phenotypic changes in many plant species in apparent response to the press of climate change on a decadal scale. The question is how much of this phenotypic change represents phenotypic plasticity versus adaptive evolution. Anderson *et al.* [63] combined data from 38 years of field observations of flowering phenology in the Colorado Rocky Mountains with measurements of selection and heritability in a quantitative genetic field experiment with the perennial mustard *Boechera stricta*. They observed strong selection for earlier flowering, and predicted that evolutionary response to this selection could account for more than 20% of the accelerated phenology observed in the long-term field study.

A few other studies have documented contemporary evolution in plant populations in apparent response to rapid climate change. Nevo *et al.* [64] used a common garden resurrection experiment to demonstrate rapid evolution of earlier flowering from 1980 to 2008 in wild cereal populations across Israel. Thompson *et al.* [65] observed an increase in frequency of frost-sensitive but summer drought-tolerant phenolic chemotypes in populations of Mediterranean wild thyme (*Thymus vulgaris*) associated with a recent decline in severe freezing events.

Is adaptive evolution in plant populations fast enough to keep up with the pace of contemporary climate change? This question can be addressed by provenance trial experiments in which accessions from a range of climates are planted into common gardens across that climatic range. Wilczek *et al.* [66] used banked seeds from geographically diverse accessions of the annual plant *Arabidopsis thaliana* to establish common garden experiments spanning the species' European climate range. Although they found evidence of historical adaptation to local climate, the year of the field experiment was unusually warm compared with historical averages. Consequently, accessions from lower latitudes with historically warmer climates had higher fitness than did local genotypes—an example of adaptational lag [58] in an extreme year. McGraw *et al.* [67] also observed adaptational lag in a reciprocal transplant experiment with the long-lived sedge *Eriophorum vaginatum* across a climate gradient in Alaska. Seeds were planted in 1980, and a 1993 census demonstrated local adaptation: local genotypes had the highest fitness in each site. However, when the experiment was recensused in 2010, genotypes transplanted from the south had higher fitness than local genotypes, suggesting that rapid warming has created a mismatch between local genotypes and their new climate.

7. Species interactions and evolution

Evolutionary consequences of extreme events may frequently be mediated indirectly via species interactions. Both pulse and press extreme events frequently alter the abundance of multiple species within communities [12]. These changes can disrupt mutualisms, competition and antagonistic interactions. In this way, extreme events are expected to alter the strength and direction of (co)evolutionary dynamics.

An example of how extreme events affect species interactions is seen with herbivorous insects. Numerous studies show that climatic extremes affect herbivore performance and population dynamics. The most common observation is that pulsed stresses, such as increased temperature and drought, are associated with herbivore population outbreaks [68]. For example, Europe experienced an unprecedented heat wave and drought during 2003, which was associated with outbreaks of multiple insect species [69]. Similarly, population outbreaks of caterpillars in *Nothofagus* forests in Patagonia have been associated with unusually warm and dry periods over the past 155 years [70]. By contrast, prolonged (press) climatic stresses frequently lead to decreased performance and abundance of herbivores [68]. Thus, pulse and press perturbations can both increase and decrease the size of local herbivore populations.

Herbivores may also respond to extreme events by expanding their range to form new populations and associations with novel hosts [12]. In southern Europe, for example, the pine processionary moth (*Thaumetopoea pityocampa*) expanded its latitudinal range 87 km northward and its altitudinal range 230 m higher in response to climate warming between 1972 and 2004 [71]. In the record hot summer of 2003, this species expanded its altitudinal range by an additional 33% on top of all previous altitudinal range expansions [72]. This expanded range persisted and facilitated *T. pityocampa*'s use of novel host plants. These and similar results show that extreme climate events can dramatically alter the ecology of plant–herbivore interactions, but how might this affect evolutionary dynamics?

Recent experiments show that plant populations can evolve rapidly in response to changes in herbivore populations. Herbivores frequently impose strong selection on plant traits [73] and most plant populations contain substantial genetic variation in plant defences against herbivores [74]. Thus, any change in the abundance of herbivore populations brought about by extreme events is expected to alter subsequent selection on plant populations. This prediction has been experimentally supported in field experiments that manipulate the abundance of herbivores, as discussed below.

In the first example, Agrawal *et al.* [75] used insecticides to manipulate densities of arthropods feeding on genetically diverse experimental field populations of evening primrose (*Oenothera biennis*). They then followed the evolutionary dynamics of these populations for four generations. Populations exhibited rapid genetic and phenotypic divergence in response to the manipulation of arthropod abundance, with the fastest changes occurring in the first generation. In the presence of herbivores, plant populations evolved by flowering later and producing more chemical defences against specialist seed predators. This manipulation was not a direct result of an extreme climatic event, but it clearly shows that large changes in herbivore populations can cause rapid evolution in plants.

The second example involves rabbit grazers native to Europe. Rabbits and other mammalian populations frequently exhibit population cycles, but natural or human-facilitated disease represents an extreme event that causes drastic population declines. In rabbits, such declines are caused by the myxoma virus, which was introduced to rabbit populations in Europe and Australia [76]. Recent evidence indicates that plant populations can evolve in response to the loss of rabbit grazers. Didiano *et al.* [77] experimentally manipulated the presence or absence of rabbits in British grasslands for up to 34 years, approximating the timeframe of change that occurs following the spread of myxoma virus. They found that multiple plant species evolved diverse morphological and life-history responses to decreased grazing, including lower tolerance to damage, slower growth and more upright growth forms. Although these evolutionary changes happened simultaneously across multiple species following the elimination of a grazer, the evolutionary dynamics were species-specific and non-convergent.

Despite the evidence reviewed above, large gaps remain in our understanding of how extreme events can affect evolution via altered species interactions. In the case of plant–herbivore interactions, convincing evidence shows that extreme events frequently lead to changes in the abundance of populations. Mounting evidence suggests that changes in herbivore abundance can cause rapid evolution of plant traits. However, no study has yet provided a complete demonstration of the links between extreme events, herbivore populations and plant evolution. All of the necessary ingredients for these links are in place, so an explicit demonstration is an important goal for future research.

Although we have focused on plant–herbivore interactions, extreme events can affect the evolution of any type of species interaction. For example, endosymbionts facilitate the evolution of increased heat tolerance of aphids following a pulsed heat stress [78]. Competing microbes rapidly use novel resources as a result of evolving when their environment changes [79], and beak shape of Darwin's finches evolves in response to interspecific competition for food during a drought (§5). Such indirect effects of extreme events on evolution have not been well studied owing to their inherent complexity, and they represent an important frontier in linking climate, community ecology and (co)evolution.

8. Lessons from the past

The geologic record makes it clear that humans have experienced only a limited subset of the extreme climatic events recorded through Earth history. What can we learn from geologically extreme events? Does their sheer magnitude limit their relevance to twenty-first century issues? Or, might they underscore a continuity of pattern applicable to climatic extremes at all scales? Indeed, might geologically extreme events provide our best guide to predicting biological responses to climate change at rates not previously experienced by humans?

Extinction is the most commonly recorded response to geologically extreme events. Extinction, of course, is inevitable for eukaryotic species, and last appearances of fossil taxa occur more or less continuously throughout the Phanerozoic Eon. Such 'background' extinctions probably reflect, at least in part, minor climatic events not easily distinguished by geologists. At rare moments, however, many species have gone extinct simultaneously, disrupting ecosystem fabrics and, on million-year time scales, providing new evolutionary opportunities for survivors. Palaeontologists recognize five mass extinctions during the past 500 million years, along with a dozen or fewer events of elevated extinction [80]. All reflect rapid and transient environmental disruptions of global extent, but they differ in terms of both causation and evolutionary consequences.

Despite this, several features unite major extinction events, and these are relevant to concerns about our environmental future. First, enhanced rates of extinction correspond to times of rapid climatic change, not to absolute maxima and minima in temperature and precipitation. When change is protracted, both physical and biological components of the Earth system can accommodate. Populations respond adaptively or migrate, while geophysical processes buffer environmental effects. When change is rapid, however, adaptation, migration and geophysical buffering are all challenged. Although temperatures anticipated for the end of the twenty-first century fall well below those characterizing much of Earth history, the rates at which CO_2 and, hence, temperature are increasing are unique within the past 66 million years [81].

The underlying state of the Earth system also appears to influence the biological effects of rapid environmental perturbation. For example, mass extinction near the end of the Ordovician Period, some 445 million years ago, is associated with a short-lived ice age [82]. Why did Ordovician ice sheets result in widespread species loss, when relatively few marine extinctions are associated with Pleistocene glaciation? A reasonable answer is that Pleistocene ice sheets expanded in a world in which continents were arrayed across wide stretches of latitude, while sea level lay near its Phanerozoic minimum. By contrast, the Ordovician ice age began in a world with isolated, commonly equatorial continents inundated by historically high levels of continental flooding. In consequence, sea-level drop associated with Ordovician ice sheets removed much more habitable area for marine benthos than an equivalent drop during the Pleistocene. At the same time, Pleistocene continental distribution allowed more effective migration in the face of climate change than was probable in the Ordovician [82].

Other extinction episodes also suggest the importance of longer-term context of transient environmental perturbations [83]. Relative to other times of enhanced volcanic activity, the catastrophic biological consequences of end-Permian massive volcanism may relate to both the state of late Permian oceans (widespread subsurface dysoxia in the hemispheric Panthalassic Ocean, amplifying the climatic and physiological consequences of volcanism [84]); and the locus of volcanic eruptions (Archean crust overlain by thick Proterozoic carbonates [85]). And it may be that the uniquely disruptive effects of end-Cretaceous bolide impact reflect a world already stressed by Deccan Trap volcanism [86]. Indeed, the Holocene extinction of large mammals in North America is thought to reflect the combined influences of expanding human populations and rapid environmental change characterized by non-analogue vegetation [87,88].

It is not straightforward to align these one–two punches of deep Earth history with press and pulse dynamics argued for contemporary events, as the sustained stresses identified as presses to ecologists may look like a pulse to geologists. Nonetheless, the idea that longer-term context may condition biological responses to short-term events has relevance for today. In the twenty-first century, ‘hit 1’ is surely the direct effects of humans on habitat disruption, pollution and overexploitation, but the interaction of these processes with ‘hit 2’—global warming—has yet to be fully explored or experienced. Geologic history suggests that by mitigating the stresses of ‘hit 1’ we may minimize the biological consequences of emerging climate stress. For better or worse, the coming century may prove a unique moment when the large extremes recognized by geologists and ecologically observed biological responses coalesce.

The third commonality among mass extinctions lies in the pattern and timescale of recovery. On million-year timescales, extinction pays an important evolutionary dividend: a permissive ecology in which novel innovations fuel new radiations. Mammals famously diversified in the wake of dinosaur extinction, and marine teleosts radiated after end-Cretaceous extinction extirpated the ammonites [89]. More generally, key Phanerozoic shifts in the structure and composition of marine communities occurred during the recovery intervals following mass extinctions [90]. Unfortunately for us and for our grandchildren, the timescale on which twenty-first century extinctions will pay evolutionary dividends carries us a million years into the future.

9. Projections and conjectures for the future

Natural selection has been studied and quantified in numerous species and environments but anticipating evolutionary change in the future is still poorly grounded. The main reason is that direct evidence for evolutionary responses of organisms to extreme events in nature is almost entirely lacking, because not enough information is available to distinguish between genetic and non-genetic explanations for observed change in use of habitats, morphology, physiology and diets. The scarcity of genetic information is particularly acute in the marine environment where calcareous organisms such as corals and plankton are imperilled by increasing acidity arising from elevated atmospheric CO_2 levels [91]. Compounding the problem for these organisms, extreme increases in sea surface temperature associated with intense El Niño events cause mass mortality of corals as well as fish [92]. El Niño events are expected to increase in intensity and frequency in the future [16], and the unanswered question is whether marine organisms are capable of an evolutionary response in the race against extinction [90–92].

Attempts to predict evolutionary consequences of extreme climatic events have languished, and few studies have advanced beyond identifying factors promoting future evolutionary change (rescue) in the face of gradual climate change: reviewed in [93,94]. Three important factors are fluctuating climate, because organisms that experience them are already adapted to change; large, widespread and inter-connected populations, because they have large amounts of standing genetic variation; and short-generation times because evolutionary responses are potentially rapid.

How can we be prepared to take advantage of opportunities arising unpredictably in the future to learn about evolution caused by extreme events? Long-term field studies offer the best prospects [11,13,29], opportunistically after the event as in the case of new populations of sticklebacks (§4) or prospectively in a suitable system with information prior to the event, as in the case of Darwin’s finches (§5). A good choice would be organisms amenable to *trans*-generational study, known to have evolved rapidly in the past, and living in environments known to change rapidly. *Ex situ* preservation of genotypes sampled from present day populations, such as seeds being banked by Project Baseline [62], will also be important for resurrection studies of evolutionary change during future extreme events.

10. Conclusion

Few demonstrations of evolutionary change in nature can be tied unambiguously to an extreme climatic event, yet, for many reasons described in this article, microevolutionary responses are likely to be widespread. A combined ecological and evolutionary research programme is needed to anticipate the potential resilience of populations facing both gradual climatic change and extreme events.

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