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REVIEWS

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Forum

The Silver Lining of Extreme Events

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Extreme climatic events cause devastating impacts to species and ecosystems, precipitating significant mortality. However, emerging empirical evidence is revealing that such mortality can drive directional selection and result in increased tolerance. We discuss the novel opportunities for promoting climate resilience presented by this 'silver lining' of extreme events.

The Destructive Nature of Extreme Events

Extreme climatic events such as floods, cyclones, heatwaves, and cold spells have precipitated significant impacts to species and ecosystems over evolutionary and contemporary time scales [1] and are predicted to increase in intensity and frequency under climate change [2]. By definition, extreme events exceed the norms of environmental conditions and therefore drive significant mortality, resulting in range shifts, local extinctions, and transitions to novel ecosystem states [3]. This causes significant loss of economic, social, and ecological values derived from natural systems. Consequently, extreme events are overwhelmingly perceived as negative and receive significant scientific, societal, financial, and media attention. However, emerging empirical research is demonstrating that mortality induced by extreme events is often not random but can drive directional selection and rapid adaptation to climate stressors [1,4–7]. Acknowledging this positive 'silver lining' of extreme events presents unique opportunities to boost resilience of natural populations under future climates.

Extreme Events Promote Selection and Increased Resilience

Theory predicts that extreme events cause selection against weak phenotypes and, where species maximum thresholds are approached, but not exceeded, promote the persistence of stress tolerant phenotypes (Figure 1). When this has a heritable basis, rapid adaptation to the prevailing stressor can occur. As such, selection driven by extreme events may be one of the few natural mechanisms through which species and populations can increase their resilience to the rapid advance of climate change. However, despite a strong theoretical basis for extreme events driving selection, studies have empirically demonstrated this process only recently. For example, comparisons of genomic and physiological data before and after a severe cold snap demonstrated increased cold tolerance in green anole lizards (*Anolis carolinensis*) [4]. Similarly, cyclones induced widespread selection favouring heritable traits in group-living spiders that enhanced competitive resource acquisition, reproduction, and survival (*Anelosimus studiosus*) [6]. In the marine environment, an extreme marine heatwave caused significant loss of genetic diversity and signatures of directional selection towards increased thermal tolerance in kelp forests (*Scytothalia dorycarpa*, *Sargassum fallax*, and *Ecklonia radiata*) [5,7]. In all cases, these extreme events precipitated significant, but nonrandom mortality, favouring certain traits or genotypes that confer greater fitness to the climate stressors (e.g., cold, heat) underpinning the extreme events. With extreme events predicted to increase in the future [2], selection may confer increased resilience and accelerated adaptation under climate change by increasing the frequency of strong, climate-proof genotypes. This 'silver lining' of the otherwise destructive impacts of extreme events is only just being realised, but provides novel opportunities for managing future resilience of species and ecosystems under climate change (Figure 1).

Harnessing the 'Silver Lining' of Extreme Events

There is increasing support for conservation, restoration, and management of natural ecosystems to proactively anticipate future climatic conditions. This involves strategies

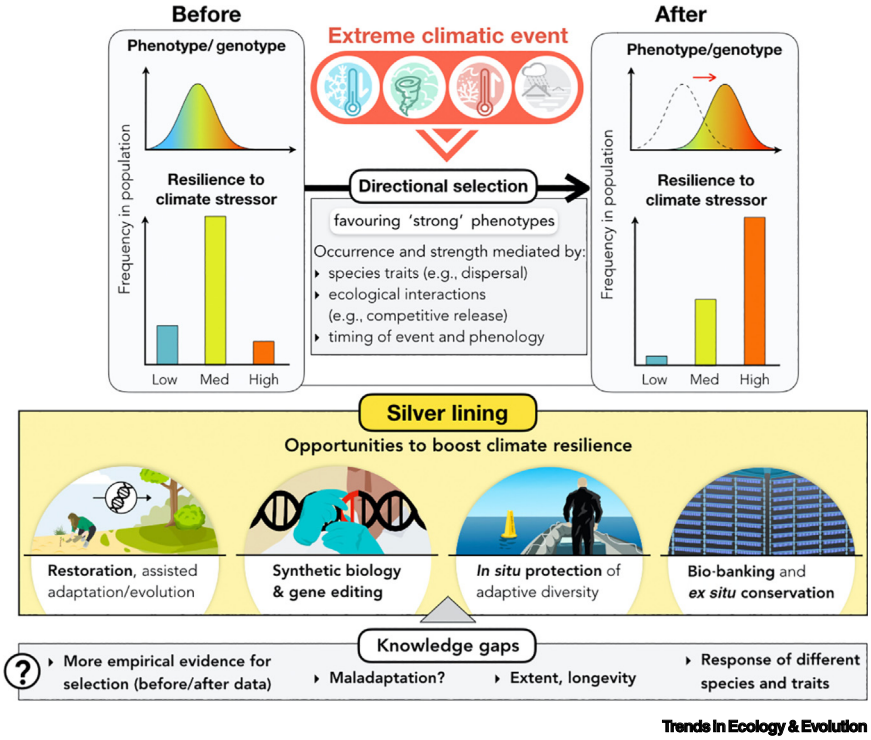

Figure 1. The Silver Lining of Extreme Events: Opportunities for Boosting Climate Resilience. Emerging empirical evidence is revealing that extreme climatic events such as cold snaps, heatwaves, cyclones, and floods can drive directional selection towards increased tolerance to the climate stressors characterising extreme events. Although the occurrence, strength, and detection of selection is mediated by factors such as species traits, ecological interactions, and the timing of the event, where directional selection does occur, there is a silver lining that can be harnessed to boost climate resilience. Areas or populations that have undergone selection could be used as targets for restoration, assisted adaptation, and gene editing to boost climate resilience in natural populations. Such areas could also be used in management strategies that seek to protect climate refugia or adaptive diversity either *in situ* or *ex situ*. Realising this silver lining will require filling knowledge gaps, including further empirical demonstration of selection and the circumstances under which it manifests in natural populations and the potential for maladaptation to additional stressors. Reframing our perception of extreme events towards the positive and beneficial impacts can yield transformative opportunities for boosting climate resilience.

ranging from assisted adaptation and assisted evolution [8] through to the use of synthetic biology and gene editing to boost resilience in natural settings [9]. Application of these cutting-edge approaches requires identification of 'beneficial' genotypes to introduce into vulnerable populations. This can be problematic for nonmodel species and requires extensive background research. However, selection induced by extreme events can be harnessed for such strategies when the management aim is to enhance future resilience to the same stressors. For example, programs that seek to enhance thermal resilience of restored populations could source donors from areas that have been subject to recent heatwaves [5,7,8]. Importantly, this could be done without extensive background data and could be an accessible approach for community groups who often implement restoration programs. In addition, selection induced by extreme events could help pinpoint target genes and pathways for gene editing that have a demonstrated causal link to stressors in natural environments. This strategy could even replace the need for experimental approaches when they are not amenable or ethical.

There is increasing interest in protecting climate refugia and adaptive genetic diversity both *in situ* and *ex situ* [10] to ensure species have the latent capacity to respond to climate change. Areas that have undergone selection following extreme events may be ideal targets for sourcing propagules or individuals for inclusion in *ex situ* breeding or bio-banking programs if they contain naturally higher frequencies of genotypes that confer climate resilience. Similarly, protection of such areas *in situ* (e.g., national parks or marine reserves) may represent resilient refugia or important source populations under future conditions. Harnessing the rapid evolutionary change induced by extreme events allows identification of target areas that could be considered for protection and provides a natural impetus for such approaches.

Emerging Questions and Knowledge Gaps in Realising the Silver Lining

The destructive nature of extreme events and their importance in shaping species distributions and ecosystem configurations has been acknowledged for decades, but impacts have largely been considered uniform and research focused on negative impacts. In contrast, most studies have neglected survivors or where extreme events only cause partial mortality. Switching focus to understand mechanisms behind survival, rather than death, may reveal processes that can be harnessed to increase climate resilience. Consequently, research questions should shift from focusing on mean population dose–response relationships to determining within-population variation and outliers of maximum tolerance.

Extreme events are superimposed onto other short- and long-term stressors that interact to impact organisms in complex ways [11]. Consequently, the long-term success of populations will require versatility to face a broad range of stressors and their interactive effects, rather than resistance to a single, dominant stressor. Experimental studies are beginning to

reveal that acclimation towards resilience for one stressor could drive maladaptation to other stressors, but the extent to which this persists across generations and traits remains a critical knowledge gap. Moreover, the role of phenotypic plasticity relative to the strength of climate stressor in determining species response is unknown. Understanding the potential for maladaptation and the role of plasticity will be vital for sensibly harnessing the silver lining presented by extreme events.

Other challenges remain for understanding the effects of extreme events on selection. Foremost, robustly disentangling the impact of extreme events from natural temporal stochasticity is still hindered by a lack of pre-event data for most species because extreme events are rare and difficult to predict. Further, species have variable responses to single extreme events depending on their respective traits [5,12] and factors such as the timing of event relative to phenology, strength of demographic impact, and species ecological interactions can dictate how signatures of selection are entrenched and detected. Therefore, realising the silver lining of extreme events will rely on multifaceted knowledge from genes through to entire ecosystems.

Reframing Perceptions of Extreme Events to Enhance Climate Resilience

Extreme climatic events are increasing in intensity and frequency with climate change and have devastating impacts globally. However, where thresholds are not fully exceeded and mortality is partial, there is a silver lining that can be harnessed to enhance climate resilience. Shifting focus towards understanding mechanisms conferring survival is revealing that extreme events can drive directional selection favouring genotypes that are resilient to the climate stressors that characterise extreme events. Therefore, extreme events can drive rapid climate adaptation and may be one of the only ways that species and populations can cope with the increasing pace of climatic change. When recognised, this silver lining can be harnessed to boost resilience of populations to future change through management, intervention, and conservation programs. Reframing our perception of extreme events, shifting focus towards the positive and beneficial impacts, can yield transformative opportunities for boosting climate resilience.

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