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Biological Extreme Events: A Research Framework

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Efforts designed to understand and predict adaptation responses of organisms and populations to global climate change must make a clear distinction between responses to changes in average conditions (e.g., doubling of atmospheric carbon dioxide concentration accompanied by an average increase of 1°–3°C in global air temperature by the end of this century) and responses resulting from increased incidence of extreme events [*Loehle and LeBlanc,* 1996; *Easterling et al.,* 2000; *Garrett et al.,* 2006]. Such distinction is critical because, unlike changes in average conditions, extremes (e.g., megadroughts, fire, flooding, hurricanes, heat waves, and pest outbreaks) are typically short in duration but challenge organisms and populations considerably further beyond their ability to acclimate than those expected from average trends in climate changes.

There is growing evidence that climatic extremes have been rising in frequency or magnitude during the last part of the twentieth century and will continue to increase during the remainder of this century [*Easterling et al.,* 2000; *Meehl et al.,* 2000; *Parmesan and Yohe,* 2003; *Barnett et al.,* 2006]. More important, the frequency of extremes is likely to increase even if the climatic means do not change substantially [*Intergovernmental Panel on Climate Change* (*IPCC*), 2001, chapter 10]. Therefore, it makes sense to pay special attention to extremes as major agents of biological adaption (genetic change) when considering global climate change.

Documented Examples of Extremes Causing Biological Shifts and Feedbacks

More than a decade and half ago, *Gaines and Denny* [1993] brought to focus the importance of extremes in shaping ecological and evolutionary processes. Their work was motivated by observations that clearly indicated that the force of incoming waves on tidal organisms was more adequately explained by maximum wave forces rather than by means and variances [*Denny and Gaines,* 1990]. This study unambiguously showed that effects on Darwinian fitness—ultimate reproductive success and escape from extinction—are concentrated in these extreme events (Figure 1).

Moreover, biological extremes couple back to the climate system, such as by changing the carbon, water, and energy fluxes. A prime example is the dieback of coniferous trees over an area of western North America exceeding 130,000 square kilometers (Figure 2). This event cascaded from a surprisingly rare and unappreciated meteorological extreme, a combination of moderately warmer weather and drought [*Breshears et al.,* 2005], and it was conditioned by the "availability" of bark beetles to do the actual killing, a fully biological overlay to the event. The carbon cycle continues to be affected, with an expected release of 270 teragrams of carbon from decay of the killed trees over the next 20 years [*Raffa et al.,* 2008]. Large-scale biological extremes also couple back to geochemical processes such as rock weathering and nitrogen cycling.

While plant communities are highly sensitive to extreme events, their impact extends to animals and microbes. The shift in average beak depth in Darwin's finches in the Galapagos after the severe drought of 1976–1977 is a classic example of a disproportionate effect of an extreme episode on population dynamics [*Grant and Grant,* 1995].

Nonetheless, responses of humans often take center stage. The 2003 heat wave in Europe took at least 10,000 human lives and altered water and carbon cycles over much of Europe.

A Framework for Study: What Is a Biological Extreme Event?

Scientists can accumulate many examples of biological extreme events, but without the comprehensive intellectual framework to study them, insights these events hold for understanding genetic shifts and climatic feedbacks will be lost. To avert this loss, characteristics of biological extremes were established [*Gutschick and BassiriRad,* 2003].

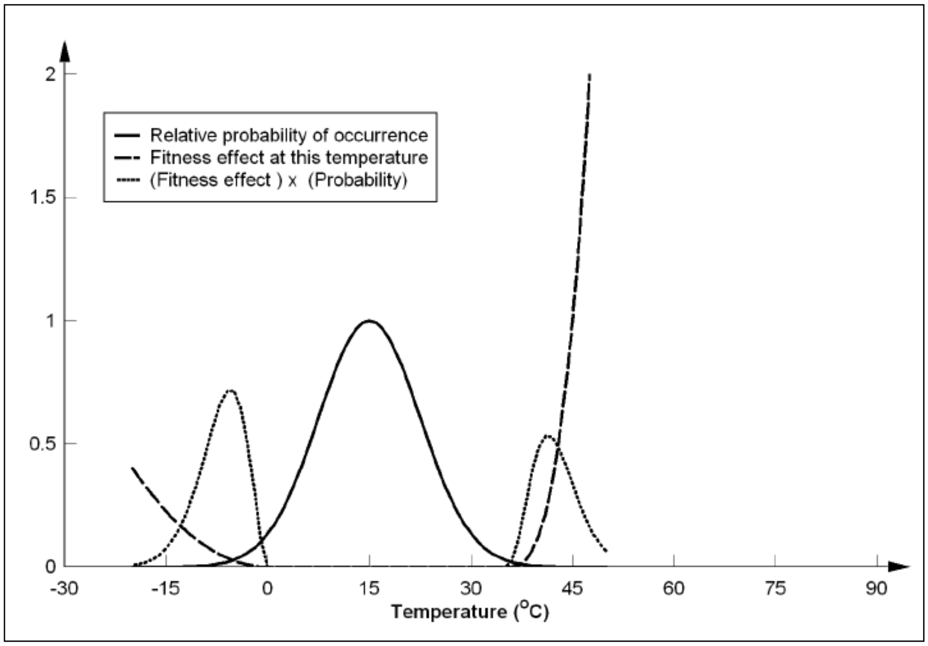

Fig. 1. Notional example of concentration of fitness effects of biological conditions at their extremes in temperature. Only very high and very low temperatures damage the organism and lower its Darwinian fitness (the fitness effect), which is the expected lifetime reproductive output, expressed above in arbitrary relative units. The expectation value of the fitness effect of an event is the product of its probability of occurrence and the fitness effect of the specific event.

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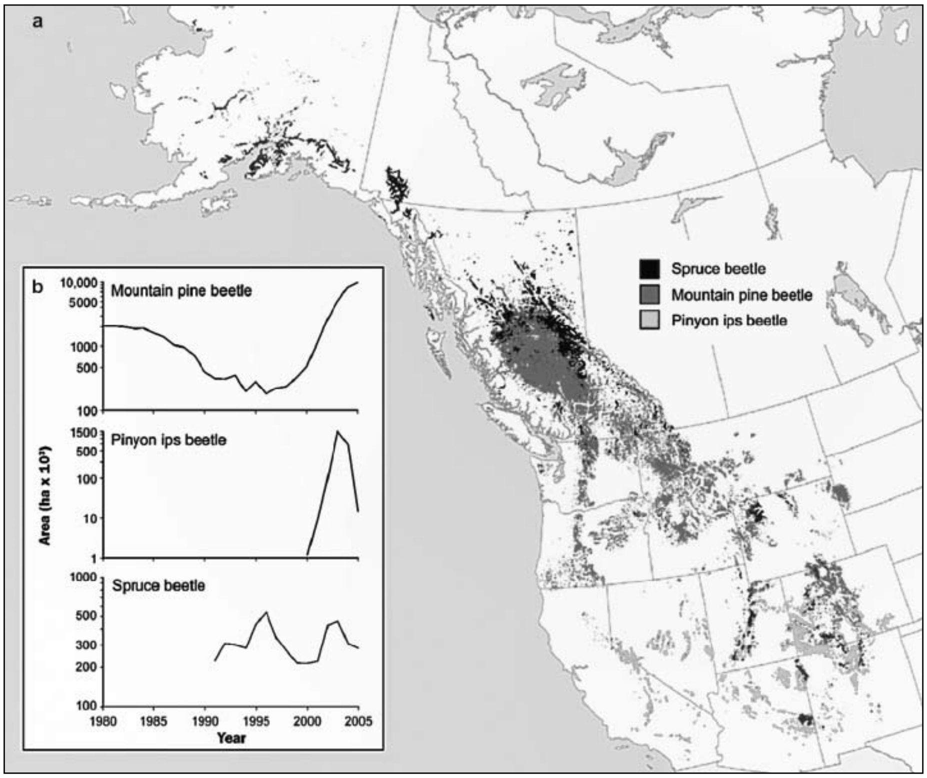

Fig. 2. Recent mortality of major western conifer biomes attributed to bark beetles. (a) Map of western North America showing regions of major population eruptions by three species. (b) Sizes of conifer biome area affected by these three species over time. Reproduced from Raffa et al. *[2008], courtesy of the American Institute of Biological Sciences.*

Foremost, extremes emerge from the interaction of a physical driver with a biological entity, and so the identification of a biological extreme event will be organism-specific. For example, extreme high air temperature is defined differently for native desert species and domesticated species.

Fundamentally, the organism's performance is strongly debited or enhanced by an extreme event. Negative extremes are perhaps more recognizable and are characterized by the environment exceeding the conditions to which (1) the individual organism can acclimate at low cost (e.g., energetic cost) by adjusting its physiology or development or (2) the population can adapt by changing its genetic structure, except by massive natural selection. In the latter scenario, necessary loss of weaker members leads to excess genetic deaths [see, e.g., *Hoffmann and Parsons,* 1997].

Further, extreme events typically are defined by sequences of abiotic phenomena rather than by point events. *Gutschick and BassiriRad* [2003] present the case that biological extremity most commonly derives from environmental conditions exceeding significantly the capacity of the organism to acclimate. This is an important subtlety: Acclimation comes from the past run of environmental conditions, so a desert plant in summer, for example, is most likely to be well acclimated to an air temperature of 40°C, but the same temperature in spring, preceded by a sequence of much milder temperatures, culminates in an extreme event. Thus, the extreme is determined by the whole sequence, not only by the final trigger or a simple "step height" in temperature, aridity, or other variable factor.

Extreme events often involve multiple, correlated environmental variables. The conifer dieoff illustrated in Figure 2 resulted from drought, a run of high annual temperatures, and the condition of bark beetle populations. The separate factors unfolded in a sequence—the order of events mattered. For instance, high beetle populations have occurred in the past but not coincident with drought and higher temperatures, giving very different (far less extreme) outcomes.

While responses of individuals and organisms during the extreme are important, responses during the recovery phase are just as important or more so. Species experience different levels of biological extremity, and they recover from such extremities with different trajectories [*BassiriRad et al.,* 1999]. Such differential tolerance and recovery rates from extremes influence local biogeography and biodiversity. Thus, scientists must look at the full range of temporal and spatial scales to account for biological extreme events. The relevant time scale is that of the organismal responses.

A Closer Look at Plants

Plant leaves have low thermal inertia and are affected by temperature extremes on the scale of minutes. Droughts entail effects in weeks or months. The rise of atmospheric carbon dioxide requires decades but is a rapid extreme on both geochemical and evolutionary scales. It is also a driver of several types of biological extremes, including wholesale changes in species dominance. Indeed, the physiological effects of carbon dioxide are developing much faster than time scales of evolution for major long-lived organisms such as trees.

Plant adaptation by genetic change requires tens to hundreds of generations and the probably alarming selective deaths of "old" genotypes. Genetic change is needed because adaptive forms of genes (alleles) to cope well with high carbon dioxide levels have not been actively selected over the past 25 million years of low atmospheric carbon levels. These alleles have likely been lost by random genetic drift [*Hoffmann and Parsons,* 1997].

Areas of Further Study

Several critical areas demand study. An immediate candidate is the physiology of acclimation to sequences of temperature for major species, primarily plants. Key conceptual models of important extreme events, such as the continental-scale outbreak of bark beetles, need to be converted into quantitative algorithms for testing. To track the important and perhaps extended sequences of multiple environmental drivers that create biological extreme events, new statistical methods are needed [*Gutschick and BassiriRad,* 2003]. Manipulative experiments [*Jentsch et al.,* 2007] rather than purely observational studies must also be expanded, but with dynamic changes, not simply static warming or precipitation alterations.

Further, climate models, regional to global, need to be tested for their ability to reproduce the observed statistical patterns that constitute biological extreme events. Additionally, new genetic compositions and resultant physiologies of populations will be poorly predicted by considering only new environmental averages and not true biological extremes [*Loehle and Leblanc,* 1996]—for example, very little is known about the variability in responses among even the relatively few dominant species of plants. Thus, biogeographic changes are likely to be very different from predictions that use models that incorporate only average conditions such as climate envelopes [*Gutschick,* 2007].

In the absence of concerted efforts on these fronts, the scientific community is rather certain to be uncomprehending observers of large changes in landscapes, climate, and biogeochemical cycles. The ability to estimate thresholds for mitigation action will be much compromised, as will society's ability to adapt social and economic systems that rely on agricultural and biological diversity.

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NEWS

U.S. National Science Foundation Slated for Large Budget Increase

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Although the Obama administration has promoted its proposed $3.8 trillion federal budget for fiscal year (FY) 2011 as one that works toward reining in budget deficits and living within the nation's means, research is among the areas slated for increases. The National Science Foundation (NSF) would receive $7.42 billion, an 8% increase above the FY 2010 enacted level of $6.87 billion, which pleases NSF administrators. This proposal would keep the agency on track for doubling its budget between about 2007 and 2017.

"The president sees science as a way to build our economy. It's a way to make the nation strong in the future. It's a way of bringing change in society, and in addressing some of the global challenges that we are facing," NSF director Arden Bement Jr. explained at a 1 February briefing. Bement, who has been at the helm of the agency for more than 6 years, announced in early February that he is leaving later this year to head up the Global Policy Research Institute at Purdue University.

Within the proposed NSF budget, the Research and Related Activities account, which includes funding for the geosciences, would increase to $6.02 billion, 8.2% more than the FY 2010 figure of $5.56 billion; and Education and Human Resources would rise to $892 million, up 2.2% from $872.7 million for FY 2010.

The Major Research Equipment and Facilities Construction (MREFC) account would rise to $165.2 million, a dramatic increase of 40.8% above the FY 2010 mark of $117.3 million. Within the MREFC account, the Ocean Observatories Initiative (OOI) is slated to receive $90.7 million for a ramp-up in operation and management support; the figure is up substantially from the FY 2010 estimate of $14.28 million provided for the initiative. OOI will include deep-sea buoys, regional cabled nodes on the seafloor, and a network of coastal observatories. The MREFC account also would include $23.58 million for the Advanced Laser Interferometer Gravitational Wave Observatory (AdvLIGO), $13.91 million for the Atacama Large Millimeter Array (ALMA), $17 million for the Advanced Technology Solar Telescope (ATST), and $20 million to begin constructing the National Ecological Observatory Network (NEON).

Agency-wide funding for the U.S. Global Change Research Program (USGCRP) would increase to $369.9 million, $50.9 million, or 15.9%, above the $319.1 million figure in FY 2010. NSF's Directorate for Geosciences (GEO) would receive $225 million of that funding, $31 million more than the $194 million it received in FY 2010. Of the USGCRP funding, $123.31 million would be for climate variability and change research, $75.67 million for terrestrial and marine ecosystems research, and $57.73 million for carbon cycle research, with funding also slated for research on atmospheric composition, the water cycle, land use and land cover, and human contributions and responses to climate change.

The new Science, Engineering, and Education for Sustainability (SEES) investment portfolio of programs would receive $765.5 million and span 10 NSF directorates and offices. SEES would incorporate the Climate Research Initiative and other programs, including renewable energy technology research and activities in large-scale networking. The proposed budget calls for GEO to receive $230.7 million for SEES.

Funding for Networking and Information Technology Research and Development would bump up to $1.17 billion, from $1.09 billion, while agency funding for the National Nanotechnology Initiative would dip to $401.3 million from $417.7 million. Funding for the Office of Polar Programs would increase to $528 million, 17% above the FY 2010 level of $451.16 million.

Outlook for the Geosciences Directorate

The $955.29 million proposed FY 2011 budget for GEO is 7.4% higher than the $889.64 million estimated FY 2010 level, which in turn was a 10.2% increase above FY 2009 levels. GEO funding for research would go up 8.8% to $505.17 million; education up 7.9% to $44.68 million; infrastructure up 5.4% to $387.6 million; and stewardship up 9.2% to $17.84 million.

Within GEO, funding for Atmospheric and Geospace Sciences (AGS) would increase to $280.8 million, 8.1% more than the $259.8 million 2010 estimate; Earth Sciences (EAR) would bump up to $199 million, 8.7% more than the earlier $183 million; and Ocean Sciences (OCE) would receive $377.89 million, 8.3% above the FY 2010 level of $348.92 million. Funding for Integrative and Collaborative Education and Research would ease down $320,000.00, or 0.3%, to $97.6 million.

At a 1 February briefing following the agency-wide budget rollout, Tim Killeen, NSF assistant director for geosciences, said GEO "is building off the momentum of the past year," including the strong FY 2010 budget and funding received through the American Recovery and Reinvestment Act