

Impact of extreme events on pollinator assemblages

Hilary E Erenler; Michael PGillman; and Jeff Ollerton

Insect pollinators face a number of well-documented threats that challenge their survival at an individual and community level. The effect of extreme events on pollinator assemblages has received little attention to date, partly due to a lack of consensus on what constitutes extreme, but also because robust pre-event data is often lacking. Here, the term SHOCK (Sudden, High-magnitude Opportunity for a Catastrophic 'Kick') is used to encompass attributes of extreme events that carry the potential to add additional challenges to insect communities already facing environmental stressors. Selected events from two SHOCK categories are explored (those with natural origins and those that are human-mediated). The value of studying single events is considered in the context of a third category; human-enhanced SHOCKs.

Introduction

Diverse insect pollinator communities, including wild and managed bees (Hymenoptera), butterflies and moths (Lepidoptera), flies (Diptera) and beetles (Coleoptera), provide mutually beneficial ecosystem functions for natural and agricultural systems [1–3]. Declines in insect pollinator species richness and abundance are well documented and linked to habitat loss, agricultural intensification and the spread of non-native species and pathogens, all of which may be exacerbated by anthropogenic climate change [4,5,6•].

The impact of extreme events on pollinator communities has received less attention, partly due to a lack of consensus on what constitutes an extreme event [7•], but more commonly because of a paucity of robust pre event data against which to measure short and long- term pollinator responses. Despite their sporadic nature, single high-impact events have the potential to temporarily or permanently disrupt mutualistic insect-plant interactions [8,9]; causing alterations to the availability of pollinator foraging and nesting resources [10,11] and leading to changes in pollinator community composition, including an increase in generalist species [12,13].

This synthesis identifies known responses of pollinator assemblages to a selection of natural and directly human-mediated extreme events. Separately, in accepting that human-enhanced extreme events, that is, natural events exacerbated by human actions, are likely to increase in frequency, we consider the importance of pre-event data gathering and the usefulness of studying single events.

What is an extreme event?

Extreme events comprise some combination of low frequency, high unpredictability and high magnitude. They exist as outliers against a backdrop of observed variation in occurrence and severity of different processes and states. The terms 'perturbation' [14] and 'abruptness' [15] have both been used to describe deviations from continuous background processes. In acknowledging the difficulties of setting parameters (and collecting data) against which to benchmark extreme events as anthropo- genic activities alter natural processes at an increasingly rapid pace [16–18], we have deliberately avoided fixed definitions of what constitutes 'extreme' in the context of frequency, predictability, magnitude and geographical reach. Instead, we use the term SHOCK (Sudden, High-magnitude Opportunity for a Catastrophic 'Kick') to encompass attributes of extreme events that have the potential to adversely affect pollinator communities (Figure 1).

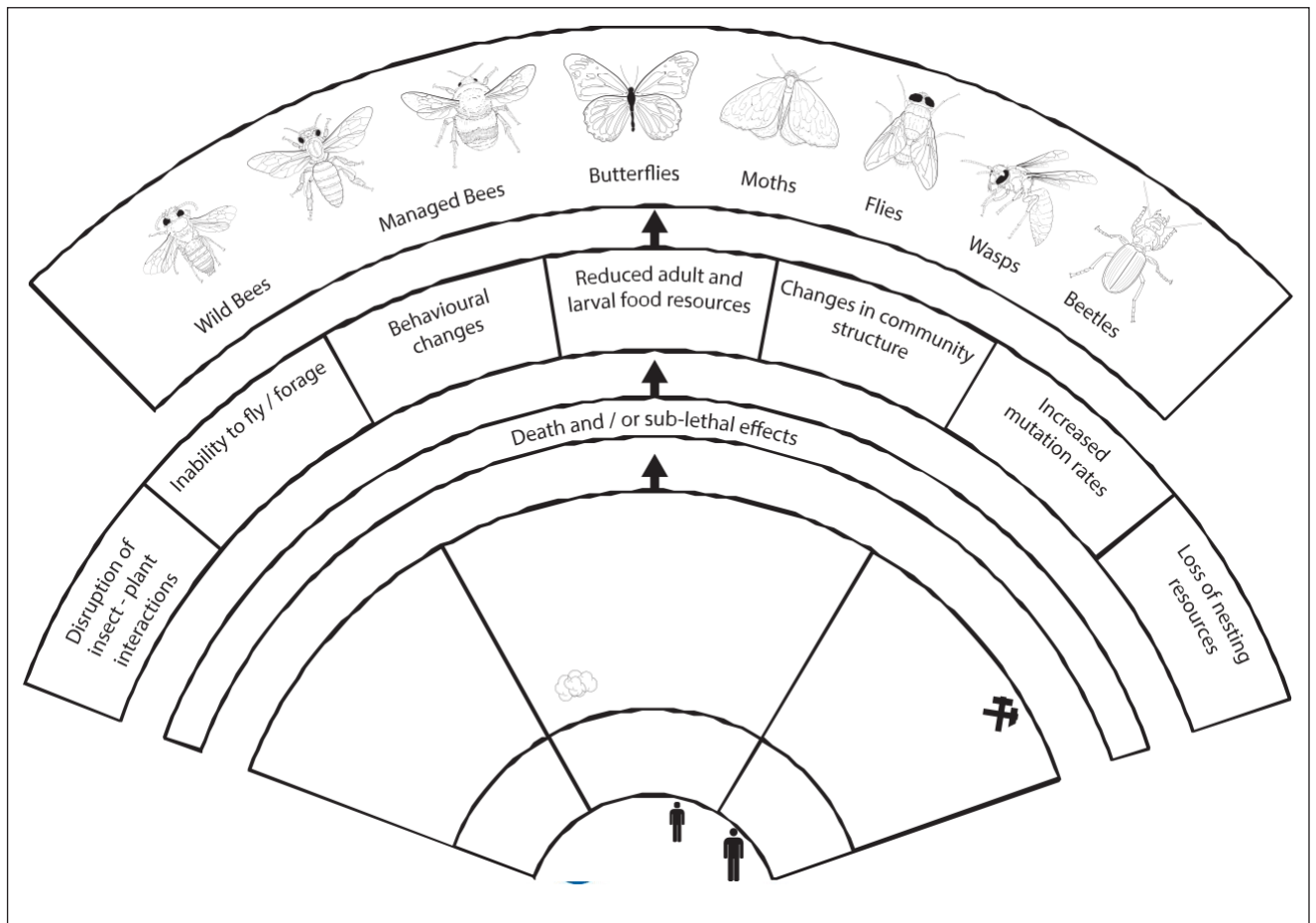


Figure 1 - A selection of natural SHOCKs, human-enhanced natural SHOCKs and directly human-mediated SHOCKs which have the potential to affect pollinator assemblages in various ways. Some of these are direct, immediate and lethal, such as loss of nest sites and future generations in diapause as a result of inundation, for example, flooding or dam collapse at mining sites. Others are sublethal but limit flight and the ability to forage, for example, the result of exposure to, or ingestion of, atmospheric volcanic ash particles. Finally, there are longer-term effects, expressed as deleterious genetic mutations resulting from exposure to increased levels of radiation following nuclear accidents.

Natural SHOCKs

Volcanic eruptions

Erupting volcanoes can lead to multiple lethal and sub-lethal SHOCKs for insect communities [19]. Ash, gas and lahars reduce or eliminate flowering resources used for food or brood nutrition [20]. Insect exoskeletons are vulnerable to physical damage caused by the abrasive nature of ash, leading to rapid desiccation, whilst the ingestion of ash contaminated pollen and nectar causes internal chemical and physical damage [21]. Ground nesting bees may suffer complete loss of nest sites or be reproductively compromised following exposure to ash and gas [22]. Other consequences include damage to wing structures which alters foraging patterns and causes loss of flight [23], as well as an increase in aggressive behaviour [24 and references within].

Not all outcomes are negative, however. Following a substantial Chilean ash fall event, declines in an invasive social wasp species were noted [25], which favoured the recovery of native wasp communities. This suggests that whilst disturbance may aid initial invasion processes, SHOCKs may facilitate the re-occupation of vacated niches by native communities [20].

Despite the potentially devastating losses of flora resulting from volcanic episodes, butterflies and other generalist pollinators, as well as specialist fig wasps and their fig tree hosts, may be able to rapidly re-colonise an area [26– 28]. Indeed, in spite of their highly specialised pollination systems, it seems figs have a remarkable ability to quickly re-establish their relationships with pollinators following an extreme event [29,30].

In the case of repeated volcanic SHOCKs, network studies have established that mutualistic plant-pollinator communities may exhibit resilience to these episodic events, thereby aiding post-SHOCK recovery [31•].

Alterations in solar flux

Suboptimal flying conditions occur when there are alterations in solar flux. This can follow an increase in atmospheric dust concentrations after a volcanic explosion [32], but also occur during solar eclipses [33••]. Solar eclipses therefore represent SHOCKs that have the potential to alter pollinator behaviour through curtailment of flight. Whilst the temporary, but significant, temperature drop associated with a 90-minute solar eclipse in 2017 was not found to be a driver in reduced flight [33••], possibly due to the broad thermal tolerances exhibited by many bee species [34], alterations in solar flux resulted in flights ceasing altogether during the complete darkness phase of the eclipse [33••]. The implications are that natural SHOCKs can limit or halt flight, leading to a reduction in foraging for individual or brood nutrition, and that this has a consequence for insect- pollinated plants.

Human-mediated SHOCKs

Nuclear incidents

Enhanced radiation levels produce elevated rates of genetic damage and increased mutation rates in a range of organisms, leading to physiological, developmental, morphological and behavioural changes [35,36]. Human-mediated releases of radionuclides via Level 7 nuclear incidents have occurred only twice to date; the Chernobyl Nuclear Power Plant (NPP) disaster of 1986 and the Fukushima Dai-ichi NPP accident in 2011. In the highly radioactive area of the Chernobyl Exclusion Zone 25 years after the event, bumblebees and butterflies were both found to exhibit significant declines in abundance with increasing levels of radiation. However, in Fukushima, six months after the event, whilst the abundance of butterflies was negatively affected along gradients of radiation, bumblebees did not exhibit a similar response [37]. This suggests that in the immediate aftermath of a nuclear incident, radiotoxicity is the biggest SHOCK, whilst over longer time-frames a mixture of radiotoxicity and mutation-accumulation effects combine, which results in pollinator taxa responding in different ways [37,38]. Haplodiploidy, associated with pollinating bees and wasps (Hymenoptera), is believed to facilitate the rapid elimination of lethal and deleterious genes [39]. This process may be important in the wake of a nuclear incident.

In laboratory conditions, increasingly severe abnormalities in successive generations of the pale grass blue butterfly, *Zizeeriyama*, exposed externally (as larvae and pupae) and internally (via ingested food) to Fukushima nuclear contaminants have been observed [40]. This suggests that the strong trans-generational legacy effects of exposure to human released radionuclides are likely to impose an, as-yet, potentially underappreciated burden on populations in the wild [41••].

Running contrary to the reported negative effects of nuclear disasters is the potential upside associated with humans being absent from an area, as shown by studies of mammals in the Chernobyl Exclusion Zone [42]. These benefits could include habitat regeneration following the abandonment of intensive agriculture, which is a known driver of pollinator loss [4].

Mining and industrial accidents

Unusually high levels of heavy metal contaminants occur in the environment as a result of mining and industrial activities [43,44]. These contaminants enter pollinator biological cycles via plant resources including plant tissue, pollen and nectar [45,46], and, in the case of several insect groups, including bees and butterflies, can lead to mortality, developmental abnormalities and an alteration in female reproductive success [47–49]. Mining and industrial accidents represent human-mediated SHOCKs through the sudden release of large quantities of contaminants into the environment, often over short periods. The collapse of the Funda~o dam in Brazil, built to hold back iron ore tailings from mining activities, unleashed 43 million m³ of mining waste into the environment on a single day in 2015, and is considered the world's worst mining dam disaster [50]. The outcome for pollinator assemblages after this, and other industrial accidents, remains largely unknown [6,51]. Studies have shown that some insects may unwittingly expose themselves to lethal doses of contaminants. For example, honey bees are unable to discern that a lethal dose of selenium is present in a sucrose solution and readily consume it [52]. Whilst some taxa, including bumblebee, ant and beetle species, have been shown to exhibit resilience under different gradients of heavy metal pollution (by means of accumulation, concentration-regulation and subsequent excretion [53,54]), the effects on pollinators of a cocktail of pollutants, including the flocculants and coagulants present in mining tailings, is currently undocumented [51].

Human-enhanced SHOCKs

In addition to natural and human-mediated SHOCKs, a third category (human-enhanced SHOCKs) exists. This represents natural events whose frequency and/or magnitude have been altered through human actions. Prime examples of this are extreme climatic events (ECEs) such as: hurricanes, cyclones and typhoons; prolonged or extreme drought or flooding; increased frequency or severity of wild fires, and extremely high or low temperatures. It is hypothesised that an increase in the frequency of these human-mediated SHOCKs will pose additional challenges to pollinator communities already compromised due to environmental stressors [55]. A systematic review across four categories of natural hazard (including examples from our natural and human-enhanced SHOCKs) emphasises the need for greater understanding of the effects on pollination for both conservation and agriculture [56].

Examining specific climate change effects on pollinator assemblages, and the myriad of approaches and challenges involved with measuring these, is beyond the scope of this paper, and has been covered elsewhere [5,6,7,57,58]. However, some of the detailed considerations regarding species and ecosystem responses to ECEs have wider application to non-climate-related extreme events (SHOCKs), and to pollinators in particular. Determination of the (nonlinear) biological response function to ECEs and its underlying mechanisms [7] is certainly desirable for natural and human-mediated SHOCKs. Likewise, the use of spatial and temporal observational data is not necessarily appropriate (or available), for all SHOCKs (unlike most ECEs), but the use of experimental manipulations and models may prove to be beneficial [7,59].

An important emerging theme is the value to be gained from studying single events particularly, but not exclusively, when they punctuate a long-term study [59]. Despite potential criticism that the results from these events fail to meet statistical norms for replication and lack availability of controls against which to measure responses, they help meet the current 'call to arms' to better understand how pollinators might fare in the future as the frequency of extreme climatic events increases [60,61]. Even in the absence of long-term, pre-event data, studying the outcomes of a single SHOCK, regardless of its cause, can provide valuable insights into the biological responses of pollinators [41,62].

Concluding remarks

SHOCKs take many forms and vary in their origin and the responses they elicit. Natural and human-mediated SHOCKs can collide to generate unpredictable human-enhanced events. This means pollinator communities that are already facing environmental stressors may be more frequently exposed to events that can alter community composition and even their existence.

Volcanic eruptions of varying severity occur regularly around the globe; however, supervolcanic eruptions, and their potential effects on biological communities, including pollinators, remain the subject of speculation [63]. The recent work on pollinator responses to solar eclipses [33••] provides a useful insight into how altered light levels from volcanic dust might affect pollinators' ability to forage following larger or global-level volcanic events.

Nuclear incidents remain rare, but increased demand for non-fossil-fuel energy means the ageing infrastructure of some existing nuclear power plants can combine with an unfortunate sequence of events (such as an earthquake then a tsunami), resulting in immediate and severe local and regional effects on pollinators. The transgenerational effects of such SHOCKs on pollinator populations in the wild are only now being appreciated. Similarly, previously unimagined extreme events, such as the infrastructure failure of a dam holding back mining tailings, can become SHOCKs that destroy habitats, and initiate a cascade of catastrophic consequences for pollinator assemblages.

Depending on the ecological and behavioural traits of pollinator communities, food resource availability can become significantly compromised following a SHOCK, resulting in reductions to the quantity or quality of adult and larval food resources including flowers and prey for carnivorous species. Separately, bees and wasps may be affected to a greater or lesser extent by SHOCKs such as volcanic events, inundation following mining disasters or nuclear incidents depending on whether they are aerial or ground nesting species.

Reports of outcomes from single-event studies can provide valuable insights into how pollinators respond both in the immediate aftermath of SHOCKs and through subsequent generations. Moreover, they offer the opportunity to contribute to a wider base of knowledge against which practical responses can be evaluated and a theoretical framework built.

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