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OPINION

Rethinking species' ability to cope with rapid climate change

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Abstract

Ongoing climate change is assumed to be exceptional because of its unprecedented velocity. However, new geophysical research suggests that dramatic climatic changes during the Late Pleistocene occurred extremely rapid, over just a few years. These abrupt climatic changes may have been even faster than contemporary ones, but relatively few continent-wide extinctions of species have been documented for these periods. This raises questions about the ability of extant species to adapt to ongoing climate change. We propose that the advances in geophysical research challenge current views about species' ability to cope with climate change, and that lessons must be learned for modelling future impacts of climate change on species.

Keywords: adaptation, biodiversity, dispersal, extinction, habitat fragmentation, phenotypic plasticity, rapid climate change

Our planet has undergone severe climatic changes in the past, most recently the glacial–interglacial cycles of the Pleistocene. Global change biologists generally assume that climatic changes during and after the Pleistocene were gradual, while contemporary climate warming occurs at an unprecedentedly rapid rate [see e.g. the fourth report of Intergovernmental Panel on Climate Change (IPCC) working group II, Fischlin *et al*., 2007, but see Chapter 6 'Paleoclimate' of WG I, Jansen *et al*., 2007, which gives a more differentiated picture]. The IPCC report recognizes that rapid climatic changes occurred in the past, but it also states that 'it is very likely that the global warming of 4–7 °C since the Last Glacial Maximum (21 000 BP) occurred at an average rate about 10 times slower than the warming of the 20th century' (IPCC, 2007, p. 435). This perception is based upon the fact that Earth's mean temperature has increased by 0.74 °C from 1906 to 2005, and projections of global mean temperature increase for the end of the century (2090–2099) range from 1.8 to 4 °C (IPCC, 2007).

Recent geophysical studies challenge the view that the speed of current and projected climate change is unprecedented. Based on high-resolution Greenland ice core data, Steffensen *et al*. (2008) showed that local temperature changed up to 4 °C yr^{-1} near the end of the last glacial period (14 700 BP). Their results revealed that 'polar atmospheric circulation can shift in 1–3 years, resulting in decadal- to centennial-scale changes from cold stadials to warm interstadials' associated with Greenland temperature changes of 10 °C (Steffensen *et al*., 2008). Brauer *et al*. (2008) reported an abrupt increase in storminess within a single year in Western Germany during the Younger Dryas cold climate period (12 700 BP), and linked this event to the inception of deglaciation (see also Bakke *et al*., 2009). The existence of abrupt historic climate change has been acknowledged previously (Alley *et al*., 2003). However, the newer studies not only support the view that abrupt climatic changes might have been more common than expected, they also document on a fine temporal resolution that they occurred over very short time periods. Although such abrupt changes are so far documented as regional to continental phenomena, their global implications are still being discussed (see also Shakun & Carlson, 2010). The fact that the documented abrupt climate changes do not coincide with any of the known major extinction events raises questions about species' abilities to cope with climatic changes, and whether we fully understand this process.

The view that ongoing climate change is unprecedentedly fast has fuelled the prediction that it will have unprecedented effects on Earth's biodiversity (e.g. Tho-

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mas *et al*., 2004; Pereira *et al*., 2010). In this context, it is worth noting that the rapid climate changes in the Quaternary period (spanning approximately 2.5 million years to the present) did not cause a noticeable level of broad-scale, continent-wide extinctions of species; instead, it appeared to primarily affect a few specific groups, mainly large mammals (Koch & Barnosky, 2006) and European trees (Svenning, 2003). This taxonomically biased extinction might partly be due to the fact that not all groups are equally represented in the fossil record; for instance, detailed data on Quaternary extinctions is vastly lacking for herbaceous plants and many invertebrate groups. Nevertheless, overall it appears evident that relatively few taxa became extinct during the Quaternary (Botkin *et al*., 2007). Further, and more importantly, the vast majority of extant species in, e.g., Europe and North America, which are now exposed to contemporary rapid climate change, have been exposed to the last glacial cycles of the Pleistocene, and thus have coped successfully with the abrupt climatic changes of the past.

In simplified terms, responses of species to climate change may be synthesized as evolutionary adaptation, dispersal and extinction (Holt, 1990; Parmesan, 2006), supplemented by behavioural, physiological and anatomical variability within and among individuals and populations. When modelling the effects of climate change on species distributions, the prevailing consensus is that current climate change simply outpaces microevolutionary processes. So, there is no time for evolutionary adaptation (Jump & Peñuelas, 2005). Dispersal, on the other hand, has been identified as widespread response of species to recent climate change, usually via range shifts from lower to higher latitudes and altitudes (Parmesan & Yohe, 2003); it is also regarded as the main response of species to past climatic changes. However, in light of abrupt climatic changes of the past, we need to move beyond modelling approaches where dispersal across large distances is regarded as the only predominant strategy for species to successfully cope with changing climate (Fig. 1a). By the same token, microevolutionary adaptations comprising small-scale changes in genetic diversity in a population over a few generations are even more difficult to imagine as a potential response to rapidly changing historical climate regimes.

The fact that extant species did not become extinct as a result of the drastic, rapid climatic changes at the end of the Last Glacial indicates that species may have used strategies other than shifting their geographical distributions or changing their genetic make-up. If abrupt climatic changes were, by en large, a continent-wide phenomenon, one possibility is that adaptation might have been a consequence of phenotypic variability in the populations. In other words, intraspecific variation in physiological, phenological, behavioural or morphological traits may have allowed species to cope with rapid climatic changes within their range (Davis & Shaw, 2001; Nussey *et al*., 2005; Skelly *et al*., 2007). This phenotypic variability is based on the preexisting genetic variation within and among different populations, which is an important prerequisite for adaptive responses. Furthermore, the phenotypic plasticity of individuals, e.g., in their behaviour or anatomy, may also enable organisms to respond successfully to environmental changes. As both intraspecific phenotypic variability and individual phenotypic plasticity may allow for rapid adaptation without actual microevolutionary changes, they may have been important strategies for species to cope with rapid climatic changes of the past. In addition, retreats to nearby pockets of suitable microclimates (Fig. 1b and c), permitting species to endure adverse climatic conditions, could have played a role for various taxa and regions (Willis *et al*., 2000; Scherrer & Körner, 2010). These pockets may have been located within species' ranges, especially for species with wider distributions, or may have been reached by small-scale dispersal events – presumably over much shorter distances than those implied by range shifts. These potential strategies to cope with rapid climate change are not necessarily independent, but may have complemented each other. In any case, no matter which strategy was most important, the fact of interest is that extant species have coped successfully with the extremely rapid climatic changes of the Late Quaternary.

These novel perspectives on species' responses to past climate change may challenge our perception of how species will respond to current and future climatic changes. Currently, the perception prevails that the vast majority of species will heavily struggle under the burden of current and future climate change (Thomas *et al*., 2004). The reports on extremely rapid climatic changes in the Late Quaternary may give rise to the question of whether high estimates of extinction risk due to current and future climate change are inflated. One might be tempted to jump to the conclusion that most species would be able to respond successfully by either of the aforementioned suggested strategies. However, such a conclusion is ill-founded because current and projected future climatic changes are not the only threats that species have to cope with today.

The ability of species to survive rapid climate change is different today than it was in the past, with current landscapes and ecosystems being severely modified by humans (Sala *et al*., 2000). These modifications include land-use change and concomitant habitat destruction, degradation and fragmentation at large spatial scales. In fact, habitat destruction and fragmentation, not climate

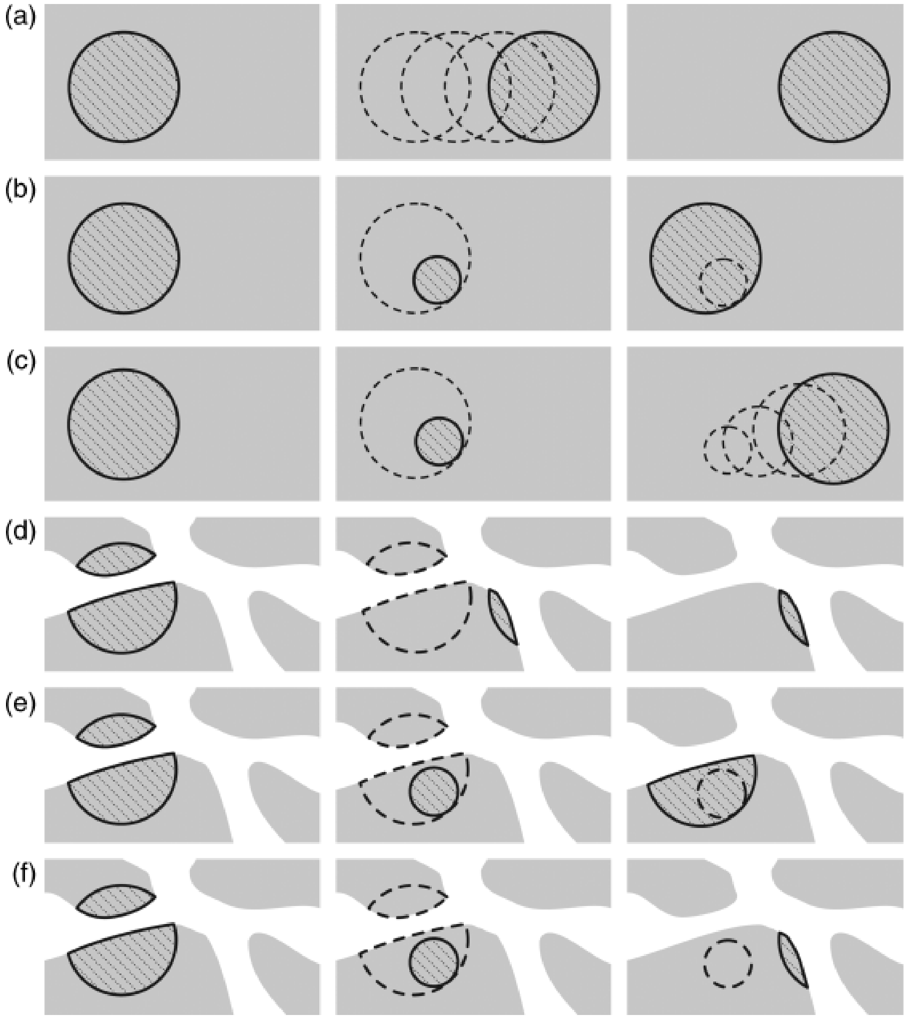

Fig. 1 Schematic illustration of potential changes in ranges of species as a result of climatic changes. Grey areas indicate suitable habitat for species occurrence, whole circles represent the distribution of a species and dashed circles its distribution in the previous time step. (a)–(c) illustrate a pristine world before human impact on habitat continuity and (d)–(f) a world where habitats are modified by humans (note that in these scenarios adaptation of species to climate change is not considered important for the persistence of the species). In (a), species are assumed to track in distribution gradual changes in climate. In (b), climatic changes are assumed to be extremely rapid and species may survive by enduring in small areas of suitable microclimates within the current ranges and expand when suitable climatic conditions return. In (c), species are also assumed to endure in small areas of suitable microclimates within the current ranges, but this time followed by subsequent tracking of suitable climate conditions. (d)–(f) correspond to (a)–(c), but illustrate a world of habitat destruction and fragmentation, where the area containing suitable microclimatic conditions is smaller, which reduces the probability of endurance (central panel), as well as the probability of successful range shifts (right-hand panel).

change *per se*, are usually identified as the most severe threat to biodiversity (Pimm & Raven, 2000; Stuart *et al*., 2004; Schipper *et al*., 2008). But beyond affecting species directly, land-use changes have a marked impact on the ability of species to deal with climate change (see e.g. Travis, 2003), and climate change enhances the negative impact of habitat and landscape changes.

Habitat destruction and fragmentation may reduce the possibilities of species to survive climate change in suitable microclimatic pockets. Smaller and fewer habitat patches contain, by definition, fewer microclimatic areas suitable for the endurance of species during climatic changes (Fig. 1d–f). Additionally, smaller habitat patches sustain smaller populations, which show lower genetic and phenotypic variability (Jump & Peñuelas, 2005) – a prerequisite for rapid adaptive responses. Even pristine landscapes are geographically heterogeneous (see Fig. 1a–c for a schematic illustration) so phenotypic and the underlying genotypic variability are not evenly distributed in space. Consequently, even without the negative anthropogenic impact, the potential of species populations to adapt to climate change is unevenly distributed across space. Increasing fragmentation of the remaining habitat patches is likely to exacerbate this uneven distribution of the adaptive potential, due to the decline of phenotypic and genotypic variability both within and between populations. Thus, habitat fragmentation reduces the potential of a species to respond with trait shifts due to lower phenotypic variability across its range. Fragmentation also impedes short- and long-distance dispersal processes (Fig. 1d–f, Fahrig & Merriam, 1994). This does not only reduce the potential of species to respond via range shifts; a reduced dispersal probability also impedes the exchange of individuals among populations, thus lowering gene flow and therefore genotypic and phenotypic variability (Young *et al*., 1996), and, in turn, the ability of species to adapt to changing environmental conditions (Davis & Shaw, 2001).

The graphical illustration of habitat destruction and fragmentation in Fig. 1d–f is simplified and might provide too optimistic scenarios. In many regions, the extant degree of habitat fragmentation is much more severe than illustrated in the figure. Furthermore, the vast majority of species have smaller distributions than assumed in the figure. For small-ranging species, independently of whether their distributions are naturally small (e.g. island endemics) or small because of anthropogenic pressures (e.g. exploitation), habitat destruction and fragmentation are particularly detrimental irrespective of adding climate change as an additional pressure or not.

That extant species have survived abrupt, historical climatic changes might be – at least partly – good news. It suggests that species' ability to survive drastic climate change is greater than hitherto recognized, perhaps due to the phenotypic variability of populations, or to their ability to survive in microclimatic pockets in a heterogeneous landscape. In other words, species are probably more resilient to climatic changes than anticipated in most model assessments of the effect of contemporary climate change on biodiversity (see also Willis & Bhagwat, 2009). However, the synergetic effects between climate change and the ongoing destruction and fragmentation of natural habitats (leaving aside further anthropogenic pressures for biodiversity) should by no means be underestimated.

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