Extinction risks from climate change: macroecological and historical insights

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Abstract

Human-induced climate change may threaten a large proportion of Earth's biota, but the uncertainties involved in projecting the future geographical distributions of species make quantitative predictions of extinction risk difficult to make. I discuss how insight from recent advances in macroecology and knowledge about species responses to past climate change can help predict extinction risks more accurately.

Introduction and context

Current rates of species extinction have been inferred to be orders of magnitude above background levels, based on well known groups with a fossil record [1,2], but whether these taxa are representative for biodiversity in general is not known. There is concern that we are currently entering a mass extinction event comparable to the previous five greatest mass extinctions in the history of life [3]. Currently, most human-induced extinctions result from habitat destruction and overexploitation of species [4]. Climate change caused by greenhouse gas emissions may become a similarly severe threat [5], and will add to present challenges for global biodiversity. The ability to assess the potential species loss is hampered by insufficient knowledge about biodiversity. The number of species on Earth is not known even to the order of magnitude [6], and the geographic distributions and ecology is poorly known for most taxa described by science.

Extinctions of species where climate change is thought to be the ultimate cause may have already occurred [7], but pinpointing the ultimate cause of an extinction event is difficult. To assess the magnitude of the problem in the future, modelling is required. Despite the challenge of incomplete knowledge, rough predictions of the number of species threatened with extinction by climate change

have been made [8-10]. The general method in such predictions has been to project the degree of habitat loss expected as a result of geographic range adjustments in response to climate change, and then use species-area equations to assess potential species loss as a result of range contractions. Depending on the climate change scenario used and dispersal ability of species, Thomas *et al.* [9] projected that 18-35% of species are at risk of extinction in their sample of regions across the Earth. The paper and similar efforts are controversial, however, and both the methods [11] and the way the results have been presented in the media [12] have been criticized. Nevertheless, realistic predictions of climate-driven extinction risk are needed for climate mitigation and species conservation efforts.

The accuracy of extinction risk predictions depends on the ability to project how species will adjust to climate change. To survive climate change that is beyond its tolerance, a species may either adapt to the new climate locally, or shift its geographical distribution to climatically suitable areas. A critical question is whether species will be able to evolve tolerance to new climatic conditions at the pace of climate change. Species distribution models utilize species distribution records and correlations with climate to project where species will occur in the future under the assumption of no

evolutionary change [13]. These models are not only used to predict extinction risk, but by providing projections of where species may occur in a future climate, they form the basis of adaptation strategies to conserve biodiversity [14]. When the ability of species distribution models to predict future distributions has been checked, however, their performance has been less than satisfying [15], although the methods are rapidly improving [16]. Reasons for poor model performance and inconsistencies among models include variation among climate change scenarios, poor species distribution data, variation in modelling methods, and violation of model assumptions. One way of gaining insight into the constraints and opportunities offered by extinction risk assessments is to examine how species have responded to similar climatic challenges in the past, and to examine how biodiversity is distributed at large spatial scales and the underlying causes of this distribution, sometimes referred to as 'macroecology'.

Major recent advances

Below I highlight recent advances in the knowledge of how species adjust their ranges in response to climate change now and in the past, which may help assess the risk for climate-induced species extinctions.

Adaptations and evolutionary responses to climate change

If species can evolve rapidly enough in response to climate change, projections of extinction risk based on species distribution modelling may be overestimated. Recent empirical evidence suggests that evolution is responsive to climate variation and may occur at rates that make evolutionary change a plausible alternative to geographical range shifts [17]. Adaptive evolution in local populations may, however, be counteracted by competition from immigrating organisms pre-adapted to the new climate [18]. The dominant response to Quaternary climate changes comprised geographical range shifts rather than morphological adaptation *in situ* [19]. Evolutionary change and geographic range shifts are, however, not mutually exclusive alternatives. Both *in situ* persistence and range shifts may involve evolutionary processes that enhance adaptations to new climatic conditions - for example, by selection for enhanced tolerance in migrating populations [20].

Observed responses to present climate change

An increasing body of data documents that species and assemblages respond to warming as predicted by models, adjusting their ranges polewards and towards higher elevations. This lends support to bioclimatic modelling approaches and projections of species extinction. The most common data record latitudinally expanding range limits of temperate taxa colonizing

habitats that have become climatically suitable [21-23]. Records of latitudinal range contractions are mostly anecdotal [24], but a few recent studies document elevational range shifts [25-27]. Range shifts on tropical mountains in response to warming raise double concerns [28]; many high-elevational species are at risk of becoming extinct if mountains are 'too low' to offer them habitat after the climate zones have shifted upwards. In addition, tropical lowlands might be depleted of species as more and more species shift their ranges towards higher latitudes and elevations [28]. Data on range shifts from tropical mountains have been mostly missing, but recently Chen *et al.* [25] documented 102 insect species shifting their distributions an average of 62 m upwards on Mount Kinabalu, Borneo, between 1965 and 2007. Raxworthy *et al.* [27] found that 30 species of reptiles and amphibians had shifted their elevational midpoints upslope by 19-51 m on Madagascar, in agreement with recent regional warming.

The role of climate and dispersal in limiting species ranges

Some climate types are predicted to completely disappear, threatening species assemblages living in these vanishing environments with extirpation [29]. In the majority of cases, however, the environments of species will shift geographically to various degrees, necessitating modelling of range adjustments and extinction risk. Species distribution modelling rests on the assumption that ranges are bounded by climate. Beale *et al.* [30] found that null models of species-climate associations established using bioclimatic models were no better than chance for 68 of 100 European bird species. Many factors other than climate, such as species interactions and human impact, set the limit of species ranges, all contributing to weaken species-climate associations. If species do not occur everywhere their climatic requirements are met (global dispersal) due to migration barriers, this will also reduce the ability of projecting future geographic distributions. As a result, modelled climatic tolerances will be more narrow than real ones, overstating extinction risk. On the other hand, such a situation also implies that many species are likely to have problems colonizing new areas that become climatically suitable. Svenning and Skov [31] found that European tree species occupy only 38% of their calculated potential climatic ranges. Frequent successful naturalizations of tree species outside their native ranges confirm the climatic suitability of modelled potential ranges. If dispersal limitation is common, species or species diversity patterns cannot be expected to be in steady-state with contemporary climate. The pattern of diversity for European tree species with restricted ranges was best explained by climatic conditions occurring at the last glacial maximum about 21,000 years ago, whereas the

diversity of widely distributed species correlates with present day climate [31]. This suggests that some species were unable to expand their ranges following deglaciation and Holocene warming to occupy their potential niches. This interpretation is supported by the demonstration that species richness of tree species in northern Europe can be explained by differential rates of dispersal out of glacial refugia [32]. In line with these results, Araújo *et al.* [33] demonstrated that species richness of narrow-ranging amphibians and reptiles in Europe was better explained by climatic stability between the last glacial maximum and the present day than by the present climate.

A question related to dispersal limitation in explaining present distributions is whether species will be able to keep up with future climate change. Models of species' future distributions usually assume either full adjustment of species ranges - that is, that species can colonize any suitable habitat - or no range adjustment at all, implying only range contraction in response to climate change [9]. The truth should be somewhere in between. The finding that species richness of butterflies in Britain increases with climate change, but that species richness change lags behind climate change [34] sheds some light on this question. Generalist species responded quicker than specialist ones, suggesting that species with high specialization and low vagility will have the greatest difficulties in tracking their habitat. Lag times should be longer and dispersal barriers more difficult to overcome in taxa less vagile than butterflies.

When using information on how species responded to past climatic shifts, we are faced with a conundrum. Climate shifts during the Quaternary were thought to be as rapid and large as those expected during the 21st century [35]. Despite that, extant species survived many such events, and documented extinctions were few [36]. Does this imply that the problem of climate-induced extinctions has been overstated? Closer examination of the data demonstrates that this is probably not the case. First, assemblages that have been 'filtered' by a previous challenge or catastrophe usually experience little extinction when faced by similar subsequent challenges [37]. For example, the first continental glaciation in Europe in the Plio-Pleistocene caused a wave of extinction in, for example, tree species [38], but the following glacial periods resulted in few extinctions, despite an increase in the amplitude of climate shifts. The first cooling event pruned the European tree species pool of cold-intolerant taxa, whereas the remaining taxa could persist. Secondly, present global climate is close to the peak average temperature attained during the Quaternary [35]. Future warming will result in a climate warmer than recorded

for millions of years [35]. Many species have never experienced such a situation, potentially resulting in extinction of intolerant taxa. Thirdly, during previous climatic shifts, species were able to shift their distributions without interference from humans. Humans now dominate most ecosystems, resulting in barriers to dispersal and combined threats of climate change, habitat destruction and overexploitation of species. The combined effect of human overexploitation and climate change has been implicated in the extinction of the megafauna in Eurasia and America at the beginning of the Holocene. Bioclimatic models show that the ranges of many species, such as the woolly mammoth, drastically declined during deglaciation [39], but megafaunal species had survived many similar climate shifts in the past, and the *coup de grâce* was probably caused by human hunting [40].

Geographic patterns in species vulnerability

Where are species most at risk from climate change? Given that observed and projected climate change is larger towards the poles, most attention has been directed towards high-latitude environments [41], with polar bears as iconic species in the public mind. Depending on the vulnerability of species, geographic patterns of extinction risk may, however, deviate from geographic patterns of warming. Deutsch *et al.* [42] showed that tropical insects are more sensitive to warming than high-latitude ones, because they already live close to their limit of climatic tolerance, whereas the fitness of many high-latitude species may increase as a result of warming. Moreover, tropical assemblages contain more species with poor dispersal ability, high specialization and small geographic ranges [43], all characteristics that make them vulnerable to climate change. McCain [44] recently found support for Janzen's hypothesis [45] that the elevational range sizes of organisms are smaller on tropical than high-latitude mountains, making them more vulnerable to warming and upslope range shifts. Narrow range-sizes also mean that for many tropical mountain species there will be no overlap between present and projected future distributions, increasing the risk for dispersal failure and extinction [28]. In an assessment of global extinction risk in birds, Jetz *et al.* [46] projected many extinctions of tropical narrow-ranged species, although land conversion is presently a greater threat than climate change. As a result of narrow climatic tolerances, relatively small temperature changes may have large effects on species distributions in the tropics. In a record of forest turnover during 48,000 years in the Amazon basin, forest cover was found to be continuous, but a temperature change of only 1°C during the transition from glacial to Holocene resulted in a large turnover in species composition [47].

Future directions

Even if the assumptions in bioclimatic models are frequently violated, they remain a primary strategy to project the future of biodiversity. The methods are also developing rapidly, with prospects of accounting for variability among models and relaxing some of the critical assumptions [13,48]. Information on how species responded to climate change in the past serves as a 'reality check' of model projections. Further advances could be made by taking advantage of new knowledge about past climate change. For example, studies of species responses to Pleistocene climate oscillations have focused on the role of refugia, with recent interest in microrefugia (survival of taxa in small habitat pockets), to explain the speed of post-glacial recolonization [49]. The concept of microrefugia should also be relevant in projecting the effects of climate change [50]. Survival in small patches may be incorporated into models, and management and creation of microrefugia could be used as an active adaptation strategy.

An area in need of more research is the relationship between species tolerances and climate change. Some species may be more tolerant than indicated by present species-environment relationships, whereas others live close to their tolerance limits. Better information about the vulnerability of taxa in different regions is also desirable. Much of our present knowledge is derived from studies of Europe and North America, which may not be relevant for the rest of the world, such as the hotspots of species richness and endemism where most of Earth's biodiversity reside. Rapid progress in this field is urgently needed to avoid the prospect of a wave of climate change-induced extinction becoming inevitable.

Competing interests

The author declares that he has no competing interests.

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