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Research Focus

Range retractions and extinction in the face of climate warming

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Until recently, published evidence for the responses of species to climate change had revealed more examples of species expanding than retracting their distributions. However, recent papers on butterflies and frogs now show that population-level and species-level extinctions are occurring. The relative lack of previous information about range retractions and extinctions appears to stem, at least partly, from a failure to survey the distributions of species at sufficiently fine resolution to detect declines, and from a failure to attribute such declines to climate change. The new evidence suggests that climate-driven extinctions and range retractions are already widespread.

Declines can be difficult to detect

A consensus has emerged that many species are expanding their distributions towards the poles and to higher elevations in response to climate change, but corresponding evidence for range retractions at low-latitude and low-elevation boundaries has been comparatively weak [1–4]. It is not clear why we are not seeing more species retreating in these regions, given that widespread climate-driven extinction has been predicted [5].

One possibility is that retreats are already occurring, but we have either not yet detected them or have failed to attribute them to climate change. If distributions are mapped on a coarse-resolution grid, the extinction of many local populations must occur before a grid cell is deemed empty; thus, decline rates are likely to be underestimated [6]. Even if a decline is detected, attributing it to a climatic cause is difficult. When large numbers of species are expanding towards higher latitudes across degraded habitats, climate change is an obvious candidate cause, but when species are declining at their low-latitude boundary, it is hard to apportion extinction among a host of potential causes, including habitat loss and the presence of invasive species. Evidence from recent studies of butterflies [7] and frogs [8] suggests that we have so far failed to detect and attribute declines appropriately.

Butterfly range boundaries are retreating

In a recent study, Robert Wilson and colleagues [7] compared population-level censuses of butterflies in 2004 in the Sierra de Guadarrama mountain range in central Spain with the results of a comparable survey carried out in the same region between 1967 and 1973. Using a re-sampling strategy that controlled for recording effort, the authors estimated that the low-elevation boundaries of 16 montane butterfly species had moved uphill by an average of 212 m (Figure 1). Wilson *et al.* used data from nearby meteorological stations to show that the temperature had increased by 1.3 °C over the same 35-year period, equivalent to isotherms shifting uphill by ~225 m. As their distributions retracted toward the tops of the mountains, the butterflies lost, on average, a third of their distribution area. Because several other low-elevation butterfly species that use the same host plants in the same area survived over the same period, it is unlikely that the retreats recorded in the 16 butterfly species could have been caused by habitat degradation.

Other studies of butterfly species have produced similar results. In North America, population-level extinctions of Edith's checkerspot *Euphydryas editha* produced a 92-km shift northwards during a period when isotherms shifted north by ~105 km [1,9]. In Britain, relatively fine-resolution (1-km^2) mapping revealed extinction gradients since 1970 for three of four northern butterfly species: the northern brown argus *Aricia artaxerxes* and Scotch argus *Erebia aethiops* retreated northwards by an estimated 73 km and 80 km, respectively, and the mountain ringlet *Erebia epiphron* retreated uphill by 149 m [10]. Shifts of 88 km north and 98 m uphill would have been expected for

Figure 1. De Prunner's ringlet *Erebia triaria*, an endemic of mountain ranges in south-western Europe. Wilson *et al.* [7] estimated that the lower elevational limits of this butterfly have increased by ~290 m since ~1970 in the Sierra de Guadarrama in Spain, restricting the species to ever higher altitudes.

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these species, based on warming over the same period. However, if one hundred-fold coarser 10-km grid resolution data had been used, retreats since 1970 would have been missed or underestimated, yielding estimated range shifts of 5 km south, 0.7 km north and 63 m uphill for *A. artaxerxes*, *E. aethiops* and *E. epiphron* respectively (calculated from [11]).

In combination, these population-resolution studies [7,9,10] found that 17 out of the 21 butterfly species retracted as the climate deteriorated. Although the number of species considered is still small, the percentage found to be retreating (81%) is comparable to the percentage of species (80%) reported to be expanding at high-elevation and high-latitude range boundaries [3,4]. The boundaries of these butterfly species retreated at an average rate of ~29 km per decade in latitude (mean of *E. editha*, assuming extinctions over 30 years, and of three lowland northern British species) or 63 m per decade in elevation (montane butterflies in Spain and Britain). By contrast, southern butterflies in Britain expanded northwards by an average of 17 km per decade [12]. Expansions can also be underestimated (e.g. a species can expand within a large grid square without being detected), so it is not yet possible to conclude whether rates of expansion and retraction are the same.

Frog species are becoming extinct

Retreating distributions can be expected to lead to regional declines, to major range shifts in some species and, potentially, to global extinction for species with nowhere to go. In a recent paper, Alan Pounds *et al.* [8] analysed the extinction of harlequin frogs (species in the genus *Atelopus*) in the New World tropics. Approximately 67% of the known *Atelopus* species are missing, presumed extinct, in this area [8]. The timing of extinctions had suggested a possible linkage with climate, although frogs were often seen dying from a pathogenic fungal infection. Pounds *et al*. conclude that climate has been triggering fungal epidemics: approximately 80% of the *Atelopus* species that have disappeared were last seen following a hot year. Cold nights inhibit fungal growth at high elevations, whereas hot days constrain it at low elevations. In recent decades, night-time temperatures have increased and peak day-time temperatures have decreased (because of increased cloudiness), both of which favour the fungus. The optimal climate range for the fungus has moved up into the geographical ranges of susceptible frogs. As a result, over 90% of the harlequin frog species that used to be restricted to mid-elevations (1000–2400 m) are thought to have become extinct [8].

Conclusions

Linking extinction and climate change involves problems of detection and attribution. Unless detailed survey data are available, it is difficult to detect the initial stages of decline, such that recognition of the association between extinction and climate change will lag after the event. Lags can also occur between the climate changing and the species responding, analogous to delays following habitat fragmentations [13]. Attributing a cause is also difficult, requiring detailed study. It is the combined effect of climate change and an emerging infectious disease [14] that has proven so deadly for harlequin frogs. Should we attribute extinction either to climate change or to an emerging species? Alteration of the outcome of interactions among species is likely to be a common consequence of climate change, just as concurrent climate change and habitat loss will cause problems in other cases [15]. Hence, multi-factor causes of extinction are likely to be typical.

Climate appears to have been a contributory factor in the extinction of many of the missing ~67–74 harlequin frog species [8], representing ~1.2% of the ~5743 amphibian species that have been described worldwide (http://www.redlist.org/). Similarly, the study of butterflies in northern Britain concluded that approximately half of the recent population-level extinctions were likely to have been caused by climate change, and the remainder by habitat degradation [10]; climate is also the most plausible cause for montane butterflies retreating uphill in Spain [7]. For ectothermic animals with relatively short generation times, at least, climate change already appears to have joined habitat loss, invasive species and overexploitation as a major driving force of population- and species-level extinctions.

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