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Climate, climate change and range boundaries

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ABSTRACT

Aim A major issue in ecology, biogeography, conservation biology and invasion biology is the extent to which climate, and hence climate change, contributes to the positions of species' range boundaries. Thirty years of rapid climate warming provides an excellent opportunity to test the hypothesis that climate acts as a major constraint on range boundaries, treating anthropogenic climate change as a large-scale experiment.

Location UK and global data, and literature.

Methods This article analyses the frequencies with which species have responded to climate change by shifting their range boundaries. It does not consider abundance or other changes.

Results For the majority of species, boundaries shifted in a direction that is concordant with being a response to climate change; 84% of all species have expanded in a polewards direction as the climate has warmed (for the best data available), which represents an excess of 68% of species after taking account of the fact that some species may shift in this direction for non-climatic reasons. Other data sets also show an excess of animal range boundaries expanding in the expected direction.

Main conclusions Climate is likely to contribute to the majority of terrestrial and freshwater range boundaries. This generalization excludes species that are endemic to specific islands, lakes, rivers and geological outcrops, although these local endemics are not immune from the effects of climate change. The observed shifts associated with recent climate change are likely to have been brought about through both direct and indirect (changes to species' interactions) effects of climate; indirect effects are discussed in relation to laboratory experiments and invasive species. Recent observations of range boundary shifts are consistent with the hypothesis that climate contributes to, but is not the sole determinant of, the position of the range boundaries of the majority of terrestrial animal species.

Keywords

Adaptation, biological invasions, climate warming, distributions, extinction, range margins, thermal ecology.

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INTRODUCTION

Understanding the factors determining the distributions and abundances of species has been a major focus throughout the history of ecology (e.g. Andrewartha & Birch, 1954; MacArthur, 1972), an interest that remains undiminished as we face practical issues that relate to both shrinking (extinction) and expanding (invasives) ranges. If climate is, *inter alia*, one of the important determinants of species' range boundaries, then we can expect anthropogenic climate change to generate both range expansions and range contractions, potentially threatening large numbers of species with extinction (e.g. Thomas *et al.*, 2004; McClean *et al.*, 2005; Malcolm *et al.*, 2006).

Research on the factors that determine range boundaries has often resorted to the interpretation of unintended, large-scale 'experiments'. For example, the success of introduced species provides numerous examples of how geographical barriers to dispersal can limit species' ranges and also of how biological interactions determine large-scale distribution patterns (native species that are reduced or eliminated by invasives). Until

recent decades, the impact of climate on species' contemporary distributions has been much harder to assess because the climate had been thought of as moderately stable since 1800, the period for which most distributional data are available. Palaeoecological studies have shown that changing climates affect species' distributions (e.g. Pitelka *et al.*, 1997; Hewitt, 1999), as have studies of biological responses to the Little Ice Age (Maunder Minimum) between 1645 and 1715 (Grove, 1988). But fossil data and pre-1800 documented records are inevitably sparse and rarely of sufficient resolution to identify the precise locations of range boundaries. Given the nature of the data, most such data document the past distribution responses of relatively common and widespread species. Anthropogenic climate change provides the ideal opportunity to test the hypothesis that climate is an important determinants of species' range boundaries more generally.

The death of an individual near the edge of a species' range might be caused directly by the climate; by extreme cold, heat or drought. However, most deaths in most species appear to be caused by natural enemies or through a failure to compete successfully for resources, rather than by climate *per se* (e.g. Sih *et al.*, 1985; Cornell & Hawkins, 1995). Similarly, birth rates are affected by other species as well as by the physical environment. The abundance and diversity of natural enemies, of competitors, of mutualists and of other species that constitute the resources used by an organism may nevertheless be affected by climate. In addition, the ability of an individual to avoid or resist natural enemies or compete with other species can be affected by climate. Therefore, climate may affect range boundaries indirectly through changes to species interactions and through climate-driven changes to the physical structure of habitats, as well as having direct impacts on birth and death rates (Fig. 1).

This article uses recent climate change to assess the frequency with which climate contributes to the position of range boundaries, analysing the frequencies with which species have responded to climate change by shifting their distributions in the 'expected' direction. In addition, it discusses some alternative means of assessing the impact of climate on the positions of range boundaries.

TERRESTRIAL RANGE LIMITS

Most species are highly localized, with a small minority being geographically widespread (Gaston, 1996, 2003). Thus, most species have at least some range boundaries that are not coastlines; continental centres of endemism contain many such species. Why do all of these species not spread from their existing boundaries into adjacent land? Some kind of limit (climatic or otherwise) must logically exist or have existed until quite recently, *at their existing boundaries* that prevents them from spreading.

The fact that at least part of the existing/recent range boundary of most terrestrial species is/was limited by climate is compatible with the idea that it may be possible to find other, disjunct parts of the world that are suitable for these species,
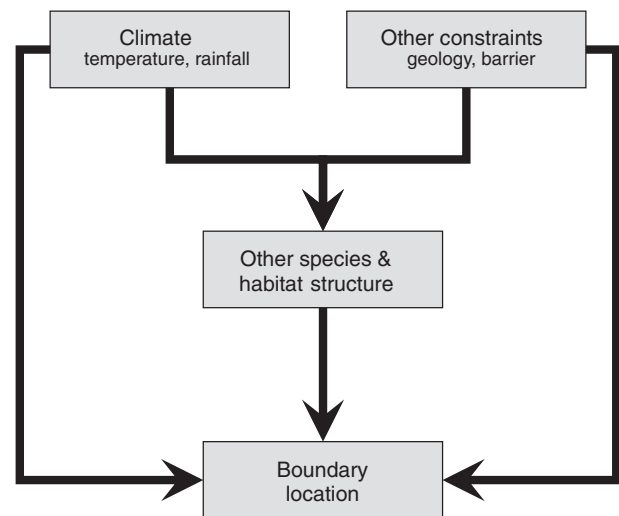

Figure 1 Schematic diagram of the effects of climate on the location of the range boundary of a species. Climate may affect the boundary directly (e.g. through physiological and life history responses; left-hand arrow), as may other constraints (right-hand arrow). Climate and other constraints also combine to determine which other species are present at a given location, and their abundances, as well as to determine the structure (e.g. vegetation height and complexity) of habitat; these indirect species/habitat effects act together to affect the location of the range boundary. 'Other species' effects include positive (mutualists, resources) and negative (competitors, enemies) impacts. Note that human activities are combined with those of other species.

but which are too distant to have been colonized naturally (e.g. Williamson, 1996; Peterson, 2003; Svenning & Skov, 2007; Duncan *et al.*, 2009). A combination of population/species history and inadequate time to colonize represent important constraints on species' distributions at a global scale. This article concentrates, instead, on evaluating whether climate plays a role in affecting the edges of existing ranges (i.e. within relatively easy colonization range).

CLIMATE-DISTRIBUTION CORRELATIONS

Aside from the palaeo-record, which is beyond the scope of this article, deductions that climate is an important determinant of species' current distribution margins have mainly been based on indirect information. The most frequent approach is to match (correlate) the existing distribution of species to the spatial distribution of climatic variation; variously termed distribution, climate envelope or niche modelling (Elith & Leathwick, 2009). Correlations between climate variables and distributions are widely observed.

One interesting approach is to compare the match between climate variables and the distributions of real species with the match of climate variables with the distributions of fictional 'null' species that have the same spatial attributes (range size and level of distributional aggregation) as the real species. Taking this approach, Beale *et al.* (2008) conclude that 68% of

bird species have distributions that are no more closely associated with spatial variation in the climate than expected at random; alternatively, 32% *are* statistically associated with spatial variation in the climate. However, 32% may be an underestimate (Araújo *et al.*, 2009) for several reasons, including: (1) if the spatial characteristics (range size and aggregation) of real species are genuinely generated by spatial patterns of climatic variation, then 'null' species are not truly 'null' but can be thought of as potential climatic niches that species could have, were there to be an infinite number of species on Earth; and (2) it is not clear how the null distribution analysis performs when some but not all range boundaries of a species are set by climate and when many of the species are not restricted (endemic) to the region analysed (Peterson *et al.*, 2009). This is a useful approach, but it is ultimately difficult or impossible to deduce causation from correlation.

A potentially stronger approach is to evaluate whether the distributions of species in their native ranges can be used to predict the ranges of the same species in parts of the world to which they have been introduced (and *vice versa*). This approach has had mixed success, identifying that both climate and other factors (species' traits, human activities, propagule pressure, time since arrival) contribute to species' distributions within their introduced ranges (e.g. Beerling *et al.*, 1995; Peterson, 2003; Roura-Pascual *et al.*, 2004; Thuiller *et al.*, 2006; Richardson & Thuiller, 2007; Duncan *et al.*, 2009). These studies provide strong support to the view that climate contributes to the success and distribution of a species, following introduction, but (1) time since arrival is a predictor of introduced range size (Wilson *et al.*, 2007; Williamson *et al.*, 2009), which implies that the range boundaries of many species have not yet have come to 'equilibrium' in the introduced range, and (2) introduced species interact with new continental biotas after translocation, such that their realized climatic niches may differ between their native and introduced ranges (Broennimann *et al.*, 2007). For both of these reasons, this approach is likely to provide a minimum estimate of the role of climate in determining stable or native range boundaries.

Another approach is to evaluate whether climate envelopes can be used to predict changes to the distributions of species that have already been observed (e.g. Walther *et al.*, 2005; Berger *et al.*, 2007). Araújo *et al.* (2005) analysed bird distribution changes in Britain and found rather inconsistent matches between predicted and observed changes, depending on the species and modelling approach used. Green *et al.* (2008) concluded that bird population changes did tend to track predicted changes in climatic suitability at a European scale, although this study did not specifically examine changes to the locations of range boundaries. Because realized *rates* of response (which determine the statistical match between projected and observed changes) depend not only on climate but also on the traits of the species and the landscapes through which the distributions are shifting (e.g. Warren *et al.*, 2001; Willis *et al.*, 2009; Wilson *et al.*, 2009), it is not clear whether these results should be regarded as providing strong or weak support for climate as an important determinant of range boundaries.

OBSERVED SHIFTS IN RANGE BOUNDARIES

Recent climate change represents a large-scale experiment to test directly whether species' boundaries are shifting in the 'expected' direction. Here, I examine the frequency with which the positions of range boundaries have moved along thermal gradients. The reason for concentrating on thermal gradients is because it is possible to make clear predictions for the direction of range shifts, whereas shifts along moisture gradients are less easy to interpret. I only consider studies in which all species within a specified group/region are considered (given specified data quality inclusion criteria). The reason for concentrating on multi-species studies is because single-species studies are prone to publication bias and could therefore bias estimates of the proportion of species showing distributional responses to climate change.

Parmesan & Yohe (2003) reviewed then-available multi-species studies, the majority from the temperate zone. Of studies classified by these authors as regional/continental (as opposed to local, which I do not consider), and where multiple (≥10 spp. in each study) terrestrial species were examined, 106 range boundaries were classified as shifting in the direction expected on the basis of climate warming (shifting northwards in the northern hemisphere), 84 as stable, and 36 as shifting in the opposite direction. Significantly, more range shifts were in the direction expected from climate change than expected by chance (Parmesan & Yohe, 2003). These numbers provide an estimate of 47% of range boundaries shifting in the direction expected. This may exaggerate the percentage responding because some of the 106 boundaries shifting polewards might have done so for other reasons (e.g. land use changes, changes in persecution), just as the 36 boundaries that moved towards the equator are likely to have been responding to other pressures. Simplistically, we might conclude that an *excess* of 31% of boundaries of these 226 species' boundaries shifted towards higher latitudes; i.e. 100*(106−36)/226. Conversely, most of the studies included by Parmesan & Yohe (2003) were relatively early within the recent phase of anthropogenic warming, so they might under-estimate the climate sensitivity of range boundaries; the 84 'stable' boundaries may hide small changes in one direction or another. If we ignore the 'stable' species, 75% of species shifted in the direction expected, an excess of 49%.

The other compilation of regional range shifts was provided by Hickling *et al.* (2006), who considered data for the northern (high latitude, or poleward) range boundaries of many different taxonomic groups in Britain (millipedes; woodlice; harvestmen; spiders; aquatic bugs; butterflies; carabid, long-horn & soldier beetles; dragonflies & damselflies; grasshopper relatives; lacewings; fish; herptiles; birds; mammals). These are arguably the most reliable data in the world available to assess such changes. Of 329 species meeting data quality criteria, 275 (84%) boundaries expanded northwards, two remain exactly
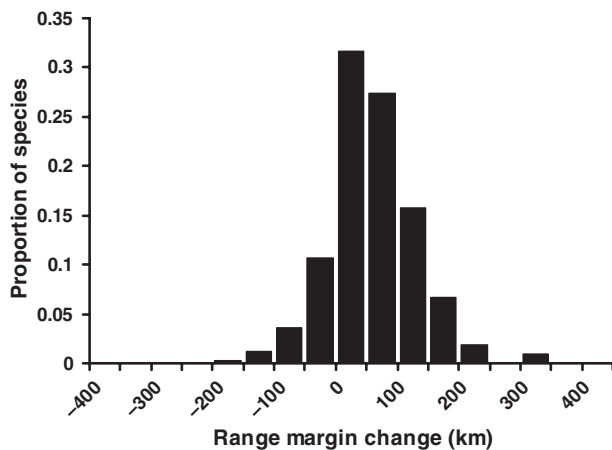
Figure 2 Shifts at the northern range boundaries of southerly distributed animal species in Britain. Northwards shifts are positive values, and southwards shifts are negative, with distances moved over approximately 25 years. Data are for 329 species from the following taxa: millipedes; woodlice; harvestmen; spiders; aquatic bugs; butterflies; carabid, longhorn & soldier beetles; dragonflies & damselflies; grasshopper relatives; lacewings; fish; herptiles; birds; mammals. Data and further details from Hickling *et al.* (2006).

the same and 52 retreated southwards (Fig. 2). Again, some northwards shifts are likely to be related to non-climatic factors, so the excess northwards shift is approximately 68%; i.e. 100*(275−52)/329. The data in Hickling *et al.* (2006) are only up to 2000, so these estimates may already be exceeded.

Evaluating whether low latitude range boundaries are retreating with equal frequency is harder to assess, mainly because the data are inadequate (Thomas *et al.*, 2006). Parmesan & Yohe (2003) found that expansions at leading edges was potentially more frequent than contractions at trailing edges. However, expansions are typified by increases in abundance and expansion as a 'front', which is reasonably easy to detect, whereas retreats more usually proceed by increasing fragmentation of populations (Wilson *et al.*, 2004; Hampe & Petit, 2005), making it harder to identify when the last local population in a region has disappeared, and whether climate change is a possible cause. Thomas *et al.* (2006) estimated that 17 out of 21 (81%, an excess of 62%) butterfly species for which there had been detailed surveys of their trailing edges had shown elevational or latitudinal retreats – comparable to the expansion figures for leading edges.

It is possible that the species that have been assessed could represent a biased sample, even in multi-species studies. Species for which there are sufficient records for comparison across time may disproportionately be relatively common species (i.e. they meet 'data quality' criteria for inclusion more frequently than do rarer species because they have many records in two or more time periods). Habitat generalists that are relatively common and widespread within their distributions will normally (1) meet data quality criteria, and (2) not find barriers to dispersal, and hence they will have the greatest

capacity to spread into new regions (Warren *et al.*, 2001). In contrast, the most rapidly retreating species are likely to be those that experience a combination of deteriorating climate and other pressures, and declining species that are rarely recorded may tend to be excluded on the basis of low data quality. Therefore, it is conceivable that data selection results in an over-estimate of the fraction of range boundaries showing expansion at potentially leading range edges and an under-estimate of retreat rates at trailing edges. However, it is also possible that many additional (rarer) species are responding at more local scales, such as expanding into new habitats (Davies *et al.*, 2006), which have not yet been detected in geographical-scale analyses.

Another complication is whether land use changes or other environmental drivers might themselves show latitudinal gradients of intensity and hence mimic the effects of climate change. For most of the British taxa considered by Hickling *et al.* (2006), this seems unlikely, given that most of the southern species are spreading northwards across human-dominated landscapes; land use appears to be responsible for limiting the level of response, in this case, rather than accelerating it.

Comparable analyses of the distribution boundaries of individual plant species require further development; Harsch *et al.* (2009) report advances of the tree line since 1900 at 52% of sites, whereas retreat was observed at only 1% of sites, an excess of 51%.

The direction of response is relevant simply to ask whether climate *contributes* to the location of range boundaries. On the above evidence, I conclude that over half, and perhaps around two-thirds, of observed animal range boundaries have already shown a response to 1970–2000 anthropogenic warming.

ARE TROPICAL SPECIES SIMILARLY LIMITED?

The above studies were from the temperate zone, and there is a dearth of studies of geographical-scale range boundary shifts for tropical species. More local studies provide evidence of upwards shifts on tropical mountains, in Costa Rica, Madagascar and Borneo (Pounds *et al.*, 1999; Raxworthy *et al.*, 2008; Chen *et al.*, 2009), but they are insufficient to draw strong conclusions about the frequencies with which species have shown geographical-scale boundary shifts. Combining data for Costa Rican birds (Pounds *et al.*, 1999) and Madagascar herptiles (Raxworthy *et al.*, 2008), 91 (75%) upper boundaries moved upwards, 18 moved downwards and 12 remained stable, an excess of 60% shifting upwards. For the lower boundaries of montane species, however, no such pattern was apparent; 48 (38%) lower boundaries shifted upwards, 40 downwards and 38 remained stable, an excess of only 8% moving upwards. However, both studies failed to detect some high elevation species in the more recent surveys (and hence they were excluded from comparisons of boundaries between time periods), and if these species are extinct, then the true proportion retreating upwards is higher than the above figures suggest. I-C Chen *et al.* (unpublished) found quite comparable

upwards shifts of the lower and upper boundaries when considering all geometrid moth species on Mt. Kinabalu, in Borneo, although this overall result hid differences at different elevations on the mountain (greater expansion upwards than retreat at some elevations, but the opposite elsewhere).

Over large parts of the tropics, moisture availability is probably a more important determinant of range boundaries than temperature. The tree Aloe, *Aloe dichotoma*, appears to be showing population decreases in the driest parts of its geographical range, an observation that is consistent with climate change (Foden *et al.*, 2007). However, multi-species geographical studies of distribution responses to drying and wetting trends are not yet available. Part of the difficulty is that predictions are far from straight-forward; would species be expected to expand into drier areas because of increased water use efficiency (atmospheric CO_2 enrichment enables plants to keep stomata closed more of the time), or retract because of increased desiccation arising from higher temperatures or reduced precipitation?

Whilst further data would be desirable, these preliminary analyses suggest that the responses of the range boundaries of tropical montane species are not obviously different from those observed at larger geographical scales in the temperate zone; the majority of upper boundaries have already shifted upwards in response to climate warming. Responses of lower boundaries on tropical mountains, and especially distributional responses to changing moisture gradients, are poorly documented. The importance of climate to species range boundaries' in the tropics receives some further support from the observation that centres of endemism tend to be located in climatically unusual regions and in regions with steep climatic gradients (Ohlemüller *et al.*, 2008).

THE CLIMATE–SPECIES INTERACTION

The main indirect means by which climate affects the locations of species' range boundaries is likely to be through its impact on the interactions between species (Fig. 1) (MacArthur, 1972). Evidence that 'other species' are major determinants of distribution boundaries comes from studies of invasive species (e.g. van Riper *et al.*, 1986; Channell & Lomolino, 2000a,b; Short & Turner, 2000) and from competition/ predation experiments (Davis *et al.*, 1998a,b; Pople *et al.*, 2000). From Gause onwards, researchers have commonly observed that it is difficult to maintain two species in culture together in a single controlled environment but that the outcome (which species 'wins') of the interaction can be changed by altering the environment. If this holds in general with respect to climatic environments, then climate is expected to be a critical determinant of the locations of species transitions and so indirectly affects range boundaries.

Two microcosm articles by Andrew Davis and colleagues (Davis *et al.*, 1998a,b) are particularly relevant. Davis *et al.* kept local *Drosophila* populations (in different incubators) at different temperatures, and linked the populations by connecting tubes, forming a thermal cline spanning 15°C

(10–25°C and 15–30°C). Experiments considered three *Drosophila* species on their own, and in two- and three-species mixtures, with and without a shared parasitoid (natural enemy), and with and without dispersal (by opening and blocking the connecting tubes). The *Drosophila* species and the parasitoid affected the thermal ranges and abundances of each other in these experiments, showing very clearly that distributions arise from a combination of biotic and physical (temperature) factors in these simplified environments. A major message that has been taken up in the literature citing this work (over 300 and 100 citations of Davis *et al.*, 1998a,b, respectively; Web of Science, December 2009) is that responses to climate change will be unpredictable because of complex species interactions.

The conclusion that multi-species boundaries are unpredictable seems premature. In Davis *et al.*'s results, the 'winner' of pairwise competition experiments between *Drosophila* species was entirely predictable at each temperature (but the winner was different at different temperatures). The 'optimum' temperature of each species was also largely unaffected by which other species were in the experiment (they always lined up with *D. subobscura* being most abundant in the coolest cages, *D. simulans* in intermediate cages and *D. melanogaster* in the hottest). And, the *standard errors* of the mean abundances (in chambers of a given temperature) in multi-species clines were just as small as in single-species replicates; densities in multi-species experiments were just as predictable as in single-species chambers. In other words, the outcomes of species interactions were highly predictable throughout the sequence of experiments, for a given temperature, and given a particular set of species, etc. These effects might be indirect (Fig. 1), but temperature strongly determined the observed patterns. When the experimenters applied climate change to the thermal clines (cline of 15–30°C vs. 10–25°C), the differences in abundance were largely predictable on the basis of the previous patterns. My own interpretation is that thermally driven changes to multi-species interactions will in most cases not produce major surprises, although this will happen sometimes; most of the surprises will arise when entirely different species or functional groups, usually from other continents (invasive species), join the set of interacting species.

Invasive species often show variation in their propensity to impact negatively on native species along environmental gradients; threatened species commonly survive (last) at the margins of their former distributions (e.g. Clout & Craig, 1995; Channell & Lomolino, 2000a,b; Short & Turner, 2000). For all species that eventually co-exist with an invader in a subset of their previous distributions, the locations of new boundaries are likely to be set by factors that limit the occurrence or virulence of the invader or increase the capacity of the native species to resist it; such as climate, geology or dispersal failure (e.g. failure to reach offshore islands). The pervasive impacts of some non-native species on others do not in any way disprove the hypothesis that climate contributes to the locations of existing range boundaries; it reminds us, rather, that climatic limits must be seen in the context of multi-species interactions.

If climate change drives malaria-resistant introduced birds, mosquitoes and bird malaria to higher elevations in the Hawaiian Islands, we might expect them to make further inroads into the susceptible (now largely montane) native bird fauna (van Riper *et al.*, 1986; Freed *et al.*, 2005).

In conclusion, laboratory experiments and observations of invasive species commonly show that the outcome of interactions between species depends on the environment. In as much as that 'climate' is part of the environment, this implies that climate does contribute to range boundaries. When the climate shifts, so do those range boundaries that are set by the outcomes of interspecific interactions.

NON-CLIMATIC LIMITS

Some species have range boundaries set by factors that are completely unrelated to climate. A land species that is endemic to and occurs throughout a particular oceanic island or an aquatic species that occurs throughout the waters of a single lake are obvious examples. There are also many other island-like environments, particularly geologies (e.g. Serpentine outcrops), which may constrain range boundaries irrespective of the climate (this does not include cold mountain tops where the island-like nature of the environment is determined largely by climate). Narrowly distributed endemics associated with these localized environments may exhibit realized climatic niches that are a small fraction of their potential climatic niche, such that their distributions are not immediately affected by climate change (see below). Even so, quite a high proportion of local endemics still show range limits within these areas, such as species that are restricted by elevation on an island, by depth in a lake, or by aspect or soil moisture on an unusual geological outcrop (e.g. van Riper *et al.*, 1986; Daniel & Fox, 1999; Mackay *et al.*, 2006). These species are expected to shift their local distribution boundaries higher, deeper, or to a shadier aspect, with climate warming.

As an aside, we should not presume that local endemics with no current climatic limits at their range boundaries will be safe from future climate change. First, the narrow distributions of local endemics may, in some species, have led secondarily to evolutionary specialization in physiological attributes over that last 10,000 years of relatively stable climate and hence may have caused them to be susceptible to climate change. It is possible to argue the opposite because they have survived climate change over hundreds of thousands of years, but a demonstrated capacity to survive much colder 'glacial' temperatures is not necessarily an indication that they will be able to survive novel high temperatures. Second, these species may not respond initially to climate change, as they remain limited by other factors. But with further warming, the unusual environment (outcrop) may quickly pass outside the potential climatic niche of the species, causing rapid population collapse with little forewarning. Thirdly, these species are now likely to be living in ecosystems in which the identities and relative abundances of other species have already changed as a result of climate change (Menéndez *et al.*, 2006; González-Megías *et al.*,

2008). When the climate changes, almost all species are likely to be affected indirectly through the responses of species that are affected directly (Fig. 1). Such species are potentially susceptible to changes in ecosystem productivity and species interactions wrought by climate change (O'Reilly *et al.*, 2003).

CONCLUSION

Climate change has now provided a preliminary answer to the old question of whether climate is an important determinant of the recent range boundaries of species. Over half of species' boundaries that have been examined have already responded to the quite modest level of global warming already experienced between 1970 and 2000. It seems likely that climate *contributes to* (but is not the sole determinant of) the locations of distribution boundaries for the majority of terrestrial species in continental regions; even higher fractions of range boundaries are likely to respond to further warming. The contribution of climate to range boundaries is in many cases likely to be indirect, through alterations to species' interactions (Fig. 1). Because responses to climate change are already so common, virtually every species is already experiencing changes to these interspecific interactions, and hence feeling at least the indirect impacts of climate change.

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