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Proc. R. Soc. B published online 17 October 2012
doi: 10.1098/rspb.2012.1890

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Review

How does climate change cause extinction?

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Anthropogenic climate change is predicted to be a major cause of species extinctions in the next 100 years. But what will actually cause these extinctions? For example, will it be limited physiological tolerance to high temperatures, changing biotic interactions or other factors? Here, we systematically review the proximate causes of climate-change related extinctions and their empirical support. We find 136 case studies of climatic impacts that are potentially relevant to this topic. However, only seven identified proximate causes of demonstrated local extinctions due to anthropogenic climate change. Among these seven studies, the proximate causes vary widely. Surprisingly, none show a straightforward relationship between local extinction and limited tolerances to high temperature. Instead, many studies implicate species interactions as an important proximate cause, especially decreases in food availability. We find very similar patterns in studies showing decreases in abundance associated with climate change, and in those studies showing impacts of climatic oscillations. Collectively, these results highlight our disturbingly limited knowledge of this crucial issue but also support the idea that changing species interactions are an important cause of documented population declines and extinctions related to climate change. Finally, we briefly outline general research strategies for identifying these proximate causes in future studies.

Keywords: climate change; extinction; physiological tolerances; species interactions

1. INTRODUCTION

Anthropogenic climate change is recognized as a major threat to global biodiversity, one that may lead to the extinction of thousands of species over the next 100 years [1–7]. Climate change is an especially pernicious threat, as it may be difficult to protect species from its effects, even within reserves [8,9]. Furthermore, climate change may have important interactions with other anthropogenic impacts (e.g. habitat loss [2,6]). Given this, understanding the responses of species to modern climate change is one of the most pressing issues facing biologists today.

But what do we actually know about how climate change causes extinction? It might seem that limited physiological tolerances to high temperatures should be the major factor that causes climate change to threaten the persistence of populations and species, and many studies have justifiably focused on these tolerances [10–13]. However, there may be many other proximate causes of extinction, even when anthropogenic climate change is the ultimate cause. These proximate factors include negative impacts of heat-avoidance behaviour [14], the climate-related loss of host and pollinator species [15,16] and positive impacts of climate change on pathogens and competitors [17,18], among others. The relative importance of these factors is unclear and has not, to our knowledge, previously been reviewed, despite increasing interest in mechanisms underlying the impacts of climate change [19].

Identifying these proximate causes may be critical for many reasons. For example, different proximate factors may call for different conservation strategies to ameliorate their effects [20]. These different proximate factors may also influence the accuracy with which the impacts of climate change are predicted and may drive populations to extinction at different rates.

In this paper, we address three topics related to how anthropogenic climate change causes extinction. First, we briefly review and categorize the many proposed factors that potentially lead to extinction from climate change. Second, we argue that there is already abundant evidence for current local extinctions as a result of climate change, based on the widespread pattern of range contractions at the warm edges of species' ranges (low latitude and low elevation). Third, and most importantly, we perform to the best of our knowledge, the first large-scale review of empirical studies that have addressed the proximate causes of local extinctions related to climate change. This review reveals some unexpected results. We find that despite intensive research on the impacts of climate change, only a handful of studies have demonstrated a proximate cause of local extinctions. Further, among those studies that have identified a proximate cause, very few implicate limited physiological tolerance to high temperatures as the main, direct cause. Instead,

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2012.1890 or via http://rspb.royalsocietypublishing.org.

Received 13 August 2012
Accepted 24 September 2012

a diverse set of factors are supported, with species interactions being particularly important. Finally, we outline some of the research approaches that can be used to examine the proximate factors causing extinction from climate change.

2. PROXIMATE FACTORS CAUSING EXTINCTION FROM CLIMATE CHANGE

We briefly review and categorize the diverse proximate factors that may cause extinctions due to climate change. We organize these factors by distinguishing between abiotic and biotic factors (following the literature on species range limits [21]). However, all factors are ultimately related to abiotic climate change.

We make several caveats about this classification. First, we emphasize broad categories of factors, so some specific factors may not be included. Second, some factors are presently hypothetical and have not yet been demonstrated as causes of extinction. Third, we recognize that these factors are not mutually exclusive and may act synergistically to drive extinction. They may also interact with other, non-climatic factors (e.g. habitat modification [2,6]) and many different ecological and demographic factors may come into play as populations approach extinction [22]. Finally, we do not address factors that impede climate-induced dispersal.

(a) *Abiotic factors*

(i) *Temperature (physiological tolerances)*

Many effects of anthropogenic climate change follow from an increase in temperature. The most obvious proximate factor causing extinction is temperatures that exceed the physiological tolerance of the species [10,12]. This factor may be most important in sessile organisms and those with limited thermoregulatory ability, and in regions and time scales in which temperature increase is greatest.

The impacts of temperature may also be more indirect, but still related to physiological tolerances. For example, in spiny lizards (*Sceloporus*), local extinctions seem to occur because higher temperatures restrict surface activity during the spring breeding season to a daily time window that is overly short [23]. Similarly, increased air temperatures may both decrease activity time and increase energy maintenance costs, leading organisms to die from starvation rather than from overheating [14]. In aquatic organisms, increased water temperatures may lead to increased metabolic demand for oxygen while reducing the oxygen content of the water [24]. Variability in temperature may also be an important proximate cause of extinction [25], including both extreme events and large differences over the course of a year. In temperate and polar latitudes, a mismatch between photoperiod cues and temperature may be important, with fixed photoperiod responses leading to activity patterns that are inappropriate for the changed climate [26]. Here, both low and high temperatures could increase mortality rates and lead to population extinction.

(ii) *Precipitation (physiological tolerances)*

Anthropogenic changes are also modifying precipitation patterns [27], and these changes may drive extinction in a variety of ways. For example, decreasing precipitation may lead directly to water stress, death and local extinction for terrestrial species [28], and loss of habitat for freshwater species or life stages [29,30]. There may also be synergistic effects between heat and drought stress (e.g. in trees [31]). Changing precipitation may be more important to some species than changing temperature, sometimes leading to range shifts in the direction opposite to those predicted by rising temperatures [32].

(iii) *Other abiotic factors*

Other abiotic, non-climatic factors may drive extinctions that are ultimately caused by climate change. For example, climate change can increase fire frequency, and these fires may be proximate causes of extinction (e.g. in South African plants [33]). Similarly, increases in temperature lead to melting icecaps and rising sea levels [27], which may eliminate coastal habitats and modify the salinity of freshwater habitats [34].

(b) *Biotic factors*

The biotic factors that are the proximate causes of extinction from climate change can be placed in three general categories.

(i) *Negative impacts on beneficial species*

Climate change may cause local extinction of a given species by causing declines in a species upon which it depends. These may include prey for predators [35], hosts for parasites and specialized herbivores [16], species that create necessary microhabitats [36] and species that are essential for reproduction (e.g. pollinators [15]).

(ii) *Positive impacts on harmful species*

Alternately, climate change may cause extinction through positive effects on species that have negative interactions with a focal species, including competitors [37,38], predators [39,40] and pathogens [41–43]. Warming temperatures can also benefit introduced species, exacerbating their negative effects on native flora and fauna [44].

(iii) *Temporal mismatch between interacting species*

Climate change may also create incongruence between the activity times of interacting species [45]. These phenological mismatches may occur when interacting species respond to different environmental cues (e.g. temperature versus photoperiod for winter emergence) that are not congruently influenced by climate change [46]. We consider this category to be distinct from the other two because the differences in activity times are not necessarily negative or positive impacts on the species that are interacting with the focal species.

3. ARE THERE CURRENT EXTINCTIONS DUE TO CLIMATE CHANGE?

Our goal is to understand which proximate factors cause extinctions due to climate change. However, we first need to establish that such extinctions are presently occurring. Few global species extinctions are thought to have been caused by climate change. For example, only 20 of 864 species extinctions are considered by the International Union for Conservation of Nature (IUCN) [47] to potentially be the result of climate change, either wholly or in part (using the same search criteria as a recent review [9]), and the evidence linking them to

Table 1. Studies documenting the proximate causes of local extinction due to anthropogenic climatic change.

species	location	hypothesized proximate cause of local extinction	reference
American pika (*Ochotona princeps*)	Great Basin region, USA	limited tolerance to temperature extremes (both high and low)	[25,63]
planarian (*Crenobia alpina*)	Wales, UK	loss of prey as result of increasing stream temperatures	[35]
desert bighorn sheep (*Ovis canadensis*)	California, USA	decrease in precipitation leading to altered plant community (food)	[64]
checkerspot butterfly (*Euphydryas editha bayensis*)	San Francisco Bay area, CA, USA	increase in variability of precipitation corresponding with reduction of temporal overlap between larvae and host plants	[66]
fish (*Gobiodon* sp. A)	New Britain, Papua New Guinea	destruction of obligate coral habitat due to coral bleaching caused by increasing water temperatures	[36]
48 lizard species (genus *Sceloporus*)	Mexico	increased maximum air temperature approaches physiological limit, seemingly causing decreased surface activity during the reproductive season	[23]
Adrar Mountain fish species	Mauritania	loss of water bodies due to drought	[30]

climate change is typically very tenuous (see the electronic supplementary material, table S1). However, there is abundant evidence for local extinctions from contractions at the warm edges of species' ranges. A pattern of range shifts (generally polewards and upwards) has been documented in hundreds of species of plants and animals [48,49], and is one of the strongest signals of biotic change from global warming. These shifts result from two processes: cold-edge expansion and warm-edge contraction (see the electronic supplementary material, figure S1). Much has been written about cold-edge expansions [21,50], and these may be more common than warm-edge contractions [51]. Nevertheless, many warm-edge contractions have been documented [52–58], including large-scale review studies spanning hundreds of species [48,59]. These warm-edge populations are a logical place to look for the causes of climate-related extinctions, especially because they may already be at the limits of their climatic tolerances [60]. Importantly, this pattern of warm-edge contraction provides evidence that many local extinctions have already occurred as a result of climate change.

We generally assume that the proximate factors causing local extinction from climate change are associated with the death of individuals. However, others factors may be involved as well. These include emigration of individuals into adjacent localities, declines in recruitment, or a combination of these and other factors. The question of whether climate-related local extinctions occur through death, dispersal or other processes has received little attention (but see [61,62]), and represents another important but poorly explored area in climate-change research.

4. WHAT CAUSES EXTINCTION DUE TO CLIMATE CHANGE? CURRENT EVIDENCE

Given that there are many different potential causes of extinction as a result of climate change, and given that many populations have already gone extinct (as evidenced by warm-edge range contractions), what proximate causes of climate-related extinction have actually been documented? We conducted a systematic review of the literature to address this question.

(a) *Causes of extinction: methods*

We conducted three searches in the ISI Web of Science database, using the following keywords: (i) ((‘locally extinct’ OR ‘local extinction’ OR ‘extinc*’) AND (caus*) AND (‘climate change’ OR ‘global warming’)); (ii) ((‘locally extinct’ OR ‘local extinction’) AND (‘climate change’ OR ‘global warming’)); and (iii) ((‘extinc*’ OR ‘extirpat*’) AND (‘climate change’ OR ‘global warming’ OR ‘changing climate’ OR ‘global change’)). The first two were conducted on 7 December 2011 and the third on 4 February 2012. Each search identified a partially overlapping set of studies (687 unique studies overall). We then reduced this to 136 studies which suggested that climate change is associated with local extinctions or declines (see the electronic supplementary material, appendix S1).

Among these 136 studies, we then identified those that reported an association between local extinction and climatic variables and that also identified a specific proximate cause for these extinctions (see the electronic supplementary material, appendix S1). The evidence linking these proximate causes to anthropogenic climate change varied considerably, but included studies integrating experimental and correlative results [23,63], and those that also accounted for factors unrelated to climate change [64]. Although we did not perform a separate, comprehensive search for all studies of climate-related declines, we also include studies of population declines that were connected to potential local extinctions as a second category of studies. Studies of declines should also be informative, given that the factors causing population declines may ultimately lead to extinctions [65]. All studies reported declines in abundance but some also considered declines in other parameters (e.g. fecundity). We also included studies of impacts from natural oscillations (such as the El Niño-Southern Oscillation, ENSO) as a third category of results.

(b) *Causes of extinction: results*

(i) *Proximate causes of local extinctions*

Of 136 studies focusing on local extinctions associated with climate change (see the electronic supplementary material, appendix S1), only seven identified the proximate causes of these extinctions (table 1 and figure 1*a*). Surprisingly, none of the seven studies shows a straightforward relationship between local extinction and limited tolerances to high temperature. For example, for the two studies that relate extinctions most directly to changing temperatures, the proximate factor is related either to how temperature

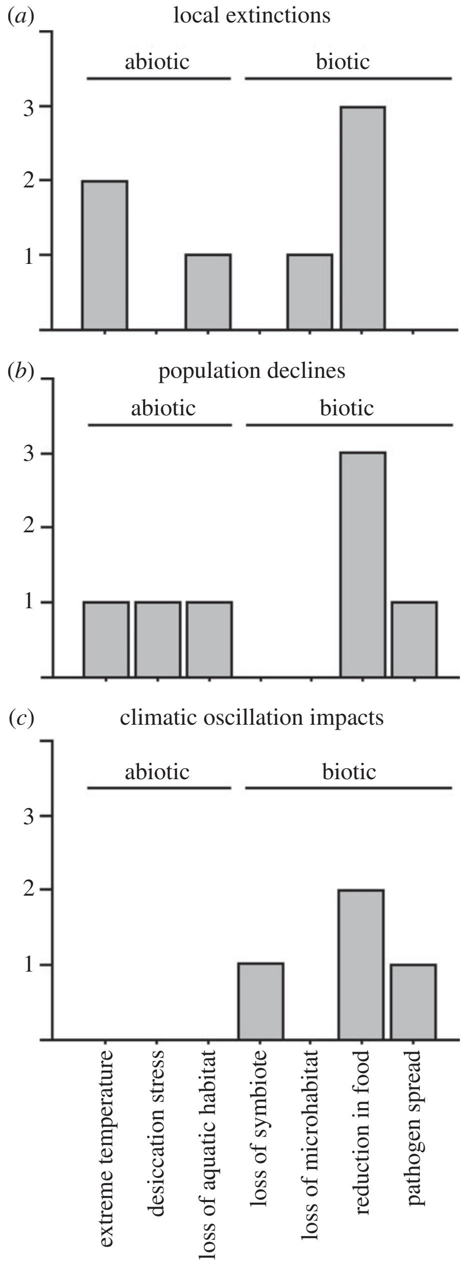

Figure 1. Summary of the frequency of different proximate causes of extinction due to climate change, among published studies. (*a*) 'local extinctions' refers to studies of local extinctions related to anthropogenic climate change (table 1), (*b*) 'population declines' refers to studies of declines in population abundance related to anthropogenic climate change (table 2), whereas (*c*) 'climatic oscillation impacts' refers to studies showing declines related to natural climatic oscillations (table 3) (but these oscillations may also be influenced by human factors, see relevant text). We note that there is some ambiguity in assigning some studies to a single, simple category.

limits surface activity time during the breeding season [23] or to a complex relationship between extreme temperatures (both cold and hot), precipitation and physiology [25,63]. Most studies (four of seven) implicate species interactions as the proximate cause, especially decreases in food availability [35,64,66]. Many authors have predicted that altered species interactions may be an important cause of extinction resulting from climate change (e.g. [67,68]), and our results empirically support the importance of these interactions (relative to other factors) among documented cases of local extinction.

(ii) *Proximate causes of population declines*

Seven studies identified proximate causes of population declines (table 2). The frequency of different proximate causes is intriguingly similar to those for population extinctions (figure 1*a*,*b*). Specifically, species interactions are the proximate cause of declines in the majority of studies, with declines in food availability being the most common cause [69,71,72], along with disease [70]. Drying of aquatic habitats is the cause in one study [29]. Two studies show physiological tolerances to abiotic factors as responsible for declines, with the declines being due to desiccation stress in desert trees [28], and due to oxygen limitation at high temperatures in a fish [24]. However, we find again that no studies show a straightforward relationship between population declines and temperatures exceeding the critical thermal limits of physiological tolerance.

(iii) *Proximate causes of extinction due to 'natural' climatic oscillations*

Among the 136 studies, four documented proximate causes of climate-change related extinctions that were associated with climatic oscillations (table 3). These oscillations may increase in frequency and severity due to anthropogenic impacts ([77], but see [78]). All four studies reinforce the importance of species interactions as the proximate cause of many extinctions attributable to climate change (figure 1*c*), including climate-related losses of food resources [73,75], loss of an algal symbiont ('coral bleaching'; [74]) and pathogen infection [76].

Two of the most widely discussed examples of climate-change related extinctions involve chytrid fungus in amphibians and coral bleaching (including many examples given above [36,70,74,75]). In both cases, local extinctions are strongly connected to natural climatic oscillations (e.g. [74]), but the links to anthropogenic climate change are still uncertain. For example, Pounds *et al.* [42] concluded that chytrid-related declines and extinctions in the frog genus *Atelopus* are related to anthropogenic warming, but Rohr & Raffel [70] subsequently suggested that chytrid spread in *Atelopus* was largely due to El Niño events. The link between anthropogenic climate change and local extinction of coral populations through bleaching also remains speculative [79]. For example, severe climate anomalies can cause bleaching and coral mortality [80], but bleaching itself does not always lead to mass mortality [81].

(c) *Proximate causes of extinction: synthesis*

Our review of the proximate causes of population extinctions and declines due to climate change reveals three main results, which are concordant across the three categories of studies (extinctions, declines and climatic oscillations). First, very few studies have documented proximate factors (18 of 136). Second, a diversity of proximate causes are empirically supported. Third, changing interspecific interactions are the most commonly demonstrated causes of extinctions and declines (figure 1). Specifically, changes in biotic interactions leading to reduced food availability are the single most common

Table 2. Studies documenting the proximate causes of declines in abundance due to anthropogenic climatic change.

species	location	hypothesized proximate cause of decline	reference
aloe tree (*Aloe dichotoma*)	Namib desert	desiccation stress owing to decreasing precipitation	[28]
four species of amphibians	Yellowstone National Park, USA	increasing temperature and decreasing precipitation cause a decline in habitat availability (pond drying)	[29]
plover (*Pluvialis apricaria*)	United Kingdom	high summer temperatures reduce abundance of craneflies (prey)	[69]
eelpout (*Zoarces viviparus*)	Baltic Sea	oxygen limitation at high temperatures	[24]
frogs (genus *Atelopus*)	Central and South America	climate change facilitates spread of pathogen (chytrid fungus)	[70]
grey jay (*Perisoreus canadensis*)	Ontario, Canada	warm autumns cause rotting in hoarded food, compromising overwinter survival and breeding success in the following year	[71]
Cassin's auklet (*Ptychoramphus aleuticus*)	California, USA	changes in upwelling timing and strength lower both adult survival and breeding success by changing food availability	[72]

Table 3. Studies that report proximate causes of declines in abundance or fitness associated with El Niño-Southern Oscilliation (ENSO) events.

species	location	hypothesized proximate cause of decline	reference
fig wasps (Hymenoptera: Agonidae)	Borneo	ENSO event causes obligate host trees (*Ficus* sp.) to fail to produce inflorescences, resulting in local extinction of pollinating wasps	[73]
corals	Panama and Ecuador	high sea surface temperatures cause bleaching and mortality	[74]
butterflyfish	Indian Ocean	climate-related loss of coral food source	[75]
toad (*Bufo boreas*)	Western USA	warming reduces water depth in ponds, which increases ultraviolet-B exposure of embryos, which in turn increases risk of fungal infection	[76]

proximate factor (figure 1). In contrast, limited physiological tolerances to high temperatures are supported only infrequently and indirectly (figure 1). Interestingly, the impacts of species interactions may be particularly difficult to document, inviting underestimation. However, we caution that these generalizations are based on few studies. For example, all three datasets (tables 1–3) are dominated by vertebrates, with only one plant study represented. Thus, the frequencies of documented proximate causes may change as the pool of studies becomes more taxonomically representative.

Finally, we note that we did not specifically address global species extinctions associated with climate change in our review. However, IUCN lists 20 species as extinct or extinct in the wild that potentially declined because of climate change (see the electronic supplementary material, table S1). Of these 20 species, seven are frogs that were possibly infected by chytrid fungus, which may be facilitated by climate change (see above). Four are snails, which may have become extinct as a result of drought. Two are freshwater fishes that lost their habitats because of drought. Among the six birds, two were also potentially affected by drought. The other four birds are island species possibly impacted by storms (the severity of which may be related to climate change), but these all had clear non-climatic threats. A similar pattern occurs in one island rodent species. In almost all cases, the links between extinction and anthropogenic climate change are speculative (but see [82]), which is why these cases were not included previously in our review. Intriguingly, none of the 20 is clearly related to limited tolerances to high temperatures (see the electronic supplementary material, table S1).

5. APPROACHES FOR FINDING THE PROXIMATE CAUSES OF CLIMATE-RELATED EXTINCTION

Our review demonstrates that disturbingly little is known about the proximate causes of extinctions due to recent climate change. How can this important gap be filled? Many approaches are possible, and we very briefly summarize two general frameworks that are beginning to be used. One focuses on individual species at multiple localities [23,25,63], the other on species assemblages at a particular locality [83–85]. These approaches are summarized graphically in the electronic supplementary material, figure S2.

Focusing on individual species (see the electronic supplementary material, figure S2), one must first document local extinctions or declines. To test whether populations have gone extinct, the present and past geographical ranges of the species can be compared. These analyses need not require surveying the entire species range, but could focus on a more limited series of transects (e.g. near the lowest latitudes and elevations, where ranges may already be limited by climatic factors [69,86]). The historical range can be determined from literature records and/or museum specimen localities [87]. These latter data are becoming increasingly available through online databases (e.g. GBIF; http://www.gbif.org/). Next, the species range (or select transects) should be resurveyed to document which populations are extant [23,56]. Evaluating whether populations persist is not trivial, and recent studies [56,88] have applied specialized approaches (e.g. occupancy modelling [89]). Furthermore, resurveys should account for false absences that may be misinterpreted as extinctions and for biases created by unequal sampling effort in space and time [87,90,91].

Documenting climate-related declines presents different challenges than documenting extinctions, given that most species lack data on population parameters over time. Some populations have been the focus of long-term monitoring, facilitating detailed studies of climate change impacts [86,92]. Large-scale databases on population dynamics through time are now becoming available. For example, the Global Population Dynamics Database [93] contains nearly 5000 time-series datasets. However, for many species, resurveying ranges to document local extinctions may be a necessary first step instead.

Given demonstrable local extinctions or declines, the next step is to determine whether these are related to large-scale trends in global climate change. Peery *et al.* [94] summarize six approaches that can be used to relate environmental factors to population declines [95]. These same approaches can be applied to connect global climate change and local extinctions. Relationships between changes in climate over time and population extinction versus persistence can be tested using GIS-based climatic data for relatively fine time scales (e.g. each month and year; PRISM; [96]). These analyses should preferably include data on other potential causes of local extinction not directly related to climate change, such as human habitat modification [64]. These analyses should help establish whether the observed local extinctions or declines are indeed due to climate change. If so, the next step is to understand their proximate causes.

Correlative analyses can be carried out to generate and test hypotheses about which proximate causes may be involved. Biophysical modelling [97] may be especially useful for these analyses, as it can incorporate many important factors, such as microclimate [98] and related variables (e.g. shade, wind speed, cloudiness, humidity) and relevant behavioural, ecological, demographic and physiological parameters [14,23]. Dissecting the specific aspects of climate that are most strongly associated with local extinctions may be important (e.g. is it warmer temperatures in the hottest part of the year, or the coldest?). Correlative studies can also test potential biotic factors, including the association between population extinctions or declines and the abundance of other species with negative impacts on the species in question (e.g. competitors, pathogens) or reductions in species necessary for persistence (e.g. prey, hosts). Two-species occupancy models [99] could be applied to test for the impacts of these and other types of interspecific interactions. Identifying the particular interactions that are responsible for climate-related extinctions may be challenging, given the diversity of interactions and species that may be involved. However, our results suggest that changing biotic interactions may be the most common proximate causes of climate-related extinction (figure 1).

Once potential factors are identified with correlative studies, these can be tested with mechanistic analyses. These could include experimental tests of physiological tolerances to relevant temperature and precipitation regimes [10,24,86,100], and laboratory and field tests of species interactions [39]. Transplant experiments that move individuals from extant populations into nearby localities where the species has recently gone extinct [100] may be particularly useful (for species in which this is practical). In many ways, experimental analyses can provide the strongest tests of the hypothesized causes of local extinctions. However, these should be informed by broader correlative studies. For example, simply testing the physiological tolerances of a species to extremely high temperatures may say little about the causes of climate-associated local extinction in that species if those extinctions are actually caused by warmer temperatures in winter or the spread of a competitor.

The second major approach (see the electronic supplementary material, figure S2) is to focus on species assemblages at single localities over time [83–85], rather than analysing multiple localities across the range of one or more species. Given data on species composition at different points in time, the local extinctions or declines of certain species can be tested for association with temporal changes in climate. These losses can then be related to specific biological traits (e.g. greater loss of species with temperature-cued flowering times versus those using photoperiod, or species for which the site is near their southern versus northern range limits [84]). These relationships can then point the way to more mechanistic and experimental studies.

6. QUESTIONS FOR FUTURE RESEARCH

Understanding the proximate factors that cause climate-related extinctions should be an urgent priority for future research and should open the door to many additional applied and basic questions. Are there specific conservation and management strategies that can be matched to specific extinction causes? Are there phylogenetic trends or life-history correlates [20] of these factors that may allow researchers to predict which factors will be important in a species without having to conduct lengthy studies within that species? Do different factors influence the ability of niche models to accurately predict range shifts and extinctions due to climate change (e.g. physiological tolerances versus species interactions)? Can species adapt to some potential causes of extinction and not others?

7. CONCLUSIONS

Climate change is now recognized as a major threat to global biodiversity, and one that is already causing widespread local extinctions. However, the specific causes of these present and future extinctions are much less clear. Here, we have reviewed the presently available evidence for the proximate causes of extinction from climate change. Our review shows that only a handful of studies have focused specifically on these factors, and very few suggest a straightforward relationship between limited tolerance to high temperatures and local extinction. Instead, a diverse set of factors is implicated, including effects of precipitation, food abundance and mismatched timing with host species. Overall, we argue that understanding the proximate causes of extinction from climate change should be an urgent priority for future research. For example, it is hard to imagine truly effective strategies for species conservation that ignore these proximate causes. We also outline some general approaches that may be used to identify these causes. However, we make the important caveat that the relative importance of different proximate causes may change radically over the next 100 years as climate continues to change, and limited physiological tolerances to high temperatures may become the dominant cause of extinction. Nevertheless, our review suggests the disturbing possibility that there may be many extinctions due to other proximate causes long before physiological tolerances to high temperatures become predominant.

We thank H. Resit Akçakaya, Amy Angert, Steven Beissinger, Doug Futuyma, Spencer Koury, Javier Monzón, Juan Parra and anonymous reviewers for discussion and helpful comments on the manuscript.

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