ARTICLES

Widespread amphibian extinctions from epidemic disease driven by global warming

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As the Earth warms, many species are likely to disappear, often because of changing disease dynamics. Here we show that a recent mass extinction associated with pathogen outbreaks is tied to global warming. Seventeen years ago, in the mountains of Costa Rica, the Monteverde harlequin frog (*Atelopus* sp.) vanished along with the golden toad (*Bufo periglenes*). An estimated 67% of the 110 or so species of *Atelopus*, which are endemic to the American tropics, have met the same fate, and a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) is implicated. Analysing the timing of losses in relation to changes in sea surface and air temperatures, we conclude with 'very high confidence' (>99%, following the Intergovernmental Panel on Climate Change, IPCC) that large-scale warming is a key factor in the disappearances. We propose that temperatures at many highland localities are shifting towards the growth optimum of *Batrachochytrium*, thus encouraging outbreaks. With climate change promoting infectious disease and eroding biodiversity, the urgency of reducing greenhouse-gas concentrations is now undeniable.

Humans are altering the Earth's climate[1–4] and thus the workings of living systems[5–8], including pathogens and their hosts[9–11]. Among the predicted outcomes is the extinction of many species[10,12], but detecting such an effect is difficult against a backdrop of other changes, especially habitat destruction. One approach is to focus on organisms for which current rates of extinction exceed those expected from habitat loss. Amphibians are a case in point. Thousands of species have declined, and hundreds are on the brink of extinction or have already vanished[13]. The Global Amphibian Assessment (GAA) lists 427 species as "critically endangered", including 122 species that are "possibly extinct"[13]. A majority of the former, and nearly all of the latter, have declined even in seemingly undisturbed environments.

The causes have remained unclear, in part because of their complexity[14–16]. Although pathogens are implicated[14–28], their relationship to environmental change is poorly understood. Here we test the "climate-linked epidemic hypothesis"[29–34], which predicts declines in unusually warm years but does not assume a particular disease or chain of events. Recent studies have considered this idea[15,18,21,23,28], yet data have not permitted a geographically broad test that examines landscape alteration, global warming and climate fluctuations on the timescale of El Niño. Suffering widespread extinctions often despite habitat protection, harlequin frogs (*Atelopus*) afford such a test. A new database, produced by 75 researchers, documents the case in unprecedented detail, owing to the nature of

these members of the toad family (Bufonidae)[26]. Brightly coloured and active during the day near streams, most are readily observed and identified. For the first time, data indicate when each of numerous species was seen for the last time.

Our analyses capitalise on insights gained by alternating between large and small spatial scales[35] (Supplementary Fig. 1). Since epidemics of *Batrachochytrium* are implicated in *Atelopus* extinctions in Central and South America[26], we first explain that the predicted association with warm years, if juxtaposed with theory regarding this chytrid, is a paradox. We then: (1) assess large-scale altitudinal patterns of extinction risk with this paradox in mind; (2) consider determinants of local climate in the case of the golden toad and the Monteverde harlequin frog to select large-scale temperature signals for analysing the biological patterns; (3) show that the timing of the widespread extinctions is strongly tied to these signals; and (4) explore local climate from a chytrid's viewpoint to frame a solution to the paradox.

The climate–chytrid paradox

The climate-linked epidemic hypothesis predicts amphibian declines in unusually warm years, because shifts in temperature or related variables often influence disease dynamics[9–11]. As temperatures rise, climate fluctuations may cross thresholds for certain pathogens, triggering outbreaks. Many diseases are expected to become more lethal, or to spread more readily, as the Earth warms[9–11].

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Chytridiomycosis, caused by *Batrachochytrium*, is thought to be an exception[10]. This chytrid grows on amphibian skin and produces aquatic zoospores[22,24]. Widespread and ranging from deserts and lowland rainforests to cold mountain tops[27], it is sometimes a non-lethal parasite and possibly a saprophyte[19,25]. It is associated with host mortality in highlands or during winter[22], and, according to theory, becomes more pathogenic at lower temperatures[19,22]. Hence, the idea that it causes declines in warm years is paradoxical. Moreover, the fungus is apparently more lethal under moist conditions[24,26], yet, at many affected sites, warm years are comparatively dry.

Ideas of two sorts could resolve this paradox. First, warm or dry conditions may stress amphibians, possibly increasing susceptibility to disease[29]. Second, warm years could favour *Batrachochytrium* directly. The prevailing idea—that lower temperatures benefit the chytrid[19,22]—might be an oversimplification of the pathogen's response to climate.

Altitudinal patterns of extinction risk

This prevailing idea predicts greater extinction risk for higher-elevation species. Many are already prone to extinction, because geographic ranges tend to decrease in size with increasing elevation. The probability of disappearance might thus be expected to increase from lowlands to mountain tops.

For a preliminary test with *Atelopus*, we consider 100 species for which data indicate the last year of observation (LYO). We recognize two tiers. According to La Marca *et al.* (ref. 26), the population data are sufficient to judge whether tier-one species ($n = 51$) have declined, but not tier-two species ($n = 49$). Throughout our analyses, patterns are similar for tier one and for tiers one and two combined. Adding tier two increases error but provides insights. We score species as having disappeared if the LYO is 1998 or earlier.

The altitudinal patterns are more complex than expected (Fig. 1). Using a sliding window to assess how the probability of disappearance varies with species' lower elevational limit, we find three breakpoints. The percentage of species lost increases sharply at 200 m, and again at 1,000 m. It decreases, however, at 2,400 m, and thus peaks at middle elevations, suggesting that low temperatures as
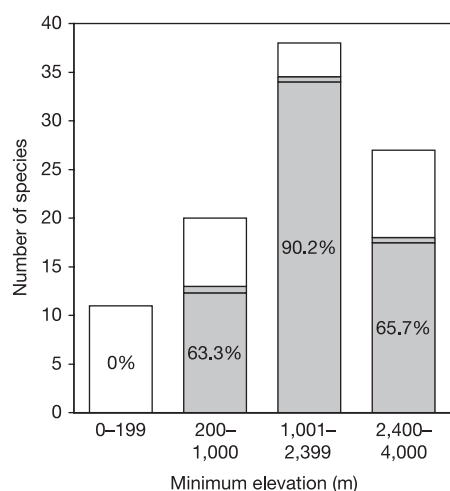
well as high ones may limit the impact of *Batrachochytrium*. The altitudinal effects remain significant when we control for range size, which also influences extinction probability. Average range size decreases from lower to higher zones as defined in Fig. 1, but is similar for the upper two.

These altitudinal patterns contribute to the severity of losses. For instance, the zone losing the highest percentage of species had the greatest diversity (Fig. 1). Our overall estimate that 67% of the species have disappeared is weighted by the number of species per zone. Although extinction probabilities are independent of tier, an unweighted estimate based on tier one alone (57%) under-represents the severely affected mid-elevation species.

GAA data for New World amphibians[13] suggest similar altitudinal patterns (Supplementary Fig. 2). The percentage of species extinct or threatened is largest at middle elevations, even though higher-elevation species generally have smaller ranges. Clearly, the role of climate needs re-evaluating.

Temperature signals

To select temperature signals, we consider the scale at which local climates are determined. In Costa Rica's Monteverde cloud forest, reduced mist frequency in warm years is associated with shifts in populations of birds, reptiles and amphibians, including the disappearance of the golden toad and the Monteverde harlequin frog[31]. Whereas nearby lowland deforestation might have influenced conditions[36], temperatures in Central and South America agree with simulated responses to greenhouse-gas accumulation[3]. Here we quantify the extent and timing of deforestation upwind of Monteverde, model regional climate, and consider how local trends relate to sea surface temperature (SST) and air temperature (AT) on varying scales.

We focus on warming and the growing number of dry days, which reflects increasing precipitation variability and declining mist frequency[31]. While the latter probably affects many organisms, impacts of correlated climatic changes are hard to separate, and not all *Atelopus* extinctions have occurred in habitats where mist is vital[26]. In any case, large-scale temperature shifts, integrating various aspects of climate change, are a likely common denominator.

The chiefly historical deforestation probably enhanced sensitivity to warming but cannot easily explain the trends. Using LANDSAT images and aerial photos, we assess changes in a 35-km-wide belt representing the trade-wind path from the Caribbean shore to the 500-m contour. Clearing through the year 2000 claimed about 38% of this belt. The loss, however, was only 11% during 1975–2000, when the changes occurred at Monteverde, and 9% during 1960–1975. The area of the San Carlos Plain directly upwind was cleared before 1940 (ref. 36).

In contrast, global temperatures have climbed steeply since the early 1970s (refs 1–4). In the tropics, all forest regions have warmed[37,38], and mountain glaciers are rapidly melting[39]. During 1975–2000, SST and AT for the tropics, both of which are averages for 30° N–30° S, were highly correlated (Fig. 2a). The latter increased by 0.18 °C per decade, which is triple the average rate of warming for the twentieth century. It is 18 times the inferred average rate for a mid-elevation cloud forest in the Andes during the 8,000-year transition from the ice ages to modern times (Pleistocene–Holocene)[40]. It is similarly more rapid than the non-directional changes of the preceding 30,000 years.

The recent warming, our work suggests, has reduced mist frequency at Monteverde by raising heights of orographic cloud formation. These altitudes depend on relative humidity in the trade winds ascending the mountain slopes, and thus on moisture content and temperature[41]. In our simulations, large-scale warming reduces relative humidity locally much more than the observed deforestation (Supplementary Fig. 3). The growing number of dry days is consistent. It is correlated with SST in each of six regions: offshore Caribbean (near Costa Rica), offshore Pacific, equatorial

Figure 1 | Altitudinal patterns in the *Atelopus* extinctions. Bars indicate the number of species known per altitudinal zone (total $n = 96$), and the grey-shaded portions represent the estimated percentage of species lost from each. This percentage differs among zones ($\chi^2 = 31.4$, degrees of freedom = 3, $P < 0.0001$), but not between the tier-one species-set and the species-set that combines tiers one and two (Fisher exact tests, $P > 0.9$). The double lines indicate the values for each of these two species-sets; the percentage labels are the averages of the two. The percentage for the zone affected most severely differs from that of each adjacent zone (Fisher exact tests, $P < 0.036$).

Pacific (Niño-3 region), deep tropics (10° N–10° S), tropics, and the globe. A residual trend remains, however, unless we consider the tropics or the globe (Supplementary Fig. 4). Large-scale and local climatic changes are strikingly concordant, with fluctuations related to El Niño superimposed on the trends (Fig. 2b, c). Thus, analysis of AT or SST for the tropics should capture temperature shifts influencing the relevant ecological processes.

Signatures of warming

Accordingly, the biological changes at Monteverde are associated statistically with AT and SST for the tropics but not with Niño-region SST alone (Supplementary Fig. 5). Correlations are evident for the shift of lower-elevation breeding birds up the mountain slopes, and for the decline of highland lizards. Likewise, the episodic losses of amphibians occurred in years that were unusually warm across the tropics. To examine the overall biological pattern in relation to AT for the tropics, we randomize this signal for 1979–1998. In each of 10,000 iterations, we assign the annual means at random to the 20 years and recalculate indices of association. The results confirm that none of the observed relationships is likely to have arisen by chance (Supplementary Table 1). Moreover, in only one iteration are the modelled values all as extreme as the observed ones, indicating a high probability that large-scale warming is affecting local ecology.

We examine the timing of the widespread *Atelopus* extinctions in relation to the same temperature signals. The Jambato toad (*Atelopus ignescens*) of Ecuador and the Monteverde harlequin frog suggest the working hypothesis that species tend to be seen for the last time right after a relatively warm year[21,29,31]. Both were last found in 1988, following a temperature peak in 1987. Before 1988, the Jambato toad was present during 64% of visits to sites throughout its 10,234-km^2 range[21]. After 1988, it was absent at all sites, implying synchronous declines across localities. The degree of synchrony, however, differs

among species, and survivors of population crashes persist for variable lengths of time. Furthermore, the spatial and temporal coverage of sampling varies, introducing error.

At any rate, the climate-linked epidemic hypothesis predicts an association between disappearances and warm years, but not a one-to-one correspondence[33]. An *Atelopus* population might survive despite warm weather if the pathogens are absent from particular sites within their range, or if they are spreading but have not reached certain areas. Factors that discourage pathogen transmission, such as low host-density, may likewise forestall declines[10]. Although temperature shifts can entrain multiple outbreaks, fast-moving waves of infection might also synchronize declines across localities, and an *Atelopus* population experiencing normal weather could succumb to a wave set in motion elsewhere.

Despite the potential variability, the extinctions show signatures of warming. Like the biological changes at Monteverde, they are associated statistically with AT and SST for the tropics but not with Niño-region SST alone (Fig. 3 & Supplementary Table 2). Around 80% of the species that have disappeared were seen for the last time right after a relatively warm year. For tier one, and for tiers one and two combined, we use Monte Carlo methods to generate 10,000 random frequency distributions for comparison with the observed distributions. These analyses confer 'very high confidence' (>99%, following the IPCC[1,5]) that the tendencies are not due to chance and that large-scale warming is a key factor. Patterns for the two species-sets are comparable despite differences in error rate and time period. Spanning a longer period, the combined data indicate depletion of the most vulnerable species by the late 1990s.

Results are consistent when we repeat the analyses with various subsets of species to consider sources of variation, error and uncertainty (Supplementary Table 2). For instance, because some undescribed species are poorly known, we repeat the analyses including only described ones. Likewise, we consider occurrence in protected
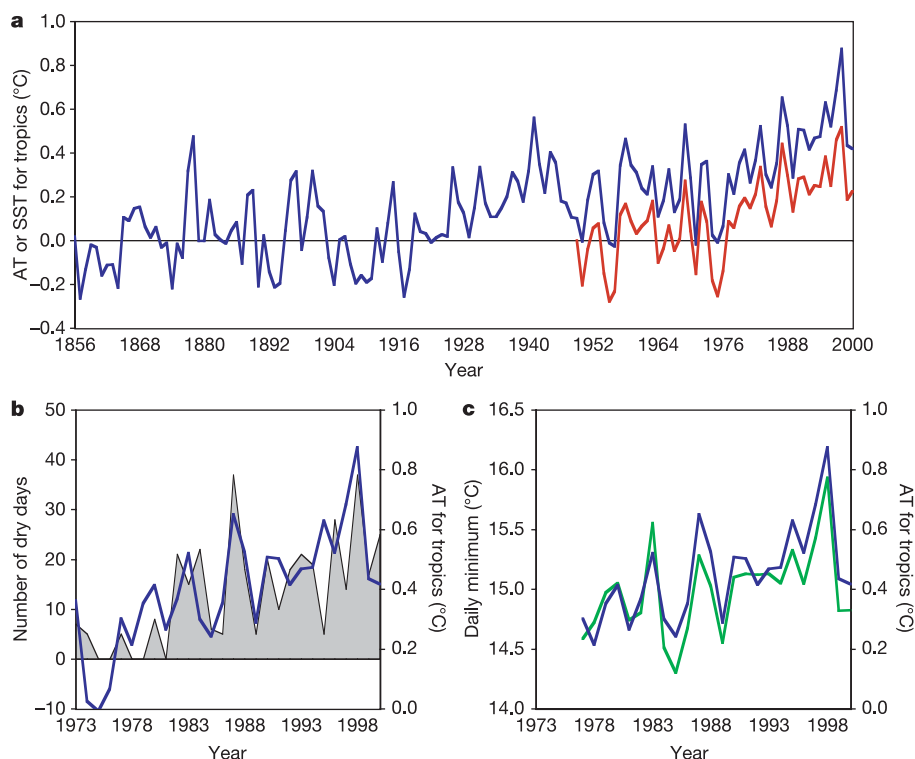

Figure 2 | **AT and SST for the tropics and their relationship to climatic trends at Monteverde.** AT for the tropics (blue line) is correlated with: **a,** SST for the tropics (red line) ($r = 0.97$, $P < 0.0001$, $n = 51$); **b,** number of dry days in runs ≥5 days (grey-shaded area) ($r = 0.70$, $P < 0.0001$, $n = 28$);

and **c,** local daily minimum AT (green line) ($r = 0.91$, $P < 0.0001$, $n = 24$). Temperatures are annual averages. AT and SST for the tropics are departures from a baseline mean (for 1856–1895 and 1951–1979, respectively).
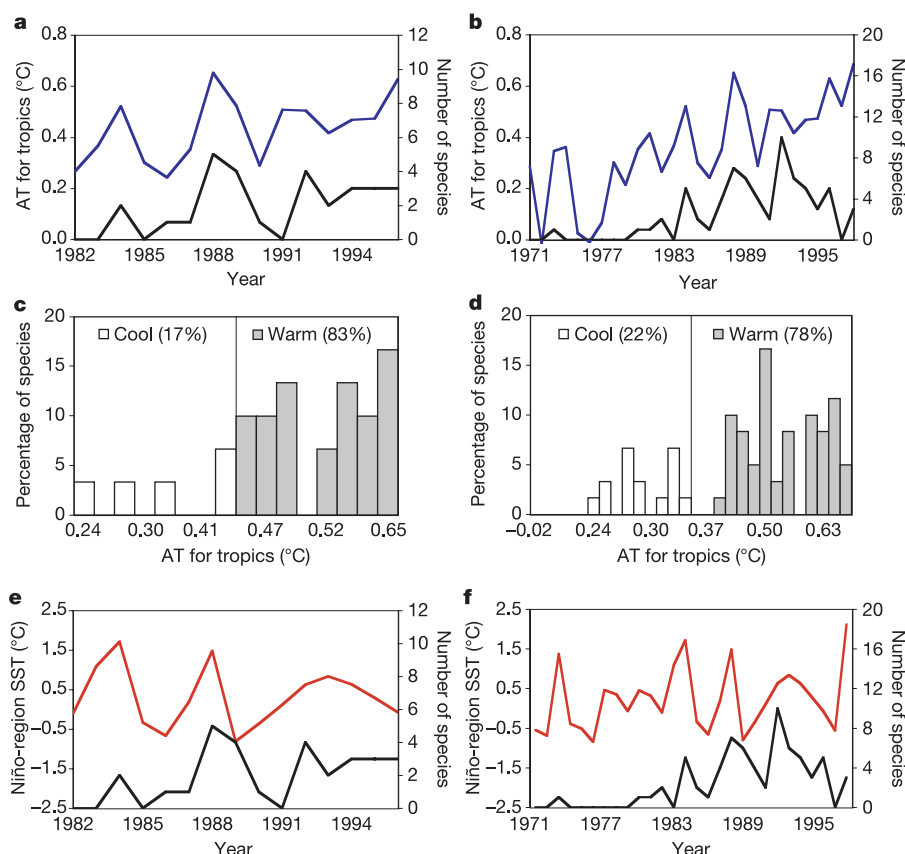
Figure 3 | Signatures of warming in the *Atelopus* extinctions. For tier one (**a**) and tiers one and two combined (**b**), the number of species observed for the last time (black line) is related to AT for the tropics in the preceding year (blue line). **c, d**, Percentage of species observed for the last time following a relatively warm year exceeds that expected by chance (**c**, tier one, 83%, $P < 0.002$, $n = 29$; **d**, tiers one and two, 78%, $P < 0.0001$, $n = 68$). **e, f**, The same patterns (black lines as in **a, b**) are not significantly related to Niño-region SST (red line). The corresponding percentages do not exceed those expected by chance (**e**, tier one, 55%, $P > 0.43$; **f**, tiers one and two, 62%, $P > 0.12$). Temperatures are calculated as in Fig. 2.

areas, accessibility of regions, and factors that might influence the timing of extinction. Several analyses provide independent tests of our hypothesis. The strength of association between warm years and disappearances is not related to altitude, latitude or range size. Accordingly, conclusions are similar for 'northern' and 'southern' species, and for 'higher-elevation' and 'lower-elevation' ones.

In these analyses, AT or SST for the tropics serves as a relative index, often registering smaller shifts than local indices. In 1987, the former averaged 0.65 °C above the baseline (Fig. 2), whereas local temperatures relevant to the Jambato toad's extinction in the highlands of Ecuador were almost 2.0 °C above a century-long mean[21]. The difference may reflect, in part, increasing atmospheric moisture, which can amplify the signal at higher altitudes[42,43]. Global warming accelerates evaporation and raises the air's capacity to hold water. As water vapour rises and condenses, latent heat is transferred to the atmosphere.

A climate for chytrids

Increased water vapour can also translate into enhanced cloud cover—often with the help of condensation nuclei from particulate air pollution (aerosols)[44]—creating additional feedbacks that influence surface temperatures[45]. This may be notable in places where air rises strongly, such as in mountainous regions. Reducing heat loss at night, cloud cover adds to nocturnal warming. By impeding solar radiation, however, it moderates daytime trends and may reverse them. In many areas, the daily temperature range is declining as the minimum rises faster than the maximum[45].

Such trends are evident in the highlands of Central and South

America[46–48]. At Monteverde, regardless of the season, the daily minimum is rising while the daily maximum is falling (Fig. 4a). For 11 Colombian and Venezuelan stations with quality-checked, long-term data[47], we compare 1941–1970, preceding the *Atelopus* extinctions, to the first decade with major losses (1981–1990). The minimum again shows an increase and the maximum a decrease (Fig. 4b). At some localities both are rising, but the former disproportionately so[46–48]. These trends imply increasing cloud cover that contributes to warming at night but diminishes it during the day[45].

Cloudiness should favour the chytrids. These fungi reportedly grow best at 17 to 25 °C, peaking at 23 °C (refs 19, 22, 24). They stop growing at 28 °C and die at 30 °C. Shielding them from excessive warmth and fostering moist conditions, cloud cover may promote their survival, growth and reproduction. At Monteverde, where ambient daytime temperatures are usually chytrid-friendly, temperatures inside sunlit moss mats, bromeliads or leaf litter often exceed 30 °C (ref. 34). Cloudiness, however, largely shuts down radiant heating, forcing thermal environments to mirror ambient conditions. Microscale trends can thus dwarf local ambient trends, which, in some places, might even be of opposite sign. If amphibians seek warmth to combat infection, increasing cloudiness might hamper their defences[34]. In any case, local or microscale cooling should often benefit the chytrids.

So why should these pathogens flourish in the highlands during warm years? The answer, we suggest, lies in the difference between night and day. To consider this difference, we plot daily minimum and maximum temperatures in relation to altitude for 50 localities, from Costa Rica to Peru, along with the optimal temperatures for
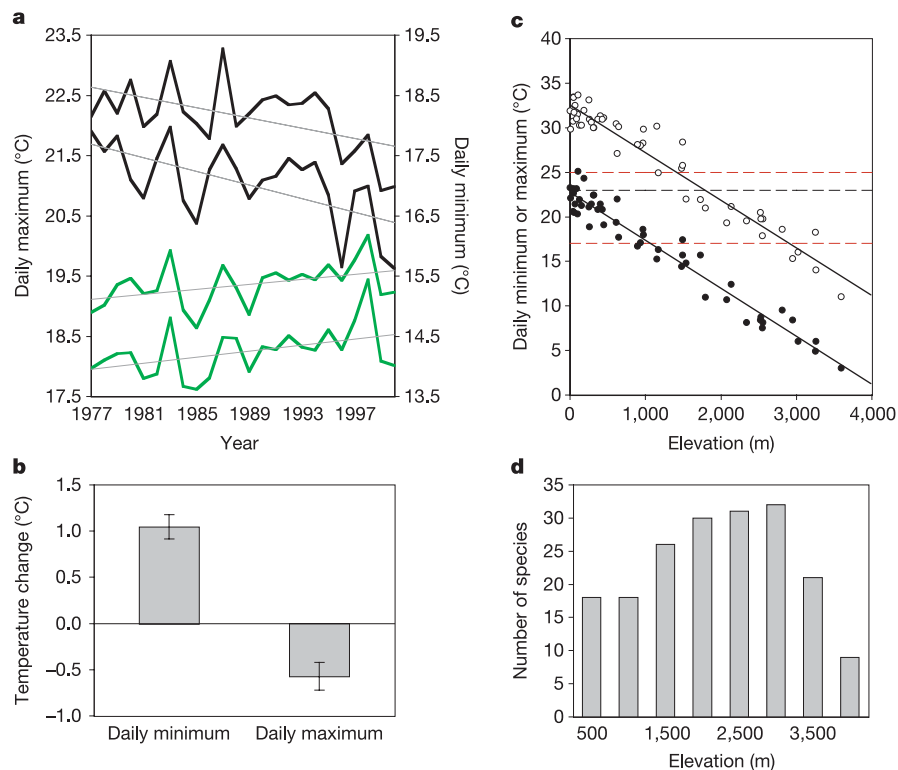
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Figure 4 | Daily minimum and maximum temperatures and the chytrid-thermal-optimum hypothesis. a, At Monteverde, the average daily minimum (green lines) and maximum (black lines) for warmer months (March–October) and cooler months (November–February) show trends ($|r| \geq 0.43$, $P < 0.038$, $n = 24$). **b**, In Colombia and Venezuela, station averages during the extinctions differed from those of earlier decades. Values are mean changes ($\pm$s.e.m.). **c**, For Costa Rica to Peru, annual average daily minimum (closed circles) and maximum (open circles) vary by altitude. Dashed lines give reported optimal temperature range (red dashed line) and optimum temperature (black dashed line) for *Batrachochytrium*. **d**, Number of *Atelopus* species per 500-m belt is labelled by upper limit. Six ranged above 4,000 m.

growth of *Batrachochytrium* (Fig. 4c). We also plot the altitudinal distribution of *Atelopus* (Fig. 4d). Two patterns are clear. First, just as the lowlands are often too warm for the chytrids during the day, the highlands are often too cool for them at night. Second, most *Atelopus* extinctions have occurred at elevations where the minimum temperature is shifting towards the growth optimum for these pathogens. Thus, we propose the chytrid-thermal-optimum hypothesis, in which daytime cooling (local or microscale) and night time warming accelerate disease development. The impacts at night may explain the association with warm years and thereby resolve the climate–chytrid paradox.

Conclusions

We establish that global climate change is already causing the extinction of species. Taking our results and recent findings that tie the same losses to disease, we conclude that climate-driven epidemics are an immediate threat to biodiversity. Our study sheds light on the amphibian-decline mystery by showing that large-scale warming is a key factor. It also points to a chain of events whereby this warming may accelerate disease development by translating into local or microscale temperature shifts—increases and decreases—favourable to *Batrachochytrium*. The case illustrates how greenhouse warming and the resultant intensification of the hydrological cycle, together with aerosol pollution, may affect life on Earth. Influencing patterns of cloud formation, these agents alter the thermal, light and moisture environments of many organisms, changing ecological interactions and threatening species survival.

METHODS

Assessing extinction probability in relation to altitude. We examine the influence of altitudinal distribution while considering range size. Data indicate the last year of observation (LYO) for 104 of the 113 species of *Atelopus* (see Appendix A in the Supplementary Information). Focusing on recent losses, we exclude four species known only from historical records (1950 or earlier). Variables include minimum and maximum elevations[26], elevational midpoint and longest axis of the range polygon (GAA data[13]). For statistical analyses, we use logistic regression and contingency tables. Sample sizes vary because some data are missing, particularly for undescribed species. Although extinction probability is related to each altitudinal variable, we focus on minimum elevation, because it indicates whether populations occur at low elevations, which may provide a refuge from chytridiomycosis. Ranking species by minimum elevation, from lowest to highest, we use a sliding window to compare extinction probabilities between successive subsets of ten, shifting the window one species at a time. The first ten encompass the altitudes (<200 m) at which no species has disappeared.

Selecting temperature signals. The regional modelling generates climate-change scenarios, which we test by analysing local trends in relation to temperature on varying spatial scales. In the simulations, we prescribe realistic partial clearing, based on the remote-sensing data. We compare its impact to that of an increase in AT and SST approximating tropical warming over 1973–2000 and, in a separate run, the 1986–1987 El Niño. We examine aerial photos from Costa Rica's National Geographic Institute for 1960, LANDSAT Multispectral Scanner images for 1975, and LANDSAT Thematic Mapper 7 images for the year 2000. Detecting forest fragments ≥ 0.03 km^2, and classifying areas as forest if canopy density is $\geq 80\%$, the techniques[49] produce land-cover maps at a scale of 1:250,000. We run our simulations with the Regional Atmospheric Modelling System (RAMS)[50] at a maximum horizontal resolution of 1.6 km. To prescribe initial and boundary conditions, we use the ECMWF Global Reanalysis (2.5°-resolution ERA-15 Pressure Level Analysis) from the European Centre for Medium-range Weather Forecasts. The GDTOPO30 digital elevation model from the US Geological Survey defines terrain. To examine local trends in relation to temperature on varying scales, we examine SST data (2°-resolution) from the National Oceanic and Atmospheric Administration's (NOAA's) National Centers for Environmental Prediction (NCEP), and AT data (5°-resolution) from the Climate Research Unit (CRU), University of East

Anglia. The local data, including tallies of dry days for January–May, are from 1,540 m on Monteverde's upper Pacific slope[31].

Testing for a link to global warming. We use resampling methods to analyse biological patterns in relation to large-scale temperature signals. 'Warm years' are above average for the period of analysis. For Monteverde, we examine 1979–1998, which encompasses the field observations[31]. To produce a single time series for anoline lizards, we average data for the two declining species, which are highly correlated. The *Atelopus* data are from various independent studies[26]. To prevent bias, persons contributing or compiling these data were not told how they would be analysed in relation to climate. We consider AT for the tropics over the last year of observation (LYO) of each species, for one, two and three years before, and for averages across these years. The period of analysis is defined accordingly. We find an association, however, only for one year before. To examine the strength of this association in relation to altitudinal and latitudinal distribution and range size, we use logistic regression. Latitudinal variables include northern and southern limits and range midpoint. The analyses of biological patterns in relation to Niño-region SST (departures relative to 1950–1979) yield similar conclusions regardless of the signal examined: Niño-1 and -2, Niño-3, these combined, or Niño-1 and -2 combined with Niño-3 and -4. We present results for the latter, composite, signal.

Resolving the climate–chytrid paradox. We focus on temperature, since altitudinal patterns in the declines underscore its importance and because the extinctions are strongly associated with it. Temperature shifts are presumably more coherent spatially than attendant climatic changes. Our premise is that any pathogen with an optimal range for growth and reproduction will be sensitive to low temperatures as well as high ones, as suggested by the altitudinal patterns of extinction risk. (see the Supplementary Notes pertaining to "A climate for chytrids", which explores the meaning of the observed breakpoints.) Comparing temperatures for the warmer and cooler months at Monteverde shows that, seasonally, night time temperatures in the highland tropics often lie even farther below the optimal range for *Batrachochytrium* than average conditions suggest. To examine daily minimum and maximum temperatures for the 11 Colombian and Venezuelan stations, we use the published averages for particular decades[47]. The 50 localities from Costa Rica to Peru mostly represent inland areas. The corresponding analyses do not control for latitude or sampling period, yet provide a generalized altitudinal profile of minimum and maximum temperatures. Numbers of *Atelopus* species that inhabited the different altitudinal zones are based on $n = 96$. Some inhabited more than one zone.

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