**LETTER**

# Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate

Christy M. McCain[1]* and
Robert K. Colwell[2]

[1]*Department of Ecology & Evolutionary Biology and CU Museum of Natural History, MCOL 265 UCB, University of Colorado, Boulder, CO 80309-0265, USA*
[2]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA*
*Correspondence: E-mail: christy.mccain@colorado.edu*

## Abstract

Mountains are centres of global biodiversity, endemism and threatened species. Elevational gradients present opportunities for species currently living near their upper thermal limits to track cooler temperatures upslope in warming climates, but only if changes in precipitation are sufficiently in step with temperature. We model local population extirpation risk for a range of temperature and precipitation scenarios over the next 100 years for 16 848 vertebrate species populations distributed along 156 elevational gradients. Average population extirpation risks due to warming alone were < 5%, but increased 10-fold, on average, when changes in precipitation were also considered. Under the driest scenarios (minimum predicted precipitation), local extirpation risks increased sharply (50–60%) and were especially worrisome for hydrophilic amphibians and montane Latin America (c. 80%). Realistic assessment of risks urgently requires improved monitoring of precipitation, better regional precipitation models and more research on the effects of changes in precipitation on montane distributions.

## Keywords

Amphibians and reptiles, bioclimatic models, birds, climate change, elevation, mammals, mountains, precipitation, range contraction, temperature.

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## INTRODUCTION

Scientists and conservation planners urgently need to understand how the rapid changes associated with anthropogenic climate modification may impact species' distributions, extinction risks, phenology and biotic interactions (e.g. Parmesan & Galbraith 2004; Rosenzweig *et al.* 2007). To meet this need, given the uncertainties, one step is to bracket the potential magnitude of risk associated with various types of change (e.g. temperature, precipitation, sea-level change) and their interactions (e.g. Rosenzweig *et al.* 2007). To date, empirical research on terrestrial organisms has focused overwhelmingly on detecting and interpreting species' shifts latitudinally, elevationally and phenologically in terms of global increases in temperature (e.g. Grabherr *et al.* 1994; Parmesan 1996; Pounds *et al.* 2006; Lenoir *et al.* 2008; Moritz *et al.* 2008; Chen *et al.* 2009; La Sorte & Jetz 2010; see Appendix S1 for additional citations). Likewise, much of the biogeographic modelling work on range shifts under contemporary climate change has also focused on temperature change (e.g. Buckley 2008; Colwell *et al.* 2008; Deutsch *et al.* 2008; Appendix S1).

Although many studies acknowledge the importance of changes in precipitation regimes, and empirical work supports the importance of such changes (Pounds *et al.* 1999; McLaughlin *et al.* 2002; Epps *et al.* 2004; Kelly & Goulden 2008; Crimmins *et al.* 2011), we lack an overview of the interaction between temperature and precipitation under global climate change in a biogeographic context. We know that most species responded individualistically to changing temperature and precipitation during the Pleistocene, producing range shifts more complex than simple thermal zone shifts (Graham & Grimm 1990; Davis & Shaw 2001; Lyons 2005; Appendix S1). Yet the overall effort to detect species' range shifts, population reductions and extinction risks associated with contemporary changes in precipitation regimes

(e.g. Crimmins *et al.* 2011) has thus far been minimal compared with temperature changes, particularly for fauna.

There are some good reasons for this imbalance. On annual to decadal time scales, temperature is easier and less costly to measure and much more accurately predictable on broad geographical scales than precipitation, given the nearly linear decline in mean temperature with elevation (Barry 2008). Precipitation, in contrast, is more costly to measure. Accurate measurement of precipitation is complicated by the various types of monitors needed to detect rainfall, snow, cloud condensation and evaporative effects. Thus, high quality or at least adequate temperature data are readily available for much of the world, whereas accurate precipitation data are relatively scarce, especially for less developed regions. Moreover, because precipitation trends are nonlinear latitudinally, elevationally and seasonally, climate models predicting changes in precipitation are highly sensitive to model assumptions (Christensen *et al.* 2007; Barry 2008 and references therein).

From a physiological perspective, energetic costs and performance implications may be more straightforward under temperature models than under precipitation models, particularly for ectotherm animals (e.g. Chamaillé-Jammes *et al.* 2006; Buckley 2008; Deutsch *et al.* 2008; Kearney *et al.* 2009; Rosenzweig *et al.* 2007; Sunday *et al.* 2010). But both temperature and precipitation are critical physiological niche axes for all organisms, especially in arid environments (e.g. Pounds *et al.* 1999; McLaughlin *et al.* 2002; Epps *et al.* 2004; Kelly & Goulden 2008; Crimmins *et al.* 2011). For many animals, temperature and water influences extend beyond direct physiological impacts to indirect impacts on habitat requirements and on food resource abundance and quality (e.g. Hawkins *et al.* 2003; McCain 2007). Thus, it is critical to assess whether focusing on temperature, alone, provides an adequate indication of proportional risk associated with climate change as a

whole. A focus on temperature alone might be potentially misleading if climate change risks are substantially and disproportionately higher or quite differently patterned when precipitation change is considered.

Here, we apply simple models of climate-driven range shifts to compare the risk of population extirpation associated with temperature change alone to the corresponding risks with both temperature and precipitation change. We apply these models to the elevational ranges of vertebrate species from around the globe. Mountains harbour a preponderance of global biodiversity (e.g. Grabherr *et al.* 1994; Orme *et al.* 2005; Grenyer *et al.* 2006; Pauli *et al.* 2007; La Sorte & Jetz 2010) as well as many species of especially high extinction risk, owing to their small geographic range sizes and narrow endemism (e.g. Ricketts *et al.* 2005; Thuiller *et al.* 2005; Appendix S1). Mountains have also been predicted to have the highest level of risk associated with disappearing climatic regimes (Williams *et al.* 2007). Both temperature and water are highly correlated with biodiversity of flora and fauna (e.g. Hawkins *et al.* 2003 and references therein; Appendix S1) and have been shown to strongly affect elevational patterns of diversity (e.g. McCain 2007; Sanders *et al.* 2007; Appendix S1). Therefore, examining climate change effects on mountain organisms around the world should offer a valuable assessment, as they encompass a majority of the world's diversity, endemism and species already at high risk of extinction.

We base our study on a previous compilation of datasets from studies on montane vertebrate distributions (McCain 2009 and references therein) that includes 16 848 vertebrate populations distributed along 156 elevational gradients (Fig. 1a). For each population on each gradient, we apply a battery of range-shift projection models based on climates projected ahead 100 years. Our models bracket predictions of least, average and maximum predicted change in temperature and precipitation from the 'best 21 models' in the IPCC 2007 report for regional changes (Christensen *et al.* 2007). Given the substantial variability among models in predicted precipitation changes, this approach encompasses a broad range in potential precipitation change from wetter to drier conditions on each mountain. Although limited to the multimodel dataset for the A1B scenario (e.g. moderate emissions and a balanced emphasis on all energy sources) and available only at relatively low resolution, the regional IPCC models have the advantage of global availability at a uniform spatial scale, with the same modelling assumptions and similar accuracy and precision for each montane area.

Ideally, we would simulate change not only for populations along these individual montane gradients, but also for the full extent of each species' entire geographic range, taking topography and dispersal into account. Although this approach is indeed feasible for well-known species in well-studied regions (e.g. La Sorte & Jetz 2010; Engler *et al.*

in press), it is not currently feasible for the taxa we consider on a global scale, given the lack of appropriate distributional data for all mountains within their geographic ranges. For this reason, the projected risk we model for each species is, conservatively, at the level of its population on an individual mountain, rather than for the species as a whole. Of course, for species whose entire geographic range is encompassed by the local gradient or mountain region, the



**Figure 1** Distribution of study sites and examples of temperature and precipitation change along elevational gradients. (a) Location of montane gradients studied for well-sampled assemblages of birds (red), non-volant small mammals (green), bats (blue), reptiles (yellow), salamanders (black) and frogs (orange). Only gradients with high, unbiased sampling effort across more than 70% of the elevational gradient and minimal impact of habitat destruction were included. Lower panels show empirical examples of elevational climate patterns under current conditions and for three levels of climate change (minimum, median and maximum, IPCC; Christensen *et al.* 2007): (b) a temperate example, (c) a tropical example and (d) an arid example. Black areas indicate current and blue areas projected precipitation as function of elevation. Black dashed lines show current, and red, orange and yellow lines show projected temperature regimes as a function of elevation.
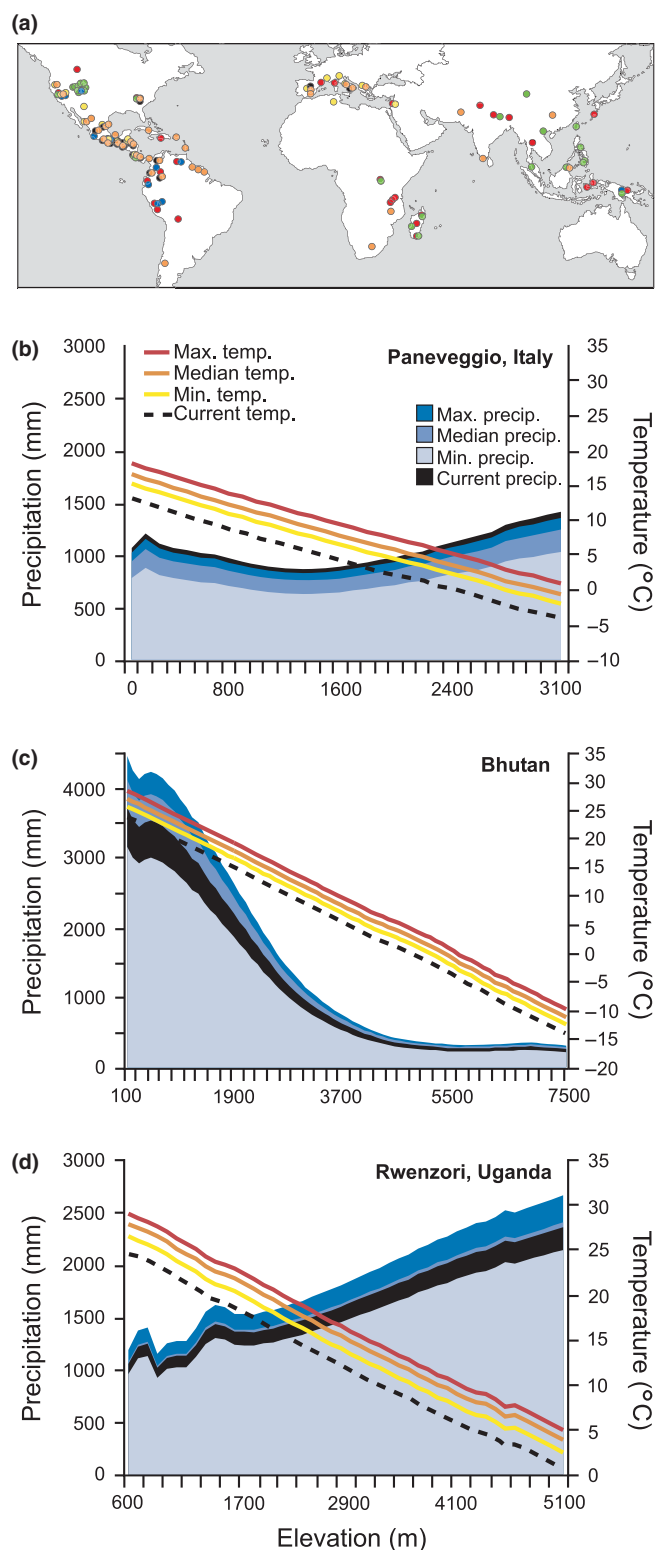
modelled risk of local extirpation is equivalent to the risk of species extinction.

Our range projections consider only temperature and precipitation, and we model limited scenarios of precipitation response. Our projections could be improved by integrating population dynamics, migratory potential, range discontinuity, thermoregulatory behaviours, acclimation, biotic interactions, co-evolutionary relationships and countless other factors. But this range of detail is not available for each species, nor would such detail be tractable at this scale of modelling. Our aim is not an exact predictive model for each species. Instead, we argue that using range-shift projections based on this comprehensive montane dataset to contrast the two main predictors of change – temperature and precipitation – will give us a relative weight of their importance in risk assessment (e.g. Pearson & Dawson 2003; Lawler *et al.* 2009), while decreasing the level of model uncertainty by incorporating an additional niche axis. Such an analysis is a vital first step towards assessing the adequacy of the current focus on climate warming for conservation forecasting.

## METHODS

### Geographical range data

The elevational ranges of frogs, salamanders, reptiles, birds, bats and non-volant small mammals (16 848 species populations) on 156 mountains were compiled for meta-analyses of elevational diversity (Fig. 1a, Appendices S1 and S2; McCain 2007, 2009). Ranges were taken directly from published articles, field guides or online databases. Study grain was local scale – field transects of samples along an elevational gradient – or regional scale, including data compiled from all potential records for an entire mountainous region. Elevational range extents were determined with range interpolation, assuming that a species was present between its highest and lowest reported elevation, in almost all of the published studies.

A dataset was used only if it met several *a priori* sampling criteria (e.g. McCain 2007; Nogués-Bravo *et al.* 2008; Appendix S1). First, sampling must have covered at least 70% of the elevational gradient. Second, sampling effort had to be substantial and not strongly biased elevationally. Third, gradients with strong elevational trends in wide-scale habitat disturbance were excluded. Fourth, published elevational ranges had to be available for all species of a vertebrate taxon. This final, high-quality subset represents only a fraction (*c.* 20–40% by taxonomic group) of the overall number of vertebrate elevational studies initially considered. Of the 16 848 populations, 8% were based on single locality occurrences or were lowland species reported as occurring below 100-m elevation. Because our range-shift model was scaled to 100-m elevational intervals (see below), the estimated range size was set at 100 m for each such species. This approximation represents a conservative assumption, with regard to the risk of extirpation, for any species whose range was smaller.

### Contemporary climate data

Mean annual temperature (MAT) and mean annual precipitation (MAP) were calculated from WorldClim data (Hijmans *et al.* 2005) at 1 km-pixel resolution for the entirety of the each mountain range and then averaged for each 100-m elevational band from the mountain base to the summit on each mountain using ArcGIS (ESRI, Redlands, CA, USA).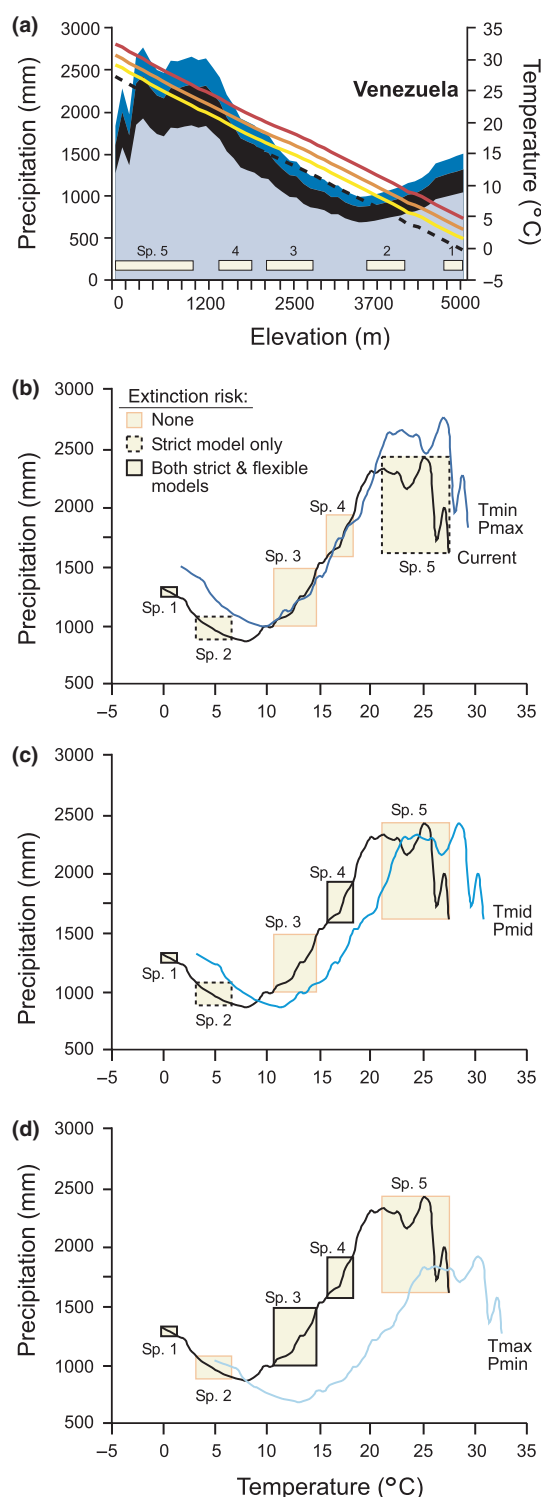 For examples of the spatial resolution of the montane environment, climate and climate change analyses, see Figs 1b,c and 2a and Appendix S3. This resolution was the finest currently possible for global precipitation data of consistent quality. For each species on each gradient, we recorded the current maximum and minimum MAT and MAP within its documented elevational range as a lower-bound estimate of tolerance limits under future conditions (e.g. Fig. 2a). Average temperatures on mountains generally decrease linearly with increasing elevation (Barry 2008); the average lapse rate for these gradients was 5.4°C per 1000 m. In contrast, precipitation trends are generally nonlinear and vary greatly among mountain gradients (Figs 1b–d and 2a). MAP increases with elevation on mountains in arid regions and at temperate latitudes (Fig. 1b,d). Tropical and subtropical montane precipitation regimes are diverse, including decreasing, increasing, bimodal and unimodal trends (e.g. Figs 1c and 2a).

### Projected climate scenarios

We recorded the temperature increase and per cent precipitation change for each gradient predicted by recent climate change models (Christensen *et al.* 2007). These predictions are regional averages for temperature and precipitation projections summarised from 21 global models in the multimodel dataset for the A1B scenario (see table 11.1 in Christensen *et al.* 2007). These climate change values for each gradient were then applied uniformly across all elevations as displacements from the current, empirical patterns for that gradient (Figs 1 and 2a). Temperature projections were examined for three levels of warming for each gradient: minimum (+1.4 to +2.8 °C), median (+2 to +3.8 °C) and maximum (+3.2 to +6.1 °C). Precipitation projections, which varied markedly among mountains and climate models, were also examined at three levels of projected change: maximum precipitation (−4 to +28%), median precipitation (−13 to +11%) and minimum precipitation (−48 to +2%). Everywhere but in southern Europe, the maximum precipitation projection was wetter than current conditions. As would be expected, the median precipitation projection tended to be moderate – slightly wetter or drier than current – with an overall average decrease of 3%. Minimum precipitation projections were highly variable regionally, but averaged 26% drier than current precipitation levels.

### Modelling range shifts

We modelled range shifts, range contractions and local population extirpation risk based on projected climate warming, alone, for the three levels of warming, then examined the combined effects of warming and precipitation change for all nine combinations of three levels of warming and three levels of precipitation change. We explored two *precipitation response scenarios* to bracket the potential response of species to changes in precipitation (Fig. 2). The first, the *strict response scenario*, assumes a fixed bioclimatic niche envelope: the future elevational range for each species is projected only at elevations that included temperature and precipitation values experienced by that species within its current range. The second, the *flexible response scenario*, assumes a more optimistic response to changes in precipitation: each future range includes elevations with precipitation greater (but not less) than in the corresponding current range, as long as predicted temperature lies within limits currently experienced by the species. The flexible response scenario expresses the possibility that species may be more likely to be limited by drier than by wetter climatic conditions than they presently experience, within their present range

**Figure 2** Examples of extirpation risk, under the strict and flexible precipitation response scenarios, for hypothetical species on an elevational gradient of temperature and precipitation. In panel (a), the spatial distributions of five hypothetical species (horizontal yellow bars) are shown along an empirical Venezuelan elevational gradient (see Fig. 1 for explanation of lines and areas). Panels (b), (c) and (d) plot the current (black line) and predicted (blue lines) temperature and precipitation conditions for three climate change projections: (b) least change (minimum temperature increase, maximum precipitation), (c) median change (median temperature increase, median precipitation) and (d) maximum change (max temperature increase and minimum precipitation). (Note that elevation decreases from left to right in panels (b), (c) and (d), inversely with temperature.) In panels (b), (c) and (d), the bioclimatic niche envelope of each hypothetical species is shown in yellow based on the climatic limits of its corresponding current geographical distribution in (a). Under the strict precipitation response scenario, if current niche limits for a species do not include predicted climatic conditions (blue line) when both temperature and precipitation are considered, at any elevation on the gradient, the species is at risk of local extirpation. Under the flexible response model, a species is expected to survive even if precipitation lies within or exceeds its current niche limits. In (b), only Sp. 1 is at risk under both models, whereas Sp. 2 and 5 are expected to survive under the flexible model (wetter conditions than those presently occupied are tolerated), but not under the strict model. In (c), Sp. 4 and, in (d), Sp. 3 and Sp. 4 are at risk of extirpation because their niches do not include the predicted climate at any point on the gradient.

Vertebrate niche responses to the interaction between precipitation and temperature may include indirect influences through habitat and food resource quality and quantity (e.g. Hawkins *et al.* 2003; McCain 2007). Indeed, most terrestrial biomes and habitats are classified based on their interacting temperature and precipitation regimes. Food resources are often related not only directly to temperature and precipitation, but also indirectly to composite temperature–precipitation effects on ecosystem variables such as net primary productivity.

Thus, for the 16 848 populations on 156 mountain gradients, we assessed 21 models: 3 temperature only and 18 combined temperature and precipitation changes under two precipitation response scenarios (nine strict vs. nine flexible). For each gradient under each model, we present results for *local population extirpations*, defined as those cases in which no portion of a species' current bioclimatic niche (as defined by temperature and/or precipitation) for a particular mountain gradient, is represented in a specified future climate projection for that mountain. To be conservative with regard to the estimation of risk, our models assume no dispersal limitation or other constraints on range shift, as long as suitable climate is available on the mountain. Taking dispersal limitation and constraints such as range-shift gaps (Colwell *et al.* 2008) into account would amplify the levels of risk we estimate.

**RESULTS**

Under projected temperature increases alone, the only population extirpations expected are 'mountaintop extirpations' in which no part of the gradient is projected to remain cool enough to allow population persistence (e.g. Colwell *et al.* 2008; La Sorte & Jetz 2010). The percentage of species predicted to have no suitable climate in 100 years on local gradients as a consequence of climate warming alone was relatively low (Table 1): 3%, on average, among all vertebrate groups (Fig. 3) and 4% among all montane regions (Fig. 4). Most vertebrate diversity lies in the bottom third of elevational gradients (McCain 2009 and references therein) and vertebrate elevational ranges are relatively large (averages herein = 920 m) compared with the projected upslope shift of thermal zones (minimum *c.* 350 m, median *c.* 600 m, maximum *c.* 930 m shift). Thus, as climate warms, most species, even those at high

of temperature. In support of this possibility, several studies have noted greater range contraction at aridifying range edges than at more mesic edges (Pounds *et al.* 1999; Epps *et al.* 2004; Parmesan & Galbraith 2004; Kelly & Goulden 2008).

Both temperature and precipitation have direct physiological repercussions on all living organisms, but vertebrates are more predictably sensitive to temperature and precipitation at high aridity (e.g. McLaughlin *et al.* 2002; Epps *et al.* 2004; Chamaillé-Jammes *et al.* 2006; Buckley 2008; Deutsch *et al.* 2008; Kearney *et al.* 2009).

**Table 1** Average population extirpation risk for montane vertebrates given 100-year predicted climate changes [per cent risk (variance)]. Three models are presented: temperature only, a flexible precipitation response scenario allowing occupation of wetter, but not drier, conditions, and a strict precipitation response scenario allowing occupation of temperature and precipitation levels in current range.

| | $n$ | Temperature only (%) | Flexible temperature and precipitation (%) | Strict temperature and precipitation (%) |
|---|---|---|---|---|
| **Region** | | | | |
| Africa | 13 | 6 (0.5) | 39 (8.7) | 49 (5.9) |
| Europe and Mediterranean | 17 | 4 (0.7) | 25 (7.1) | 31 (7.4) |
| Asia | 23 | 6 (0.9) | 13 (1.6) | 48 (5.6) |
| North America | 29 | 4 (0.8) | 5 (0.8) | 49 (6.3) |
| Central America | 52 | 3 (0.3) | 41 (1.6) | 57 (1.2) |
| South America | 22 | 3 (0.8) | 42 (4.8) | 53 (3.7) |
| **Vertebrate group:** | | | | |
| Small mammals | 33 | 7 (0.9) | 19 (5.7) | 56 (3.8) |
| Bats | 12 | 0.4 (< 0.001) | 28 (5.8) | 46 (3.8) |
| Birds | 28 | 3 (0.6) | 21 (3.8) | 39 (5.0) |
| Reptiles | 19 | 4 (0.7) | 25 (6.4) | 46 (6.7) |
| Frogs | 41 | 3 (0.6) | 33 (4.5) | 49 (3.9) |
| Salamanders | 23 | 3 (0.5) | 45 (2.9) | 63 (2.6) |

$n$ = number of montane gradients.

elevations, could survive an upslope range shift without the lower elevational range limit exceeding the top of the gradient. Elevational range size does become smaller with decreasing latitude, however, for all of these vertebrate groups except small mammals (McCain 2009), and, unlike plants (Körner 1999), relatively few vertebrate species are endemic to high alpine regions.

Incorporating predicted precipitation changes into the models produced a 10-fold increase in local population extirpation risk for montane vertebrates (Fig. 3, Table 1). Under strong precipitation limitations, the nonlinear nature of montane precipitation regimes created high variability in local extirpation risk among taxonomic groups and geographic regions. Although temperature change alone yielded only mountaintop extirpations, when precipitation changes were also taken into account, discordant shifts in temperature zones and precipitation levels also predicted low elevation and mid-gradient local extirpations, where temperature was predicted to remain suitable but precipitation was not (Fig. 2). Not surprisingly, the highest population extirpation risks were predicted under models that assume the strict response scenario ($c.$ 50% extirpation). Models implementing the flexible response scenario, which assumed that wetter, but not drier, conditions than at present allowed survival (as long as temperatures were appropriate), predicted population extirpation risks midway between those predicted for temperature alone and the strict scenario models ($c.$ 28% extirpation; Figs 3 and 4, Appendix S2).

Population extirpation risk, which generally increased with both warming and drying trends, peaked at minimum precipitation levels globally ($c.$ 56% extirpation; Fig. 5), although species already adapted to arid conditions may be more resilient to additional aridification than the models assume. Species inhabiting arid-based mountains had significantly lower population extirpation risk (strict response scenario models < 10%; flexible response scenario models < 26%) than species inhabiting humid-based mountains under both precipitation response scenarios (strict: Mann–Whitney U = −2.74, $P = 0.003$;

flexible: U = −3.51, $P = 0.0002$). The spatial scale had only a minor impact on the results, as population extirpation risks based on locally sampled transects and regionally compiled data were nearly indistinguishable. Local transects predicted slightly higher extirpation risks ($c.$ 8%) than regional data, but the difference arises primarily from slightly smaller average range sizes on local gradients (Mann–Whitney U = −3.56, $P < 0.0001$).

Under both precipitation response scenarios, salamanders and frogs were subject to the most extreme population extirpation risks, particularly at the lowest precipitation levels, with more than 80% of the amphibian species on each mountain gradient consistently facing local population extirpation (Fig. 3, Table 1). With the most drastic drying scenarios and the highest concentration of amphibians, Central America had the highest predicted level of local population extirpations (27–93%; Fig. 4), followed by South American and sub-Saharan African vertebrates. In contrast, vertebrates in Asia, Europe and the Mediterranean region, where smaller changes in precipitation are predicted, had lower predicted population extirpation risks, although this result may be in part due to a research focus on groups with lower risks (e.g. birds, reptiles, Fig. 3). The North American species, dominated by terrestrial small mammals, were most sensitive to varying the precipitation response scenario (Figs 4 and 5). These datasets were mostly from western, arid-based mountains, where wettest conditions lie at higher elevations. In our models, as ranges shifted upslope with temperature increases, species encountered wetter conditions than their current niches, demonstrating how critical the assumed response to precipitation is to climate change risk assessment. Globally, both the precipitation response scenarios we simulated revealed an interaction between warming and precipitation change (Figs 3 and 4). Regardless of whether precipitation was projected to increase or decrease, the spatial discordance between temperature and precipitation resulted in considerably higher population extirpation risks than for temperature changes alone.

## DISCUSSION

Species distribution models, especially simple bioclimatic models like ours, can be inaccurate due to a multitude of biological characteristics that are not included in the models (Davis $et\ al.$ 1998; Pearson & Dawson 2003; Buckley 2008; Appendix S1). Again, our goal here is not to produce detailed risk models for each species, but to contrast the relative risk of a focus on climate warming alone, vs. a more comprehensive focus on both warming and precipitation changes for montane communities. In this context, simple range projection models using a globally informative dataset may be quite illustrative.

Nonetheless, several caveats should be mentioned. Certain kinds of increased biological realism might well result in higher modelled estimates of population extirpation risk. The percentage and connectedness of intact habitats in highly fragmented landscapes, strong species interactions like host plant specificity (e.g. Pelini $et\ al.$ 2009; Appendix S1), variable dispersal distances (e.g. Deutsch $et\ al.$ 2008; Engler $et\ al.$ 2009), disease interactions (e.g. Pounds $et\ al.$ 2006), seasonal precipitation shifts, and many population and energetic relationships (e.g. Kearney $et\ al.$ 2009; Appendix S1) could well reduce the chance for population survival under climate change. The prospects may be worse for other groups; vertebrate elevational range sizes tend to be larger than most insect and plant elevational ranges and vertebrates may thus have a greater scope of niche response to climate change (e.g. Gaston 1996 and references therein).
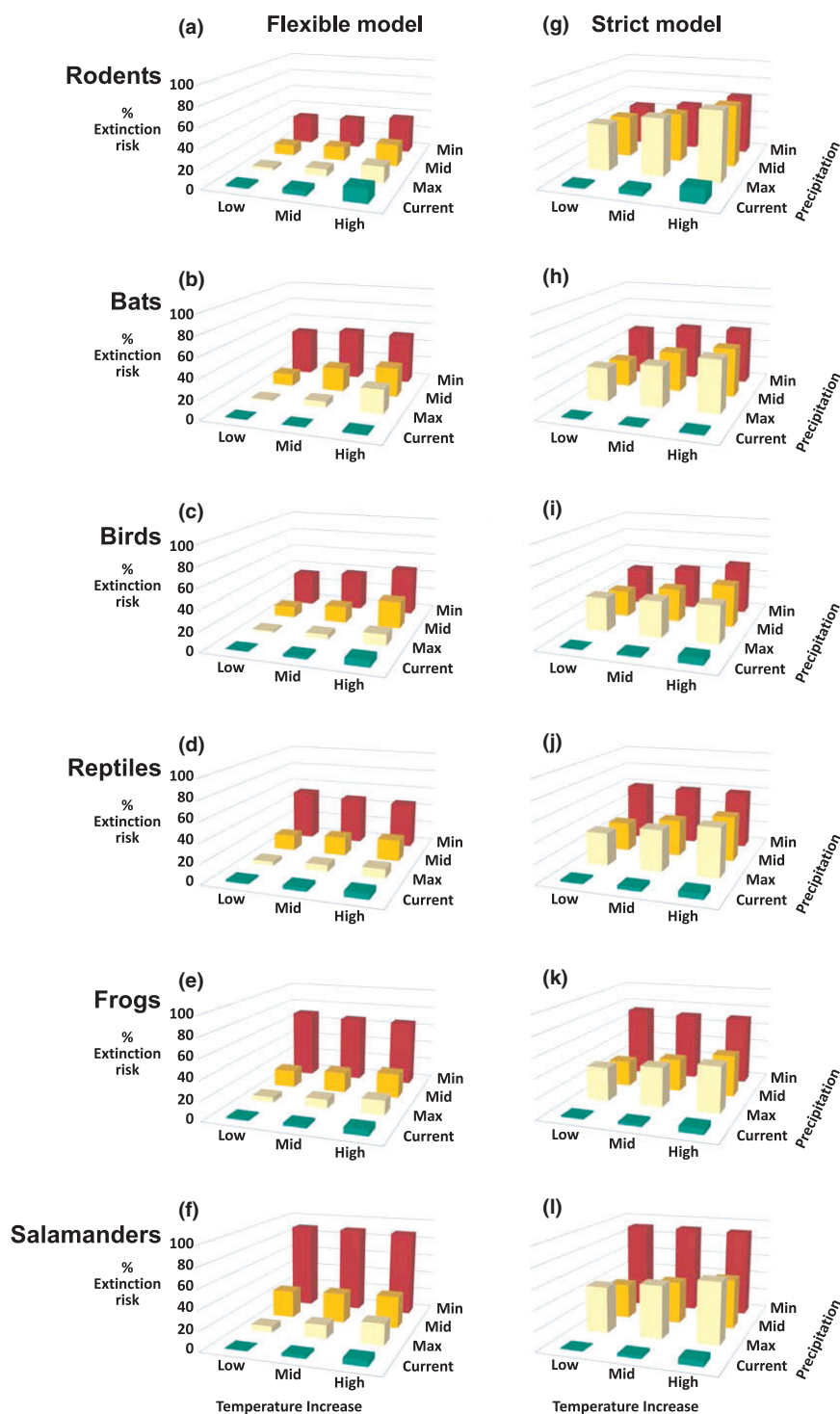
**Figure 3** Extirpation risk for montane vertebrates given 100-year predicted changes in temperature and precipitation for each taxon (Christensen *et al.* 2007). Three levels of temperature increase were modelled: lowest (Low), median (Mid) and highest (High) predicted increase. Four levels of precipitation were modelled: no precipitation effect (Current) and the highest (Max), median (Mid) and minimum (Min) precipitation. Two models of species' responses to climate change were tested: a strict precipitation response scenario (right column), in which only temperature and precipitation levels found within the species' current range were used to predict the future range; and a flexible precipitation response scenario (left column), in which elevations with increased (but not decreased) precipitation were also included in predicting future ranges.

Other types of biological realism might result in lower estimates of population extirpation risk for vertebrates. Because our estimates of elevational range size are based on local or regional elevational gradients, they may underestimate the true elevational range (and thus the climatic tolerances) for many species, especially those with large geographical ranges. La Sorte & Jetz (2010) showed that incorporating 'lateral dispersal' to suitable montane climates 100–1000 km away reduced bird extinction risks, but this benefit would be reduced for less
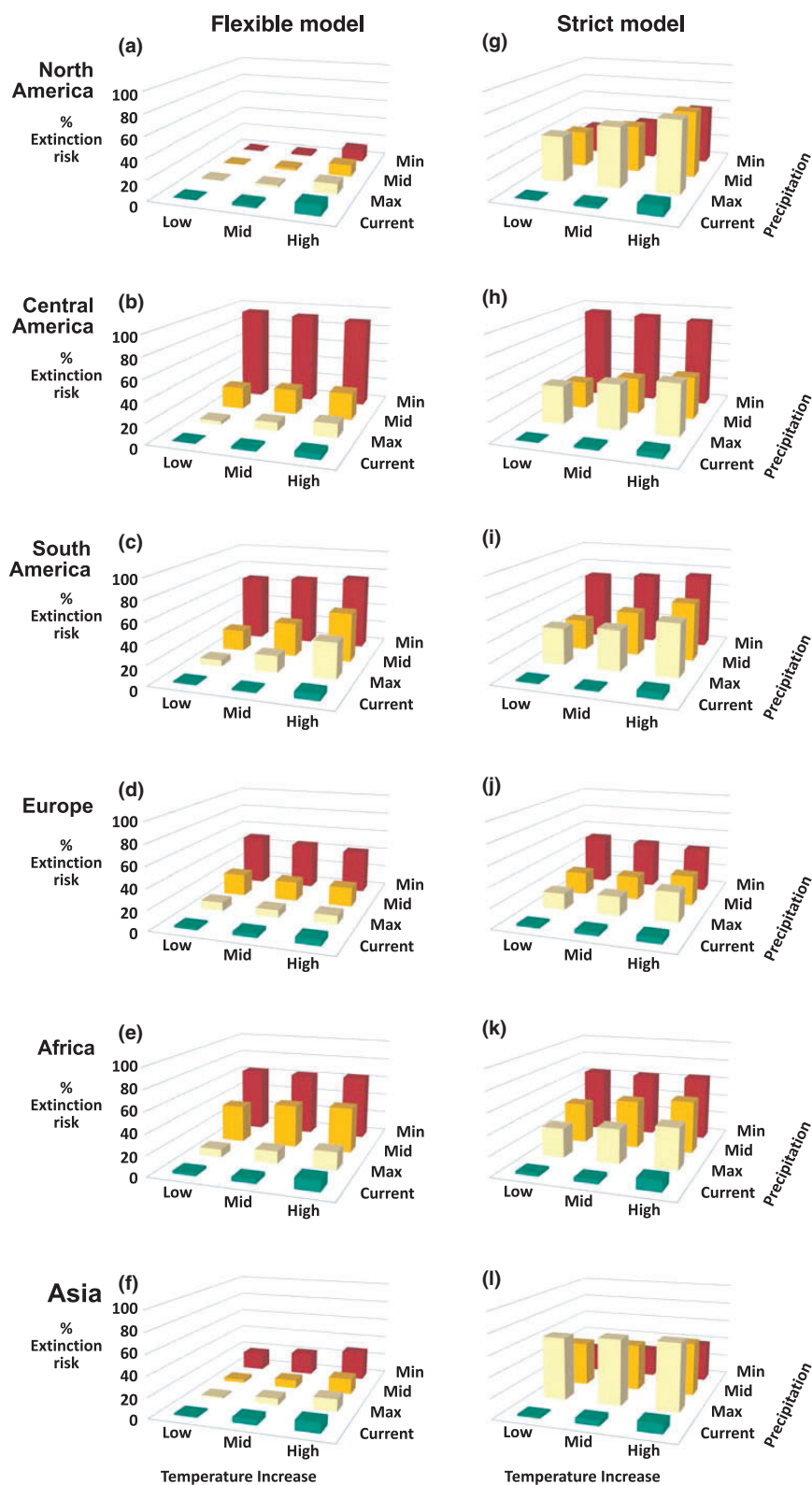
**Figure 4** Extirpation risk for montane vertebrates given 100-year predicted changes in temperature and precipitation for each geographic region. Three levels of temperature increase were modelled: lowest (Low), median (Mid) and highest (High) predicted increase. Four levels of precipitation were modelled: no precipitation effect (Current), the highest (Max), median (Mid) and minimum (Min) precipitation. Two models of species' responses to climate change were tested: a strict precipitation response scenario (right column), in which only temperature and precipitation levels found within the species' current range were used to predict the future range; and a flexible response scenario (left column), in which elevations with increased (but not decreased) precipitation were also included in predicting future ranges.
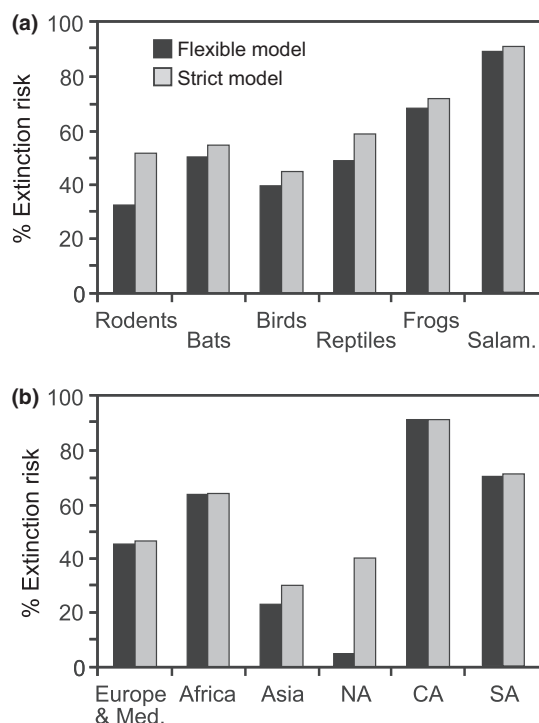
**Figure 5** Average extirpation risk for montane vertebrates estimated for all three levels of temperature and the minimum precipitation predictions for each taxonomic group and geographic region. The strict precipitation response scenario (grey bars) assumes range projections in which only temperature and precipitation levels found within the species' current range were used to predict the future range; and the flexible precipitation response scenario (black bars) is based on simulations where elevations with increased (but not decreased) precipitation were also included in predicting future ranges.

vagile vertebrates. Climatic tolerances may also be underestimated even when full ranges are known (Sunday *et al.* 2010; see also Appendix S1). Climate on a smaller spatial scale than we were able to model could also be important in reducing risk. Microhabitat refuges are increasingly thought to play a critical role in protecting local populations from climatic extremes (e.g. Randin *et al.* 2009). Flexibility in acclimation abilities, rapid evolutionary adaptation, release from historical land-use limitations and positive population responses to aridity could also offer more optimistic projections (e.g. Davis & Shaw 2001; Chamaillé-Jammes *et al.* 2006; Rowe 2007; Kearney *et al.* 2009; Crimmins *et al.* 2011). In light of the complexity of response to climate change, the results presented here must be interpreted with caution, in a qualitative context for global conservation and research priorities.

With climate warming, mountain gradients, if they have sufficient intact habitat, are thought to mitigate extinction risks for biodiversity by providing threatened species with access to cooler temperatures at relatively small dispersal distances (e.g. Pounds *et al.* 1999; Davis & Shaw 2001; Parmesan & Galbraith 2004; Colwell *et al.* 2008; Moritz *et al.* 2008; Chen *et al.* 2009; Engler *et al.* 2009; Randin *et al.* 2009). As temperature increases, species can track thermal zones to higher elevations to stay within their current temperature niche. But this temperature-tracking scenario assumes either that species have little dependence on precipitation or that the montane precipitation regime changes concordantly with directional temperature change. Using range-shift projections that contrast the importance of temperature

and precipitation change for various assumed levels of response to precipitation change (no dependency, a flexible response or a strict response), we show that the discordance in projected temperature and precipitation regimes on mountains under alternative climate change scenarios can have a drastic impact on extirpation risk for montane vertebrate populations.

Mountains would indeed appear to reduce local extirpation risks by allowing species to track thermal zones when temperature is the only critical niche element; our models estimate low extirpation risks for montane vertebrate communities when only temperature changes (3–4%; Table 1). Because temperature-change extirpations are mountain-top extirpations, under assumptions of unhindered migration ability, only those species with narrow elevational ranges at the highest elevations are at high risk for extirpation. Already species are shifting their ranges upslope on mountains with increasing temperatures for both plants (e.g. Grabherr *et al.* 1994; Pauli *et al.* 2007; Lenoir *et al.* 2008; Appendix S1) and animals (e.g. Parmesan 1996; Pounds *et al.* 1999; Moritz *et al.* 2008; Chen *et al.* 2009; Appendix S1), although, to date, claims of mountain-top extinction have been rare (Pounds *et al.* 1999). In all of these empirical studies, however, only a subset of the species shifted upslope as expected, whereas many species' ranges remained unchanged elevationally, contracted *in situ* or expanded downward. In some of the cases of downward shifts or expansions, authors attributed the shift to a strong precipitation response or a land-use change (e.g. Rowe 2007; Moritz *et al.* 2008; Chen *et al.* 2009; Crimmins *et al.* 2011). Clearly, niches of species and hence their geographic and elevational ranges are based on a multitude of climatic and biotic factors. The individualistic nature of reconstructed Pleistocene range shifts suggest that species respond in complex ways to these myriad factors (Graham & Grimm 1990; Davis & Shaw 2001; Lyons 2005).

When a species' range is forced upslope by a warming climate but the species encounters a substantially novel precipitation regime at higher elevations, local, small-scale environmental gradients may be inadequate to mitigate extirpation risks through niche tracking. Precipitation increases with elevation on most arid-based and temperate mountains, whereas, on tropical and semi-tropical mountains, precipitation can be unimodal, bimodal, and decreasing or increasing with elevation depending on local climatic and geographic characteristics (Fig. 1; Barry 2008). This discordance in spatial climatic trends and with climate change is critical to predicting extirpation risks for montane species (Fig. 2), as illustrated clearly by the 10-fold increase in population extirpation risk when models include both temperature and precipitation change on mountains (Figs. 3 and 4). Some empirical work has already detected the importance of precipitation in range shifts and population extinctions (Pounds *et al.* 1999; McLaughlin *et al.* 2002; Epps *et al.* 2004; Parmesan & Galbraith 2004; Kelly & Goulden 2008; Crimmins *et al.* 2011). Additionally, several climate change experiments with plants have found strong, species-specific phenological trends with precipitation change and precipitation–temperature interactions (Cleland *et al.* 2007 and references therein; Appendix S1). Other plant manipulation studies have found a smaller role for precipitation, particularly those experiments that augmented water (Cleland *et al.* 2007 and references therein; Appendix S1).

Temperature and precipitation are the two abiotic niche axes most often associated with species range limits and trends in biodiversity (e.g. Hawkins *et al.* 2003; Parmesan & Galbraith 2004; McCain 2007; and references therein) and are key factors in global climate models (e.g. Christensen *et al.* 2007; Rosenzweig *et al.* 2007). On probabilistic

grounds alone, we may expect that the greater number of niche axes included in an analysis of risk, the greater the calculated risk values. Indeed, incorporating additional niche axes (e.g. habitat, food or host availability) in our models, if it were feasible, might well yield increased risk values. In contrast, if the effects of precipitation on species' ranges could be modelled independent of temperature, the predicted risk might be generally lower than for interacting temperature and precipitation, just as it was lower for temperature alone. Niche-based range projections based on precipitation changes alone, however, are much more challenging to model, due to nonlinear precipitation trends. For example, if precipitation is symmetrically bimodal elevationally (e.g. Fig. 2) and a species occurs only within the lower mode, it becomes difficult to project species ranges into the future based solely on precipitation regime without making a series of *ad hoc* decisions about elevational range continuity and other range determinants. Indeed, these complications emphasise the importance of the interaction between the two pre-eminent determinants of floral and faunal niches – temperature and precipitation – in determining both species range limits and response to climate change. And in that context, our results are quite clear – species extirpation risks may well be an order of magnitude higher when their interaction is included.

The range-shift projections based on the IPCC regional models with the highest drying conditions (Christensen *et al.* 2007) were the most worrisome for extirpation risk of montane vertebrate populations (Fig. 5). Regardless of the level of temperature change and flexible or strict response to precipitation, extirpation risks rose steeply, on average to 50–60%, under the highest aridification scenarios globally (red bars in Figs 3 and 4). Water-dependent ectotherm vertebrates displayed the highest risks with aridification (salamanders = 89–91%; frogs = 68–71%), particularly in Central and South America, where drastically drier conditions are predicted in 100 years, in some cases dropping as low as 50% of current precipitation levels (Christensen *et al.* 2007). Salamanders and frogs are dependent on water for reproduction and reach high diversities on tropical wet mountains (e.g. Pounds *et al.* 1999; Ricketts *et al.* 2005), particularly in Latin America, which is thus predicted to experience the majority of the extreme risks for amphibians on mountains. A higher extirpation risk has been detected for a few montane populations experiencing aridification, including American pika (*Ochotona princeps*; Parmesan & Galbraith 2004) and desert bighorn sheep (*Ovis canadensis*; Epps *et al.* 2004), cloud forest birds and frogs (Pounds *et al.* 1999), and Mediterranean-adapted trees and plants (Kelly & Goulden 2008). Variability in precipitation increased the speed of population extirpation in checkerspot butterfly populations (McLaughlin *et al.* 2002). A few climate change modelling studies have found that precipitation change can be critical, particularly in arid environments (e.g. Kueppers *et al.* 2005; Li *et al.* 2009; Appendix S1).

The dominance of particular species-specific responses to the interaction of temperature–precipitation change will determine the accuracy of our estimates of population extirpation risk for each mountain. If most species respond critically only to temperature, then overall montane extirpation risks are low for vertebrates. In contrast, if most species respond strongly to both temperature and precipitation, risks are much higher. In reality, species will fall along this continuum and overall risk will be intermediate to these two extreme cases. Nonetheless, even intermediate risk levels, according to our models, are dangerously high for montane biodiversity – 30–40% population extirpation risk for local montane vertebrate communities. Thus, our models have the potential to reduce model uncertainty and increase realism and complexity by incorporating these two principal niche axes. We advocate not only a more focused effort to study combined temperature and precipitation effects on natural populations, but also an agenda shift towards increased funding for global and elevational monitoring of precipitation and for improved modelling of regional precipitation change. A 10-fold or even a threefold increase in population extirpation risk associated with discordant changes in precipitation and temperature is too high to disregard because precipitation is more difficult to model, assess and measure.

## AUTHOR CONTRIBUTION

CMM designed the study, gathered the data and ran the analyses; RKC contributed to the research ideas, conceptual formulation and methodology of data analysis; and both CMM and RKC wrote the paper and prepared the figures.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Supplemental Literature Cited.

**Appendix S2** List of the elevational gradients for each vertebrate group used to model climate change risk, including details on locality, citation, mountain height, study scale, number of species, percentage of species only at single elevation, climate, region of IPCC climate change predictions, and the average extirpation risk under the various models.

**Appendix S3** Supplementary methods.

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