



Altitudinal Range Shifts of Montane Amphibians and Changing Rainfall Patterns: A Review of the Evidence

Aurelie Ndlovu^{1*}, Suresh Sato², Magnus Eze³

¹Department of Life Sciences, Danube School of Life Sciences, Uzbekistan

²Department of Life Sciences, Tagus Institute for Advanced Life Sciences, Australia

³Department of Life Sciences, Parana Graduate Institute of Life Sciences, Canada

Article Info

Volume 1, Issue 1, 2026

[doi: 10.62715/ijzs.2026.v1.i1.pp1-7](https://doi.org/10.62715/ijzs.2026.v1.i1.pp1-7)

Received: 14 December 2025

Accepted: 24 February 2026

Published: 04 May 2026

Abstract

Most accounts of how mountain animals respond to climate change are written in terms of temperature: as the air warms, species are expected to move upslope. Amphibians fit this account poorly. Their permeable skin, their unshelled eggs and their dependence on standing or flowing water for breeding tie them to moisture at least as closely as to heat, and on many mountains rainfall, mist and cloud are changing in ways that do not follow temperature. This narrative review examines what the published literature says about altitudinal range shifts in montane amphibians and about the part that changing rainfall plays in them. It sets out the physiological and reproductive reasons for expecting a moisture effect, describes the directions of shift that different combinations of warming and wetting or drying should produce, and then considers the observational record from tropical cloud forests, the high Andes, Madagascar and temperate ranges. The record is thin, geographically uneven and entangled with disease and land-use change. Upslope movement has been documented, yet few studies separate the effect of rainfall from that of temperature. The review closes with the survey designs and measurements that would allow that separation.

Keywords: *Montane amphibians, Elevational range shift, Rainfall change, Cloud forest, Water balance, Resurvey studies*

© 2026 Aurelie Ndlovu et al. This is an open access article under the CC BY license (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

1. Introduction

Mountains compress climate. A walk of a few hours up a tropical slope crosses a range of temperature and humidity that would take weeks to cross on level ground, and amphibian communities change almost completely along the way. Many frogs and salamanders occupy elevational bands only a few hundred metres deep. Janzen (1967) argued that this narrowness is itself a product of climate: where seasons are weak, organisms never experience the conditions of the slope above or below them and evolve narrow tolerances, so that a tropical mountain pass is a greater physiological barrier than a temperate one of the same height. A fauna built in this way has little room to absorb change.

The broad pattern of response to recent warming is well established. Syntheses across plants and

* Corresponding author: Aurelie Ndlovu, Department of Life Sciences, Danube School of Life Sciences, Uzbekistan. E-mail: aurelie.ndlovu@danube.edu

© 2026 Aurelie Ndlovu et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

animals show that distributions have moved toward the poles and toward higher ground in a direction consistent with warming (Parmesan and Yohe, 2003; Chen et al., 2011). Amphibians are poorly represented in those syntheses, although they are the most threatened class of vertebrates and their unexplained declines have been concentrated in montane, stream-breeding species (Stuart et al., 2004). The gap matters because amphibians are not simply small ectotherms that follow isotherms. Water governs where they can live, when they can be active and whether they can breed.

This article reviews the published evidence on altitudinal range shifts of montane amphibians with particular attention to rainfall. It asks three things of the literature: why changes in moisture should be expected to move amphibian ranges, what shifts have in fact been documented, and how far those shifts can be attributed to rainfall as distinct from temperature, disease or habitat loss.

2. Scope and Approach

The article is a narrative review of the published literature. It draws on resurvey studies, long-term monitoring, physiological work and modelling papers that bear on elevational distributions of frogs, toads and salamanders, together with studies of other taxa where they clarify a mechanism. No systematic search was carried out and no quantitative synthesis is attempted, because the studies are too few and too varied in method to be pooled. Rainfall is taken broadly to include the amount, timing and intensity of precipitation and, on cloud-affected slopes, the frequency of mist and the height of the cloud base.

3. Why Moisture Constrains Amphibian Ranges

Three features of amphibian biology link distribution to water. They are treated separately here because each responds to a different aspect of rainfall.

3.1. Water balance and activity

Amphibian skin offers little resistance to evaporation in most species, and an animal away from water loses mass at a rate set by the vapour pressure deficit of the air around it (Wells, 2007). Foraging, calling and dispersal are therefore confined to humid nights and to the hours after rain. A drier climate does not need to kill adults outright to reduce a population. It shortens the time in which they can feed and find mates, and it does so most severely for terrestrial and arboreal species that cannot retreat to a stream. Because warm air holds more water vapour, warming without added rainfall increases evaporative demand, so temperature and moisture effects are physiologically coupled even when they are statistically distinct.

3.2. Breeding sites and hydroperiod

Most montane amphibians with aquatic larvae depend on pools, seeps and low-order streams whose persistence is set by seasonal rainfall. If a pool dries before metamorphosis the cohort is lost, and a run of short hydroperiods can remove a local population within a few generations. Direct-developing species, which lay eggs in moss or leaf litter, are freed from pools but are exposed to desiccation of the clutch itself. Reviews of precipitation effects stress that extremes count as much as means: both drought and scouring floods reduce recruitment, and the spacing of rain events can matter more than the annual total (Walls et al., 2013).

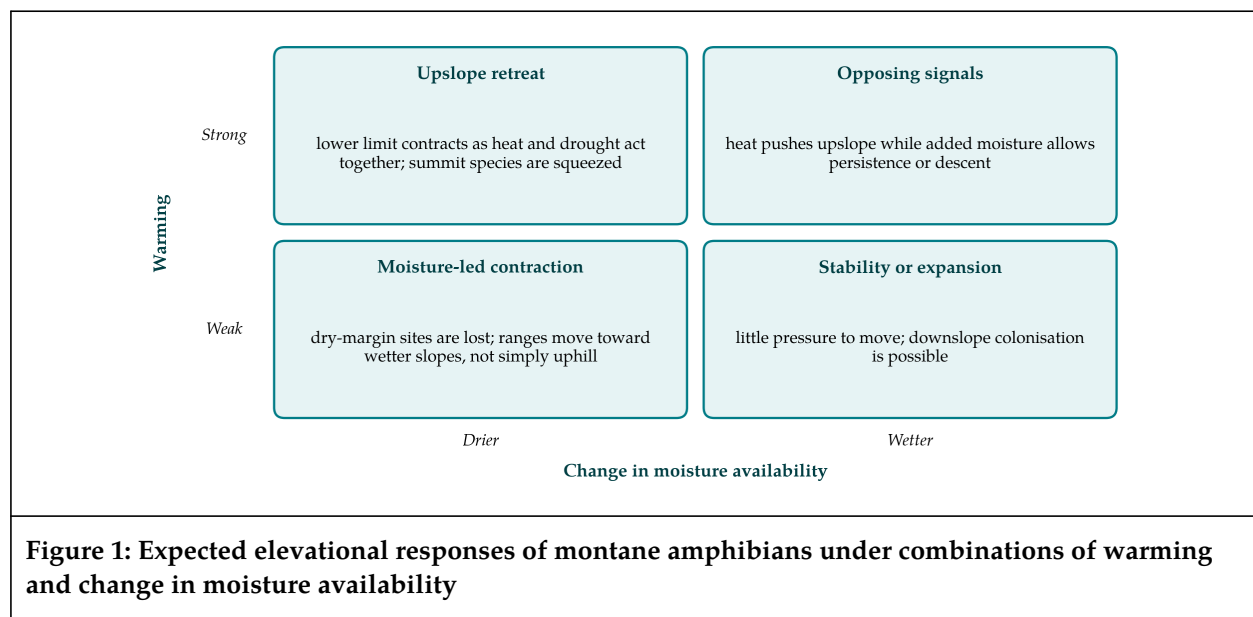
3.3. Cloud, mist and the montane moisture regime

On many tropical mountains a large share of the moisture reaching the forest arrives as cloud water intercepted by vegetation, and dry-season mist keeps litter and epiphytes damp when rain is absent. Climate simulations indicate that warming raises the altitude at which cloud forms during the dry season (Still et al., 1999), and regional modelling for Costa Rica suggests that clearing lowland forest upwind has a similar effect on the clouds of the adjacent cordillera (Lawton et al., 2001). A rising cloud base is, for a cloud forest frog, a change in rainfall regime that no rain gauge at the foot of the mountain will record.

4. Expected Directions of Shift

If temperature alone set range limits, the expectation would be simple: lower limits retreat upslope, upper limits advance, and species already at the summit run out of ground. Colwell *et al.* (2008) added that tropical lowlands have no warmer source fauna to replace the species that leave, and that gaps between a species' current and future ranges may be too wide to cross. Moisture complicates this picture. Figure 1 sets out the directions of shift that follow from combining the two drivers. Where warming is accompanied by drying, both push the lower limit upward. Where it is accompanied by wetting, the two pull in opposite directions and the net movement may be small, absent or downhill.

Evidence from other groups shows that the off-diagonal cases are real. Plant species in California moved their elevational optima downhill over the twentieth century, tracking an improved climatic water balance despite warming (Crimmins *et al.*, 2011). Resurveys of birds in the Sierra Nevada found that rising temperature tended to push species upslope while increased precipitation pulled them down, giving a heterogeneous set of shifts (Tingley *et al.*, 2012). A global synthesis concluded that a substantial fraction of documented shifts run against the simple poleward and upward expectation (Lenoir and Svenning, 2015). McCain and Colwell (2011) modelled montane vertebrates on elevational gradients worldwide and showed that projected risk rises sharply once changes in precipitation are considered alongside temperature. Amphibians, as the most water-dependent land vertebrates, should show these effects most strongly.



5. The Observational Record

Direct documentation of elevational shifts in amphibians comes from a small number of mountains. Table 1 summarises the principal studies and the role each assigns to moisture.

5.1. Tropical cloud forests

The Monteverde study remains the clearest case in which moisture, and not temperature as such, was proposed as the driver. Pounds *et al.* (1999) linked the collapse of anuran populations in the late 1980s, including the disappearance of the golden toad, to an increase in the number of dry-season days without mist, and related that trend to sea surface temperatures. Over the same period bird species from lower slopes established themselves in the cloud forest and highland lizard populations declined. The pattern is one of a whole community responding to a lifting cloud base. What it does not show is a measured upslope movement of the amphibians themselves: on an isolated ridge with little higher ground, the response was loss.

Table 1: Representative studies bearing on elevational change in montane amphibians and the role each gives to moisture

Region and source	Evidence	What was reported	Role of moisture
Monteverde, Costa Rica (Pounds et al., 1999)	Long-term monitoring	Anuran population crashes; lowland birds colonising upslope	Central: fewer dry-season mist days
Cordillera Vilcanota, Peru (Seimon et al., 2007)	Repeat field surveys	Three anurans breeding in newly deglaciated terrain	Indirect: meltwater ponds created by ice retreat
Tsaratana, Madagascar (Raxworthy et al., 2008)	Resurvey after a decade	Upslope displacement of amphibians and reptiles	Not separated from warming
Andes of Ecuador (Bustamante et al., 2005)	Historical comparison	Losses of species and abundance in seven communities	Considered with warming and disease
Neotropical highlands (Pounds et al., 2006)	Timing of disappearances	Harlequin frog extinctions clustered at mid elevations	Cloud cover altering temperature for a pathogen
Philippine forest (Scheffers et al., 2014)	Microclimate measurement	Microhabitats buffer frogs against extremes	Humid refuges may delay shifts

5.2. The high Andes

At the other extreme of the gradient, [Seimon et al. \(2007\)](#) recorded three anuran species breeding in ponds on ground exposed by retreating glaciers in southern Peru, at elevations above any previously known for amphibians. Here the upper limit advanced because warming created new aquatic habitat, a hydrological effect and not a thermal one in the narrow sense. The same surveys detected the chytrid fungus *Batrachochytrium dendrobatidis* in these populations, a reminder that pathogens can travel upslope with their hosts. Historical comparisons in Ecuador found marked losses from Andean anuran communities, with climate, disease and their interaction all considered as causes ([Bustamante et al., 2005](#)).

5.3. Madagascar and other resurveys

On the Tsaratana massif, [Raxworthy et al. \(2008\)](#) repeated elevational surveys of amphibians and reptiles after about a decade and reported that the ranges of many species had been displaced upslope, in the direction expected from regional warming. The authors described the appraisal as preliminary, since two survey periods cannot distinguish a trend from year-to-year fluctuation. The century-long resurvey of small mammals in Yosemite ([Moritz et al., 2008](#)) shows what a fuller record looks like: upward contraction of high-elevation species set against expansion of some lowland ones, with detection modelled at both dates. No amphibian data set of similar length and design has yet been published for a tropical mountain, and for the species-rich ranges of South and Southeast Asia the published assessments are largely projections ([Bickford et al., 2010](#)).

6. Confounding Factors

Attribution is difficult for amphibians because the period of climatic change coincides with the spread of chytridiomycosis. [Pounds et al. \(2006\)](#) proposed that warming, acting through cloud cover, had shifted temperatures at mid elevations toward the optimum of the fungus and so triggered the extinctions of harlequin frogs. [Lips et al. \(2008\)](#) reanalysed the timing of declines and argued that they are better explained by the wave-like spread of an introduced pathogen, with no need for a climatic trigger. Later work pointed to temperature variability associated with El Niño events as a contributing factor ([Rohr and Raffel, 2010](#)). The debate is unresolved in detail, but its lesson for range-shift studies is clear. A lower

range limit that retreats upslope may record drought, heat, disease, or disease made worse by weather, and occurrence data alone cannot tell these apart.

Land use adds a further difficulty. Forest clearance is usually concentrated on lower slopes, so the loss of low-elevation populations to habitat conversion produces the same apparent upward shift in a species' lower limit as climate would. Clearance also alters local humidity and, as noted above, may change cloud formation over neighbouring mountains. Studies that report a shift without a record of habitat change at the resurveyed sites leave this alternative open.

7. Problems of Detection

Amphibians are hard to find, and how hard depends on the weather. Calling activity and surface movement rise after rain, so a survey in a dry year will record fewer species at the dry margin of a gradient than a survey in a wet year, even if nothing has changed. This creates a specific hazard: a change in rainfall can generate an apparent range shift through detection alone. Occupancy models, which estimate the probability of detection from repeated visits, were developed for this problem ([MacKenzie *et al.*, 2002](#)), and [Tingley and Beissinger \(2009\)](#) showed how they can be applied to comparisons between historical and modern surveys. Few amphibian resurveys have used them, partly because the historical surveys were rarely repeated within a season.

Microhabitat adds a second complication. Tree holes, epiphytes, deep litter and rock crevices hold moisture and damp temperature swings, and animals using them experience a milder climate than a weather station records ([Scheffers *et al.*, 2014](#)). Buffering of this kind may allow populations to persist at an elevation for years after the open-air climate has become unsuitable, so that the distribution lags behind the climate and then changes abruptly.

8. Gaps and Future Work

Four needs stand out. The first is repeated, standardised elevational transects with several visits per season, so that detection can be modelled and trends separated from fluctuation. The second is moisture data collected on the slope itself: rainfall, mist frequency, litter moisture and pool hydroperiod at the surveyed elevations, since lowland gauges and gridded climate products resolve mountain moisture poorly. The third is concurrent screening for chytrid infection and recording of habitat condition, without which disease and land use cannot be excluded. The fourth is geographic. The Western Ghats, the eastern Himalaya, the mountains of Southeast Asia and New Guinea, and the Eastern Arc of Africa hold large endemic amphibian faunas and have little published resurvey work.

Physiological measurements would strengthen inference. Rates of evaporative water loss, dehydration tolerance and the hydroperiod required for larval development can be measured for a species and used to predict where on a gradient a given change in rainfall should bite. Agreement between such predictions and observed changes at range margins would be stronger evidence for a rainfall effect than correlation with climate records alone.

9. Conclusion

The published record shows that montane amphibian distributions have changed on several mountains over recent decades and that some of those changes are upslope. It does not yet show how much of the change is due to rainfall. The physiological case for a strong moisture effect is sound, and studies of plants and birds confirm that water balance can move ranges against the direction set by temperature. For amphibians the decisive observations, long resurvey series with on-slope moisture measurements and disease screening, remain to be made. Until they are, projections of upslope retreat based on temperature alone should be read as one scenario among several.

Conflict of interest

To be declared by the author(s) before publication.

Funding

To be declared by the author(s) before publication.

References

- Bickford, D., Howard, S.D., Ng, D.J.J. and Sheridan, J.A. (2010). [Impacts of climate change on the amphibians and reptiles of Southeast Asia](#). *Biodiversity and Conservation*, 19: 1043-1062. <https://doi.org/10.1007/s10531-010-9782-4>
- Bustamante, M.R., Ron, S.R. and Coloma, L.A. (2005). [Cambios en la diversidad en siete comunidades de anuros en los Andes de Ecuador](#). *Biotropica*, 37: 180-189.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D. (2011). [Rapid range shifts of species associated with high levels of climate warming](#). *Science*, 333: 1024-1026. <https://doi.org/10.1126/science.1206432>
- Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. and Longino, J.T. (2008). [Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics](#). *Science*, 322: 258-261. <https://doi.org/10.1126/science.1162547>
- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. and Mynsberge, A.R. (2011). [Changes in climatic water balance drive downhill shifts in plant species' optimum elevations](#). *Science*, 331: 324-327. <https://doi.org/10.1126/science.1199040>
- Janzen, D.H. (1967). [Why mountain passes are higher in the tropics](#). *The American Naturalist*, 101: 233-249. <https://doi.org/10.1086/282487>
- Lawton, R.O., Nair, U.S., Pielke, R.A. and Welch, R.M. (2001). [Climatic impact of tropical lowland deforestation on nearby montane cloud forests](#). *Science*, 294: 584-587. <https://doi.org/10.1126/science.1062459>
- Lenoir, J. and Svenning, J.-C. (2015). [Climate-related range shifts: a global multidimensional synthesis and new research directions](#). *Ecography*, 38: 15-28. <https://doi.org/10.1111/ecog.00967>
- Lips, K.R., Diffendorfer, J., Mendelson, J.R. and Sears, M.W. (2008). [Riding the wave: reconciling the roles of disease and climate change in amphibian declines](#). *PLoS Biology*, 6: e72. <https://doi.org/10.1371/journal.pbio.0060072>
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. and Langtimm, C.A. (2002). [Estimating site occupancy rates when detection probabilities are less than one](#). *Ecology*, 83: 2248-2255.
- McCain, C.M. and Colwell, R.K. (2011). [Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate](#). *Ecology Letters*, 14: 1236-1245. <https://doi.org/10.1111/j.1461-0248.2011.01695.x>
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. and Beissinger, S.R. (2008). [Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA](#). *Science*, 322: 261-264. <https://doi.org/10.1126/science.1163428>
- Parmesan, C. and Yohe, G. (2003). [A globally coherent fingerprint of climate change impacts across natural systems](#). *Nature*, 421: 37-42. <https://doi.org/10.1038/nature01286>
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. and Young, B.E. (2006). [Widespread amphibian extinctions from epidemic disease driven by global warming](#). *Nature*, 439: 161-167. <https://doi.org/10.1038/nature04246>
- Pounds, J.A., Fogden, M.P.L. and Campbell, J.H. (1999). [Biological response to climate change on a tropical mountain](#). *Nature*, 398: 611-615. <https://doi.org/10.1038/19297>
- Raxworthy, C.J., Pearson, R.G., Rabibisoa, N., Rakotondrazafy, A.M., Ramanamanjato, J.-B., Raselimanana, A.P., Wu, S., Nussbaum, R.A. and Stone, D.A. (2008). [Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the](#)

- highest massif in Madagascar. *Global Change Biology*, 14: 1703-1720.
- Rohr, J.R. and Raffel, T.R. (2010). Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences of the USA*, 107: 8269-8274. <https://doi.org/10.1073/pnas.0912883107>
- Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E. and Evans, T.A. (2014). Microhabitats reduce animals' exposure to climate extremes. *Global Change Biology*, 20: 495-503.
- Seimon, T.A., Seimon, A., Daszak, P., Halloy, S.R.P., Schloegel, L.M., Aguilar, C.A., Sowell, P., Hyatt, A.D., Konecky, B. and Simmons, J.E. (2007). Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Global Change Biology*, 13: 288-299.
- Still, C.J., Foster, P.N. and Schneider, S.H. (1999). Simulating the effects of climate change on tropical montane cloud forests. *Nature*, 398: 608-610. <https://doi.org/10.1038/19293>
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. and Waller, R.W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306: 1783-1786. <https://doi.org/10.1126/science.1103538>
- Tingley, M.W. and Beissinger, S.R. (2009). Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology & Evolution*, 24: 625-633. <https://doi.org/10.1016/j.tree.2009.05.009>
- Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. and Beissinger, S.R. (2012). The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, 18: 3279-3290.
- Walls, S.C., Barichivich, W.J. and Brown, M.E. (2013). Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology*, 2: 399-418.
- Wells, K.D. (2007). *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago.