



Escalator to extinction

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Thirty years ago, biologists began to predict how climate change would alter species' ranges, extinctions, and their roles in ecosystems (1). Since then, evidence has begun to confirm these nascent predictions. The current global temperature rise of $\sim 1^\circ\text{C}$ has shifted species up mountains and latitudes (2), altered the timing of key life events such as flowering and migration (3), and eradicated populations and species (4). As the climate continues to change, these impacts on biodiversity are expected to accelerate (5). In PNAS, Freeman et al. (6) add to the growing drumbeat of climate change's pervasive impacts on nature by demonstrating the mountaintop extirpations of five tropical bird populations.

In 1985, tropical biologists charted an elevational transect in the mountains of Cerro de Pantiacolla, which rise from the Amazonian lowlands in Peru. Along this transect, they recorded each bird they encountered. Three decades later, biologists returned to resurvey the original transect. Such historical resurveys offer a particularly effective way to gauge biotic changes in response to long-term environmental responses, assuming they apply similar methods and effort. Oftentimes, these comparisons are difficult to ascribe to climate change because other factors, such as land use, also change during this time. In this study, the study area remained undisturbed, making it an exceptional long-term catalog of nature's history. What did change was temperature, which rose 0.4°C between surveys.

After comparing observations between 1985 and 2017, the biologists discovered that the upper elevational ranges of birds had shifted upslope an average of 68 m, which was consistent with the temperature rise. Mountaintop species suffered the most. High-elevation species lost on average 110 m of elevational range and substantial habitat area because their lower elevational limits shifted upward but their upper limits could not. Species living above 1,200 m declined in abundance. At the extreme, researchers did not find five of the mountaintop species in 2017 that were

observed repeatedly in 1985. The authors offer multiple lines of evidence to demonstrate that these species were most likely extirpated from the mountaintop, including statistical analyses that account for incomplete detectability.

Mountain range shifts and contractions fueled by climate change have now been recorded for many species (2, 7, 8). As temperatures warm, the climatically suitable habitat of species shifts upslope. If species can disperse sufficiently, then they will shift ranges upslope as if on an escalator. However, species at the top have nowhere else to go. Consequently, climate change threatens mountaintop species with the aptly and alliteratively named "escalator to extinction" (9, 10) (Fig. 1). Despite many observations of elevational range shifts, few studies have yet to demonstrate mountaintop extinctions or population extirpations. In one study, the last Quino checkerspot butterfly population declined due to a warming climate, only to reappear on a nearby mountaintop, where it adapted to a new host plant (11). At least 15 American pika populations have disappeared along the species' southern boundary (12). Hence, a small, but growing, list of studies suggests increasing risks to mountain flora and fauna.

I use "extirpation" to refer to lost populations and "extinction" to refer to lost species. The Freeman et al. (6) study documents the loss of populations, not species. We should not yet sound the death knell for the Buff-browed Foliage gleaner, Hazel-fronted Pygmy-tyrant, Variable Antshrike, Fulvous-breasted Flatbill, or White-eared Solitaire. Understanding extinction risk—in contrast to population extirpation—requires understanding the demographic status of populations across the entire range, but most especially on the cool range edge where they might be expanding into newly suitable climates. Population extirpations can lead to species extinction when few populations exist or if the poleward range is not expanding, as might often characterize poorly dispersing species.

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Author contributions: M.C.U. wrote the paper.

The author declares no conflict of interest.

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See companion article on page 11982.

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Published online November 5, 2018.

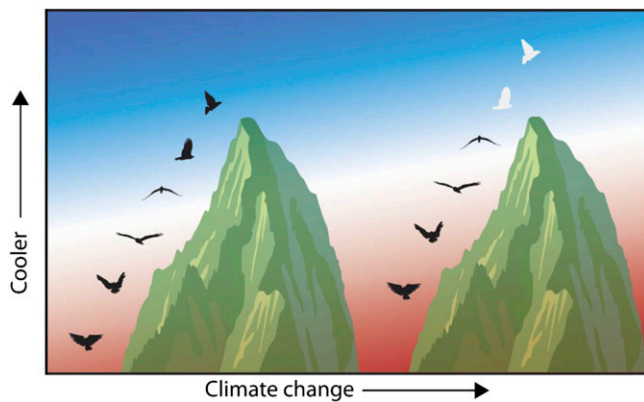


Fig. 1. Climate change causes an “escalator to extinction” as it warms elevational gradients and causes species to shift their ranges upslope. Mountaintop extirpations result when cool-adapted summit species cannot shift further and become extirpated (in white). Under some circumstances, population extirpations can lead to species extinction.

A nearby mountain at higher latitude or elevation could rescue mountaintop species by providing cooler habitat. However, peak-to-peak rescue assumes that the species can get there. Like oceanic islands, these islands of cool high-elevation habitat exist in a sea of inhospitable conditions, and thus colonizing other mountains requires high dispersal capacity and the ability to survive the trip (13). The bird species in this study could endure further climate change by mountain-hopping to the poles given the avian group’s generally high dispersal capacity. However, not all birds disperse well, including tropical birds that inhabit microhabitats in intact forests (14). Most other species disperse far worse than birds and thus face higher extinction risks (12, 15).

These climate-induced risks are heightened in the tropics, where the change in temperature with latitude is smaller than elsewhere (16). Therefore, peak-jumping in the tropics to cooler summits usually requires the juxtaposition of higher-elevation, not just higher-latitude, mountains. Also, lower seasonal temperature variation in tropical relative to temperate regions decreases the overlap between temperatures across elevational gradients. Consequently, tropical organisms often adapt narrower thermal tolerances. These lower tolerances can make mountain passes seem higher and thus greater barriers to expanding tropical organisms (17). For the same reasons, valleys might seem deeper in the tropics, making the journey to the next cooler peak that much more difficult in response to climate change.

Mountaintop extirpations suggest several questions unanswered by this study. First, to what degree are they driven by direct physiological responses to climate versus indirect impacts via biotic interactions? One study on facilitation suggests that the

slow responses of woody plants to climate change will affect Kenya’s avian diversity far more than climate’s direct effects on the birds (18). Competition also could intensify losses. Even if a species can physiologically persist at higher temperatures on the mountaintop, competing species from lower elevations could decrease the fitness of mountaintop species by moving upslope and competing for limited resources (8). You cannot just stop on a moving escalator, or the people behind you crash into you. This competition can constrain and slow climate-induced range shifts [i.e., the boxcar effect (19)]. Second, why do summit species fail to adapt to the changing climate? Oftentimes, populations possess sufficient genetic variation to respond to climate variation (20), and mountaintop habitats are often isolated from maladaptive gene flow. Climate change might be too rapid, especially for long-lived species. Alternatively, the combination of climate change and altered biotic interactions might prove too strong to mount a multipronged evolutionary response. Third, to what degree does dispersal already link mountaintop habitats into a metapopulation? If so, observed mountaintop extirpations might be a natural and sustained pattern of random extirpations and colonizations rather than climate-driven events. Answering this question requires observations collected not just in time but also across landscapes. Unfortunately, such datasets are rare for most species and regions on Earth.

Why should we care about mountaintop extinctions? The same isolation that threatens mountain species with extinction also has allowed them to proliferate, innovate, and speciate. Mountaintops provide habitat for many endemic species found nowhere else (21). Mountaintop isolation is an incubator for genetic innovations that result in novel traits. For instance, alpine insect species have evolved reduced body sizes, atrophied wings, black bodies for solar absorption, desiccation resistance, and freeze tolerance, among other traits unique to their extreme environment (22). Thus, climate change on mountains might result in losing a disproportionate number of species as well as evolutionary novelties.

Since climate scientists became certain about climate change, biologists have been predicting its effects on species (1). One of the first predictions was that climate change would shrink mountaintop habitats and eliminate mountain species (13). This study provides evidence that this prediction is now being realized. Thus, this study highlights the successful application of predictive science. However, what is a success story for science is a failure for policy. We have yet to make the difficult decisions as a society to reverse climate change. Until we do, we will continue to affirm climate change’s increasingly grim predictions.

Acknowledgments

This work was supported by NSF Grants DEB-1555876 and PLR-1417754 (to M.C.U.) and the Center of Biological Risk at the University of Connecticut.

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