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Evolutionary conservatism will limit responses to climate change in the tropics

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Rapid species turnover in tropical mountains has fascinated biologists for centuries. A popular explanation for this heightened beta diversity is that climatic stability at low latitudes promotes the evolution of narrow thermal tolerance ranges, leading to local adaptation, evolutionary divergence and parapatric speciation along elevational gradients. However, an emerging consensus from research spanning phylogenetics, biogeography and behavioural ecology is that this process rarely, if ever, occurs. Instead, closely related species typically occupy a similar elevational niche, while species with divergent elevational niches tend to be more distantly related. These results suggest populations have responded to past environmental change not by adapting and diverging in place, but instead by shifting their distributions to tightly track climate over time. We argue that tropical species are likely to respond similarly to ongoing and future climate warming, an inference supported by evidence from recent range shifts. In the absence of widespread *in situ* adaptation to new climate regimes by tropical taxa, conservation planning should prioritize protecting large swaths of habitat to facilitate movement.

Ever since Francisco José de Caldas [1] and Alexander von Humboldt [2] described the dramatic elevational zonation of species in the northern Andes, biologists have been fascinated by the drivers of speciation and the build-up of diverse communities in tropical mountains. How do we explain why 66 species of hummingbirds live along a single elevational gradient stretching from hot lowland Amazonian forests to chilly cloud forests at 3500 m in the Peruvian Andes [3]? Despite substantial challenges, a growing body of research has begun to shed light on this fundamental question. These results have important implications not only for our understanding of the origin of Earth's hottest biodiversity hotspots—tropical mountains—but also provide critical insight into how tropical species might respond to future climate warming.

Few patterns in nature are as striking as the rapid turnover of plant and animal species when climbing up a tropical mountain. From the New Guinea Highlands to the South American Andes, tropical mountains are biodiversity hotspots because large numbers of species segregate themselves into narrow elevational bands [4]. For example, despite their powers of flight, the 66 species of hummingbirds along the Andes-to-Amazon elevational gradient mentioned above have an average elevational range size of only 900 m, with many repeated examples of sequences where closely related species 'replace' one another across elevational zones [3].

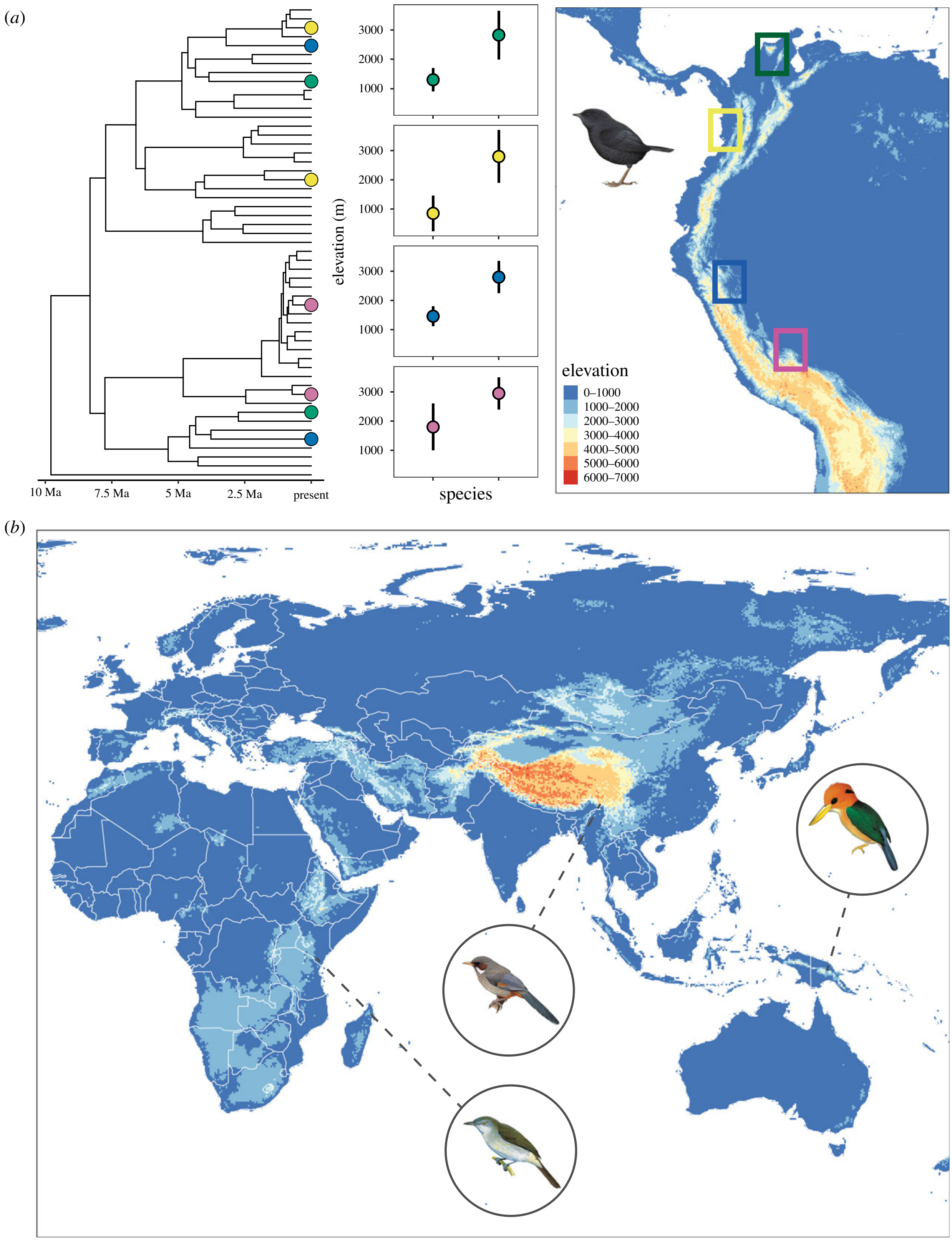

Figure 1. In tropical mountains worldwide, species that have parapatric elevational ranges are typically distantly related, rather than being each other's closest relative. This pattern indicates that the elevational niche of bird species is conserved over evolutionary timescales and suggests that *in situ* adaptation to novel climatic conditions under global warming is unlikely. (*a*) While many species of *Scytalopus* tapaculos occur in parapatry across elevational gradients, they are almost always distant relatives [8]. (*b*) Diverse bird lineages in the Afrotropics, Himalaya and New Guinea show similar patterns of ancestry, diverging in isolation long before evolving into new elevational zones [7,9,10]. Illustrations courtesy of © Cornell Lab of Ornithology's *Birds of the World*.

One prominent explanation for this extraordinary beta diversity is inspired by the observation that seasonal variation in temperature is minimal at a given elevation along a tropical mountainside, especially when compared to the large seasonal swings in temperature at an equivalent elevation in the temperate zone. This greater climatic stability at low latitudes is thought to promote the evolution of narrower thermal tolerance ranges in tropical organisms. Janzen [5] famously argued this phenomenon should reduce dispersal across tropical elevational gradients because of the increased physiological challenges of encountering cooler or warmer temperatures when travelling up or down a mountain. A potential evolutionary consequence of reduced movement and genetic exchange along tropical mountain slopes is an increased opportunity for local adaptation, evolutionary divergence and the origin of new species (i.e. parapatric or gradient speciation; [6]). Alternatively, thermal specialization may facilitate allopatric divergence between isolated populations inhabiting similar elevational zones, as mountain passes and valleys with unsuitable climates represent formidable barriers to gene flow. Under this allopatric model, subsequent range expansion by one or both daughter species could lead to secondary contact, followed by competitive interactions that lead to segregation within a formerly shared elevational niche.

The above hypotheses are impossible to distinguish with distributional data alone because they both result in a similar pattern of species turnover along elevational gradients. However, the recent explosion of molecular phylogenies of tropical species now permits us to evaluate their contrasting predictions for evolutionary relationships among elevational replacements. If parapatric speciation regularly occurs along mountain slopes, we would expect to see species that occupy adjacent elevational zones to be sister species (each other's closest relatives). If elevational replacements are instead the product of secondary contact over longer evolutionary timescales, we would expect sister species to disproportionately occur in allopatry, with similar elevational distributions.

Decades of research on the evolutionary relationships between bird species and populations in tropical mountains now suggests the latter mode of allopatric divergence followed by dispersal is more common, while parapatric speciation is vanishingly rare [7,8]. Across disparate branches of the avian phylogeny and in multiple biogeographically independent tropical mountains, species of birds replacing each other along elevational gradients are almost always not particularly close relatives, implying elevational replacements do not result from parapatric speciation, but rather from range expansions of species which originally diverged in geographical isolation (figure 1). More generally, across vertebrate taxa in the tropics, closely related species typically occupy a similar 'elevational niche', meaning they experience the same narrow range of temperatures throughout their geographical distribution. By contrast, species with different elevational ranges (hence experiencing different climatic conditions) are more distantly related [11].

What inferences can we draw from closely related species being confined to a given elevational niche throughout their ranges? First, the constancy in experienced climatic conditions across species' ranges, in conjunction with patterns of genetic diversity consistent with the presence of climate refugia, suggest that populations have responded to past environmental change not by adapting and diverging in place but instead by tightly tracking climate over time, i.e. moving upslope during hotter periods and downslope during cooler periods [12,13]. Second, there must be strong evolutionary constraints on the elevational niche of tropical lineages, at least in mega-diverse tropical mountains such as the tropical Andes and New Guinea's central cordillera. (Whether similar patterns hold for more isolated tropical mountains or regions with different climatic histories, remains an open question.) Limits to elevational distributions of tropical species may reflect reduced selection due to climatic stability, a lack of genetic variation for evolving greater thermal tolerance, or biotic interactions among species that prevent expansion [14]. So far, though evidence for the role of interspecies interactions [14,15] is stronger than that for narrow thermal physiologies [14,16,17], the consensus remains elusive. Yet while the ways in which these mechanisms jointly act to constrain elevational niche breadth in the tropics are debatable, the evidence for evolutionary conservatism is not.

The emerging picture that tropical species exhibit evolutionary conservatism in their preferred thermal niches and have used dispersal to track shifting environmental conditions over their evolutionary history has important implications in the context of anthropogenic global warming. While the ultimate drivers of evolutionary conservatism are debatable, there is little reason to expect evolutionary responses to contemporary rising temperatures if tropical species have not adapted *in situ* to past climatic changes. Consequently, as temperatures rise and habitats shift, we predict divergent responses between tropical and temperate taxa. Tropical taxa may show greater fidelity to their favoured thermal regimes than temperate taxa, shifting their elevational ranges in a way that more closely matches a changing climate. By contrast, temperate species, often with reduced niche conservatism and broader or more plastic thermal physiologies, would be expected to exhibit less pronounced shifts, even in the face of more rapid warming at high latitudes. To date, the sole comprehensive study to test this question suggests this is indeed the case: tropical communities are tracking temperatures 2.1–2.4 times more closely than temperate communities [18].

As we race to preserve tropical montane biodiversity in the face of a myriad of threats, the limited potential for adaptive evolution and reliance on dispersal to allow for climate tracking in tropical species means that large-scale approaches to management and conservation will be required. In particular, tropical conservation strategies must consider an important role for movement at the landscape level [19]. One obvious priority is to redouble our focus on gradients that connect elevational corridors. Conservation corridors were originally conceived to allow individual animals to move across a landscape. In the climate change era, these corridors must allow entire populations to move across a landscape over generations, thus conserving evolutionary processes [20]. Complicating this goal, many tropical species face significant barriers to movement as they currently occur within highly fragmented habitats in human-modified landscapes [21]. Connecting and securing protected areas is, therefore, urgently needed to establish such elevational corridors and is likely to be the most efficient long-term strategy for sustaining tropical montane biodiversity. Ultimately, the niche conservatism of tropical montane species means that conservation success cannot rest on the assumption that rapid evolutionary rescue will occur [22]. Over the next several decades, species should be able to persist by shifting upslope provided habitat is available. However, temperatures will be hotter on Earth by 2030 than at any time in the past 3 Myr [23], and these conditions, unprecedented in tropical species' evolutionary histories, represent an uncharted and ominous future.

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