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REVIEW

Building a mechanistic understanding of climate-driven elevational shifts in birds

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Abstract

Mountains hold much of the world's taxonomic diversity, but global climate change threatens this diversity by altering the distributions of montane species. While numerous studies have documented upslope shifts in elevational ranges, these patterns are highly variable across geographic regions and taxa. This variation in how species' range shifts are manifesting along elevational gradients likely reflects the diversity of mechanisms that determines elevational ranges and modulates movements, and stands in contrast to latitudinal gradients, where range shifts show less variability and appear more predictable. Here, we review observed elevational range shifts in a single taxonomic group–birds–a group that has received substantial research attention and thus provides a useful context for exploring variability in range shifts while controlling for the mechanisms that drive range shifts across broader taxonomic groups. We then explore the abiotic and biotic factors that are known to define elevational ranges, as well as the constraints that may prevent birds from shifting. Across the literature, temperature is generally invoked as the prime driver of range shifts while the role of precipitation is more neglected. However, temperature is less likely to act directly on elevational ranges, instead mediating biotic factors such as habitat and food availability, predator activity, and parasite prevalence, which could in turn modulate range shifts. Dispersal ability places an intrinsic constraint on elevational range shifts, exacerbated by habitat fragmentation. While current research provides strong evidence for the importance of various drivers of elevational ranges and shifts, testing the relative importance of these factors and achieving a more holistic view of elevational gradients will require integration of expanding datasets, novel technologies, and innovative techniques.

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1 Introduction

Mountains are foci of global biodiversity [1]. Steep environmental gradients [2] coupled with complex geological and climatic histories [3] combine to produce elevational gradients rich in species [4], endemism [5], and ecosystem function [6]. Despite only covering 25% of all land area, mountainous regions harbour more than 85% of the world's bird, mammal, and amphibian richness [1].

Global climate change poses one of the greatest threats to biodiversity [7], particularly in montane regions [8]. Increasing temperatures are generally predicted to push species to higher elevations [9], causing high rates of extinction [10], especially when combined with limited dispersal ability [11]. An ever-increasing number of empirical studies have documented upslope shifts [12–15], even resulting in localised mountaintop extinctions [16]. However, the distributional responses of populations to climate change are diverse, with shift rates lagging behind predictions [17], and many species even shifting downslope [18,19]. This variation makes understanding elevational range shifts difficult.

Birds are an exemplary group within which to study elevational ranges and shifts. Birds have been the inspiration and test subjects of numerous foundational ecological principles [20–22] and a century or more of avian research along elevational gradients has produced a wealth of data on the spatial distributions of birds. Furthermore, the ease with which birds can be monitored makes them an ideal group to test hypotheses about elevational range limits, and the ever-growing repositories of spatiotemporal [23], trait [24], physiological [25], and movement data [26] provide numerous burgeoning avenues for future research. As consumers, birds occupy a variety of trophic levels [27] and perform numerous ecosystem functions [28]. This connectivity within food webs makes birds a critical group to study. Moreover, as homeotherms, the ways in which climate change may alter bird distributions are more complex than for ectotherms [29].

Here, we review what is known about elevational range shifts in birds. We begin with an overview of evidence for elevational shifts. We then discuss the abiotic and biotic factors that determine elevational ranges and that could therefore mediate range shifts. These factors include climate, bottom-up effects, top-down control, competition, and dispersal and landscape constraints. We finish by outlining research gaps and highlighting future directions.

2 Evidence of elevational shifts

In this section we provide a brief overview of studies that have documented shifts in the elevational distributions of birds. Research tends to determine elevational shifts based on changes in range margins (e.g., minimum, maximum, or 95% range limits) or changes in central tendency (mean or median elevation). Studies make use of a wide range of methods to determine these metrics, including point counts, mist nets, audio recordings, and citizen science surveys, with measurements occurring continuously or at discrete time points. We choose to divide this section geographically into studies in temperate regions versus studies in tropical regions because the literature falls mostly into those discrete groups, although we acknowledge that latitude is, of course, a gradient. We do not go into detail for each study, and we save discussion of possible underlying mechanisms for later sections. We use this section to highlight commonalities and differences in findings and underlying methodologies across the world.

2.1 Shifts in temperate birds

As with most empirical studies of global change impacts [30,31], research on elevational shifts has been biased towards temperate regions (Fig 1). Most early research on elevational distributions came from the mountain ranges of Europe where initial signals of climate change were weak. For example, in the French Alps, Archaux [32] detected no significant change in the mean elevations of 24 bird species over 25 years. Similarly, overall shifts among 61 bird species in the Italian Alps were not statistically significant, despite the fact that upslope shifts were detected in 69% of species [33]. As an island comparison, Massimino et al. [34] found no evidence of consistent changes in elevation for 80 species over 15 years of breeding bird surveys in the United Kingdom. Indeed, in one study in the Guadarrama Mountains of Spain, 42 species were actually found on average to have shifted downslope over four decades [35].

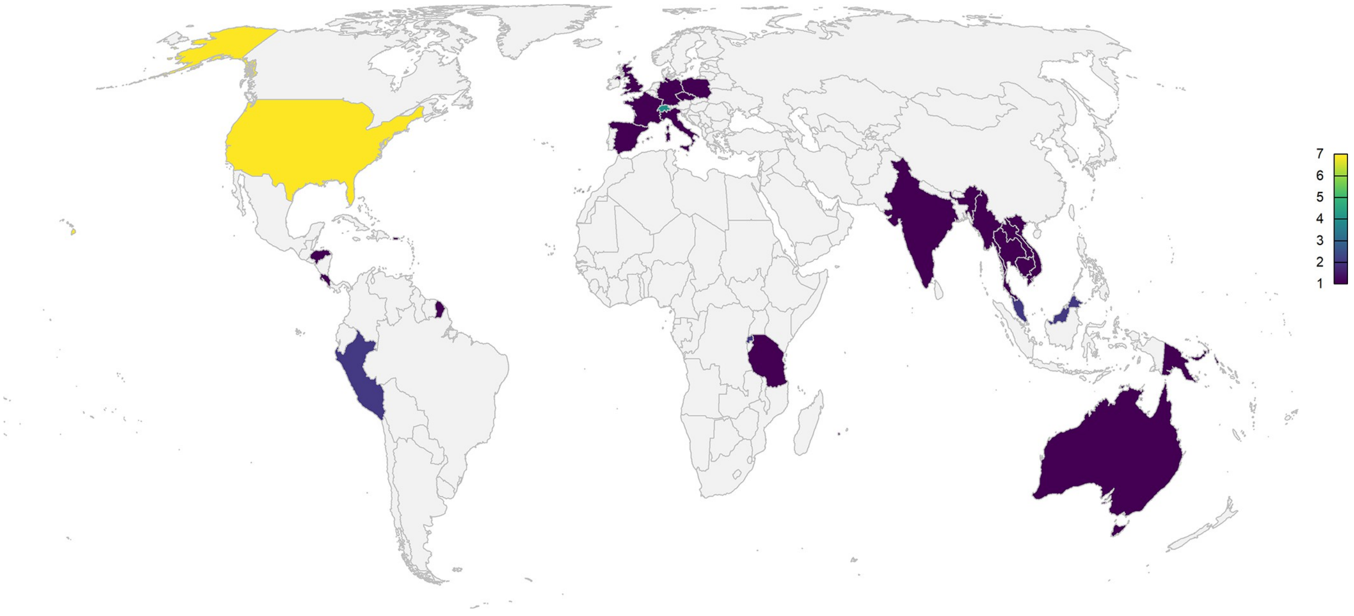

Fig 1. The distribution of research on elevational shifts in birds. Countries are coloured by the number of studies from 1 (dark purple) to 7 (yellow), with 0 studies in grey. A single study (Peh 2007) was conducted across Southeast Asia, including Myanmar, Cambodia, Laos, peninsular Malaysia, Thailand, and Vietnam.

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Other studies in Europe have managed to detect the expected signal of increasing temperatures on elevational distributions. One of the first such studies demonstrated an upward shift in White Stork (*Ciconia ciconia*) nest sites in the Tatra Mountains of Poland [36]. In the nearby Giant Mountains of the Czech Republic, Reif and Flousek [37] detected upslope shifts in 78% of species over a decade of recent warming temperatures. In the Swiss Alps, Alpine Rock Ptarmigan have rapidly shifted upslope (*Lagopus muta helvetica*) [38]. In a broader study of 95 Alpine bird species, Maggini et al. [39] found that 35% of species shifted upslope compared to 29% shifting downslope; this asymmetry in proportions has been corroborated more recently [40]. The result of these shifts is that bird communities at higher elevations increasingly resemble the community composition of lower elevations [41]. While most European studies spanned time periods of less than 30 years, a resurvey of the upper range limits of plants, insects and birds in Bavaria over a century after initial surveys demonstrated upslope shifts in birds consistent with increasing temperatures over the century [42]. Nevertheless, the elevational responses of European birds to climate change are highly variable [40].

A lack of consistent findings in Europe [43] has been mirrored in North America. For example, in the Breeding Bird Atlas of New York State, the mean elevation of 123 species shifted downslope over 20 years, despite little change in their elevational range limits and upslope shifts in resident species [44]. By contrast, another study from New York in the Adirondack mountains found a majority of upslope shifts in upper and lower range limits with an overall shift in mean elevation across 42 species [45]. Nearby in the White Mountains of New Hampshire, DeLuca and King [46] found that the upper elevational limits of low-elevation species shifted upslope over 16 years while the lower limits of high-elevation species shifted downslope [46]. Comparatively less research has taken place in the western half of the continent, but USGS Breeding Bird Surveys across Western North America have been used to show upslope shifts in the upper limits of 40 species over three decades [47], while a study from Denali National Park, Alaska, found upslope shifts in most bird species, particularly those associated with shrub-tundra [48].

Of the western states, California boasts one of the most comprehensive multi-taxa historical resurvey efforts, the Grinnell Resurvey Project [49–52]. Although the project has resurveyed habitats across the biogeographically diverse state, several papers have looked explicitly at elevational range shifts in the Sierra Nevada Mountains. Using data that spanned up to a century of environmental change, Tingley et al. [19] found that elevational range shifts were common but that across 100 species shifts were nearly evenly split between upslope and downslope movements [19]. Despite this heterogeneity in elevational direction, species were found to be tracking climate in a predictable manner [53], with particular emphasis on precipitation explaining downslope shifts and temperature–as is usual–explaining upslope shifts [19].

Across these studies from Europe and North America an overall–or "average"–signal of upslope elevational shifts can be found, however this signal is relatively weak [13], and the studies highlighted above demonstrate the lack of consistency in findings across space and time. A lack of consistent signal in elevational range shifts for temperate species could result from contrasting drivers of elevational shifts [19], from other adaptive responses such as latitudinal shifts [12,34,44,47], or from concurrent adaptations in other ways that compensate for increasing temperatures, such as shifts in breeding phenology [54]. Perhaps research on these alternative responses to climate change–especially at low elevations–has led to a relative lack of research along elevational gradients compared to other parts of the world.

2.2 Shifts in tropical birds

Tropical mountains have long been the focus of ecologists interested in the narrow elevational ranges and high species turnover of montane communities [55–57]. From a long-term monitoring study in Monteverde, Costa Rica, Pounds et al. [58] provided one of the earliest signs that tropical montane birds may be shifting upslope in response to increasing temperatures. There, between 1979 and 1998, the abundance and richness of "premontane" (cloud-forest-intolerant) species increased over time in a mid-elevation study plot, suggesting an upslope shift in that assemblage, while certain foothill species established breeding populations and increased in density over time.

Since this landmark work, the number of studies documenting upslope elevational shifts in tropical birds has remained relatively low. This paucity of research likely reflects a lack of carefully standardised and available baseline or time-series data with which to calculate trends over time [59,60]. Many attempts to quantify tropical elevational shifts have had to make use of less traditional data sources. For example, Peh [61] used field guides published 25 years apart to estimate elevational shifts for 306 common resident bird species in Southeast Asia, finding upslope shifts (>100 m) for 31% of species and downslope shifts for 12% of species. Similarly, old field guides have also been used to document birds in Rwanda occurring at elevations far higher than expected [62]. In Borneo, Harris et al. [63] used a combination of sources–including checklists, field surveys, trip reports, photos, and other historical and contemporary sources–to infer elevational shifts in birds for two-thirds of species with sufficient data [63]. Sometimes such creative and integrative methods are the only way that elevational shifts can be studied.

While not all tropical regions have the baseline data required to make temporal comparisons, tropical ornithologists, like temperate ones, have used the revisitation of elevational transects to study shifts in elevational ranges. In contrast to temperate regions, however, most tropical resurveys have been more conclusive in their findings of consistent upslope shifts. In New Guinea, for example, resurveys of a central mountain and an offshore island found that bird communities in both locations shifted their upper and lower elevational limits upslope by over 100 m over four decades, exceeding the predicted shifts based on temperature increases

[64]. In the Peruvian Andes, another resurvey found upslope shifts in the bird community over a similar timeframe [17]. These shifts were, however, one third of the expected shift based on local temperature increases. Farther south in Peru, Freeman et al. [16] recorded the first substantial evidence of localised mountaintop bird extinctions from a three-decade resurvey. Here, at least five ridgetop species historically recorded could not be re-found despite extensive survey effort, with statistical evidence supporting the disappearance of four of those species. In addition, range contractions and population declines were detected in the majority of higher elevation species, while lowland species expanded their ranges into higher elevations [16]. In comparison to these resurveys of continuous forest, a study in fragmented forest in Tanzania detected upslope shifts across 29 species over 40 years, but these shifts were driven predominantly by contractions in species' lower elevational range limits [65]. In contrast, a shorter-term study in Puerto Rico is the only published tropical resurvey to not find an elevational shift in birds [66].

Although resurveys have been able to capture changes in elevational ranges over long time periods, continuous datasets have been used to examine changes over shorter time periods. For example, a study in Rwanda used extensive point count surveys to demonstrate upslope shifts over 15 years, particularly in species' lower range limits [67]. In a similar study in Honduras, Neate-Clegg et al. [68] used standardised annual surveys to show elevation-dependent changes in bird diversity: as species richness increased at higher elevations, it decreased at lower elevations, indicating upslope shifts in the bird community, and these trends were supported by increases in the elevation of several common cloud-forest species [68]. At a larger spatial scale, bird monitoring of 42 species across the Australian Wet Tropics has revealed patterns consistent with the rest of the world, with decreases in relative abundance of high elevation species at their lower limits concomitant with increases in the relative abundance of lowland species at higher elevations [69]. While annual monitoring is costly and labour intensive to maintain [60], the fruits of this labour can be high temporal resolution of changes to elevational ranges in a way not afforded by snapshot resurveys [67].

Could citizen science data circumvent issues of monitoring cost? Girish and Srinivasan [70] recently used eBird data from fixed hotspots in the eastern Himalayas to detect elevational shifts over time. They found that lower elevation species were increasing in occurrence probability while higher elevation species decreased, findings consistent with the long-term monitoring programs above. As citizen science data continue to accumulate over time, we may have more ways to detect elevational shifts in the future and at increasingly greater scales.

2.3 Comparing temperate and tropical shifts

In contrast to studies in temperate regions, tropical studies have demonstrated consistent upslope shifts along elevational gradients [13,71]. This difference in overall signal could result from several factors [13]. First, tropical species occur over narrower elevational ranges than their temperate counterparts and are thought to be more sensitive to increased temperatures due to the reduction in daily and annual temperature variability in the tropics [57,72–74]. Second, while temperate species can respond to a warming climate by shifting along other thermal gradients, such as seasonal and latitudinal temperature gradients [44,54,75], the relative climatic stability of the tropics over time and latitude means that there are fewer thermal gradients for species to respond to, making elevational shifts the most likely response [2]. Third, the fact that there are simply more montane species in the tropics compared to temperate regions might make it easier to detect statistically-significant shifts [13], a point underscored by the lack of a consistent shift in species-poor Puerto Rico [66]. However, average signals of upslope shift in the tropics still belie a great deal of heterogeneity in shift rates and even shift direction, with many species shifting downslope despite overall upslope trends [15,71]. Some of this variation could be explained by changes in population size driven by other anthropogenic factors such as habitat change, causing range margins to expand or contract [32,40,76]. It is also important to note that, in reality, bird communities across latitudes do not fall into two discrete bins–temperate versus tropical–and avian responses to climate change are unlikely to be as neatly binned either [13]. More research is needed to fill in biogeographic gaps in montane studies (Fig 1), including subtropical mountain ranges in North America and Asia, as well as temperate regions of the Global South, such as Chile, Australasia, and Southern Africa [43].

3 Abiotic determinants of elevational ranges

To understand climate-induced elevational shifts, it is critical to understand the determinants of elevational ranges. The implicit–and sometimes explicit–assumption of upslope elevational range shifts is that the elevational ranges of species are limited by temperature. When temperatures increase over time, species are predicted to shift upslope to cooler areas in order to track their preferred thermal envelope [77]. It is also often assumed that the observed "failure" of species to perfectly track increasing temperatures is evidence for some kind of lagged response [17,78]. However, both the fundamental and realised niche of a species is defined by more than just temperature [21,79–81], including other climatic factors such as precipitation [82], non-climatic abiotic factors such as oxygen availability [78], and biotic interactions [79]. These factors may constrain elevational shifts or induce elevational shifts themselves (Fig 1). In this section we explore the abiotic factors that shape elevational ranges and how these factors might drive elevational range shifts.

3.1 Temperature

In the literature, there has long been an association between species' elevational ranges and their thermal tolerances. In particular, temperatures are thought to more strongly limit the cold edge of a species' range–that is, the upper elevational limit [22,83]. Given that elevational ranges are associated with thermal envelopes [57], the assumption that species would shift upslope with increasing temperature seems well justified. Indeed, the fact that most observed elevational shifts are upslope would appear to support this reasoning [13]. However, this evidence is largely correlational. On one hand, increasing temperatures may be causing direct changes in species distributions, but they may also be acting indirectly via biotic pathways [84]. Evidence is needed to demonstrate whether temperature actually plays a direct or proximal role in determining distributions [84]. Searching for the direct role of temperature usually involves an investigation into physiology and thermal tolerances [79]. Adult birds maintain a stable internal body temperature, usually around 39–41˚C [85]. There exists a narrow range of ambient temperatures–known as the thermal neutral zone (TNZ)–over which birds can maintain this body temperature while at their basal metabolic rate [86]. Below a lower critical temperature (LCT), they must expend additional energy on heat production; above an upper critical temperature (UCT), they must expend energy on evaporative heat loss [87]. An important question is whether species along elevational gradients are constrained by these or other thermal physiological thresholds.

There has been an increasing array of studies demonstrating the negative effects of increased temperatures on birds in wild settings. Most of these studies demonstrate sub-lethal impacts of high temperatures on birds which could plausibly lead to lower fitness consistent with temperature limiting the fundamental niche. For example, in the Kalihari Desert, hotter periods are thought to lower foraging efficiency in adult Southern Pied Babblers (*Turdoides bicolor*), causing them to lose weight [88]. Likewise, in the summer months, Rufous-eared

Warblers (*Malcorus pectoralis*) reduce preening, foraging effort, and foraging success in favour of increased evaporative cooling and time in the shade [89]. Even in larger-bodied species that are supposedly better buffered against heat [90], such as the Southern Yellow-billed Hornbill (*Tockus leucomelas*), fledging probability and fledgling weight decrease with increased temperature [91]. Species at higher elevations are not immune either, as Cape Rockjumpers (*Chaetops frenatus*) reduce provisioning rates with increasing temperature, leading to lower nestling condition [92]. Besides these single-species studies, McKechnie and Wolf [93] predicted that increasing temperatures are expected to increase water requirements and decrease the time taken to reach dehydration for desert birds. Furthermore, Conradie et al. [94] projected that future warming will bring greater exposure of Kalahari bird species to long-term, sublethal effects of temperature that result in weight reduction, lower nestling growth, and increased breeding failure [94]. Ultimately, these chronic effects could cause population declines and community collapse [95].

These studies of extreme desert climates convincingly demonstrate the negative effects of increasing temperatures in the warmest environments, but are these findings representative of birds in general, and particularly those along elevational gradients? An early study in France found that heatwaves more strongly reduced the population growth rates of those species with narrower elevational ranges [96]. In Southern California, Black-throated Sparrows (*Amphispiza bilineata*) along arid elevational gradients exhibited higher breeding success at higher elevations as lower elevations become too hot [97]. Along tropical elevational gradients, temperature has also been linked to species richness in the Bolivian Andes [98], and to the elevational distributions of species in Rwanda [99] and the Himalayas [100,101]. In Rwanda, interannual changes in the elevational distributions of birds showed little association with temperature fluctuations [67]. These studies, however, are largely correlational.

Experimental results that demonstrate direct physiological roles for temperature in structuring elevational ranges should provide better evidence than correlational studies; surprisingly, results from such physiological studies are far more equivocal than similar correlational ones. For example, in New Guinea, LCTs and thermal conductance (the rate of increase in metabolic rate below the LCT) were unrelated to the temperatures that 24 species experienced at their upper elevational limits [102]. Across >200 species in Peru, Londoño et al. [103,104] demonstrated that elevational distributions did not predict basal metabolic rates but did predict thermal conductance, body temperature, and LCT, meaning that higher elevation species were more resistant to heat loss. Nevertheless, the limits to acute cold tolerance in these species were not constrained by elevation [104], nor was there evidence that high temperatures in the lowlands would prevent downslope shifts. An even stronger experimental design is to manually transplant organisms to higher elevations and measure their physiological performance and acclimatisation [105]. While such experiments are exceedingly rare, in Anna's hummingbird (*Calypte anna*), experimental upslope shifts resulted in facultative adaptation through increased and more efficient torpor, suggesting cold temperature alone is not a limit to upslope movements in this species [106]. Thus, despite strong correlational work, experimental evidence that temperature directly constrains the elevational ranges of birds is scant.

Single-system studies limited by sample size may be unable to find consistent thermal constraints in birds; do broader-scale studies find stronger signals? Globally, Araújo et al. [107] found that variation in LCTs across 70 bird species was much higher than variation in UCTs, which are evolutionarily constrained. However, within these 70 species, there was a general lack of correlation between LCT and ambient temperature, implying little causality. On the other hand, the TNZ has been shown to correlate with the latitudinal distribution of species, driven mainly by variation in LCT [108], yet few species currently experience ambient temperatures above their UCT. In a more recent study, Pollock et al. [25] cast doubt on these findings.

Their study demonstrated that temperate species had higher UCTs and heat tolerance limits (the ambient temperature at which hyperthermia sets in) than tropical species. However, they also found that both temperate and tropical species exhibited similar thermal safety margins (the difference between UCT and maximum ambient temperature) and levels of warming tolerance (the difference between heat tolerance limit and maximum ambient temperature). Moreover, even projected warming was expected to be within the thermal safety margins of most species. In other words, most bird species–regardless of latitude–are unlikely to exceed their physiological limits to temperature even under future warming scenarios.

Across these studies it appears that most bird species (excluding those in the very hottest environments) can tolerate temperatures far warmer and far colder than they currently experience. Observed elevational shifts are therefore less likely to be driven by the physiological responses of birds to temperature change. Most studies, however, focus on adult birds which are insulated by their feathers and able to move to preferred microclimates [109]. More research is needed to investigate the thermal constraints faced by eggs and nestlings [54,92], which are expected to be more sensitive to changes in temperature [110]. Furthermore, weather-induced stress could also modulate biotic interactions such as parasite tolerance [111].

3.2 Precipitation

In matters of climate change, species distributions are generally foremost linked to temperature envelopes. A more neglected association is how species distributions are affected by rainfall, i.e., the hygric niche [82]. As with temperature, species along elevational gradients experience a range of precipitation regimes. However, unlike temperature, the mechanisms invoked to explain the hygric niche are more often biotic than abiotic. Primarily, rainfall is linked to vegetation which, in turn, provides bottom-up structure to bird communities [112]. Less often discussed, but still potentially important, is the direct role of precipitation on species distributions [82].

There is a lot of evidence to suggest that precipitation indirectly constrains the ranges of birds [113], as habitats are partly defined by their precipitation regimes so the habitat associations of birds are necessarily linked to precipitation. Even within a habitat, fluctuations in rainfall can affect population dynamics. For example, over 33 years in Panama, Brawn et al. [114] found that the population growth rates of a third of focal species were reduced in years with longer dry seasons. Similarly, in the western United States, droughts were found to reduce productivity and adult survival across 51 desert species [115]. However, responses to changes in rainfall can vary greatly within bird communities as some species respond positively to increased rainfall, and others negatively [116]. Even within a single species, rainfall regimes have contrasting effects on breeding phenology in different parts of their range [117], demonstrating the difficulty in predicting responses to changing patterns of precipitation [82]. Despite the assumed indirectness of precipitation in these demographic studies, little research has demonstrated the mechanisms involved.

In addition to indirect effects, there are numerous ways in which rainfall could directly limit a species' range [82]. At the wetter end of the spectrum, abnormally high levels of precipitation could cause damage to nests [118], lead to bacterial or mould-based mortality of eggs [119] (arguably an indirect effect), or increase thermoregulatory costs (particularly in cooler temperatures). At the drier end of the spectrum, low amounts of rainfall could limit the availability of drinking water, cause egg desiccation [120], and reduce the ability to evaporatively cool [121]. However, many of these direct effects are only likely to be felt at the extreme ends of the precipitation spectrum where most bird species do not live.

Along elevational gradients, the elevational ranges of birds can show strong associations with precipitation independent of habitat. In one region of Rwanda, van der Hoek [99] showed that precipitation was associated with the lower elevational limits of roughly half of the species studied. Can precipitation also predict elevational shifts? In another region of Rwanda, birds were found to expand their elevational ranges both upslope and downslope in wetter years [67], implying that species' elevational ranges can respond plastically to rainfall. In the temperate mountains of the Sierra Nevada, California, Tingley et al. [19] found that extensive downslope shifts of species over a century were closely associated with increasing precipitation. In addition, species that showed greater sensitivity to precipitation generally occurred at lower elevations than species that shifted in association with temperature, indicating a potentially greater role for precipitation as species escape LCT temperatures [53]. We conclude from these studies that precipitation has the potential to drive elevational shifts and should not be ignored. Given its importance, it is critical to then understand how precipitation varies over elevational gradients and how those patterns are predicted to change over time in order to understand precipitation-driven elevational shifts [122].

3.3 Non-climatic abiotic factors

While temperature and precipitation form two principal axes of climate that are subject to climate change, there are other, non-climatic abiotic factors that can shape fundamental niches. Although these factors may be relatively immutable, they can still present obstacles to shifting species (Fig 1; for a more thorough review, see [78]). Along elevational gradients, increased ultraviolet radiation at higher altitudes could be damaging for animals [123], but birds are generally well-protected by their feathers [124]. For birds, the two most important factors to consider are presumably oxygen availability and air pressure. As elevation increases, the atmosphere gets thinner, and with this decrease in pressure comes a commensurate decrease in oxygen density and air viscosity. Lower oxygen availability leads to lower levels of gas exchange, increasing the risk of hypoxia [125], especially during flight [126]. Lower air viscosity also means less air resistance, resulting in less thrust during flight [127]. However, many birds migrate at altitudes far higher than their typical breeding altitudes, suggesting at least seasonally high tolerance to both hypoxia and low air pressure [128]. At the extreme, Bar-headed Geese (*Anser indicus*) are well known to fly from sea-level to 9000 m a.s.l. [129]. Similarly, migratory songbirds that breed around sea-level migrate at altitudes around 400 to 800 m a.s.l. [130], heights that dwarf the potential elevational range shifts of most birds. Long-distance migrants are not the only flexible species: resident and altitudinal migrant species can employ different strategies to cope with hypoxia at high elevations [131]. Even hummingbirds, operating at the extremes of flight capability, are able to alter their hovering flight kinematics at lower air pressure [127]. Thus, hypobaric altitudes are not without their costs [132], but adaptations allow species to perform at such elevations [133], and these constraints may be less likely to restrict upslope shifts given the relatively small magnitudes of the shifts.

4 Biotic determinants of elevational ranges

Once within a suitable abiotic envelope, birds must interact with a suite of organisms to successfully survive and reproduce. They must locate appropriate habitat, forage for food, find a home for eggs, defend against competitors, and avoid predators, parasites, and pathogens [79]. All of these factors shape the realised niche and thus a species' geographic distribution [84] (Fig 2). In particular, biotic factors may be more critical at the warm edge of species' range limits [22,134]. In turn, these factors can be sensitive to climate change, and modulate the range shifts of birds. But which factors are most important in determining realised niches, and which

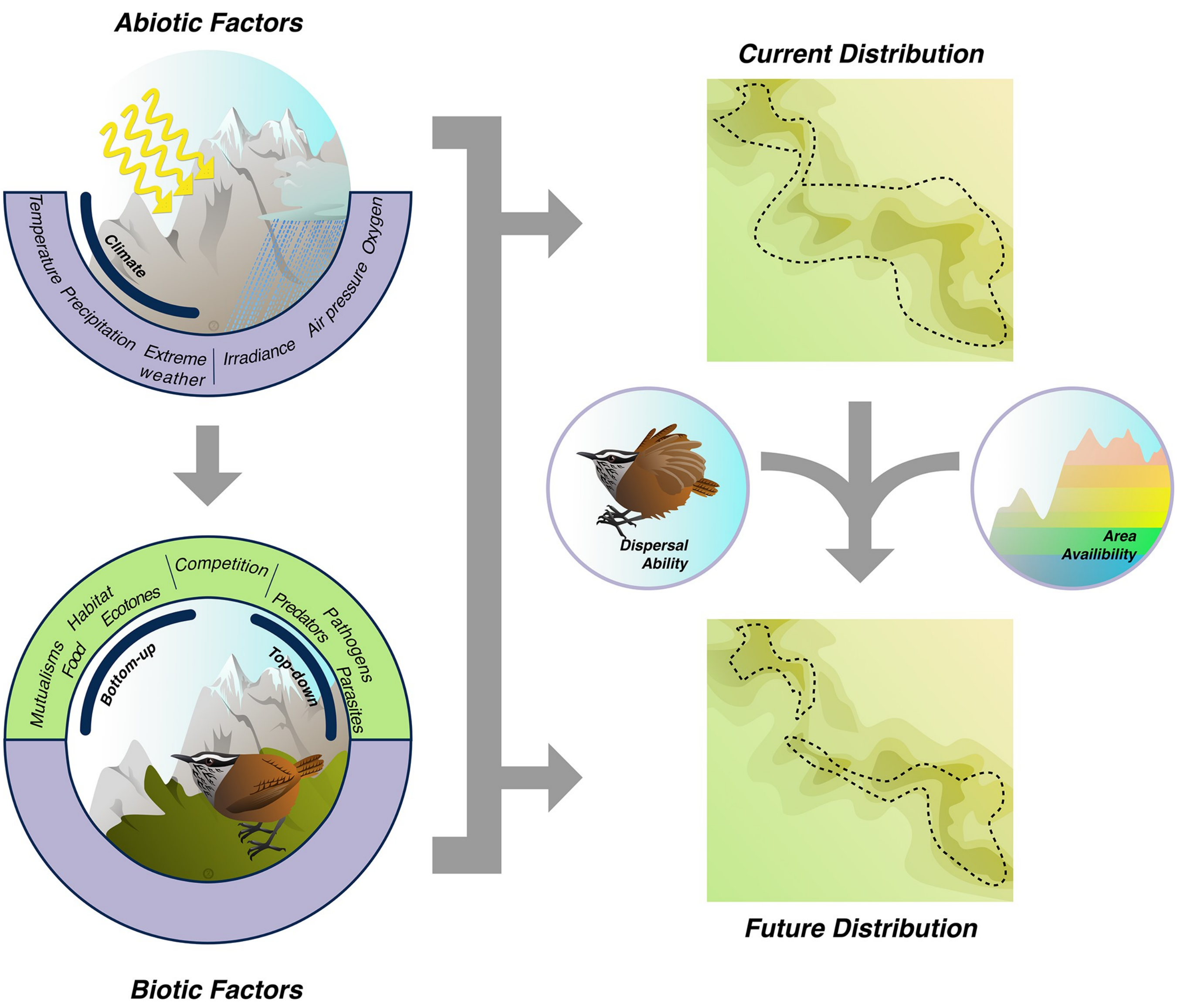

Fig 2. A conceptual framework of elevational ranges and range shifts. Elevational ranges can be shaped by abiotic factors acting directly or acting indirectly via biotic factors. All of these factors affect the realized niche of a species including its current and future distributions. In addition, intrinsic and extrinsic constraints such as dispersal ability and area availability can prevent species from reaching their predicted elevational ranges.

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are likely to influence elevational range shifts? In this section we examine the biotic factors that modify elevational ranges including bottom-up processes, top-down processes, and competition.

4.1 Ecotones, habitat, and resource availability

At a fine scale, bird distributions are often tightly linked to habitat. In the Alps, for example, birds of deciduous forest give way to species of coniferous forest at higher elevations [32]; while in the Andes, the transition from rain forest to cloud forest presents a sharp contrast in community composition [135]. Above all of these forested habitats, the timberline demarks a stark boundary between habitats and bird assemblages [136–138].

Fig 3. Multiple factors shape the elevational ranges of Black-headed Nightingale-Thrush (*Catharus mexicanus*). While habitat associations appear to drive the elevational distributions of *C. mexicanus*, the species is also aggressively dominant over its higher elevation congener Ruddy-capped Nightingale-Thrush (*C. frantzii*), displaying the importance of interactions between habitat selection and interspecific competition for elevational ranges [141]. Photo credit: Samuel Jones.

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Ecotones, the transition in plant communities between habitats, have long been tied to distributional limits in birds [55]. In the Peruvian Andes, Terborgh [139] revealed the importance of ecotones in a comparison of bird distributions between different elevational gradients. When an ecotone was found at higher elevations, Terborgh demonstrated that species inhabiting the lower elevation habitat were able to expand their upper limits upslope [139]. In the Tilarán Mountains of Costa Rica, Jankowski et al. [140] showed that turnover in the bird community was greatest at the cloud forest/rainshadow forest ecotone; while in Rwanda, habitat availability was a major predictor of bird distributions in the transition from forest to open habitat [99]. In Honduras, Jones et al. [141] determined that the transition from cloud forest to elfin forest was the principle driver of parapatry in two congeneric thrushes (Fig 3). In temperate regions, the treeline ecotone is a critical driver of bird community composition in the Swiss Alps [138], the Chilean Andes [136], and in British Colombia [137]; while in the Himalayas, the prevalence of different forest types was an important predictor of bird distributions [101], including parapatric congeners [142]. Elevational shifts have also been linked to ecotones. In Alaska, Mizel et al. [48] noted that shifts in the shrub ecotone have enabled upslope changes in shrub-tundra species, while forest species have been more limited by forest growth

[48], and similar differences in shift rates above and below treeline were found in Switzerland [40]. Thus, ecotones are critical points of turnover for montane birds, and climate-induced range shifts could well be limited by ecotones [40,48].

Besides ecotones, two important predictors of bird community patterns along elevational gradients are vegetation structure and plant composition. Diversity of vegetation structure is thought to promote niche partitioning [20], particularly for insectivores [112,135], and has been shown to predict bird species richness in Peru [55], Chile [136], Tanzania [112], and Papua New Guinea [143], as well as turnover in species composition in Peru [135] and functional and phylogenetic diversity in Bolivia [98]. Tree species diversity is thought to promote food availability, particularly for frugivores [144,145], and has been found to predict species richness in Cameroon [146], Papua New Guinea [143], and Peru [135]. Though the majority of these studies have investigated gradients in bird diversity rather than distributional limits, it seems likely that both structural diversity and plant composition would play a role in determining elevational range limits [147], as well as species' ability to adapt to change [148]. Indeed, habitat has been linked to elevational shifts in temperate regions [32,35,37,40], while in the tropics, lagged shifts in birds indicate a slow, incremental response to shifts in habitat [17,67,149].

Both structural diversity and plant species richness are connected to birds via resource availability. Birds need nest sites to breed and food to feed their young. While little is known about how habitat shapes bird distributions along elevational gradients via nest site availability, there is more evidence for the role of food availability. For example, in Papua New Guinea, Sam et al. [143] demonstrated that the abundance and biomass of insects predicted the abundance and biomass of insectivorous birds. Likewise, in the eastern Himalayas, species richness of insectivores was strongly linked to diversity of foliage arthropods [150], while in Tanzania, Ferger et al. [112] linked insectivore species richness to invertebrate biomass, and frugivore species richness to fruit abundance [112]. However, in a study investigating community assembly, food resources did not predict diversity patterns in the Bolivian Andes [98]. As most food sources are either plant products or ectothermic prey which are very sensitive to climate change [151–156], it is likely that climate-induced shifts in these resources will instigate shifts in the birds that depend on them. More studies are needed to mechanistically link resource availability to the elevational distributions of birds, but these resources are very likely to be affected by climate change and therefore modulate elevational shifts in birds. However, every species has its own individual resource requirements, whether that is bark insects, mistletoe berries, or cavity nesting sites. Using broad proxies such as invertebrate biomass may capture general trends in bird communities, but it is very challenging to quantify the resource needs of each species.

4.2 Competition

Besides top-down and bottom-up processes, another biotic factor limiting elevational ranges is competition [157]. Competition is often invoked when two congeners have abutting ranges along an elevational gradient, although competition may also be diffuse if many species are scrambling for similar resources [158,159]. Detecting signals of competition can be tricky, as parapatric distributions also result from ecotones [101,141]. One way to detect competition is to compare the elevational ranges of focal species with and without putative competitors. In an influential study from Peru, Terborgh and Weske [158] compared the distributions of a suite of species along two elevational gradients in the Andes. Compared to the Cordillera Vilcabamba in the Andes proper, they found that the isolated Cerros del Sira lacked several high elevation bird species. Due to this apparent lack of competition, the ranges of 71% of bird species expanded upslope when a higher elevation congener was absent. Similarly, 58% of species previously thought limited by an ecotone were able to expand to higher elevations in the absence of diffuse competition.

The influential results of Terborgh and Weske were recently supported by Freeman et al. [160], who found evidence of competitive release in 23 out of 52 natural experiments selected from across the Neotropics. In another natural experiment, two species of *Arremon* brushfinch were found to occupy entire elevational ranges in allopatry; yet, importantly, the relative elevational position of the two species in parapatry would flip in different regions suggesting no species-specific elevational preferences [161]. Thus, in the Andes, at least, it has long appeared as if competition plays an important role in range limitation. Similar results have also been found on isolated mountains in Borneo [159], and some advocate that competition is a key driver of elevational range limits globally [160] and that competitive release may in fact explain downslope shifts in some species [162].

While differing elevational ranges under different contexts provide circumstantial evidence of competition, several studies have used playback experiments to gain greater mechanistic insight. These experiments present a focal species with a singing parapatric congener (i.e., via playback) and compare its reaction (e.g., approach, aggression, counter-singing) to the paired reaction to a singing conspecific. For example, in Costa Rica, Jankowski et al. [163] demonstrated that high elevation Gray-breasted Wood-Wrens (*Henicorhina leucophrys*) respond aggressively to the songs of low elevation White-breasted Wood-Wrens (*H. leucosticta*) and vice versa. However, this aggression is not always symmetrical. In the same study system, low elevation Orange-billed Nightingale-Thrushes (*Catharus aurantiirostris*) behaved far more aggressively towards mid-elevation Black-headed Nightingale-Thrushes (*C. mexicanus*) than was reciprocated, while high elevation Slaty-backed Nightingale-Thrushes (*C. fuscater*) showed little aggression at all [163]. Other studies from the Neotropics have found similar support for asymmetric aggression in nightingale-thrushes (Fig 2) and wood-wrens [141,164], and yet these studies represent just two genera.

Consistent with these Neotropical findings, Freeman et al. [165] documented asymmetric aggression in New Guinea, where the lower elevation species of three out of five species pairs behaved more aggressively to its higher elevation counterpart. Similarly, in Borneo, the low elevation Ochraceus Bulbul (*Pycnonotus leucops*) dominated the high elevation Pale-faced Bulbul (*P. leucops*). Evidence for asymmetric aggression has also been building outside the tropics. For example, in temperate *Catharus* thrushes [166], asymmetric aggression from the low elevation Swainson's Thrush (*C. ustulatus*) was found towards the high elevation Bicknell's Thrush (*C. bicknelli*). In the Himalayas, however, the asymmetry was flipped [142], with the higher elevation Green-backed Tit (*Parus monticolus*) behaving dominantly over the lower elevation Cinereous Tit (*P. cinereus*). As these studies accumulate, it appears that asymmetries in aggression may actually be the norm [167], but what could explain the patterns of asymmetry?

Higher aggression from a lower elevation species might be expected if the lower elevation habitat is more optimal (e.g., more resources) [83,168]. Alternatively, higher aggression might be expected from the higher elevation species if it is also larger, following Bergman's rule [169]. One study tested these competing hypotheses in a meta-analysis of pairwise competition and aggression between congeners of various taxa [168]. Although there was no overall evidence that lower elevation species were dominant, the meta-analysis did find that, in playback studies (predominantly featuring tropical birds) lower elevation species tended to be more aggressive, and that this aggression was associated with competitive ability. However, the most important finding of the analysis was that body size was a significant predictor of competitive interactions. Large species tended to dominate smaller species, although larger species did not necessarily follow Bergmann's rule. Thus, the outcome of competition is driven more by body size than relative elevation.

These aggression studies imply that interference competition between closely related species limits range boundaries, but they do not examine the effects of scramble competition. To test the relative strength of the two putative mechanisms, a study of 118 sister species pairs along the Manu Transect in Peru compared the degree of range overlap with differences in bill morphology and territoriality [170]. While sister species with similar morphologies regularly overlapped in range, species that defend year-round territories were less likely to overlap. The results of this study indicate that interference competition is a strong driver of elevational limits. There is, therefore, increasing evidence for the role of competition in determining elevational ranges. However, most of these studies focus on parapatric and sympatric sister species pairs, which form the minority of pairwise species comparisons, especially outside of the Andes. Indeed, in comparative studies, the role of competition seems to be limited when compared to other abiotic and biotic factors [99,101]. In addition, aggression may only act to reinforce habitat-based specialism [141], with competitive advantage dependent on the abiotic or biotic context [100]. There is also disagreement about whether competition is more important in stable, resource-filled environments [6,84] compared to more variable and resource-limited environments [98,100]. More resolution is needed to weigh up the relative importance of competition versus other biotic factors [160].

When it comes to factoring competitive interactions into elevational range shifts, studies should first ask whether a potential parapatric congener is present for a given species, before asking whether that congener is larger or territorial. For a smaller species, a superior competitor at higher elevations may preclude that species from expanding upslope, while a superior competitor at lower elevations could force range contractions at a species' lower limits.

4.3 Natural enemies

Natural enemies comprise the top-down biotic factors that can limit a species' range. While there are several types of natural enemy, they generally fall into those that are either smaller than their prey and reduce prey fitness–parasites and pathogens–or those that are larger than their prey and kill to consume–predators. While both forms of natural enemy can present a constant threat to birds, their impacts on species distributions remain poorly understood.

Birds can be affected by myriad parasites, including blood-borne parasites such as malaria, ectoparasites such as ticks or *Philornis* fly larvae, and even brood parasites–other birds of the same or different species that lay their eggs in the nests of hosts, thereby reducing the reproductive success of the host. One of the most frequently studied avian parasites is *Plasmodium*, which causes both human and avian malaria. As malaria and many other avian diseases are transmitted by ectothermic arthropod vectors (e.g., mosquitoes), the prevalence of such diseases is highly associated with specific temperatures that facilitate arthropod growth, and thus the ranges of both hosts and diseases are projected to increase with global warming [171,172]. Nowhere is this threat to birds more apparent than in the Hawaiian islands, where Paxton et al. [173] linked non-native avian malaria to widescale declines in native Hawaiian avifauna [173]. Here, malaria has historically been restricted to lower elevations, but increasing temperatures have allowed the mosquito host (*Culex quinquefasciatus*) to shift upslope, endangering the honeycreepers already restricted to high elevation forest. As temperatures continue to increase, these naïve hosts are projected to become increasingly threatened [174]. However, the vulnerability of Hawaiian birds to this non-native disease may say more about issues of invasion ecology than about the general role of endemic diseases in limiting elevational ranges.

In mainland areas, by contrast, parasites and pathogens may not strongly impact range limits. In Peru, for example, a large study mapped the spatial relationships between birds and hemosporidian blood parasites across the whole country [175]. Covering almost 1,350 bird species and approximately 4,000 parasite lineages, McNew et al. [175] found little evidence that parasite diversity patterns shaped the patterns of bird communities. Conversely, the distributions of the parasites themselves were predicted by the bird communities as well as precipitation. In Central Africa, the prevalence of trypanosomes–another avian blood parasite–within a widespread sunbird host (Olive Sunbird, *Cyanomitra olivacea*) was also linked to places with lower seasonality in canopy moisture and higher precipitation, while prevalence of *Plasmodium* was once again linked to temperature [176]. Olive Sunbirds exist across a wide range of parasite prevalence, suggesting that, like Peruvian bird species, these parasites do not necessarily limit the range of this host. However, there could be thresholds of parasite prevalence above which sunbirds cannot persist.

In the Australian Wet Tropics, the idea of realised niches influenced by parasites has been developed further. Zamora-Vilchis et al. [177] found the prevalence of four genera of avian parasites (*Plasmodium*, *Haemoproteus*, *Leucocytozoon*, and *Trypanosoma*) to be positively associated with temperature, even controlling for elevation. The authors determined that if host species exist within certain parasite prevalence limits, then increasing temperatures would require the hosts to shift upslope with rising temperatures in order to track their "anti-parasitic niche". Given the high fitness cost of these parasites [178,179], shifting may be the fastest solution in the face of increased mortality or lower reproductive success [177]. The role of parasites in determining range limits requires a lot more attention, and even less is known about the role of pathogens such as West Nile Virus [180] or avipoxvirus [181].

While the effects of parasites and pathogens can vary from the chronic sublethal to acute deadly disease, the effects of predation are usually more immediate. For birds, a critical period of susceptibility is the nesting phase when predation is one of the highest causes of nest failure [182–184]. Nest predators generally fall into three groups [185,186]: mammals (e.g., rodents and monkeys), birds (particularly arboreal hawks and corvids), and reptiles (predominantly snakes). Each of these groups has their own ecologies and potential responses to climate change that could mediate predator-prey interactions. Snakes, in particular, are ectotherms whose activity directly relates to temperature [187–189]. When temperatures increase, snake activity and depredation rates are also expected to increase [190–192]. The effects of temperature on endothermic predators–i.e., birds and mammals–are more variable, with mammals showing little predatory response to higher temperatures [185]. However, changing climate regimes could still bring birds into greater conflict with predators if phenologies shift towards periods of higher predator activity [193].

There are also gradients of predation pressure that could be altered by climate change. Latitudinally, Matysioková and Remeš showed an increase in predation pressure towards the tropics, suggesting that predation is more likely to constrain the elevational ranges of tropical birds [184]. Within the tropics, predation risk also appears–at least for artificial nests in Costa Rica–to decrease with elevation, albeit exhibiting a peak around 600 m [186]. However, this gradient varied depending on the predator group, with bird depredation rates decreasing with elevation while mammal depredation rates showed a more humped pattern. Snake depredation along this gradient was almost certainly underestimated as snakes rarely attack fake nests, and yet snakes are one of the highest causes of nest failure [194]. As with blood parasites, increasing temperatures could cause this gradient to shift upslope, which would mean higher predation rates for higher elevation species that may not have evolved to combat such risk [195]. The suggestion from these studies is that predation risk would be a greater issue for the warm limit of a species' elevational range rather than the cool limit [184]. Other risk factors associated with predation include nest shape–with open nests more vulnerable [184,196]–and body size–with smaller species more vulnerable [184,197].

5 Constraints to shifting

It may be the case that every aspect of a species' fundamental and realised niche is shifting upslope concurrently and, ideally, the bird population ought to track the shifting niche perfectly. However, a shifting population necessitates movements at the individual level and this may present challenges [198]. There could be constraints that prevent a species from shifting fast enough [17], and these constraints could be intrinsic traits or extrinsic factors in the environment (though these two aspects are likely to interact; Fig 1). In this section we describe some of the barriers that may prevent species from shifting optimally.

5.1 Intrinsic constraints

Very little is known about how elevational shifts are realised, but for a species to shift its upper elevation limit upslope, there initially has to be some kind of dispersal prior to successful colonisation [199]. Dispersal, however, can be a critical limiting factor when it comes to range shifts [8,200]. In one study, La Sorte and Jetz [11] simulated elevational shifts for 1009 bird species under three dispersal scenarios, showing that the proportion of species at risk of range contractions increased dramatically under a scenario of restricted dispersal. Similarly, in the Andes, dispersal is expected to play a role in mediating elevational shifts in birds [201], while in the Australian Wet Tropics, isolated species with low dispersal ability are projected to suffer range contractions and declines [200,202]. However, the importance of dispersal ability likely varies with latitude and may not be a critical constraint for temperate bird species which tend to have broader environmental tolerances [57,73] and often engage in movements such as latitudinal migration, altitudinal migration, and nomadic behaviour [203]. In contrast, tropical bird species tend to have much lower dispersal capability [203], and several studies have shown the limited ability of rain-forest birds to cross even small gaps between forests [204–207]. Thus, dispersal ability is probably more important in limiting the shift rates of tropical birds, as supported by a meta-analysis of documented elevational shifts [71].

Another important factor that could modulate range expansions is reproductive rate [198,208]. A species at the faster end of the life-history continuum–i.e., high fecundity, fast generation times–may be able to expand faster than a species at the slow end. However, evidence for this hypothesis is mixed. For example, shift rates of birds in the Sierra Nevada, California, were actually faster for species with smaller clutch sizes [19], while the opposite was true for a study of species across the American West [47]. The importance of these vital rates may depend on the mechanisms by which species shift upslope. For example, are upslope shifts facilitated by individuals that produce many offspring each year or by individuals that live long enough to see and respond to environmental change? In the same meta-analysis of shift rates in the tropics [71], clutch size was not investigated but they did find that body size–which correlates negatively with clutch size [209]–predicted higher rates of upslope shifts for smaller species. Ultimately, this result could be driven by a number of factors, and more tests are needed to determine the roles of various aspects of life-history [210].

Beyond these fundamental morphological and life-history considerations, elevational shifts may be constrained by other ecological strategies such as territoriality or adaptive capacity. For example, highly territorial species may shift more slowly than species that are not tied to a particular area– a phenomenon with evidence from studies across the tropics [71]. However, the opposite phenomenon was found in Californian birds [19]. Species may also be more likely to shift if they are less picky about their habitat or dietary requirements–that is, if they have less ecological specialisation [198,211]. Indeed, tropical bird species with lower forest dependency tended to shift their upper limits faster than more forest dependent species [71], while birds of open habitat in the Czech Republic [37] and diet and habitat generalists in the Swiss Alps [40] were more likely to shift upslope. However, other evidence suggests that upslope shifts were greater for species with narrower diet breadths in western North America [47]. More studies of trait relationships to range shifts are needed to resolve these apparently contradictory findings, perhaps using more appropriate traits or accounting for intraspecific variation in traits [210].

5.2 Extrinsic constraints

A fundamental limit to elevational shifts is the availability of land at higher elevations. While available area does not always decrease monotonically with increasing elevation [212], at some point mountain ranges do reach their peak. For birds whose upper elevational limits already coincide with the tops of the mountains, range contractions are an inevitability of upslope shifts [15,16,67]. Perhaps suitable habitat exists on the next mountaintop over, yet dispersal to higher elevation mountains is unlikely for species with low dispersal propensity.

Besides the fundamental issue of land area availability, the most obvious impediment to elevational shifts is another anthropogenic stressor: habitat loss. Loss of habitat is one of the most pervasive threats to biodiversity [7], and has the potential to interact strongly with climate change [10,213], especially as a large fraction of elevational gradients are unprotected [214]. For a species that "wants" to shift upslope, deforestation and habitat fragmentation could limit the connectivity of a landscape [215–217]. On one hand, a species in continuous forest could slowly colonise higher and higher elevation. On the other hand, if deforestation removes suitable habitat above a species' upper elevational limit, the gap in habitat presents a barrier to upslope dispersal [202].

Studies investigating the interaction between habitat loss and elevational shifts are scant, although there is evidence that habitat loss is more of an issue for species at lower elevations [68,148,213,218,219], and projections suggest an important role for habitat availability in limiting range shifts [200,219]. In the Usambara Mountains of Tanzania, a 40-yr resurvey of 29 bird species along a fragmented elevational gradient suggested an important role for fragmentation in mediating elevational shifts [65]. Across this gradient, lower elevational limits contracted significantly over time, while upper elevational limits were slow to shift, generally moving only within continuous blocks of forest. These results indicate that the isolation of forest blocks limits upslope colonisation of understory birds [204,207]. However, this study was restricted to fragmented forest and did not include a control system of continuous forest. For example, in a spatial study of occupancy in Colombia, Mills et al. [148] suggested that high elevation bird species (~2700 m in elevation) can tolerate greater levels of habitat loss due to the naturally patchier configuration of montane forest. Perhaps habitat loss is less of an impediment to range shifts at high elevations. Future studies should attempt to compare shifts for the same species in continuous versus fragmented landscapes.

6 Conclusions and future directions

It is clear that the elevational distributions of birds can be shaped by diverse abiotic and biotic factors [79], and that these factors can in turn influence whether and how species shift their elevational ranges (Fig 1). How can we synthesise all of these factors together to gain a more holistic understanding of elevational ranges and to better predict distributions into the future?

A fundamental conundrum is whether abiotic gradients like temperature and precipitation play a greater direct or indirect role on elevational ranges [79]. Based off the current state of knowledge, the *direct* effects of temperature and precipitation seem unlikely to constrain elevational ranges and drive upslope shifts across most bird species–except perhaps in very extreme environments–but more studies are needed on vulnerable life stages, especially eggs and nestlings [54,92]. Biotic interactions, however, appear to be critical [160]. Birds tend to associate with particular habitats and food resources, so the question then becomes whether these resources are themselves sensitive to climate change [84], and ultimately, which biotic factors are most important. The overall direction of elevational shifts [13] would seem to suggest that warming temperatures are driving gradual upslope movements via changes in resources [17,67]. Where that is not uniformly the case–possibly temperate, arid environments–changes in precipitation regimes may be more important in driving the resource shifts that govern ranges [19,53].

Comparative studies can offer insight into which factors are most likely to drive elevational range limits and shifts. The role of temperature (direct or indirect) appears to be very important in temperate and sub-tropical regions [100,101] and at very high elevations in the tropics [99], while competition appears more important at lower elevations in tropical forest [158,159,170]. Across studies, habitat seems to be almost universally important [32,37,99,101,112,135,136,141], but these associations could also be driven by habitat-associated resource availability such as invertebrate abundance [112,143]. Habitat is extremely difficult to experimentally manipulate in distributional studies of birds, however, so ultimately it is unknown how plastic most species are in their habitat requirements vis à vis other potential limiting factors.

Future research in the coming years to decades is likely to improve our understanding of elevational range shifts in several ways. Increases in data availability provide opportunities to test more nuanced or complex hypotheses and to replicate studies at greater taxonomic or spatial scales. At fine scales, tracking of individual birds with GPS tags could reveal the elevational movements of individual birds [109], and how these movements temporally scale up to range shifts. For example, we could fit bird communities with trackers and test whether upslope shifts results from the directional movements of individuals over their lifetimes. Perhaps we would find that it is adults choosing nest sites at increasingly high elevations each year that push range limits upslope, or perhaps we would discover first year birds establishing new territories in newly suitable areas at higher elevations. Nest monitoring along elevational gradients could also provide more insights into pressures during the breeding season [220]. Specifically, monitoring of nest depredation could reveal whether there are gradients in predation pressure that vary by predator type, and whether these gradients are shifting upslope. Small climate loggers placed at nest sites could test whether adults are choosing nest sites in appropriate microclimates or whether hatching or fledging success is constrained by temperature in a way that adult metabolism is not. Mirroring desert studies [91,92], nest monitoring could also reveal if provisioning rates vary over elevational gradients or quantify the kinds of food brought to the nest as a function of elevation. Finally, the presence of pathogens and parasites in nestlings could be examined for possible elevation and climate effects.

At medium scales, the maturation of monitoring schemes will provide longer-term perspectives on elevational ranges including both trends and interannual variation [67,69] while accounting for imperfect detectability [98,221], especially when paired with data on other taxa. Mist-netting studies could be used to monitor the demographic rates of populations as a function of elevation [59]. Perhaps we would find that upslope expansions are driven by higher recruitment rates at higher elevations or that lower survival rates at lower limits are causing range contractions. Point counts along transects have the potential to generate huge amounts of data along elevational gradients [68], especially when paired with autonomous recording units (ARUs) [222] and machine-learning identification such as BirdNET [223]. If transects are placed systematically, they could be used to test competing hypotheses of elevational shifts. For example, we could test whether upslope shifts are more likely when a parapatric congener is absent or assess whether shift rates differ depending on the relative position of ecotones on different gradients. More studies are also needed to compare shift rates along gradients with different degrees of habitat connectivity. If other taxa such as plants, invertebrates, or predators are also monitored along elevational gradients, we could test which of these biotic gradients are shifting and which are influencing bird shifts the most. Knowledge learned from such studies could then be used to make better projections that include dispersal ability [202], landscape configuration, and joint-species co-occurrence [224].

At large scales, the availability of citizen science data coupled with comprehensive trait datasets [24,203] could be leveraged to better understand drivers of elevational ranges and shifts [71,160]. The uses of eBird [23] are exploding, as are the number of people using the platform. Instead of costly monitoring programs, we could make use of citizen science data along elevational gradients to test drivers of elevational patterns, boundaries and shifts [70,150,160]. For example, Ramesh et al. [225] used eBird data to explore drivers of bird occupancy in the mountainous Western Ghats of India. Biogeographic gaps could be filled by citizen science data where funding or research opportunities are lacking [226,227]. Citizen scientists primed with the right knowledge could also make more informed observations, such as including breeding codes on checklists. Trait datasets are already being used to predict elevational shifts with mixed results [71,210], but more traits with more relevance to elevational gradients could complement existing datasets. Examples of such relevant datasets include thermal physiology, relative competitive ability, or more specific habitat and dietary requirements. Higher resolution climate data could also aid elevational studies by testing whether range limits are associated with particular aspects of temperature and precipitation, such as variability or extremes, or whether climate-induced range limits differ between different mountain ranges or aspects. Combining all of these variables into more intuitive, interactive databases would revolutionise the ability of researchers to test hypotheses at ever-increasing scales.

As the threat of climate change increases, the need to understand elevational range shifts has never been greater. We have an increasing knowledge of the individual pieces that comprise the elevational puzzle but we still lack a holistic, all-encompassing view of elevational gradients. Although the future of montane biodiversity hotspots is uncertain, harnessing new ideas, data, and techniques will reduce that uncertainty, bringing elevational ranges into focus and providing clearer goals for conservation action.

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