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The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds

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Abstract. There is clear evidence that species' ranges along environmental gradients are constrained by both biotic and abiotic factors, yet their relative importance in structuring realized distributions remains uncertain. We surveyed breeding bird communities while collecting in situ temperature and vegetation data along five elevational transects in the Himalayas differing in temperature variability, habitat zonation, and bird richness in order to disentangle temperature, habitat, and congeneric competition as mechanisms structuring elevational ranges. Our results from species' abundance models representing these three mechanisms differed markedly from previous, foundational research in the tropics. Contrary to general expectations, we found little evidence for competition as a major determinant of range boundaries, with congeneric species limiting only 12% of ranges. Instead, temperature and habitat were found to structure the majority of species' distributions, limiting 48 and 40% of ranges, respectively. Our results suggest that different mechanisms may structure species ranges in the temperate Himalayas compared to tropical systems. Despite recent evidence suggesting temperate species have broader thermal tolerances than tropical species, our findings reinforce the notion that the abiotic environment has significant control over the distributions of temperate species.

Key words: abiotic; biotic; distribution; elevation; Himalayan birds; modeling; range limits.

INTRODUCTION

A central goal of ecology and biogeography is to understand the interplay of factors limiting the distribution patterns of species. Such knowledge is foundational to modern ecology (Grinnell 1917), yet remains incomplete and contentious despite a century of research (Sexton et al. 2009, Wiens 2011). A deeper understanding of the ecological determinants of species' ranges is also critical to predicting how species will respond to land-use and climate change (McCain and Colwell 2011), to allocating conservation investments appropriately (Dobson et al. 1997), and to designing and managing protected areas (Cabeza and Moilanen 2001).

The close association between many abiotic and biotic factors complicates efforts to disentangle their roles as primary limiting factors without controlled experiments (Terborgh 1971). Consequently, to overcome these challenges, ecologists have frequently turned to elevational gradients, which provide rapid turnover of species assemblages and habitat composition under continuous and often uncorrelated variation in climatic gradients (McCain 2009, Jankowski et al. 2013). As such, elevational gradients present perhaps the best opportunity to disentangle correlated abiotic and biotic mechanisms thought to constrain species distributions.

Abiotic factors, particularly temperature and precipitation, have repeatedly been shown to explain variation in richness and abundance patterns along elevational gradients (Thuiller et al. 2004, Boucher-Lalonde et al. 2014). For endotherms, physiological tolerances are correlated with broad-scale climate regimes, suggesting a direct role for climate as a primary limiting factor (Root 1988*a*, Khaliq et al. 2014). Yet abiotic factors may also limit species indirectly by affecting activity patterns and energy expenditures, or through the cascading effects of temperature on resource bases (Price et al. 2011, Cahill et al. 2012). Considerable evidence of species tracking their optimal or adaptive climatic niches via elevational range shifts in both temperate (Tingley et al. 2009) and tropical (Chen et al. 2011) systems further indicates a strong abiotic influence in setting species' ranges. Though species exhibit marked heterogeneity in their responses to different climatic factors (Tingley et al. 2012), temperature is particularly important as both a predictor of abundance and a determinant of range boundaries for a wide range of taxa (Root 1988*b*, Rubidge et al. 2011, Alofs and Jackson 2015).

Recently, much attention has focused on the role of biotic factors as regulators of species abundances and distributions, particularly at warm range margins (Louthan

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et al. 2015). While predator-prey dynamics and parasitic interactions can be important in structuring species distributions, habitat limitations and competition have received the most attention and support as key determinants of the occupied portion of the realized niche of species (Pearson and Dawson 2003). While competing species may co-occur through finer-scale resource partitioning (MacArthur 1958), multiple studies have demonstrated range boundaries set by competitive exclusion amongst congeneric species along environmental gradients (Terborgh and Weske 1975, Jankowksi et al. 2010, Cahill et al. 2014). Modeling techniques across taxa have illustrated that incorporating such biotic interactions into species distribution models can significantly improve projections of species ranges (Araujo and Luoto 2007, Heikkinen et al. 2007).

Similarly, habitat specialization arising, for example, from particular requirements for foraging or reproduction may narrow the range of resources a species can utilize efficiently and thereby enforce range limits (Terborgh 1985, Price 1991). Strong patterns of community turnover along elevational gradients point to an important role for habitat as a determinant of a species' range (Jankowski et al. 2013), and ecotone boundaries have been shown to limit species' distributions (Able and Noon 1976, Patterson et al. 1998).

Indeed, multiple factors likely interact simultaneously to constrain species distributions, with abiotic and biotic factors potentially limiting different portions of a species' range, such as upper and lower limits (MacArthur 1972, Brown et al. 1996). Abiotic and biotic factors may also vary in their relative importance regionally or across abiotic and biotic stress gradients, such as elevation or latitude (Louthan et al. 2015). Both experimental and empirical studies attempting to understand the factors limiting species distributions have typically focused on abiotic and biotic factors in isolation, with far fewer attempts to discern the relative contributions of each. Such studies have also typically focused on one or a few species, limiting our ability to make broader generalizations (Cahill et al. 2014).

Here, we utilize properties unique to the Himalayas that make this remote and poorly studied mountain range an exceptionally well-suited system to disentangle abiotic and biotic mechanisms limiting species distributions. The Himalayas contain the most extensive elevational gradients on Earth, support diverse sets of habitats and microclimates, and exhibit a profound longitudinal gradient in bird richness, with over twice as many breeding bird species in the east compared to the west (Price et al. 2011). This diversity gradient creates distinct communities subject to similar elevational climate gradients, but with varying species richness and numbers of congeners, facilitating tests of abiotic vs. biotic determination of range boundaries.

We surveyed breeding birds along five elevational transects in two regions of the Himalayas to test three leading hypotheses regarding the factors thought to structure species distributions. We first tested the hypothesis that temperature limits bird distributions by incorporating locally collected temperature measurements into models of bird abundance that account for imperfect detection (a common bias that can obscure true ecological relationships). Second, we tested whether habitat limits bird distributions through ecotone effects by parameterizing models with densities of tree species comprising distinct habitat types. Third, we tested whether competition limits bird distributions by searching for distributional evidence of competition between sympatric congeners and for evidence of competitive release when those congeners were absent. We assessed the evidence consistent with each hypothesis for 70 bird species by comparing the performance of each model set. By examining the relationships between bird abundance and each predictor in our models at both range margins, we determined the prevalence of abiotic and biotic factors in structuring species elevational distributions in the Himalayas.

Materials and Methods

Study regions and elevational transects

We surveyed breeding birds on five continuous transects spanning comparable elevations (~2,000–4,000 m) in two regions of the western Himalayas of northern India differing in temperature variability, habitat zonation, and bird species richness (Fig. 1). We established three separate elevational transects in Great Himalayan National Park (GHNP; Appendix S1: Table S1), located in Himachal Pradesh (31.70° N, 77.50° E), and two separate elevational transects in Askot Wildlife Sanctuary (Askot; Appendix S1: Table S1), located in Uttarakhand (29.95° N, 80.35° E) approximately 325 km southeast of GHNP. The two regions were chosen so as to maximize differences in breeding bird richness while minimizing the distances from one another in order to retain similar broad climate regimes between regions. Importantly, Askot differs from GHNP by completely lacking the lower coniferous forest zone and by containing roughly 30% more breeding bird species.

Bird surveys

Given the extreme topography of the landscape, we surveyed birds using a line transect technique along existing trail networks and, in some cases, trails of our own construction. Being situated within protected areas, all transects had minimal human disturbance. We surveyed birds between 5:00–10:30 am and 5:00–7:00 pm during the breeding seasons in late April–June in 2013 and 2014. We oriented transects in parallel with the elevational gradient so that they largely ascended straight up mountain sides and divided each elevational transect into 350 m transect subsections that formed the basis of daily sampling. We surveyed each transect subsection twice each morning (one upslope walk and one downslope

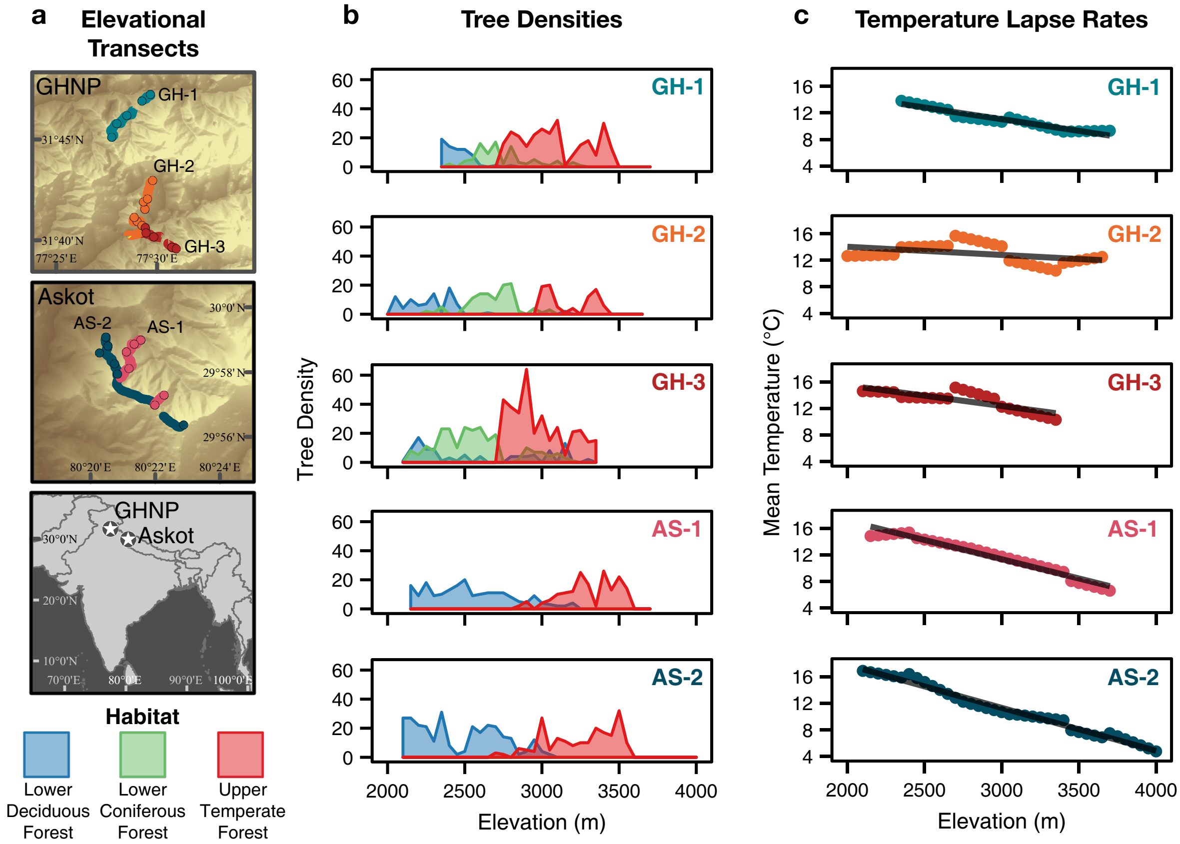

Fig. 1. (a) Map of the five elevational transects (colored lines) used to survey birds and habitat in GHNP and Askot and their position within India. Colored points along elevational transects refer to locations of temperature loggers and approximate the bounds of 350-m transect subsections. (b) Tree densities of all tree species that are characteristic of habitat types along each elevational transect (shaded polygons, see habitat key). Approximate ecotone boundaries occur where shaded polygons begin to overlap along a transect and are variable between regions and transects within a region. Note the absence of lower coniferous forest along elevational transects in Askot (AS-1, AS-2), resulting in an elevated upper boundary of lower deciduous forest compared to GHNP (GH-1, GH-2, GH-3). See Appendix S1: Table S2 for descriptions of tree species in each habitat category. (c) Mean temperature readings (points) with elevation, calculated over the period surveyed for birds along the five elevational transects with linear trend lines. Note variable lapse rates among transects, even within a region. [Color figure can be viewed at wileyonlinelibrary.com]

walk, separated by 20 min) and once each evening (either upslope or downslope), repeating surveys between six and nine times in total over the 2 yr. While surveying, we identified all birds by sight and sound and recorded the elevation, time, distance to observer, and count for all birds while walking at a slow, constant pace. We had two simultaneous observers for all surveys to maximize detectability, resulting in one combined count. The same observers conducted the surveys along all transects in both regions and across both years.

Habitat surveys and habitat type assignments

We quantified habitat characteristics along all elevational transects we surveyed for birds in order to define habitat types and determine the locations of habitat transitions along the elevational transects. To do this, we established one habitat survey plot every 50 m of elevation along each elevational transect. In each habitat survey plot, we identified and counted all woody stems ≥30 cm dbh (to species level, except for the genera *Acer* and *Abies* where the two species in each genus were grouped) within a 25 m radius of the plot center. The same team conducted the vegetation surveys along all transects in both regions and across both years.

We then followed the typology of forest types defined by Champion and Seth (1968) to delineate each habitat survey plot as being composed of distinct habitat types based on tree species composition (rare tree species with <10 total observations were excluded). We determined that all of the tree species we recorded during our surveys fell into three such habitat types, based on Champion and Seth (1968): lower deciduous forest (LDF), lower coniferous forest (LCF), and upper temperate forest (UTF). Habitat types may share tree species, but each habitat type has a unique species assemblage (Appendix S1: Table S2). LDF and UTF habitat types were present in both regions, but only GHNP contained the additional LCF habitat type (Fig. 1b). At each habitat survey plot, we summed the count of individuals of all tree species that are characteristic of each habitat type, resulting in one summed count of tree densities for each of the three habitat types. Our method allows tree species of multiple habitat types to be represented in each habitat survey plot resulting in graduated rather than discrete ecotone boundaries (Fig. 1b).

Temperature measurements

We deployed HOBO Microstation data loggers (Onset H21-002, Natick, Massachusetts, USA) fitted with temperature sensors (Onset S-THB-M002, accuracy ±0.21°C) along all elevational transects to simultaneously record temperature every 5 min during the time we surveyed for birds. We placed one data logger at the endpoints of each transect subsection, positioned within the forest (except when above treeline) and spaced approximately 350 vertical meters apart (Fig. 1a). We calculated the mean temperature over all periods surveyed for birds for each 50 vertical meters of elevation on each survey transect by linearly interpolating the temperature readings from the upper and lower loggers bounding a given subsection (Fig. 1c).

Modeling bird abundance

We used *N*-mixture models – a class of abundance model that corrects for imperfect detection (Royle 2004) – to evaluate how strongly hypothesized factors contributed to bird abundance patterns. Because we surveyed the entire bird community along each continuous elevational transect, our data comprised both true absences (the absence of observations outside the known bounds of a species' elevational range) and false absences (arising from imperfect detection of a species at elevations where it occurs in low abundance). Consequently, we used zero-inflated Poisson (ZIP) *N*-mixture models, which can accommodate both types of absence (Wenger and Freeman 2008, Denes et al. 2015). ZIP *N*-mixture models are hierarchical and simultaneously model the Poisson-distributed abundance of a species (λ), given its occupancy adjusted for zero inflation (ψ), and the probability of detecting an individual of a species (p), given true abundance. We used ZIP *N*-mixture models specifically because they (1) account for three sources of zeroes in the data (Denes et al. 2015), (2) provide greater variability in the response variable with which to model distributions, facilitating model convergence for more uncommon species, and (3) incorporate estimates of occupancy into estimates of abundance, which can appropriately model threshold effects (Wenger and Freeman 2008) and provide meaningful insight into the ecological processes underlying species distributions (Joseph et al. 2009).

The ZIP *N*-mixture model is used with repeated observation data to model the true number of individuals, N_i, based on observed counts, y_{it}, at $i = 1, 2, \ldots, R$ sites over $t = 1, 2, \ldots, T$ sample periods. Within the model, we defined a site as a 50-m elevational band on a given transect. By discretizing transects into elevational units, we were able to match continuous bird observations with vegetation sampling units and interpolated temperature measurements. We conservatively restricted all analyses to bird species that were present in both study regions with ≥30 observations at ≥20 sites over both seasons. Each y_{it} count arises from a binomial process based on N_i and p_{it} (survey-specific detection probability of each individual) as:

$$y_{it} \sim \text{binomial}(N_i, p_{it}).$$

We selected survey effort (total time spent in a 50 m elevational band divided by the traveled distance within the elevational band per survey event), time of day (when surveying began in each 50-m elevational band), and Julian day as survey-specific covariates expected to affect probability of detection (p_{it}), and used these covariates to create seven different parameterizations, which composed the detectability model set to apply to different models parameterizing abundance (Fig. 2). These covariates were modeled as a function of p_{it} using a logit-linear transformation.

The abundance of each species was modeled as a zero-inflated Poisson, formulated as:

$$N_i \sim \text{Poisson}(\lambda_i \cdot z_i)$$

$$z_i \sim \text{Bernoulli}(\psi)$$

where ψ is a zero-inflation parameter, specifying the probability that the species is present, and z_i is the Bernoulli-distributed binary outcome of this probability, indicating whether the species is truly present ($z_i = 1$) or absent ($z_i = 0$) from site *i* (Wenger and Freeman 2008). The general form of the abundance portion of the model is given by:

$$\text{logit}\left(\lambda_i\right) = \boldsymbol{\beta} \cdot \boldsymbol{\Omega}_i$$

where $\boldsymbol{\beta}$ is a vector of parameters and Ω is a matrix of covariate values including, at minimum, an intercept. We used maximum likelihood to estimate parameters following the form outlined in Royle (2004). *N*-mixture models were fit using the package *unmarked* (Fiske and Chandler 2011) in the program *R* (R Core Team 2015).

Hypothesis testing

The specification of unique covariate combinations for λ provides a framework for testing alternative mechanisms thought to limit species distributions (Royle 2004, Joseph et al. 2009). We used a multi-model information-theoretic approach (Burnham and Anderson 2002) to evaluate how strongly our abundance data fit three independent candidate sets of environmental covariates representing

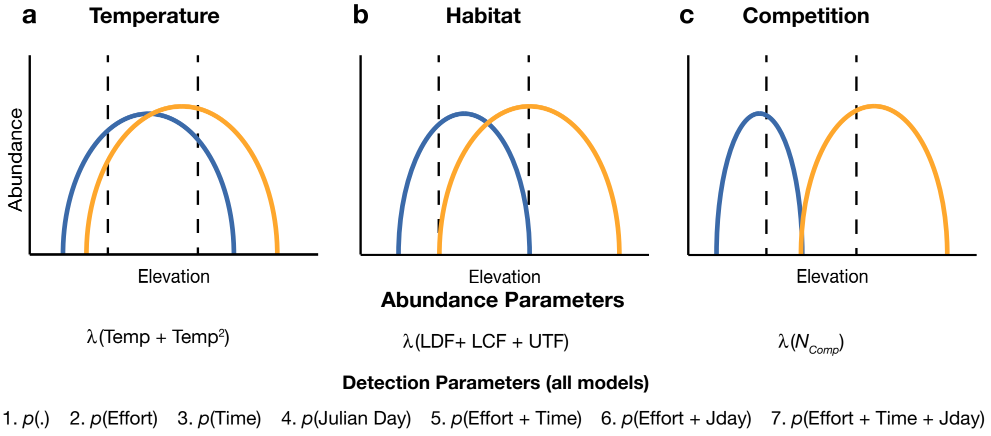

FIG. 2. Conceptual models with *N*-mixture model parameterizations representing range limit hypotheses tested. Colored lines indicate potentially competing species. (a) In the temperature model, potential competitor distributions overlap broadly (no elevational segregation between congeners) and range limits do not coincide with ecotone boundaries (dotted vertical lines). (b) In the habitat model, range limits closely correspond to ecotone boundaries (upper for blue species, lower for orange species), irrespective of congeneric competitors. (c) In the competition model, potential competitor distributions abut sharply, irrespective of ecotone boundaries. Models are not mutually exclusive, such that species can show distributions consistent with more than one hypothesis at either lower or upper range boundaries. λ parameters in the habitat model refer to summed densities of all tree species from each of three habitat types (LDF = lower deciduous forest; LCF = lower coniferous forest; UTF = upper temperate forest) and for competition refer to detection-corrected modeled abundances of congeneric species. The seven *p* parameterizations accounting for detectability were used in each of the three abundance model formulations. See Appendix S1: Tables S3, S4 for descriptions of the modeled response consistent with each hypothesis. [Color figure can be viewed at wileyonlinelibrary.com]

the hypotheses that temperature, habitat, or competition structure species distributions (Fig. 2; see also Appendix S1: Table S3). Such correlational approaches facilitate ecological generalizability and have frequently been employed in species distribution modeling and studies of range limitation (Guisan and Thuiller 2005, Louthan et al. 2015). We chose three distinct candidate sets rather than one global mixed effects model to enable appropriate calculations of model-averaged coefficients given the variable numbers of predictors across species in competition model sets (Burnham and Anderson 2002, Cade 2015). Within each candidate set, we kept abundance parameters constant and applied the abundance model to our detectability model set, calculating model-averaged coefficients for each parameter affecting abundance while accounting for imperfect detection (Burnham and Anderson 2002, see Fig. 2 for λ and *p* parameterizations).

We then evaluated the model-averaged effect size and direction of coefficients on abundance within each candidate set to determine whether relationships between bird abundance and each abiotic and biotic factor were indicative of range limitation in ways predicted by ecological theory (Fig. 2; Terborgh 1971, MacArthur 1972). We considered a modeled bird response to be significantly related to a covariate when the range of the 95% model-averaged confidence interval did not contain zero. When no covariates were found to be significant, or when covariate relationships were counter to theoretical expectations (following Terborgh 1971 and outlined in Appendix S1: Tables S3, S4), this suggested the modeled response was not consistent with the hypothesis represented by that candidate set.

To test the hypothesis that temperature limits species' ranges, we parameterized models with in situ mean temperature (linear and quadratic effects) at each site as a predictor of abundance (i.e., model averaging of abundance covariates captures the uncertainty in detectability parameterization) and applied this abundance model to our detectability model set. The explicit inclusion of temperature into our models, rather than elevation (which is typically used as a proxy), helps control for the potential influence of other abiotic factors that co-vary with elevation, such as precipitation. We expected that bird abundance distributions consistent with temperature limitation at both range margins would be hump-shaped, where maximum abundance is centered at the thermal optimum and declines as temperature increases or decreases (Fig. 2a; Terborgh 1971). Distributions consistent with temperature-limitation at only the upper or lower portions of their range would show positive or negative monotonic relationships with temperature, respectively.

To test the hypothesis that habitat limits species' ranges, we parameterized models with the three summed tree density measurements—one summed count of individuals of all tree species that are characteristic of each habitat type, for all three habitat types—as predictors of abundance (three covariates in total) and applied this abundance model to our detectability model set. We expected that bird abundance distributions consistent with habitat limitation would be positively associated with one or more habitat types, and that abundance would quickly decline in unfavorable habitats at upper, lower, or both range margins via ecotone effects (Fig. 2b; Terborgh 1971).

To test the hypothesis that competition limits bird ranges, we defined a potential competitor as a congeneric species – because congeners are typically very similar ecologically and therefore often thought to exert intense competitive force (Terborgh and Weske 1975, Jankowksi et al. 2010) – and first considered species that had congeners present across all elevational transects. We first modeled the abundance of each competitor using our detectability model set, with no covariates on abundance. Then, for each species, we used the modeled abundance of the congeneric competitor (having accounted for detectability) per site as a predictor of abundance and applied this model to our detectability model set. For species with more than one congener present, we modeled each pairwise interaction separately, independently assessing competitive interactions between all pairwise congeneric combinations. We expected bird abundance distributions consistent with competition-mediated limitation would have a significant negative relationship with the abundance of at least one of its potential competitors at upper, lower, or both range margins (Fig. 2c). We visually inspected the modeled abundance distributions over elevation for the competing species to determine the range margin(s) on which competition was operating.

Finally, we tested for competitive release by considering species that had congeners present at some, but not all, elevational transects, owing to the longitudinal bird diversity gradient (Price et al. 2011). Using the same modeling approach as described above, we expected that bird abundance distributions consistent with competition-mediated limitation would have a significant negative relationship with competitor abundance on transects where both species were present and that range limits would expand on transects where the competitor was absent.

To ensure that our competition analyses were robust to differences in phylogenetic relatedness and key morphological traits between congeneric pairs, which might influence the expected level of competition found between congeners, we performed a meta-analysis testing for effects of these parameters on the competition coefficients produced from our models. To do this, we obtained 1000 phylogenetic trees of all species considered in our competition analyses using the Ericson backbone posterior distribution from a global phylogeny of birds (Jetz et al. 2012). We then calculated the mean phylogenetic distance between congeneric species pairs over the 1000 phylogenetic trees. We considered differences in bill length and body size between congeneric pairs to potentially influence the degree of competitive interactions, given their relation to diet and prey size (Price 1991). We obtained morphometric data on bill length for each species from Ali and Ripley (1978) and body mass from Dunning (2008), using the median value of measurements taken from male individuals. We then ran a series of linear mixed effects models that used the pairwise congeneric competition coefficients obtained earlier as the response variable, all additive combinations of phylogenetic distance, pairwise difference in bill length, and pairwise difference in body mass as fixed effects, and the genus of each pairwise comparison as a random effect.

Our analytical approach allows for multiple competing hypotheses to be consistent with the data for a given species. When modeled responses were consistent with more than one hypothesis for a given species' upper or lower range limit (outlined in Appendix S1: Tables S3, S4), we followed the hierarchy outlined in Terborgh (1971), first assigning competition, followed by habitat, and finally temperature as the primary limiting mechanism when applicable. Such an approach may underestimate the number of species limited by temperature and overestimate the number of species limited by habitat or competition when range limits incidentally coincide with ecotones or competitors. However, this possibility is minimized given that range limits must incidentally coincide with ecotones or competitors across five elevational transects to be assigned incorrectly. Despite these limitations, we follow this hierarchy to retain consistency with earlier work and theory (Terborgh 1971), but we also report for each species whether its modeled distribution was consistent with each of the three hypotheses (Appendix S1: Table S5), which provides general insight as to the relative support for each hypothesis across the entire bird community.

In cases where modeled responses were not consistent with any of the three hypotheses, we re-evaluated all hypotheses by considering narrower confidence intervals (coefficient ±0.98 SE) and repeated range limit assignments as described above. When the data still were not consistent with a single hypothesis, we did not assign a limiting mechanism and concluded that other factors not considered in our models most likely determined range limits for such species.

Results

Evidence of abiotic and biotic mechanisms of range limitation

Surveys produced 13,192 bird observations of 168 bird species. Of the 168 species we recorded, 62 species were removed from analysis because they were present in only one region (largely due to the longitudinal species richness gradient). A further 36 species were removed due to sample size limitations: 10 were removed because their ranges barely extended into our surveyed elevational gradient; 15 were removed because they occur primarily in non-forested habitats or along river courses, while transects were situated on forested slopes largely away from rivers; and 11 were removed because they were generally uncommon in our survey regions (Appendix S1: Table S6). Consequently, 70 species met our criteria for inclusion in the modeling analysis (Appendix S1: Table S5). Across these 70 species, we found modeled responses consistent with all three hypotheses limiting bird ranges, with abiotic and biotic factors limiting Himalayan bird elevational ranges in approximately equal proportions (Fig. 3). Notably, the data were overwhelmingly consistent with

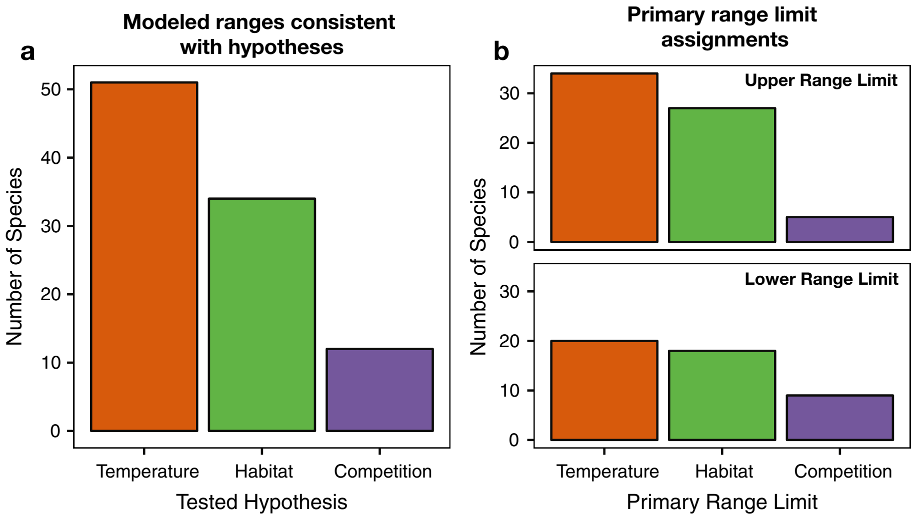

FIG. 3. (a) Number of species whose modeled elevational distributions were consistent with temperature, habitat, and competition hypotheses of range limitation (n = 70 species). Species with modeled distributions consistent with more than one hypothesis (e.g., *Tarsiger rufilatus,* see Fig. 4b) were assigned a primary limiting mechanism following the hierarchy of competition, habitat, and then temperature (see methods for further details). (b) Summaries of the number of species with upper and lower range boundaries primarily limited by each factor considered. Overall, abiotic factors primarily limited the majority of species upper range limits (top panel), whereas biotic factors primarily limited the majority of species lower range limits (bottom panel), though differences were marginal. Three species with modeled ranges not consistent with any of the three hypothesis and 22 lower range limits artificially truncated due to the sampled elevational gradient are excluded from plots. [Color figure can be viewed at wileyonlinelibrary.com]

the hypothesis that temperature is an important factor limiting species' ranges, with 51 of 70 species showing significant relationships between modeled abundance and temperature that suggested a thermal optimum for each species (Figs. 3a, 4a; Appendix S1: Table S5). Thirty-three of 70 species had modeled distributions consistent with the hypothesis that habitat limits bird ranges (Fig. 3a, Appendix S1: Table S5). Such species showed lower and/or upper range limits closely corresponding to habitat transitions across multiple transects (Fig. 4b).

Forty-six species had at least one congener present across all transects for inclusion in competition analyses, and we found evidence consistent with the hypothesis that competition limits bird ranges for 12 of these species (Fig. 3a; Appendix S1: Tables S5, S7, S8). Competitive interactions occurred at lower, upper, and both range margins in some cases (Fig. 4c). We were able to test for evidence of competitive release with 19 species that had congeners present on transects in Askot, but not in GHNP. Of these 19 tests, we found no instance of a species expanding its range to upper or lower elevations in the absence of a competitor (Fig. 5; Appendix S1: Table S8).

We additionally found no evidence that differences in bill length or body mass between congeneric pairs influenced their degree of modeled competition. Our meta-analysis results testing for a signal of phylogenetic relatedness on competition while controlling for different genera revealed a significantly positive relationship between phylogenetic distance between congeneric species and the coefficient of competition between them ($\beta = 0.025$ [95% CLs = 0.009, 0.040]), such that more closely related species showed significantly greater evidence for competitive limitation (Appendix S1: Table S5 and Figure S1).

Primary limiting mechanism assignments

By comparing the three hypotheses for each species, we independently assigned lower and upper primary range limit mechanisms as described earlier, following the hierarchy in Terborgh (1971). Because we were unable to survey elevations below 2000 m due to human disturbance, we were unable to evaluate the mechanisms setting the lower range limit for 22 species whose elevational distributions are known from the literature to extend below 2000 m. We were also unable to determine the factors setting the lower and upper range limits for one and four species, respectively, because they had weak relationships with all abiotic and biotic factors considered. Of the 67 species for which we could make range limit assignments, we found temperature accountable for limiting approximately 48% of species' total range boundaries (upper and lower ranges combined; Fig. 3b; Appendix S1: Table S5). Of the biotic factors considered, habitat was found to limit roughly 40% of species' total range limits and competition the remaining 12% of range limits (Fig. 3b). Overall, abiotic factors were found to limit a greater proportion of species' upper ranges while biotic factors were found to limit a greater proportion of species' lower ranges (Fig. 3b), though these differences were marginal.

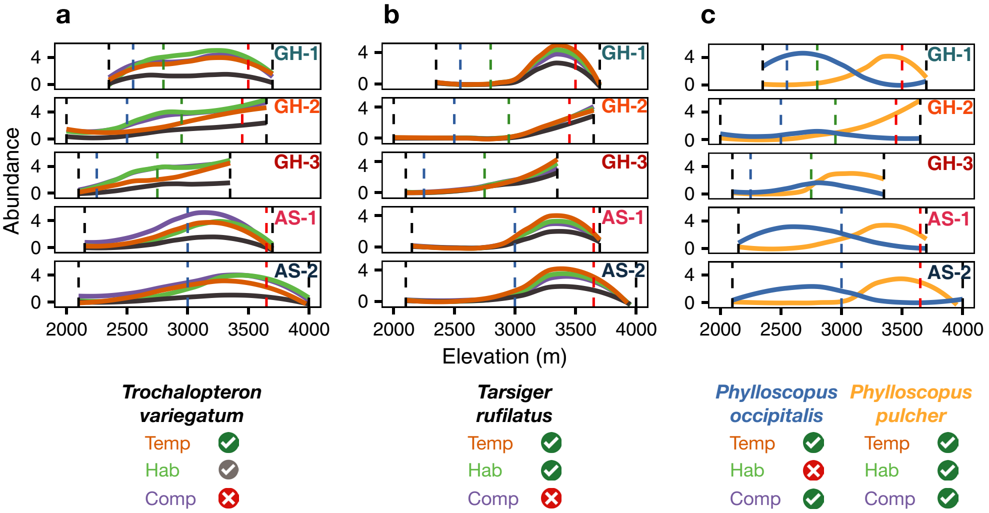

FIG. 4. Example bird species with modeled and raw abundance distributions across five elevational transects. Dotted vertical lines represent approximate upper ecotone boundaries (colored as in Fig. 1) and lower and upper sampling termini (black). In (a) and (b), colored lines represent predicted abundance based on temperature (orange), habitat (green), and competition (purple) N-mixture models, compared to raw abundance counts (black). (a) *T. variegatum* was abundant across ecotone boundaries and in the presence of a congeneric competitor, *T. erythrocephalum* (not shown), consistent with the temperature hypothesis of range limitation at both range margins. (b) *T. rufilatus* showed strong declines in abundance at lower and upper range limits that coincided with ecotone boundaries, irrespective of the presence of a congeneric competitor, *T. chrysaeus* (not shown), consistent with both temperature and habitat hypotheses. (c) Colored lines represent competition N-mixture models for *P. occipitalis* (blue) and *P. pulcher* (orange), whose modeled abundance distributions were consistent with competitive range limitation at upper and lower range boundaries, respectively. Green and grey check marks and red "x" marks indicate modeled distributions were strongly, moderately, or not consistent with the corresponding hypotheses for each species as determined by hypothesis testing using N-mixture models. [Color figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Our results demonstrate the importance of both abiotic and biotic factors in determining the elevational distributions of Himalayan birds. Compared to previous research in the tropics (Terborgh 1971), our results highlight a substantial abiotic influence in structuring bird elevational ranges, with the majority of species (73%) in our analyses showing significant relationships with temperature (Fig. 3a). This finding is consistent with the notion that both the fundamental and realized niche are strongly structured by abiotic factors as well as by recent research documenting niche tracking of temperature by birds (Pearson and Dawson 2003, Tingley et al. 2009). Temperature likely

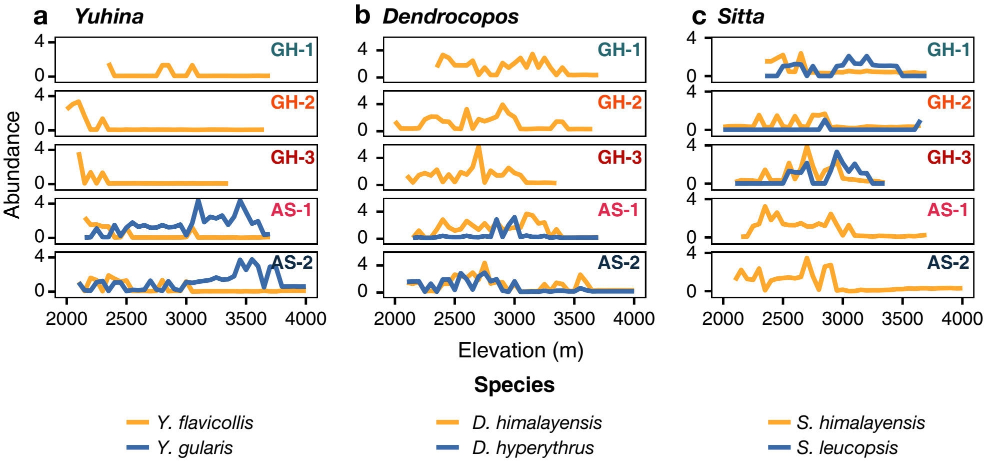

FIG. 5. Examples of tests of competitive release for species pairs in three genera where congeners are present on some – but not all – elevational transects due to the longitudinal bird diversity gradient. (a–c) Colored lines represent modeled abundance from competition N-mixture models, beginning and ending at the limits of the sampled elevational gradient per transect. Note across the three genera, species show no signs of competitive release to higher or lower elevations in the absence of their congeneric competitor. [Color figure can be viewed at wileyonlinelibrary.com]

plays a particularly important role for birds due to its direct effect on physiological tolerances (Root 1988*a,b*), but may also interact with a host of other factors to indirectly structure bird communities. For instance, temperature may structure bird ranges through its effect on prey availability (Price et al. 2011) or by influencing other dimensions of habitat not incorporated in our models. It is also possible that rather than directly influencing adult bird physiology, temperature limits bird ranges through its effect on egg and nestling development, or by inducing tradeoffs with life history traits associated with reproductive physiology, such as balancing incubation and foraging (Londoño et al. 2016). While we cannot parse out the relative influence of direct and indirect effects of temperature on range limits through our study, our results nevertheless suggest a dominant role of temperature in limiting the elevational ranges of Himalayan birds.

Tests of the hypothesis that habitat limits bird elevational ranges via ecotone effects revealed that nearly half of our species (47%) had significant relationships with one or more habitat types consistent with strong habitat-mediated range limitation, where bird abundances declined precipitously in habitat types adjacent at lower or higher elevations (Fig. 4b; Appendix S1: Table S5). Turnover of the bird community was especially high at the transition into upper temperate forest, with many bird species' elevational ranges closely corresponding to the displaced zonation of upper temperate forest across transects (Appendix S1: Figure S2). However, we also note that the majority of upper limits coincided with treeline, which could simply reflect dependence on forests in general rather than strict habitat specialization to upper temperate forests per se.

We found much less evidence that competition is a major factor limiting the elevational distributions and structuring the realized niches of Himalayan birds. From previous studies, competitive interactions are widely thought to play a dominant role in limiting bird ranges (Terborgh and Weske 1975, Jankowksi et al. 2010, Laube et al. 2013). In the Peruvian Andes, for example, competition was found to set the elevational range limits of more than two-thirds of the bird community (Terborgh and Weske 1975). Despite elevational replacement by many congeners in the Himalayas, a pattern that has previously been interpreted as demonstrating a strong role for competition along elevational gradients (Terborgh 1971, Price et al. 2011), our tests of competition between over 100 independent congener pairs revealed few significantly negative relationships indicative of competition-mediated range limitation. Assessing competitive interactions across multiple repeated transects, or in different regions of a species' geographic range, may be necessary to appropriately attribute range limitation to competition rather than to other co-varying factors, such as temperature (Cadena and Loiselle 2007). Indeed, many congener pairs whose ranges abutted on one transect were found to overlap substantially on other transects (Appendix S1: Figure S3). Statistically, most species exhibited neutral or even positive abundance relationships with their congener(s), suggesting a lack of competition in such cases (Appendix S1: Table S8).

However, competition-mediated range limitation was apparent in a few cases, most notably among the morphologically similar and closely related *Phylloscopus* warblers, the most species-rich genus of birds in the western Himalayas. While previous studies have suggested that *Phylloscopus* warblers do not show range contractions across the Himalayan bird diversity gradient as predicted by competitive forces influencing elevational distributions (Ghosh-Harihar and Price 2014), we found evidence consistent with competition as an important factor limiting both the upper and lower ranges of several species in this genus (see examples in Fig. 4c; Appendix S1: Tables S5, S7). Still, many *Phylloscopus* warbler species in our study areas exhibit overlapping distributions and, rather than competing strictly along elevational gradients, it is likely that they also partition resources in the landscape along other dimensions, such as by altering their foraging mode or position in the canopy (Price 1991), allowing varying degrees of sympatry (sensu MacArthur 1958).

We also failed to observe compelling evidence for competitive release, a hallmark of competitive exclusion, when including potential congeneric competitors that were present on only some transects into our models (Fig. 5; Appendix S1: Table S8). A species' elevational range generally did not differ whether in the presence of a congener or not, and our model results indicated that any observed shifts were better predicted by displaced habitat types or differing temperature profiles across transects. It is possible we underestimated the role of competition by not considering other forms, such as diffuse competition or direct competition from non-congeneric species, but given the weak signature of competition among congeneric species, which are often thought to aggressively compete along elevational gradients (Terborgh and Weske 1975, Jankowksi et al. 2010), as well as the general absence of competitive release, we think it unlikely that competition plays a major role in limiting bird distributions in our study area.

Indeed, our hierarchy of assigning primary limiting mechanisms ensures that competition is assigned to a species whenever there is evidence to support it, eliminating the possibility of underestimating rates of congeneric competition-mediated range limitation in our study. Moreover, our meta-analyses suggest that more closely related species exhibit greater negative interactions (Appendix S1: Figure S1), and since we included all congener pairs in our analyses, we would not expect substantial competition-mediated range limitation amongst more distantly related species pairs. Still, while our results suggest that competition plays a minor role in limiting elevational ranges of Himalayan birds, it is possible that historical interactions between species pairs contributed to evolutionary process promoting congeneric co-existence and structuring the elevational distributions we currently observe (Cadena 2007).

Previous studies in the Andes have implicated abiotic factors as important elevational range limit determinants for only a small fraction of birds (Terborgh and Weske

1975, Terborgh 1985). In contrast, we find that temperature explains the elevational distributions of at least as many Himalayan bird species as do habitat and competitive interactions combined. Because previous studies relied on elevation as a proxy for abiotic factors (i.e., temperature), they may, in fact, have underestimated the number of elevational displacements due to temperature. We found that rates of temperature change with elevation differed across transects separated by only a few kilometers within a region (Fig. 1c), facilitating the separation of the influence of temperature from other abiotic factors that co-vary with elevation; we also found a diminished correlation between temperature and habitat turnover across transects (Appendix S1: Figure S4). Complex topographic systems create complex microclimates, resulting in rates of temperature change with elevation that can even vary seasonally on a single slope (Minder et al. 2010). That we accounted for this variability in our models by incorporating local temperature as a covariate, and not elevation, could partly reconcile our results with earlier work in the Andes.

The proportion of bird species found to be limited by habitat in our study is more similar to the high rates documented in North American temperate (Able and Noon 1976) and subtropical (Navarro S. 1992) mountains than to the low rates documented in the tropical montane systems of Central and South America (Terborgh 1985, Patterson et al. 1998). Indeed, our study regions in the Himalayas at roughly 30°N latitude reflect a temperate environment more similar to the North American sites than the Central and South America sites. It is therefore possible that habitat limitation may be more prevalent in temperate systems, where competitive interactions among congeneric species have resulted in discretized habitat selection, compared to tropical systems, where outright spatial exclusion appears to be more common (Robinson and Terborgh 1995, Patterson et al. 1998).

Heightened seasonality in temperate environments, such as the western Himalayas, could also partly contribute to relatively lower rates of competition compared to more climatically stable, tropical environments. For example, resource surges during the breeding season in temperate environments may relax competition amongst congeners during this period (Fretwell 1972). In the western Himalayas, as in many northern latitudes, dramatic seasonality also drives widespread migration in birds (Somveille et al. 2013). Approximately 80% of the birds in the western Himalayas undergo regular seasonal elevational migrations (Grimmett et al. 1999), and it is conceivable that such fluidity, disrupting the holding of stable territories throughout the year, may suppress competition leading to elevational segregation.

The strong influence of both abiotic and biotic factors in structuring the elevational distributions of Himalayan birds points to likely future elevational shifts in response to climate change that, in turn, will be constrained and complicated by habitat boundaries and, to a lesser extent, competition. Though birds may track abiotic factors other than temperature, such as precipitation, and show heterogeneous responses between species (Tingley et al. 2012), there is considerable evidence that they often follow trends of upslope shifts consistent with warming temperatures (Chen et al. 2011). Current rates of warming in the Himalayas are faster than the global average (Shrestha et al. 2012), and despite potentially having increased area of occupancy at higher elevations in the Himalayas (Elsen and Tingley 2015), many bird species shifting upslope will largely depend on the simultaneous advancement of trees.

Overall, our findings are largely consistent with the long-standing theory that abiotic factors set the majority of range limits at higher latitudes and in other abiotically "stressful" environments (MacArthur 1972, Louthan et al. 2015). Together with findings from previous foundational research (Terborgh and Weske 1975), our results reveal potentially contrasting mechanisms responsible for setting the majority of avian range limits across abiotic and biotic stress gradients, with important implications for species conservation in the context of climate change. In light of recent evidence suggesting tropical species may be more sensitive to changes in temperature given potential physiological specialization to narrower climatic variability (McCain 2009, Chan et al. 2016), tropical species may also be at risk due to the presence of biotic "boundaries," be they habitat discontinuities or competitive interactions, when undergoing climate-induced range shifts (see Jankowksi et al. 2010). By contrast, while temperate species tend to have larger elevational ranges indicative of greater thermal tolerance (McCain 2009, Chan et al. 2016), our results suggest that range limits of species in climatically variable environments, such as the Himalayas, are still predominately enforced by an underlying sensitivity to temperature. Under climate change, such species are still likely to respond to the changing abiotic environment by tracking factors such as temperature and precipitation.

The regional variation and individualistic nature of species responses to abiotic and biotic factors, in addition to likely variation in abiotic and biotic sensitivities across taxa (Cahill et al. 2014, Rapacciuolo et al. 2014), present significant challenges for conservation that will ultimately require context-specific planning. Additional studies of range limitation across multiple taxa at lower elevations in the Himalayas and in the more species-rich and tropical eastern Himalayas would help further resolve how the relative importance of abiotic and biotic factors as range limit determinants changes across abiotic and biotic stress gradients.

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