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Research

Annual temperature variation influences the vulnerability of montane bird communities to land-use change

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Understanding how and why species respond to land-use change is one of the central challenges in conservation biology, yet the causes of variation in the responses of species to land-use change remain unclear. We tested whether adaptation to different abiotic environments influenced the vulnerability of bird communities to agricultural expansion in the Himalayan mountain range, which exhibits a strong east–west gradient in annual temperature variation. We did so by surveying bird communities in forest and agriculture at opposite ends of that gradient. We contrasted metrics of species richness, diversity, community composition and forest dependency across land-use types and regions, and tested whether species' thermal sensitivity influenced their response to the replacement of forest with agriculture. Agricultural land in the relatively aseasonal east harboured significantly fewer bird species than did forests, a pattern that is starkly reversed in the highly seasonal west. For species common to both regions, eastern populations used forest ~35% more than did western populations. While western species were less constrained by temperature than eastern species, western species with narrow thermal tolerances were also more forest dependent. Selection across a stark environmental gradient on a common species pool appears to have altered the vulnerability of Himalayan birds to forest loss, with communities in the relatively aseasonal east much more sensitive to forest conversion than those in the west. Adaptation to local environmental conditions appears to mediate species' responses to land use change, with thermal specialists more vulnerable to forest loss than species with greater thermal tolerances. Species' responses to global change may differ predictably along abiotic gradients even within a single region or biodiversity hotspot, and such variation must be addressed in conservation planning.

Keywords: agricultural expansion, forest use, Himalayas, temperature seasonality, thermal sensitivity

Introduction

Biodiversity is increasingly under threat from the conversion of natural ecosystems to alternative land uses, especially in the species-rich tropics (Gibson et al. 2011, Newbold et al. 2015). Across the tropics, the expansion of agriculture is the dominant

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driver of forest loss (Curtis et al. 2018), and it has led to dramatic species losses, with downstream consequences for community structure and functioning (Kremen et al. 2002). However, recent evidence indicates that in certain cases, agricultural lands may support high levels of biodiversity (Karp et al. 2012). Moreover, the conservation value of certain land-use types can vary across taxonomic groups (Barlow et al. 2007) or seasonally (La Sorte et al. 2017). In the western Himalayas, for instance, low-intensity agricultural landscapes harbour significantly more bird species than do primary forests in winter (Elsen et al. 2017a), while the summer bird community is equally speciose in primary forest and agriculture at landscape scales (Elsen et al. 2018). Therefore, understanding the specific contexts in which agricultural expansion can either benefit or harm biodiversity is crucial for effective conservation planning. To do so requires knowledge of the abiotic and biotic processes that determine community composition.

In any given habitat, abiotic conditions are thought to impose a 'filter' that allows colonization and persistence by only a subset of species that are phenotypically adapted to that particular environment (Mittelbach and Schemske 2015). This process of habitat filtering therefore acts to increase trait similarity (e.g. thermal sensitivity) between the species in a community (Silvertown et al. 2005). At the same time, biophysical attributes of the habitat, such as vegetation composition and structure, impose further constraints on habitat suitability for species, thereby influencing community composition and dynamics (Patterson et al. 1998). In addition, biotic interactions such as competition and facilitation impose still more constraints on the coexistence of species (Silvertown et al. 2005).

At regional, continental and global scales, there are strong gradients in abiotic conditions such as temperature, precipitation and intra-annual variation in temperature. The extremities of these abiotic gradients typically harbour very different ecological communities (Buckley and Jetz 2008), with species in each community adapted to the physical environment prevailing at each location (Srinivasan et al. 2018). The adaptation of species to locally prevalent environmental conditions is likely to influence their sensitivity to land-use change, because habitat modification alters the abiotic environment, especially the thermal environment. For instance, on average, tropical agricultural lands are 7.6°C warmer than tropical primary forest (Senior et al. 2017). Further, forest canopies buffer the understorey against thermal extremes, leading to lower temperature variation within forests than in anthropogenically modified habitats (DeFrenne et al. 2019). Therefore, species adapted to highly seasonal environments (i.e. species with tolerance for a wider temperature range, hereafter 'thermal generalists') might be better able to persist in human-modified habitats because such habitats are typically much warmer and more variable in temperature than primary forest, especially in the tropics. Indeed, birds adapted to dry Neotropical forests have been found to be more tolerant of the conversion of forest to agriculture (Frishkoff et al. 2016, Karp et al. 2018), and low thermal tolerances in reptiles and amphibians are associated with greater sensitivity to habitat change (Frishkoff et al. 2015). Conversely, species adapted to low annual temperature variation (i.e. those with narrower thermal tolerances, hereafter 'thermal specialists') might be more sensitive to forest loss and degradation (Nowakowski et al. 2018), especially to the replacement of forest with agriculture.

Consequently, the conservation value of different land uses and the most effective conservation strategy for a given landscape may change as a function of the underlying abiotic environment. Stark abiotic gradients exist within even seemingly homogeneous regions of conservation concern. For instance, the Himalaya Global Biodiversity Hotspot (Myers et al. 2000) spans 1500 miles and 15 degrees in latitude along a primarily east–west axis; along its length, annual variation in temperature nearly doubles (Price et al. 2011, Fig. 1). Given this trend in annual temperature variability, we might expect different responses of species to the conversion of forests to agriculture at the two extremities of the gradient, necessitating potentially different conservation strategies in different portions of the Himalayan mountain range. However, whether species' tolerances to habitat conversion are indeed influenced by the underlying abiotic environment and correlated with their thermal sensitivity is largely unknown.

We studied how the conversion of forest to agriculture affected the diversity and composition of winter bird communities at two ends of the Himalaya Global Biodiversity Hotspot (Myers et al. 2000, Fig. 1). We focused on winter bird communities for two primary reasons. First, the majority of Himalayan birds exhibit seasonal altitudinal migrations from high elevation breeding grounds (often above the extent of permanent agriculture) to lower elevation wintering grounds largely at elevations where agriculture is the dominant form of land use, but where primary forest is also present (Grimmett et al. 1999). Thus, studying winter bird communities allowed us to look at trends across a large species pool. Second, previous research has shown that western Himalayan bird communities are more tolerant of conversion of forest to agriculture in winter than during the breeding season (Elsen et al. 2018). We therefore expected that any regional differences in sensitivity to forest loss might be more apparent in winter, since western Himalayan birds already show relatively high sensitivity to forest loss during the breeding season.

The western Himalayas experience twice the annual variation in temperature as the eastern Himalayas, which have a much more tropical climate (Fig. 1). A majority of the species in the Himalayas have a common evolutionary and biogeographic history, having colonized the Himalayas from the east towards the west (Srinivasan et al. 2014). Despite similarities in their biogeographic origins, bird communities at the two ends of the Himalayas show significant differences in thermal tolerances. Western species occur in a wider range of temperatures than eastern species, and western populations have

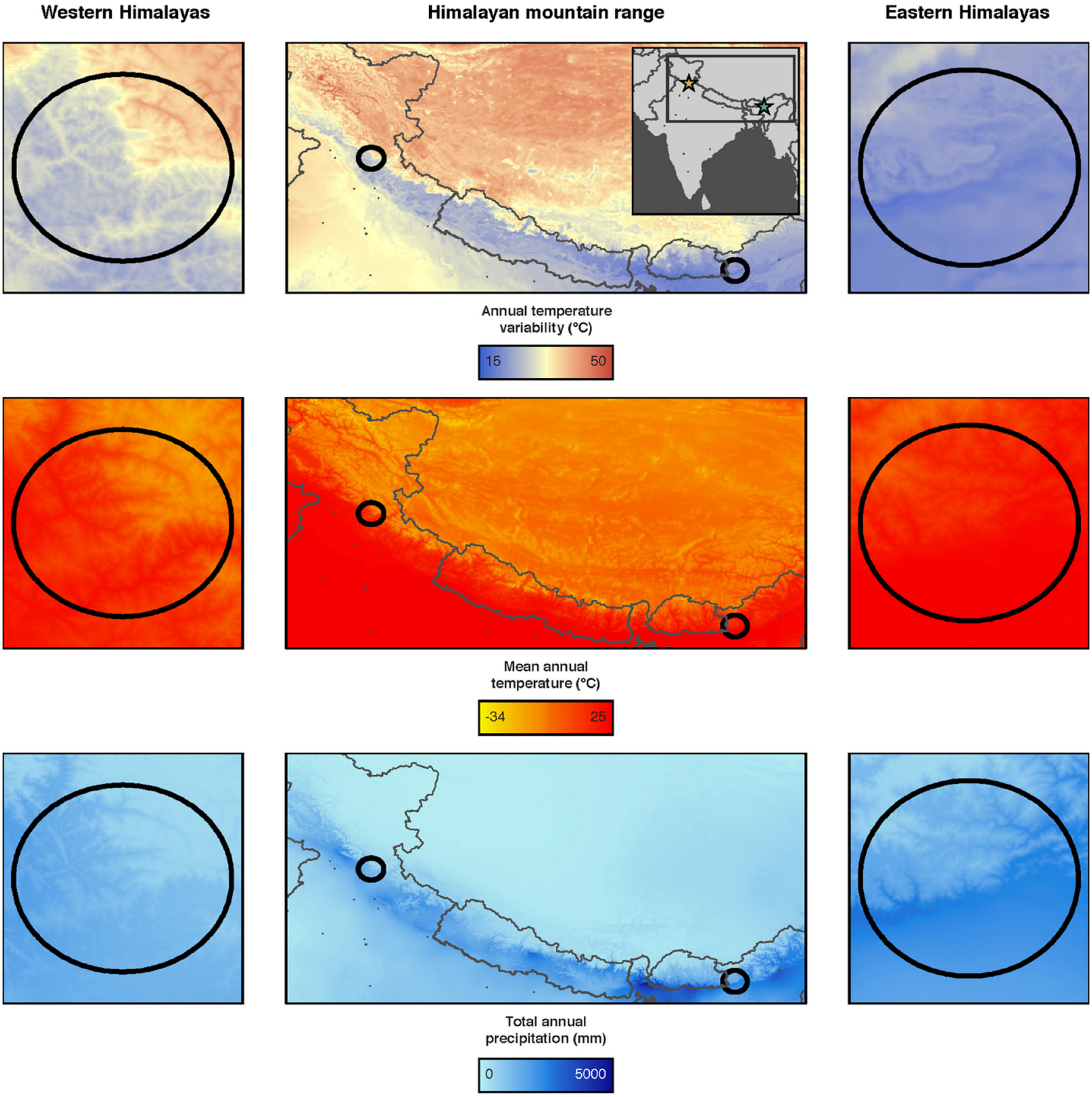

Figure 1. Differences in three climatic factors showing longitudinal trends across the Himalayan mountain range (centre panels) with detailed insets of western and eastern Himalayan study regions (left and right panels, respectively). Top row: annual temperature variability; middle row: mean annual temperature; bottom row: total annual precipitation. Circles in panels denote a 50 km radius around survey regions. Climate data from WorldClim 2.0 (Fick and Hijmans 2017).

significantly broader realized thermal niches than eastern populations of the same species (Srinivasan et al. 2018).

Given the stark differences in underlying abiotic environments and in species' sensitivities to temperature across the Himalayas, we hypothesized that community- and species-level responses of birds to the conversion of forests to agriculture would differ significantly between the western and eastern Himalayas. Specifically, we predicted that: a) eastern Himalayan species, being more constrained by the thermal environment, would be more reliant on forest than western Himalayan species; b) for species common to both regions, eastern Himalayan populations, which are thermally specialised, would be more reliant on forest than western populations, which should be better able to use warmer agricultural habitats; c) bird communities in forest and agriculture would be more similar to each other in the west than in the east, because western species would be more likely to be able to tolerate the thermal conditions of both agriculture and forest and d) across species, the degree of sensitivity to forest loss should correlate with the degree of sensitivity to temperature in both the western and eastern Himalayas.

Material and methods

Study areas and field sampling

We sampled old-growth forest and agricultural lands in and around Great Himalayan National Park (31.79°N; 77.33°E) in the western Himalayas and Singchung Bugun Village Community Reserve (27.17°N; 92.46°E) in the eastern Himalayas at elevations between 1800 and 2300 m a.s.l. Our study regions were separated by 1500 km and 15 degrees of longitude. Annual temperature variation (i.e. the difference between mean summer and winter temperatures) in the western region is one-and-a-half times greater than in the eastern region (Fick and Hijmans 2017, Srinivasan et al. 2018, Fig. 1), with large variations in temperature between summer and winter. Mean annual precipitation also varies greatly between the western and eastern Himalayas, with the east receiving significantly more rainfall than the west (Fig. 1, Supplementary material Appendix 1 Fig. A1). However, we focus on temperature and species' thermal tolerances, because temperature varies starkly between forest and agricultural land (Senior et al. 2017), whereas rainfall is similar in both habitat types within a region (although rates of evapo-transpiration and therefore moisture retention might vary between natural and anthropogenic habitats; see Discussion).

We chose survey sites in each region that were comparable in terms of their natural habitats and the types of croplands in the landscape. The natural habitat in the eastern region is montane mixed-broadleaved deciduous forest, with major tree species belonging to genera such as *Quercus*, *Betula*, *Acer*, *Alnus* and *Juglans*. In the western region, the forest is heavily dominated by broadleaved tree species of the genera *Quercus*, *Betula*, *Acer*, *Alnus*, *Juglans*, *Ulmus* and *Aesculus*, with a few individuals belonging to coniferous genera such as *Cedrus* and *Picea* at the uppermost elevations of one survey transect (Elsen et al. 2017b). In both regions, a substantial proportion of natural forest has been converted to medium-intensity agriculture, with small remnant fragments of forest embedded within more extensive actively farmed areas. Crops typically grown in agricultural plots in both regions include cabbage, potato, tomato and garlic.

We established three transects each in forest and agriculture in the western Himalayas and in the eastern Himalayas (i.e. 12 transects in total). We consciously selected study sites with similar landscape configurations in both the west and east to enable comparisons between regions (i.e. old growth forest with adjacent mixed agriculture–forest mosaic). Each transect spanned at least 350 m in elevation (or, at least 70% of the altitudinal range we studied). In the west, each transect was surveyed three times (i.e. 18 surveys in total) in November and December 2013 resulting in exhaustive bird surveys (Elsen et al. 2017a, 2018). In the east, bird species richness is twofold higher than in the west, with a large number of uncommon species. We therefore surveyed each eastern transect 20 times between December 2017 and January 2018, until species rarefaction curves saturated and we were confident that only a negligible fraction of the eastern Himalayan mid-elevation bird community was not part of the data we collected.

We conducted surveys in early morning and late afternoon. On each transect survey, two observers walked the transect line at a slow, constant, pace and recorded all bird species seen and heard. For sight records, observers also noted group size, and average species-specific group size was assigned to each aural record of a given species.

Analytical methods

We used the SPECIES package (Wang 2011) in R (R Core Team) to calculate separate jackknife species richness estimates of the bird communities in forest and agriculture in the western and eastern Himalayas, and the vegan package (Oksanen et al. 2013) to calculate community diversity for each land-use type in each region.

We used N-mixture models in the package unmarked (Fiske and Chandler 2011) to estimate species-specific abundances in forest and agriculture separately in the west and east while simultaneously accounting for imperfect detection (Royle 2004). Such models use repeated observations to estimate the true number of individuals, N_i, based on observations, y_{it} at $i = 1, 2, \ldots, R$ sites over $t = 1, 2, \ldots, T$ sample periods. We treated each transect as a site ($R = 12$). Counts are modelled as arising from a binomial process on N_i and p_{it}, which denotes survey-specific detection probabilities of each individual using the equation:

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

For this analysis, we first excluded water-dependent species, species with large home ranges (e.g. predatory birds) and nocturnal species (e.g. owls) because 1) water-dependent species are likely affected by the availability of water rather than habitat type, and 2) abundance estimates of predatory birds and owls are likely to be poor because of biases in detection. We then selected species that were detected at least three times. For each species, we fit separate N-mixture models in each region (i.e. two models per species). We included habitat type (forest or agriculture) as a covariate affecting detection in all models, specified as *p*(habitat). The abundance of each species was modelled using a Poisson mixture using the equation:

$$N_i \sim \text{Poisson}\left(\lambda_i\right)$$

The general form of abundance is formulated as:

$$\log(\lambda_i) = \beta_1 + \beta_2 \times \text{habitat}$$

where β_1 is the model-derived estimate of abundance in agricultural lands, and β_2 is the estimate of the difference in abundance between agriculture and forest. We also attempted to include all species in one model and specify abundance covariates as interactions between region (east or west) and habitat type (forest or agriculture), specified as $\lambda(\text{region} \times \text{habitat})$, but results were less desirable because 1) models failed to converge for many species and 2) the models estimated detection probabilities and abundances for some species in sites where the species were known a priori to be absent in the region (e.g. species restricted to either the eastern or western Himalayas). Because of these considerations, we opted to fit separate models for each species in each region as described above.

We compared the composition of bird communities between primary forest and agriculture using Jaccard's index on a presence–absence site-by-species matrix and the Bray–Curtis index on a raw counts site-by-species matrix, defining a site as a 50-m elevational band on our transects. We used non-metric multidimensional scaling (NMDS) to then visualize similarity in community composition between forest and agriculture in the western and eastern Himalayas using the R package vegan (Oksanen et al. 2013).

To quantify differences between forest and agricultural bird communities within a region, we calculated the Euclidean distance of each forest community in a given region to the centroid of all agricultural communities in that region (Karp et al. 2018). The Cartesian coordinates for each forest community (and the centroid for the agricultural communities) were derived from the locations of these communities in multivariate space (i.e. $x = \text{location on NMDS1}$; $y = \text{location on NMDS2}$; NMDS based on the Jaccard's similarity index). We then compared the distribution of distances between the region-specific forest communities and the region-specific average agricultural community across regions.

For each species, we calculated its proportion of forest use by dividing its detection-corrected abundance in forest habitats by its overall detection-corrected abundance. This metric thus scaled from 0, where the species was entirely absent from forests, to 1, where the species was completely restricted to forests. We contrasted the proportion of forest use by region across all species, but to ensure our results were not influenced by differences in species' natural histories, we also contrasted the proportion of forest use within foraging guilds and by migratory strategy, two ecological traits that are generally thought to be associated with sensitivity to forest loss (Newbold et al. 2013). For example, forest conversion and fragmentation are thought to particularly affect insectivorous birds (Şekercioḡlu et al. 2002) and to reduce nesting success in long-distance migratory birds (Robinson et al. 1995), but forests that have been converted to some types of agriculture can retain a substantial number of migrant species on winter territories (Bennett et al. 2018). We assigned each species in each region to a primary foraging guild and to a migratory strategy following Grimmett et al. (1999) (Supplementary material Appendix 1 Table A1). We then assessed differences in proportion of forest use by foraging guild and migratory strategy between the two regions using quasibinomial generalised linear models to account for the response variable being bound between 0 and 1. To compare forest use in the west and east by populations of species common to both regions, we used a paired t-test to test whether the difference in proportion of forest use between populations in the west and east differed from zero.

Finally, to test for the influence of a species' thermal sensitivity on its reliance on forest, we obtained species- and region-specific thermal niche overlap scores from data and methods outlined in Srinivasan et al. (2018). The data used to calculate the thermal niche overlap scores were originally collected by the authors of this study in the same study regions, thereby ensuring that metrics associated with thermal sensitivity and sensitivity to forest conversion are regionally consistent. These scores were derived from data consisting of in situ temperature measurements associated with each observation of a bird. For each species – and separately in the west and east – we calculated the thermal niche occupied in summer (breeding) and winter (non-breeding), defining the thermal niche as the area of the 95% minimum convex polygon of minimum and maximum daily temperatures associated with each bird observation (for details, see Srinivasan et al. 2018). A large number of Himalayan bird species are elevational migrants (breeding at higher and wintering at lower elevations), and therefore have the potential to maximise overlaps between summer and winter thermal niches and remain in similar thermal environments year-round. Species with high niche overlaps between summer and winter are thermally constrained, preferring similar thermal conditions year-round, while those with minimal seasonal niche overlaps are thermal generalists, capable of dealing with wide variations in temperature. Note that the niche overlap metric is corrected for available thermal space in a region to control for the differences in annual temperature variation (higher variation in annual temperature in the west) between our two study regions. Thermal niche overlap metrics are a strong indicator of a species' sensitivity to the thermal environment (Gomez et al. 2016), with higher thermal niche overlaps indicative of greater thermal sensitivity. For the complete approach to calculating thermal niche overlap, we refer readers to Srinivasan et al. (2018).

We were able to obtain thermal niche overlap scores for 20 species in the west and 47 species in the east for which we also had sufficient data to calculate proportion forest use using detection-corrected abundances (see above). We used quasibinomial generalised linear models with the proportion forest use as the response variable and an interaction term of region by thermal niche overlap as predictor to assess the influence of a species' thermal sensitivity on its reliance on forest.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7d4t0g6> (Srinivasan et al. 2019).

Results

Species richness and diversity patterns across forest and agriculture

We recorded 1326 observations of 85 species in the western Himalayas (72 species in agriculture; 38 in forest), and 5459 observations of 135 species in the eastern Himalayas (95 species in agriculture; 112 species in forest). We recorded a total of 185 species across both regions, of which 35 species were common to both the west and east. After excluding water-dependent, predatory and nocturnal species, and species with less than three detections, we were are able to fit N-mixture models to estimate the abundances of 41 species in the west, 94 species in the east and 17 species common to both the west and east (a total of 118 species).

While overall species richness was higher in the eastern Himalayas, we found strikingly different patterns of species richness in forest and agriculture between the two regions. In the highly seasonal western Himalayas, jackknife-estimated species richness was significantly higher in agriculture than in forest (86 versus 50 species, respectively; Fig. 2a). By contrast, in the relatively aseasonal eastern Himalayas, this pattern was reversed, with significantly higher species richness in forest than in agriculture (129 versus 111 species; respectively; Fig. 2a). Agricultural bird communities were also more diverse than forest bird communities in the west based on the Shannon–Wiener index (Fig. 2b). In the east, agricultural and forest bird communities were equally diverse (Fig. 2b). These patterns were not a result of differences in sampling effort between the two regions, as species richness and diversity patterns were qualitatively similar when analysing a subset of the data in the east that equalised sampling effort between the west and east (i.e. records from the first three visits for transects in the east; Supplementary material Appendix 1 Fig. A2).

When contrasting the proportion of forest use by birds in each region, we found that eastern Himalayan bird communities had greater dependence on forests than western Himalayan bird communities (Fig. 3a). These trends were also consistent across foraging guilds and migratory strategies (Fig. 3b–c). In other words, proportion of forest use was higher for all foraging guilds and for both residents and migrants in the eastern Himalayas than in the west (Fig. 3b–c), but we did not find strong differences between foraging guilds or migratory strategies within a region (Fig. 3b). Furthermore, the proportion of eastern and western species assigned to each foraging guild and migratory strategy was roughly equal across regions. Overall, these results suggest that diet and migratory behaviour have little impact on the regional differences in forest dependence we observed.

Use of forest and agriculture by species common to the western and eastern Himalayas

Of the 35 species common to the western and eastern Himalayas, we were able to robustly estimate the abundances of 17 species using N-mixture models separately in each region. For the remaining species, raw counts in one of the two habitats in one of the two regions (i.e. forest or agriculture in the west or east) were too sparse (i.e. data had too many zeros) to apply N-mixture models to estimate abundances. Forest use for the 17 species we analysed ranged from 0 (i.e. restricted to agriculture) to 1 (i.e. restricted to forest). Using these estimates to calculate proportion forest use in each region, we found that eastern populations of a given species were roughly 35% more forest-dependent than western populations (paired t-test; $\beta = 0.34$, $p < 0.01$; Fig. 4).

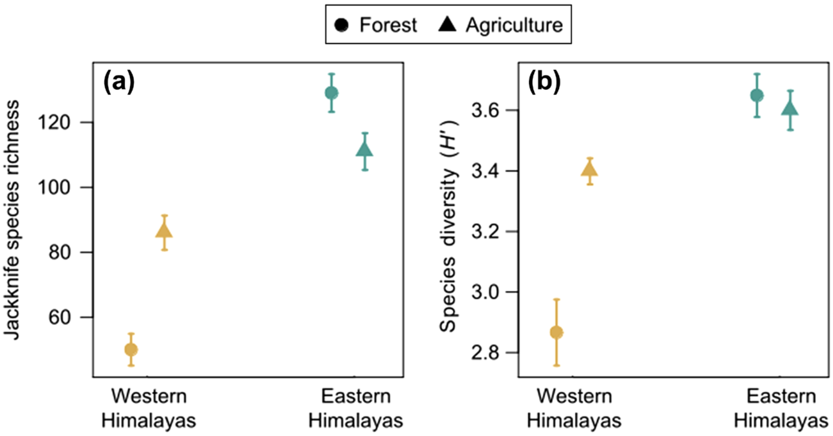

Figure 2. Estimated Jackknife species richness (a) and species diversity (*H′*) (b) metrics of bird communities in the western and eastern Himalayas by habitat type. Error bars represent 95% confidence intervals.

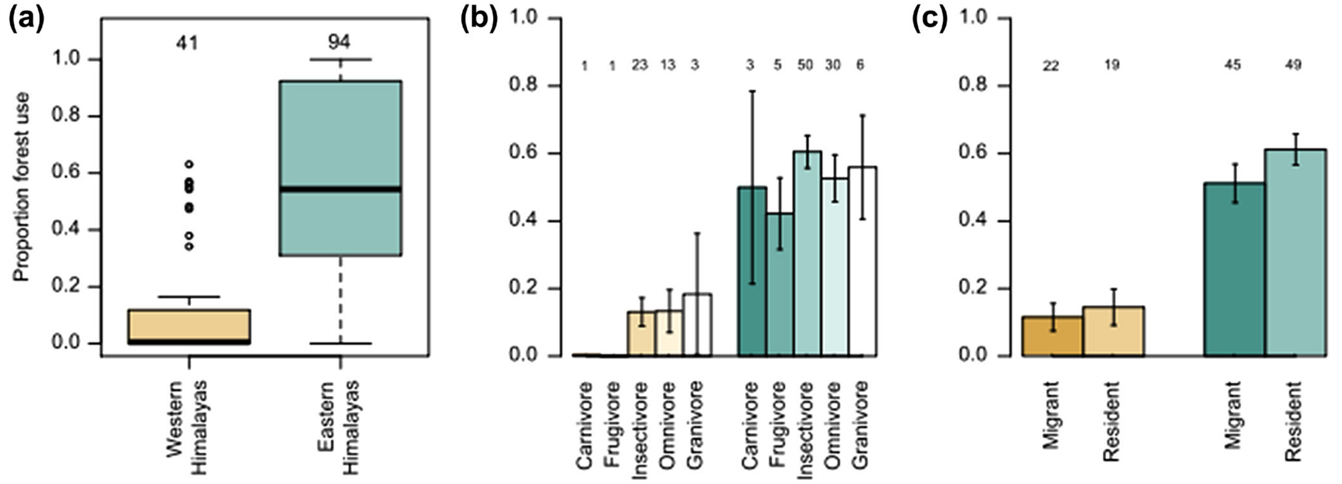

Figure 3. Overall proportion of forest use by birds in the western and eastern Himalayas (a), and by foraging guilds (b) and migratory strategy (c) for birds in the western Himalayas (brown-shaded bars) and eastern Himalayas (green-shaded bars). Heights of bars represent mean values and error bars represent standard errors. Numbers above bars show the number of species per grouping.

Community-level patterns across forest and agriculture

Bird communities differed significantly in composition both across regions (i.e. between the west and east) and habitat type (i.e. between forest and agriculture; Fig. 5). Using Jaccard's index on the presence–absence data, the first NMDS axis separated western and eastern bird communities in general, while the second NMDS axis separated forest and agricultural bird communities (Fig. 5). In general, each habitat type in each region harboured a distinct bird community. Multivariate distances from each forest site to the centroid of the agricultural sites (Fig. 5) indicated that forest and agricultural bird communities in the east were more similar to each other (median distance = 0.09; 95% CI = [0.06, 0.14]) than were forest and agricultural bird communities in the west (0.39 [0.17, 0.63]). The Bray–Curtis index on raw counts of species did not indicate any difference in the degree of difference between forest and agricultural birds communities in the west (0.24 [0.06, 0.56]) or east (0.33 [0.21, 0.42]) (Supplementary material Appendix 1 Fig. A3). With both the Jaccard and the Bray–Curtis indices, we found greater variability in differences between forest and agriculture in the west than in the east.

Influence of thermal sensitivity on forest dependence

We were able to obtain thermal niche overlap scores for 20 species in the seasonal western Himalayas and 47 species in the relatively aseasonal eastern Himalayas for which we were also able to calculate proportion forest use. Results from a quasibinomial generalised linear model (McFadden's pseudo-$R^2 = 0.28$) again revealed that western Himalayan species had significantly lower proportions of forest use compared to eastern Himalayan species ($\beta_{west} = -2.27$; $p < 0.01$), and also revealed a significantly positive correlation between seasonal thermal niche overlap and proportion of forest use in the western Himalayas ($\beta = 1.71$; $p = 0.02$; Fig. 6). Contrary to our expectations, seasonal thermal niche overlap, reflecting the degree of thermal specialisation, was unrelated to proportion of forest use in the eastern Himalayas ($\beta = -0.74$; $p = 0.20$; Fig. 6).

Discussion

Our results show that the conversion of forest to agriculture has markedly different impacts on winter bird communities at the two ends of the Himalayas. Agricultural lands harboured significantly more species than did forest in the highly

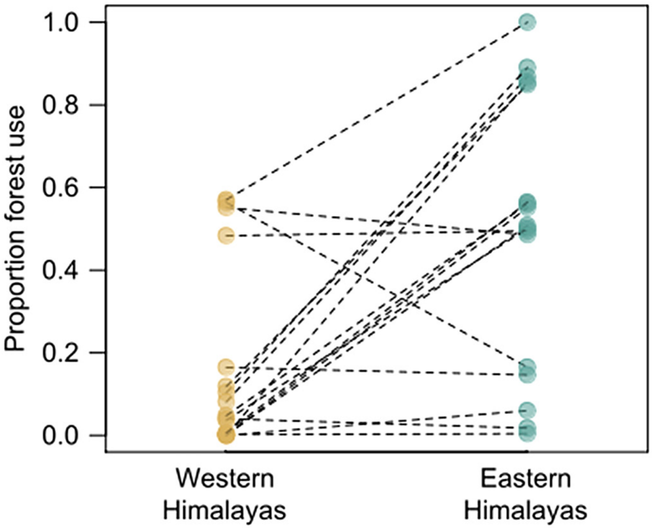

Figure 4. Proportions of forest use by bird species common to both the eastern and western Himalayas. Each point represents a species and dashed lines connect populations of the same species across regions.

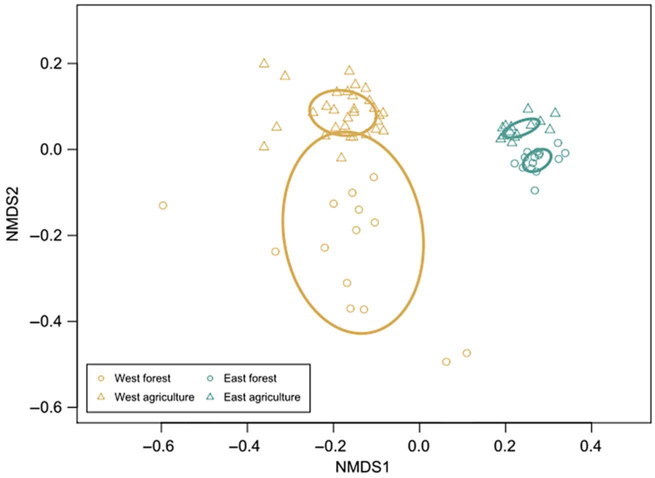

Figure 5. Non-metric multidimensional scaling visualizing dissimilarity between winter bird communities in forest and agriculture in the western and eastern Himalayas based on Jaccard's index from presence to absence matrices (stress = 0.16). Ellipsoids are centred at the mean and represent one standard deviation around the points, which are 50-m elevational bands on transects.

seasonal west, while this pattern was reversed in the relatively aseasonal east (Fig. 2a). Furthermore, for species common to both the western and eastern Himalayas, eastern populations used forest more (and agriculture less) compared with their western counterparts (Fig. 4). These striking regional differences in response to habitat conversion within the Himalayas are consistent with regional differences observed in thermal sensitivity, whereby eastern species appear to have narrower thermal tolerances (Srinivasan et al. 2018). This suggests that a species' adaptation to the abiotic conditions prevalent in its habitat might also influence its sensitivity to degradation of that habitat.

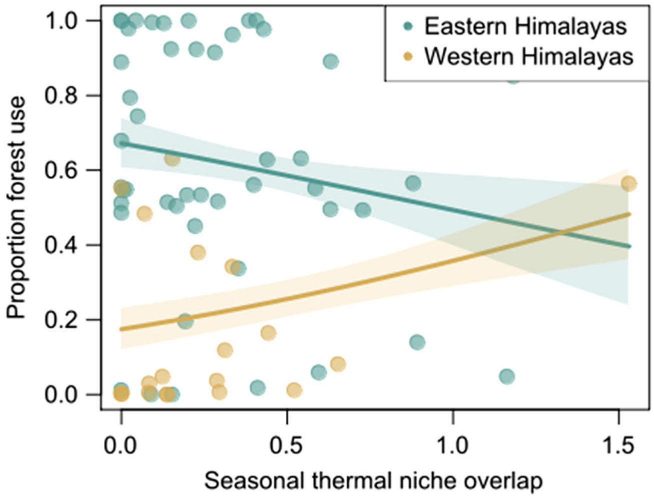

Figure 6. Relationship between seasonal temperature niche overlap (a proxy for thermal sensitivity whereby greater overlap equates to greater sensitivity) and proportion of forest use (a proxy for sensitivity to forest loss), plotted separately for western (brown points; n = 27) and eastern (green points; n = 40) Himalayan birds. Lines and shaded regions show quasibinomial model fits and standard errors for the western (p = 0.02) and eastern (p = 0.74) Himalayas.

The contemporary avifauna of the Himalayas reflects a pattern of colonization of the mountain range from the east towards the west (Packert et al. 2012). In general, species with high dispersal abilities (White 2016) and wide thermal tolerances (Srinivasan et al. 2014, 2018) have been successful in expanding their ranges westward. Therefore, although most of the Himalayan avifauna has a common evolutionary and biogeographic history, selection by a strong environmental gradient on the common species pool appears to have differentially altered the vulnerability of Himalayan bird communities to forest loss, with eastern species and populations much more sensitive to forest conversion than western species and populations. Western Himalayan species might be able to persist in, and perhaps even take advantage of, significantly warmer agricultural lands and the resources they provide (Senior et al. 2017), especially in winter (Elsen et al. 2018). By contrast, eastern Himalayan species, which are adapted to narrower thermal niches (Srinivasan et al. 2018), probably face heightened thermal stresses in modified landscapes such as agriculture. Recent technological advances in the non-invasive monitoring of stress in wild birds (Jerem et al. 2018) will be useful to understand the degree to which birds face thermal stress in anthropogenically modified habitats.

A significant finding from our study is that western populations of species common to both regions used agricultural lands roughly 35% more often than their conspecifics in the relatively aseasonal east (Fig. 4). This provides strong evidence that, beyond observed differences in the proportion of forest use at the community level, populations of the same species show differences in their tolerance to anthropogenic habitat modification. Moreover, these differences correlated with the degree of annual temperature variation in the environment and with community-level differences in thermal sensitivity across regions (Srinivasan et al. 2018). It appears that the greater thermal tolerance of western birds might allow them to use modified landscapes to a greater degree than thermally constrained eastern birds – a finding consistent with patterns in Neotropical agricultural landscapes (Frishkoff et al. 2016) – and future research should test this apparent link, perhaps through the measurement of thermal stress.

Contrary to our expectations, the analysis of distances between habitats in multivariate space indicated that forest and agricultural communities were more similar to each other in the relatively aseasonal east compared with the seasonal west (though the standard deviation ellipses of the two habitats overlapped minimally in the west, but not in the east; Fig. 5). However, of the 112 species observed in forest in the east, 77 species (~69%) also occurred in agriculture. By comparison, of the 58 species observed in forest in the west, 52 species (~90%) also occurred in agriculture, indicating that a much greater proportion of forest-dwelling species in the seasonal west are able to use agricultural lands.

In addition, our results from the NMDS analysis indicated that bird communities in agriculture in the west exhibit much greater dispersion in multivariate space, reflective of greater beta diversity within western agricultural sites compared to bird communities in eastern agricultural sites. This could at least partly explain the greater average distances we observed between forest and agricultural sites in the west, and future work could help to determine why we observe differences in beta diversity in agriculture across regions that likely give rise to the patterns we observe.

We have focused on the role of temperature variation in explaining the response of species to land-use change. An important caveat to highlight is that in the Himalayas, annual temperature variation is correlated with precipitation (Fick and Hijmans 2017, Fig. 1), such that locations with high temperature variation are also drier, whereas those with low variability in annual temperature are considerably wetter. Consequently, thermally specialist species are also those likely adapted to a wetter environment, whereas thermal generalists should be adapted to more arid habitats. Anthropogenic habitats such as agriculture probably retain less moisture and have lower humidity than forest because of higher evaporative losses. These habitats might impose desiccation stress arising from lower moisture availability, caused by a thermally altered environment. Despite the fact that higher temperatures ultimately cause greater evapo-transpiration in altered habitats, the role of differential moisture availability (both across regions and between habitats) cannot be ruled out as a mechanism generating the patterns we report (see Frishkoff et al. 2016). Future research focusing on separating species' sensitivity to temperature versus humidity in influencing their responses to land-use change will be crucial to forecast how ecological communities will fare in a warmer world with altered precipitation patterns.

However, while western Himalayan birds exhibit greater thermal tolerance and thus higher tolerance to habitat conversion than eastern birds overall (Fig. 2), our results also suggest that those western Himalayan bird species that are more thermally sensitive are also more restricted to forests (Fig. 6). This provides further evidence that the degree to which a species is thermally constrained correlates positively with forest dependence. Yet, counter to our expectations, the thermal sensitivity of eastern Himalayan birds does not appear to be directly related to their degree of forest dependence (Fig. 6). One possible explanation is that the high thermal specialisation of eastern Himalayan species (Srinivasan et al. 2018) exceeds the threshold below which thermal sensitivity is related to forest dependence. Another possibility is that an alternative metric of thermal sensitivity, perhaps based on species' physiological responses to temperature extremes (Khaliq et al. 2014, Frishkoff et al. 2015, Nowakowski et al. 2018), would provide a more robust test of the link with sensitivity to forest loss. Both of these possibilities represent promising avenues for future research.

In light of our results, and given that gradients in the abiotic environment akin to what is seen in the Himalayas also occur at subcontinental, continental and global scales worldwide, the biogeographic history of ecological communities may well be a strong determinant of species' tolerances to anthropogenic land-use change more generally (Balmford 1996). Tropical biota, having evolved narrower abiotic niches (Janzen 1967, McCain 2009) in relatively aseasonal habitats that have also been more climatically stable historically (for instance, during ice ages and inter-glacial periods; Hewitt 2004), are likely to experience heightened sensitivity to habitat disturbance compared with temperate species (Stratford and Robinson 2005, Mantyka-Pringle et al. 2012, Guo et al. 2018). As a consequence, our results support the notion that tropical species are particularly sensitive to changes in both land use and climate (Jetz et al. 2007).

Furthermore, these findings suggest that, even within a single biodiversity hotspot, observed patterns of species' responses to habitat conversion in one region may not be representative of species' responses in other regions experiencing different abiotic conditions. Although it might be expected that any particular biodiversity hotspot might generally harbour biota with a common evolutionary origin and species would therefore show consistent responses to habitat conversion, our results indicate that subsequent adaptation to local abiotic conditions might influence regional vulnerability to habitat modification. Importantly, several tropical biodiversity hotspots besides the Himalayas (e.g. Mesoamerica, the Andes, the Western Ghats (Myers et al. 2000)) span large abiotic gradients, and community responses to forest loss could differ along those gradients depending on the underlying abiotic and biotic context. Thus, in these highly biodiverse and threatened regions, conservation priorities and strategies may need to vary regionally, be individualistic and adaptable, and account for differences in species' sensitivities to global change. For example, in the case of landscape-level conservation planning in the Himalayas, our results point to potentially greater consequences of forest loss for eastern Himalayan biodiversity, at least during winter. (We note, however, that given the greater reliance of western Himalayan birds on forests in summer than in winter (Elsen et al. 2018), we expect that eastern Himalayan birds use forests to an even greater degree during the breeding season.) Overall, our results show that in the western Himalayas, landscape-level conservation measures should prioritize the retention of both primary forest and agriculture, whereas the continued protection of primary forest will be of more pressing concern to adequately conserve eastern Himalayan bird communities. Similar studies in other biodiversity hotspots with strong abiotic gradients are likely to reveal equally important lessons for conservation.

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Supplementary material (available online as Appendix ecog-04611 at <www.ecography.org/appendix/ecog-04611>). Appendix 1.

Srinivasan, U. et al. 2019. Data from: Annual temperature variation influences the vulnerability of montane bird communities to land-use change. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.7d4t0g6>.
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