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Conserving Himalayan birds in highly seasonal forested and agricultural landscapes

Paul R. Elsen,[1]* Krishnamurthy Ramesh,[2] and David S. Wilcove[1]

[1]Woodrow Wilson School, Princeton University, Princeton, NJ, 08544, U.S.A.
[2]Wildlife Institute of India, Dehradun, Uttarakhand, 248001, India

Abstract: *The Himalayas are a global biodiversity hotspot threatened by widespread agriculture and pasture expansion. To determine the impact of these threats on biodiversity and to formulate appropriate conservation strategies, we surveyed birds along elevational gradients in primary forest and in human-dominated lands spanning a gradient of habitat alteration, including forest-agriculture mosaics, mixed agriculture mosaics, and pasture. We surveyed birds during the breeding season and in winter to account for pronounced seasonal migrations. Bird abundance and richness in forest-agriculture and mixed agriculture mosaics were equal to or greater than in primary forest and greater than in pasture at local and landscape scales during both seasons. Pasture had greater abundance and richness of birds in winter than primary forest, but richness was greater in primary forest at the landscape scale during the breeding season. All 4 land-use types held unique species, suggesting that all must be retained in the landscape to conserve the entire avifauna. Our results suggest forest-agriculture and mixed agriculture mosaics are particularly important for sustaining Himalayan bird communities during winter and primary forests are vital for sustaining Himalayan bird communities during the breeding season. Further conversion of forest-agriculture and mixed agriculture mosaics to pasture would likely result in significant biodiversity losses that would disproportionately affect breeding species. To ensure comprehensive conservation, strategies in the western Himalayas must balance the protection of intact primary forest with the minimization of pasture expansion.*

Keywords: forest agriculture, grazing, habitat alteration, land-use change, mixed agriculture mosaics, pasture, primary forest, seasonality

Conservación de Aves en el Himalaya dentro de Paisajes Agrícolas y Forestales Extremadamente Temporales

Resumen: *La cordillera del Himalaya es un punto caliente de biodiversidad que está amenazado por la agricultura extensiva y la expansión de las pasturas. Para determinar el impacto de estas amenazas sobre la biodiversidad y para formular estrategias de conservación apropiadas, realizamos un censo de aves a lo largo del gradiente de elevación en bosques primarios y en tierras dominadas por humanos que abarcan un gradiente de alteración de hábitat, incluyendo los mosaicos de agricultura forestal, los mosaicos de agricultura mixta, y las pasturas. Censamos a las aves durante la temporada de reproducción y durante el invierno para explicar la migración estacional pronunciada. La riqueza y abundancia de aves en los terrenos agrícolas y forestales y en los mosaicos de agricultura mixta fueron iguales o mayores que en los bosques primarios, y mayores que en las pasturas a escala local y de paisaje durante ambas temporadas. Durante el invierno las pasturas tuvieron mayor abundancia y riqueza de aves que los bosques primarios, pero la riqueza fue mayor en los bosques primarios a escala de paisaje durante la temporada de reproducción. Los cuatros tipos de uso de suelo albergaron a especies únicas, lo que sugiere que todas deben ser retenidas dentro del paisaje para conservar a toda la avifauna. Nuestros resultados sugieren que la agricultura forestal y los mosaicos de agricultura mixta son particularmente importantes para mantener a las comunidades de aves del Himalaya durante el invierno y los bosques primarios son vitales para mantener a estas comunidades durante la época reproductiva. Una mayor conversión de la agricultura forestal y los mosaicos de agricultura mixta a pasturas probablemente resultaría en pérdidas significativas*

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*email pelsen@berkeley.edu

Article impact statement: *Comprehensive conservation in the Himalayas requires both protecting intact primary forest and minimizing pasture expansion.*

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de biodiversidad que podrían afectar desproporcionadamente a las especies en reproducción. Para asegurar una conservación completa, las estrategias en el oeste del Himalaya deben balancear a la protección del bosque primario intacto con la reducción de la expansión de las pasturas.

Palabras Clave: alteración del hábitat, agricultura forestal, bosque primario, cambio en el uso de suelo, estacionalidad, mosaicos de agricultura mixta, pastoreo, pastura

摘要: *喜马拉雅山脉是全球生物多样性保护热点地区, 但受到农业和牧场大规模扩张的威胁。为了确定这些威胁对生物多样性的影响, 并制定合适的保护策略, 我们沿海拔梯度, 对原始林和人类利用的土地间的一系列生境包括森林-农业镶嵌区、混合农业镶嵌区和牧场中的鸟类进行了调查。考虑到鸟类明显的季节性迁徙, 我们分别在繁殖期和冬季进行了调查。在这两个季节中, 森林-农业镶嵌区和混合农业镶嵌区局部水平和景观尺度上的鸟类丰度和丰富度等于或高于原始林中的情况, 同时都高于牧场的水平。在冬季牧场的鸟类丰度和丰富度比原始林高, 但在繁殖季, 原始林景观尺度上的丰富度更高。这四种土地利用类型的生境中都有特有种, 这意味着要保护整个鸟类动物群就应在景观中把各种生境都保留下来。我们的结果表明, 森林-农业镶嵌区和混合农业镶嵌区对于在冬季维持喜马拉雅的鸟类群落尤为重要, 而原始林则在繁殖季十分重要。将森林-农业镶嵌区和混合农业镶嵌区进一步转化为牧场很可能导致严重的生物多样性丧失, 而且对繁殖的物种影响更大。为了进行全面的保护, 西喜马拉雅地区的保护策略必须在原始林的完整保护和最小化牧场扩张间找到平衡。* ***【翻译: 胡怡思; 审校: 聂永刚】***

关键词: 生境变更, 原始林, 森林农业, 混合农业镶嵌区, 牧场, 放牧, 季节性, 土地利用变化

Introduction

The Himalayan mountains are rich in biodiversity despite having lost much of their natural forest cover to agriculture and pasture (Pandit et al. 2014). Trajectories of human population growth and deforestation in the region underscore the urgency of developing conservation strategies that minimize biodiversity loss (Pandit et al. 2007). Expanding protected areas in the Himalayas, which inadequately protect many of the region's rare and threatened species (Cantú-Salazar et al. 2013), could help to safeguard species that rely on intact forests. Alternatively, enhancing the conservation value of agricultural landscapes by limiting further degradation and habitat alteration could help sensitive species persist in human-dominated landscapes (Ranganathan et al. 2008). Although there are trade-offs and challenges associated with either strategy, a detailed understanding of how species respond to forest loss driven by agricultural practices is essential to developing the most effective strategy for conserving biodiversity.

Complicating this issue is the understanding that species may use different habitats during different periods of their annual cycle (e.g., during breeding vs. wintering [La Sorte et al. 2017]) or use different habitats facultatively within a season (Sekercioglu et al. 2007). In the Himalayas, dramatic seasonality brings widely fluctuating annual temperatures, resulting in seasonal surges in food resources (Ghosh et al. 2011). Consequently, the Himalayan fauna is continually in flux, with many species utilizing different habitats and resources in different seasons (Laiolo 2004). Conservation strategies derived from knowledge of only 1 season may not adequately account for this dynamism. A truly effective conservation strategy in the Himalayas must address the threats present year-round.

To inform comprehensive conservation strategies for Himalayan biodiversity, we assessed the impact of forest loss stemming from agriculture and pasture on birds. Himalayan birds represent a particularly diverse assemblage of species, totaling nearly 1000 species and representing nearly 10% of bird species globally (Pandit et al. 2014). Hundreds of species migrate to the Himalayas each year to breed or overwinter, and most resident species undergo pronounced seasonal elevational migrations up and down Himalayan mountainsides (Grimmett et al. 1999). Expanding human populations have transformed Himalayan forests to diverse agricultural systems ranging from small-scale subsistence farms to valley-wide grazing pastures. Although some forms of agriculture support diverse bird assemblages during winter (Laiolo 2004; Elsen et al. 2017*a*), intact Himalayan forests contain higher bird diversity and more unique bird species during the breeding season than nonforested areas (Brandt et al. 2013). Thus, the conservation value of forests may shift seasonally. Understanding the dynamic nature of conservation values of different land uses to biodiversity is essential for developing an effective conservation strategy in seasonal environments such as the Himalayas. We conducted bird surveys in the western Himalayas of northern India to determine the response of bird communities to land-use types.

Methods

Study Sites and Elevational Transects

We surveyed birds along 12 continuous elevational transects in Great Himalayan National Park (31.70°N, 77.50°E) and the adjacent agricultural landscape in Himachal Pradesh, India. We conducted surveys during

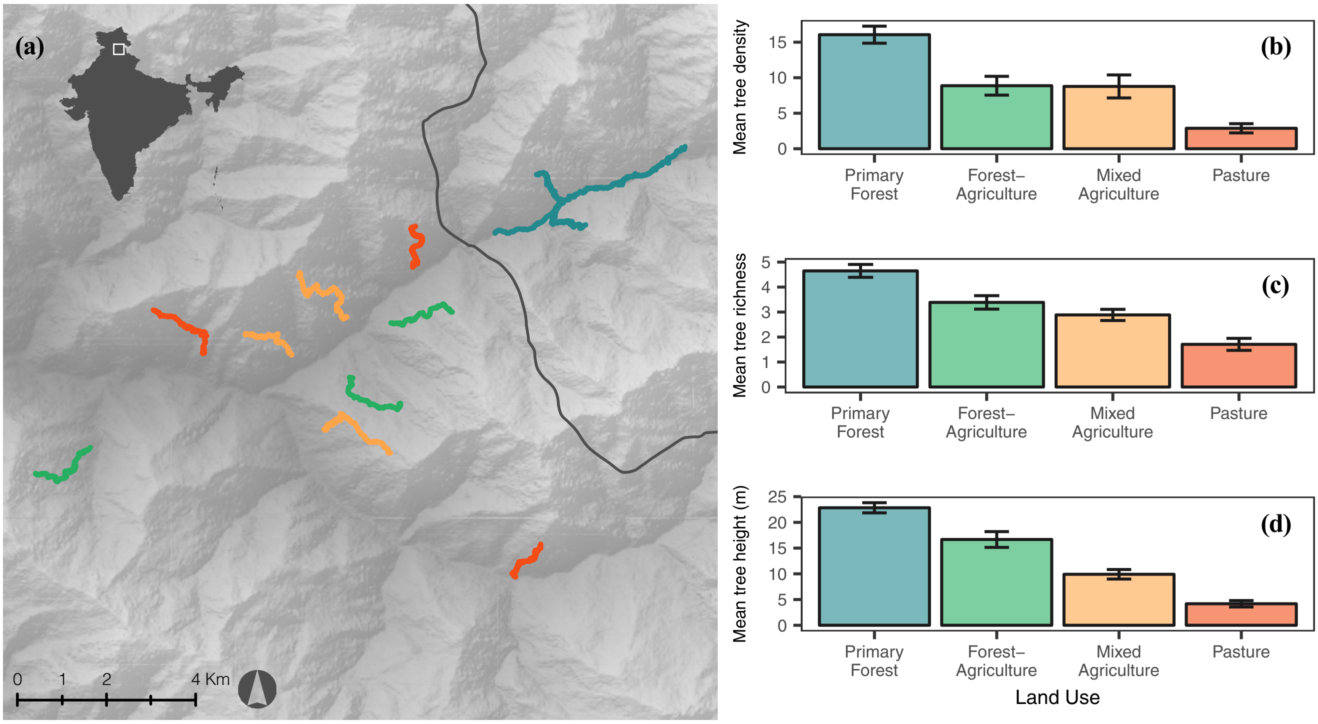

Figure 1. (a) Map of the 12 elevational transects surveyed for birds and trees in and adjacent to Great Himalayan National Park, India (lines are by land-use type depicted in [b–d]; black line, park boundary). Mean (SE) of (b) tree density, (c) tree richness, and (d) tree height per site (50-m elevational band of a given transect) across all transects in each of 4 land-use types.

2 discrete periods in the annual cycle of Himalayan birds: breeding season and winter. We conducted winter surveys throughout November–December, 2013, and breeding surveys throughout May–June, 2016. We established 3 transects within primary forest in the national park and 9 transects within the adjacent human-dominated landscape (Fig. 1). We divided the human-dominated lands into 3 distinct land-use types—forest-agriculture mosaic, mixed agriculture mosaic, and pasture—based on established local knowledge, visual inspection of satellite imagery, extensive field visits, and informal interviews with community members.

The 3 forest-agriculture mosaic transects were in community forests, primarily used for limited timber, fuelwood, and fodder extraction, and amidst a few houses that had small, localized agricultural plots. Transects within forest-agriculture mosaics featured large native trees and often had a closed canopy (Fig. 1).

The 3 mixed agriculture mosaic transects were in fields and agricultural terraces, where dozens of crops (e.g., legumes, rice, wheat, potatoes, tomatoes, and garlic) and fruit orchards were grown. Mixed agriculture featured small shrubs and hedgerows and the occasional tall tree that was heavily lopped for use as fodder. Forest stands were largely absent (Fig. 1).

The 3 pasture transects were primarily used for livestock grazing. Pastures were dominated by grasses and had few trees and shrubs due to grazing by goats and cattle, grass collection, and fires set to promote grass growth (Fig. 1).

We established transects over the largest elevational gradient possible so as to survey at comparable elevations and in similar broad-scale habitat types and climate zones. Land used for agriculture and pasture in the region extended from ~1650–2700 m. Primary forest in the national park extended from ~2000–3600 m. Consequently, we surveyed along elevational transects in primary forest, agriculture, and pasture from 2000–2700 m to minimize bias due to elevational differences among sampling locations and enable robust comparisons across land-use types.

Bird and Tree Surveys

We surveyed birds using line transects along existing footpaths and trail networks. Because we were unable to survey birds over multiple years owing to financial constraints, we performed temporal replicate surveys within each season. During each season, we repeated surveys 3 separate times: twice from 05:00 to 10:30 and once from 16:00 to 19:00. We identified all birds by sight and sound and recorded the elevation, time, and distance to observer for each observation while walking at a slow, constant pace. To minimize detection bias, the same observer (P.R.E.) performed all surveys. For each bird species recorded, we compiled ecological trait information on breeding habitat status (forest vs. open country), migrant status (resident, elevational migrant, breeding visitor, and winter visitor), and primary foraging guild following Grimmett et al. (1999).

We surveyed trees every 50 m of elevation along all transects we surveyed for birds. At each survey point, we identified all trees to species within a 25-m radius, counted all stems with diameter at breast height ≥30 cm, and measured their heights with a rangefinder. We summed the number of tree species to calculate tree species richness, summed all stems to calculate tree density, and averaged all tree heights to calculate tree height at each survey point.

Bird Abundance and Species Richness Analyses

To determine how bird abundance varies as a function of land-use type and season, we used generalized linear models (GLMs) with Poisson error and a log link to accommodate count data, using land-use type as predictor variables. We ran GLMs separately for winter and breeding data, and for data combined across seasons. We defined a site as a 50-m elevational band on a given transect, following established methodological approaches (Elsen et al. 2017*a*, 2017*b*). This resulted in 37 primary forest, 31 forest-agriculture, 35 mixed agriculture, and 41 pasture sites. To account for differences in absolute traveled distances among sites, we included the walked length of the 50-m elevational band as a covariate in our models. Because distance sampling approaches that enable accounting for imperfect detection can be unreliable along trails due to nonrandom line placement that precludes a representative sample of distances with which to derive a valid density estimate (Buckland et al. 1993) and the use of other hierarchical modeling techniques with repeated sampling would prohibit us from including rarer species in our analysis, we used raw counts as the response variable in our abundance models. For each bird species, we used the maximum count across the 3 visits per season as the raw count.

To determine how bird species richness varies as a function of land-use type and season at the local scale, we first used a presence-absence matrix to calculate total bird species richness within each site. We then used GLMs as above, controlling for variable transect length, to analyze site-level bird richness differences between land-use types separately for winter and breeding data, and for data combined across seasons. We assessed potential biases arising from the spatial configuration of survey sites by calculating Moran's I with the ncf and ape packages in R (R Core Team 2017) and analyzing the model residuals in correlograms, separately for winter and breeding data and for data combined across seasons.

To assess how bird species richness varied as a function of land-use type and season at the landscape scale, we used abundance matrices to calculate sample-based rarefaction curves in the iNEXT package in R (Colwell et al. 2012). To accommodate variable transect lengths and yield unbiased comparisons, we first performed individual-based rarefaction to a standardized length of 100 m, which removed 14 sites that were initially <100 m in length. We then performed sample-based rarefaction on the remaining sites and repeated this process separately for winter and breeding data and for data combined across seasons.

Bird Community Composition

To determine how bird community composition varies as a function of land-use type and season, we performed nonmetric multidimensional scaling (NMDS) to ordinate each site along 2 axes according to the similarity of species present at each site. We used winter and breeding presence–absence matrices to calculate Bray–Curtis similarity indices separately for each season for use in our NMDS analyses. We also used data combined across seasons to repeat this analysis. We tested for differences in community composition with perMANOVA tests (Anderson 2001) between all land-use type pairs in each season.

We assessed potential biases arising from the spatial configuration of survey sites in this analysis by first using an abundance matrix and then calculating Hellinger's distance. We then included the resulting matrix as the response variable in a partial redundancy analysis (Legendre & Legendre 2012), parameterized with land-use type and conditioned using the geographic coordinates of our survey sites. We used permutation tests with 1000 permutations to determine the significance of the model and followed this with variance partitioning to evaluate the direct and joint contributions of land-use type and spatial configuration to variation in community composition among survey sites. Using the vegan package in R, we repeated this analysis separately for winter and breeding data and for data combined across seasons.

Species-Specific Responses to Land Use

To determine how individual species respond differentially to land-use type by season, we used GLMs to model the abundance of each species as a function of land use while controlling for variable survey length. We determined whether each species' abundance in each land-use type was significantly greater, significantly lower, or not significantly different compared with the species' abundance in primary forest or whether the species was altogether absent in each land-use type. We then repeated this analysis by comparing abundances in each land-use type with respect to forest-agriculture, mixed agriculture, and pasture. We performed these analyses separately for winter and breeding data and for data combined across seasons. We also summarized these results grouping species by primary breeding habitat type, migrant status, and foraging guild, recognizing that species' ecologies along these dimensions affect their response to habitat alteration (Sekercioglu et al. 2002; Runge et al. 2014).

Drivers of Bird Abundance and Richness Patterns

To determine how habitat alteration resulting from land-use change influences bird abundance and richness patterns, we fit GLMs with our measurements of tree height, tree density, and tree richness as predictors of site-level bird abundance and richness in both summer and winter. We fit models using all additive combinations of predictors while controlling for transect length, including a model with a null intercept, and ranked models by Akaike's information criterion (AIC_c). We centered and standardized all predictors to enable unbiased comparisons and used Akiake weights (w_t) to obtain a 95% confidence set. We then performed model averaging on all predictors within the 95% confidence set to obtain 95% confidence intervals (CIs) for each predictor. We considered the model-averaged coefficients significant when the 95% CI did not overlap zero.

Results

Bird Abundance and Species Richness

Bird surveys yielded 5123 observations of 128 species during winter and 7944 observations of 139 species during breeding: 13,067 observations of 170 species. Ninety-seven species were recorded in both seasons.

Patterns of bird abundance between land-use types at the site level differed across seasons (Fig. 2a). During the breeding season, bird abundance was highest in mixed agriculture ($z_{4139} = 10.76, p < 0.001$) and forest-agriculture mosaic (hereafter forest-agriculture) ($z_{4139} = 11.11, p < 0.001$), and significantly lower in pasture and primary forest. Pasture and primary forest had comparable abundances during the breeding season ($z_{4139} = 0.004, p = 0.997$). Relative to primary forest, bird abundance in winter was highest in mixed agriculture ($z_{4139} = 16.45, p < 0.001$), followed by forest-agriculture ($z_{4139} = 13.57, p < 0.001$) and pasture ($z_{4139} = 9.17, p < 0.001$). Year-round, abundance was highest in mixed agriculture ($z_{4139} = 16.11, p < 0.001$) and forest-agriculture ($z_{4139} = 14.43, p < 0.001$), and pasture was intermediate and had significantly higher abundance than primary forest ($z_{4139} = 4.18, p < 0.001$).

During the breeding season, site-level species richness was highest in mixed agriculture ($z_{4139} = 7.85, p < 0.001$) and forest-agriculture ($z_{4139} = 8.91, p < 0.001$) and significantly lower in pasture and primary forest ($z_{4139} = -0.08, p = 0.937$). Relative to primary forest, site-level species richness in winter was highest in mixed agriculture ($z_{4139} = 12.89, p < 0.001$), followed by forest-agriculture ($z_{4139} = 10.48, p < 0.001$) and pasture ($z_{4139} = 6.37, p < 0.001$). Year-round, site-level species richness was highest in mixed agriculture ($z_{4139} = 11.86, p < 0.001$) and forest-agriculture ($z_{4139} = 10.88, p < 0.001$), followed by pasture ($z_{4139} = 2.42, p = 0.016$). Primary forest had significantly lower richness than all other land-use types. Correlograms of model residuals of richness analyses confirmed that sites >50 m apart were spatially independent during winter, and sites >100 m apart were spatially independent during the breeding season and year-round (Supporting Information). Thus, results were not strongly determined by the spatial distribution of our survey sites.

During the breeding season, species richness at the landscape scale was significantly greater in forest-agriculture than in the other 3 land-use types and was significantly greater in primary forest compared to pasture (Fig. 3). During winter, mixed agriculture and forest-agriculture exhibited the highest species richness, pasture had intermediate richness, and primary forest exhibited the lowest species richness at the landscape scale (Fig. 3). Year-round, patterns were similar to winter, except there were smaller differences in landscape-scale richness between primary forest and pasture, and between mixed agriculture and pasture (Fig. 3). These patterns were consistent when we reanalyzed data considering all sites and not just sites >100 m long.

Bird Community Composition

Primary forests harbored 20 unique species during the breeding season and 4 unique species during winter. Combined, all other land-use types harbored 27 unique species during the breeding season and 32 unique species during winter. The NMDS analyses revealed strong differences in community composition between land-use types that were consistent across seasons (Fig. 4). Pairwise perMANOVA analyses indicated that each land-use type held distinct bird communities during winter, breeding, and year-round. For all periods, bird communities in primary forest were most similar to communities in forest-agriculture (breeding: $R^2 = 0.16, p < 0.001$; winter: $R^2 = 0.12, p < 0.001$; combined: $R^2 = 0.16, p < 0.001$), followed by mixed agriculture (breeding: $R^2 = 0.28, p < 0.001$; winter: $R^2 = 0.20, p < 0.001$; combined: $R^2 = 0.27, p < 0.001$) and pasture (breeding: $R^2 = 0.33, p < 0.001$; winter: $R^2 = 0.25, p < 0.001$; combined: $R^2 = 0.34, p < 0.001$). Bird communities in forest-agriculture and mixed agriculture were also distinct during the breeding season ($R^2 = 0.08, p < 0.001$), winter

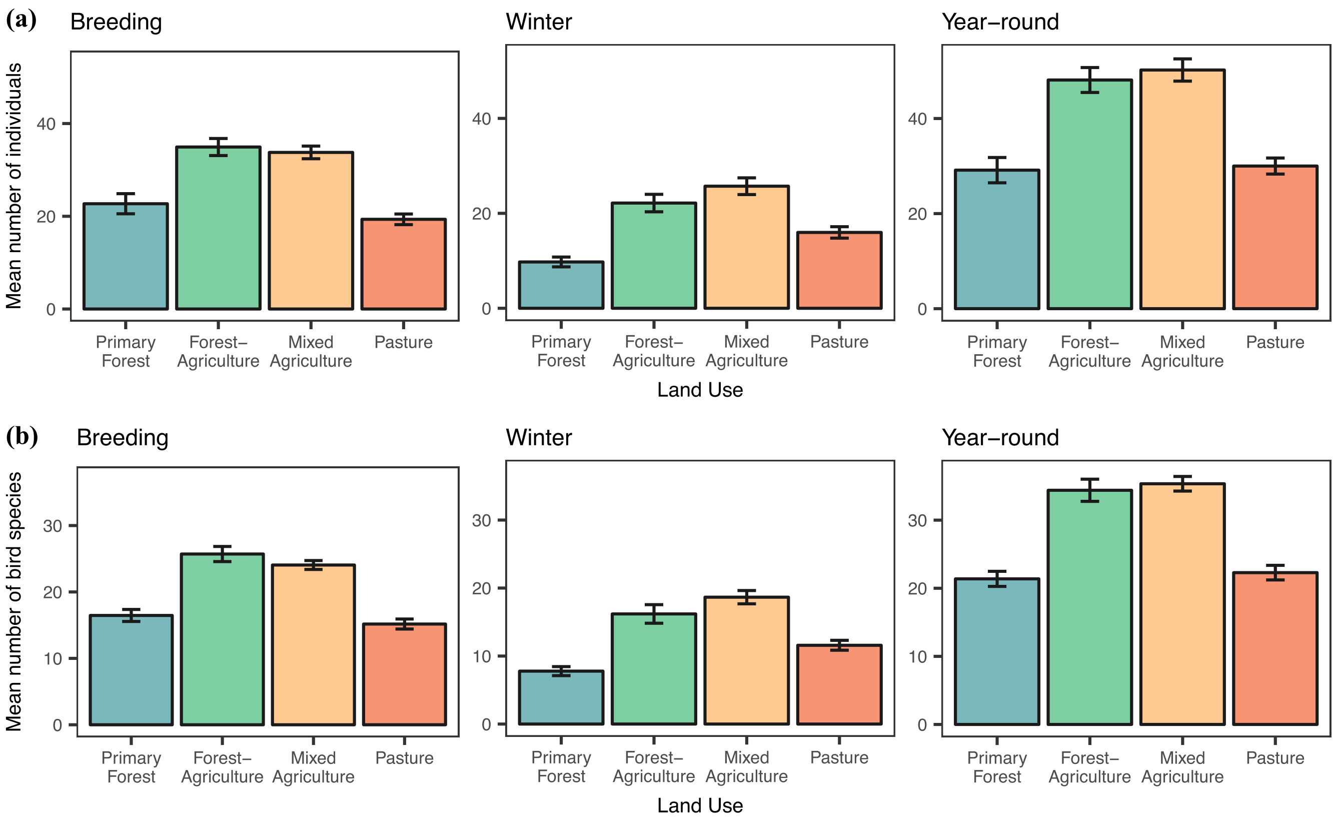

Figure 2. Mean (SE) number of (a) individuals and (b) bird species per site across 4 land-use types by season.

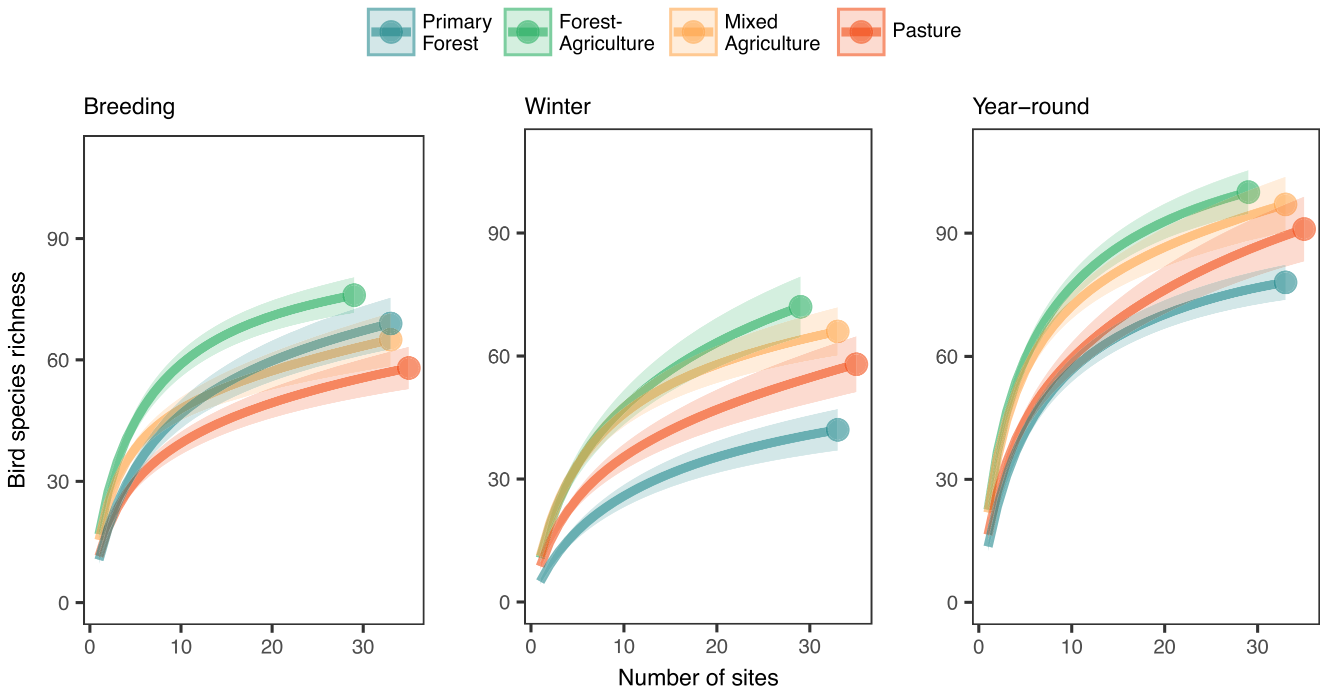

Figure 3. Sample-based rarefaction of bird species richness across 4 land-use types during the breeding season, winter, and year-round (shaded regions, 95% CI).

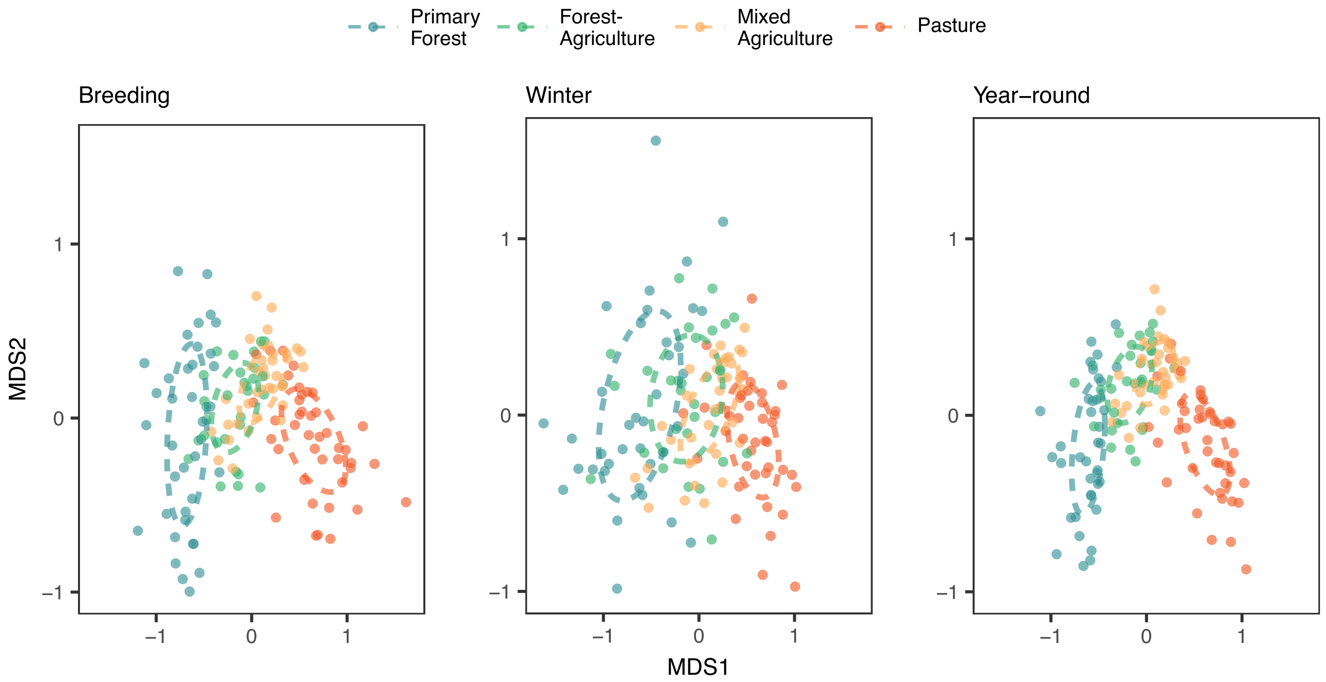

Figure 4. NMDS plots of bird community composition based on Bray-Curtis similarity indices derived from presence-absence matrices relative to land-use type during the breeding season (stress = 0.13), winter (stress = 0.21), and year-round (stress = 0.13) (ellipsoids, centered at the mean MDS value of both axes per land use by season; axis radius of ellipsoids, standard deviation).

($R^2 = 0.05$, $p < 0.001$), and with data combined ($R^2 = 0.08$, $p < 0.001$).

Variance partitioning revealed that the overall variance explained was largely driven by the pure effect of land use during breeding, winter, and year-round (Supporting Information). These results suggest that the differences in community composition we observed across land-use types largely arise from intrinsic differences in land-use types, with relatively little influence from their spatial distribution.

Species-Specific Responses to Land Use

During the breeding season, ~54% of all detected species were observed in primary forest. Of these 75 species, ~39% declined or were absent from forest-agriculture, ~61% declined or were absent from mixed agriculture, and ~73% declined or were absent from pasture (Fig. 5a). During winter, ~38% of all detected species were observed in primary forest. Of these 49 species, ~20% declined or were absent from forest-agriculture, ~35% declined or were absent from mixed agriculture, and ~53% declined or were absent from pasture (Fig. 5a). These trends were largely consistent when restricting the analysis to only forest birds and insectivorous birds (Supporting Information). By comparison, a greater proportion of granivorous birds observed in primary forest were absent from all other land-use types, but only during the breeding season (Supporting Information).

The number of resident species observed in primary forests that declined or were absent in forest-agriculture and mixed agriculture mosaics was fairly similar across seasons (Supporting Information). Only 1 long-distance migrant wintering in the Himalayas (Black-throated Thrush [*Turdus atrogularis*]) was observed in primary forest, but it was also observed in all other land-use types, with its highest abundance in mixed agriculture (Supporting Information). By contrast, 15 long-distance migrants breeding in the Himalayas were observed in primary forest. Of these species, ~60% also were observed in forest-agriculture and mixed agriculture in similar or greater abundances as in primary forest, and ~75% were either absent or declined in pasture (Supporting Information). Elevational migrants constituted most of the species we recorded, and elevational migrants observed in primary forest declined or were absent from all other land-use types in greater proportions during breeding than during winter (Supporting Information).

Drivers of Bird Abundance and Richness Patterns

During the breeding season, bird richness and abundance declined as tree density declined (richness: $\beta_{\text{tree density}} = -0.007$, [-0.013, -0.001]; abundance: $\beta_{\text{tree density}} = -0.012$, [-0.017, -0.007]) and increased as tree richness

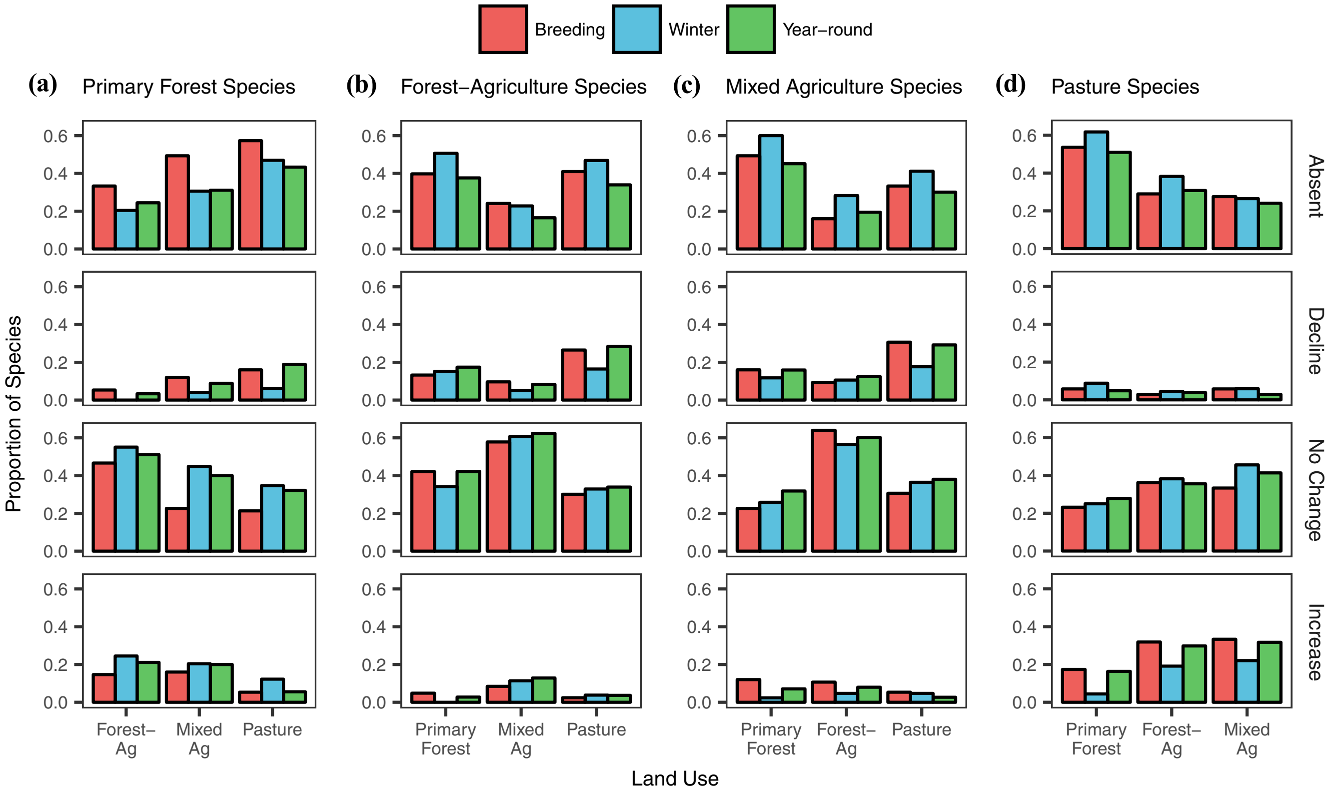

Figure 5. Proportion of bird species recorded in (a) primary forest, (b) forest-agriculture mosaic, (c) mixed agriculture mosaic, and (d) pasture but were absent, declined, showed no change, or increased across land-use types during the breeding season, winter, and year-round (x-axes differ). See text for sample sizes.

increased (richness: $\beta_{\text{tree richness}} = 0.037$, [0.008, 0.067]; abundance: $\beta_{\text{tree richness}} = 0.034$, [0.010, 0.057]). Bird richness and abundance were not associated with tree height (richness: $\beta_{\text{tree height}} = 0.001$, [-0.005, 0.007]; abundance: $\beta_{\text{tree height}} = -0.0003$, [-0.005, 0.005]). During winter, bird richness and abundance declined as tree density declined (richness: $\beta_{\text{tree density}} = -0.013$, [-0.022, -0.005]; abundance: $\beta_{\text{tree density}} = -0.018$, [-0.026, -0.011]), increased as tree richness increased (richness: $\beta_{\text{tree richness}} = 0.072$, [0.037, 0.107]; abundance: $\beta_{\text{tree richness}} = 0.076$, [0.046, 0.106]), and declined as tree height declined (richness: $\beta_{\text{tree height}} = -0.02$, [-0.028, -0.013]; abundance: $\beta_{\text{tree height}} = -0.023$, [-0.029, -0.016]).

Discussion

Habitat loss through the conversion of primary forest to agriculture is a leading driver of terrestrial biodiversity loss globally (Newbold et al. 2015), and agricultural intensification is expected to have especially strong negative impacts on Himalayan biodiversity (Kehoe et al. 2017). Our results suggest that converting primary forest to forest-agriculture and mixed agriculture mosaics in the western Himalayas does not reduce bird abundance or richness at local or landscape scales during the breeding season, winter, or year-round at this site. In addition, our results show that bird abundance and richness in pasture was similar or even greater than in primary forest year-round. Because our surveys were conducted along the typical progression of landscape conversion in the region—from primary forest to forest-agriculture, then to mixed agriculture, and finally to pasture—our results suggest that some types of agricultural conversion would not likely result in reduced overall bird abundance or species richness.

These findings superficially suggest agricultural conversion does not represent a significant threat to Himalayan birds. However, such an interpretation dangerously discounts significant changes in community composition resulting from habitat alteration and ignores profound seasonal differences in species' utilization of primary forest versus other forms of land use. Altogether, our results support the notions that forest-agriculture and mixed agriculture mosaics are particularly important for sustaining Himalayan bird communities during winter; primary forests are particularly important for sustaining Himalayan bird communities during the breeding season; and the conversion of primary forest or agricultural lands to pasture is particularly harmful to the Himalayan avifauna.

Bird community composition in forest-agriculture mosaics—the land-use type with forest composition and structure most similar to that of primary forest (Fig. 1)—was significantly different from that of primary forest, echoing research linking agriculturally driven land-use change to alterations in community structure for multiple taxa, including birds (Newbold et al. 2015). Moreover, we found that increasingly altered habitats led to increasingly altered bird communities (Fig. 4). All 4 land-use types held unique species, suggesting that conversion of primary forest to agriculture, and subsequent conversion to pasture, would likely result in some degree of species loss or replacement of species of conservation interest at each stage. Because Himalayan forests are rapidly disappearing, especially in the west (Pandit et al. 2007), bird communities could face large-scale homogenization (Devictor et al. 2008; Socolar et al. 2016). To safeguard the full suite of species occurring in Himalayan landscapes, primary forests must be retained to complement other forms of land use.

The effects of habitat alteration on Himalayan birds differed seasonally. Himalayan birds appear to be disproportionately negatively affected by forest loss during the breeding season; most species used forest-agriculture and mixed agriculture to a larger degree during winter (Figs. 4 & 5). Similar conclusions have been reached for several Neotropical migrants that preferentially use agricultural lands on their wintering grounds and forested lands during the breeding season (Johnson et al. 2006; Holmes 2007). This suggests that Himalayan birds may rely more on primary forests during the breeding season than in winter. Several lines of evidence support our conclusion. First, the number of species unique to primary forest was 5 times greater during the breeding season than during winter, suggesting that many more species can be found in at least some form of agriculture during winter. Second, the proportion of species found in primary forest that are absent or which decline in forest-agriculture was nearly twice as high during the breeding season compared to winter (Fig. 5a). This trend was consistent when considering species grouped by functional guild and migratory strategy, and was especially strong for long-distance migrants (Supporting Information). Finally, species that breed in primary forest have their highest abundances on average in primary forest, whereas species that winter in primary forest have similar or even greater abundances in other land-uses types in that season (Fig. 6). Although it is unclear why Himalayan birds extensively use agricultural lands during winter, it could be due to large reductions in arthropod abundance in forests in winter (Ghosh et al. 2011) or to seasonal diet switching (Grimmett et al. 1999) that enables species to capitalize on more diverse prey bases in agriculture.

Overall, retention of primary forest is critical to sustaining breeding populations of many species, while agricultural lands may act as an important refuge to sustain populations of forest-breeding species during the winter. For migratory species, the presence and quality of suitable habitat during 1 season can have cascading effects on reproductive performance or survival the following season (Norris et al. 2004; Runge et al. 2014). In the Himalayas, agricultural lands could bolster the reproductive success of elevational migrants and help facilitate year-round stability within the bird community. But without primary forest in which to breed, nearly 30% of species that occur in primary forest would likely decline following conversion to forest-agriculture mosaics (Fig. 5a).

More generally, our results highlight that seasonality can drive divergent patterns of species abundance, richness, and community composition across land-use types. Conclusions and policy recommendations based on patterns observed during only 1 season can be misguided (Martin et al. 2007). For example, in our case, ~20% of the species observed in primary forest year-round were absent or showed declines in forest-agriculture during the breeding season, but those same species were present at comparable abundances in forest-agriculture during winter. Although limited budgets may prevent researchers from conducting surveys over multiple discrete seasons, the influence of seasonality should be considered in drawing robust conclusions and informing management and policy (La Sorte et al. 2017). Indeed, further surveys in our study area could help inform how the use of human-dominated lands by birds might depend on the severity of winter, fluctuating resource availability, or other factors that vary annually and that we could not assess within our sampling period.

Our results also reveal that landscape conversion to pasture would be detrimental to Himalayan bird communities in both seasons, but particularly during the breeding season. Bird abundance and richness decline substantially at both local and landscape scales when mixed agriculture mosaics are converted to pasture (Figs. 2 & 4). These results are consistent with previous research linking livestock grazing to declines in forest and woodland birds in Australian agroecosystems (Martin & McIntyre 2007) and with pasture containing significantly lower bird richness than mixed agriculture and monoculture agroecosystems in Mexico (Estrada et al. 1997). The patterns we observed were consistent across foraging guilds and migratory strategies (Supporting Information) and are similar to those resulting from repeated logging or the conversion of tropical forests to plantations globally, including for birds and several other taxa (Gibson et al. 2011). Our models linking bird abundance and richness patterns to tree cover characteristics suggest that retaining a diversity of trees within pasture could help support diverse and abundant bird assemblages, but this requires further research. Furthermore, our observations of birds frequently foraging in dense shrubs within mixed agriculture suggest that limiting shrub removal may also

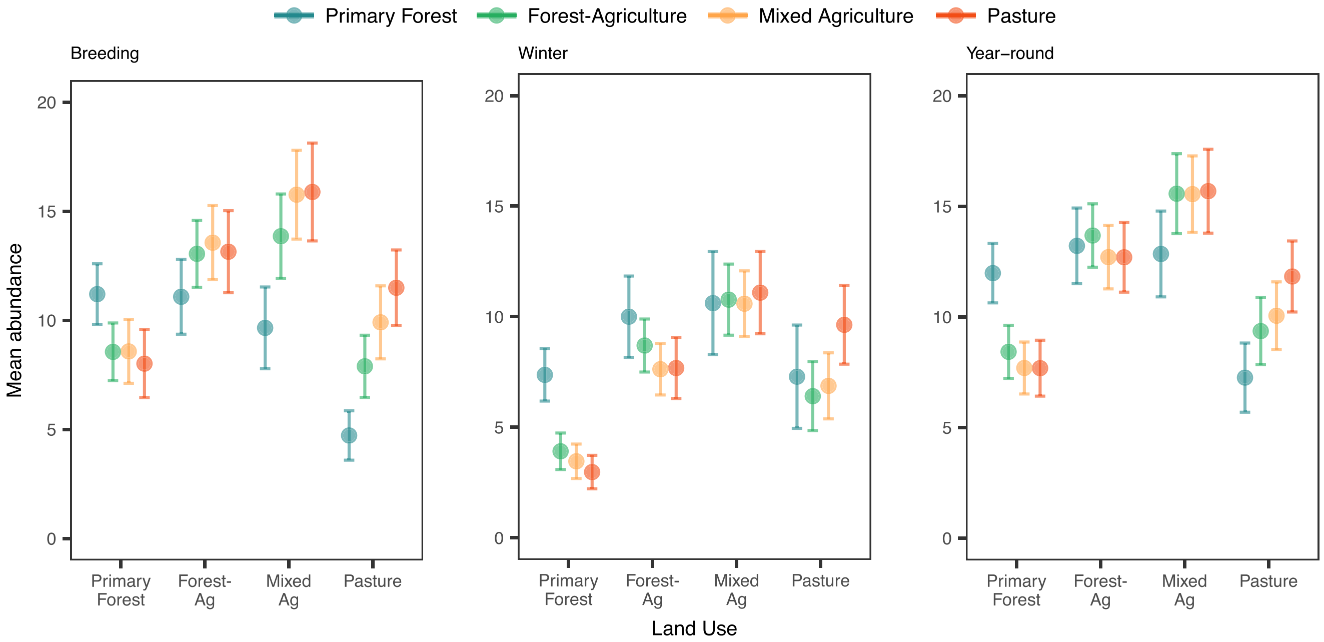

Figure 6. Mean (SE) abundance of species groups across 4 land-use types. The 4 species groups refer to the collections of species observed in primary forest, forest-agriculture mosaic, mixed agriculture mosaic, and pasture.

promote bird conservation in pasture, although we lack data to address this issue directly.

On average, species that occur in pasture tend to be more abundant in mixed agriculture and at least as abundant in forest-agriculture (Fig. 6). Less than 10% of the species found in pasture declined in forest-agriculture and mixed agriculture mosaics (Fig. 5d). This suggests that most species occurring in pasture would either benefit or at least not be negatively affected by policies restricting pasture expansion, as was also found for birds in Australian agricultural landscapes (Martin et al. 2005). Exceptions to this are the few species we recorded only in pasture, such as Blue Rock Thrush (*Monticola solitarius*), Chukar Partridge (*Alectoris chukar*), and Red-fronted Serin (*Serinus pusillus*), all of which have relatively large geographic ranges globally. However, because habitat conversion to pasture threatens many Himalayan bird species and homogenizes bird communities year-round, limiting pasture expansion to retain forest-agriculture and mixed agriculture mosaics that have substantially greater value for Himalayan birds would be an important step in conserving Himalayan biodiversity.

Our results suggest that a conservation strategy focused on either strict forest protection with agricultural intensification (land sparing [Phalan et al. 2011]) or on enhancing the value of agriculture to biodiversity (land sharing [Green et al. 2005]) may be inadequate to sustain bird populations in the western Himalayas. Intensive farming to maximize yields as part of a land-sparing strategy may not even be possible in topographically diverse Himalayan landscapes (Fischer et al. 2011). Rather, protection of intact forests should be part of a broader strategy that includes retention of forest-agriculture and mixed agriculture mosaics. For example, land-use zoning could be used to zone both intact forests and forest-agriculture for conservation (Phalan et al. 2016), thereby limiting pasture expansion in these important land-use types. In our study area, protection of intact primary forest will be essential to conserve those species that rely on forests exclusively during the breeding season, such as the endangered Western Tragopan (*Tragopan melanocephalus*), the frequently hunted Himalayan Monal (*Lophophorus impejanus*), and the range-restricted Nepal Wren Babbler (*Pnoepyga immaculata*), all of which were exclusively observed in primary forest during our breeding surveys. By contrast, retaining forest-agriculture and mixed agriculture will be important for some species, such as the near-endemic White-cheeked Nuthatch (*Sitta leucopsis*) and Himalayan Woodpecker (*Dendrocopos himalyensis*), that persist in agricultural lands at comparable densities to what occurs primary forest but are completely absent from pasture.

Consequently, benefits to Himalayan biodiversity might best be achieved by integrating principles from both land-sparing and land-sharing strategies into a more holistic framework (Kremen 2015; Socolar et al. 2016). Such policies could combine strict nature protection with sustainable and ecologically oriented agricultural practices, governance that minimizes leakage of habitat disturbance to other countries or regions, and incentives to maintain landscapes as functioning social-ecological systems (Fischer et al. 2014; Kremen 2015). In our study region, the creation of an ecodevelopment zone adjacent to the Great Himalayan National Park is an example of an approach that successfully integrates habitat protection with sustainable use and community development programs (Pandey & Wells 1997). Recent assessments of similar community-based forestry programs across the Himalayas show that they result in lower deforestation rates than programs that do not integrate local livelihood benefits with forest conservation efforts (Brandt et al. 2017). Incentives to communities to maintain ecological integrity from such programs may also aid in safeguarding biodiversity from threats other than land-use change, such as hunting. The alarming rate of landscape conversion, high levels of biodiversity at stake, and increasing food demands underscore the urgency with which such multifaceted and integrated policies are needed throughout the Himalayan mountains.

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Supporting Information

Variance partitioning of the results by partial redundancy analysis (Appendix S1); correlograms of bird species richness model residuals (Appendix S2); and population responses of forest species, insectivores, granivores, resident species, long distance migrants, and elevational migrants to land-use change (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of materials) should be directed to the corresponding author.

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