



The importance of agricultural lands for Himalayan birds in winter

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Abstract: *The impacts of land-use change on biodiversity in the Himalayas are poorly known, notwithstanding widespread deforestation and agricultural intensification in this highly biodiverse region. Although intact primary forests harbor many Himalayan birds during breeding, a large number of bird species use agricultural lands during winter. We assessed how Himalayan bird species richness, abundance, and composition during winter are affected by forest loss stemming from agriculture and grazing. Bird surveys along 12 elevational transects within primary forest, low-intensity agriculture, mixed subsistence agriculture, and intensively grazed pastures in winter revealed that bird species richness and abundance were greatest in low-intensity and mixed agriculture, intermediate in grazed pastures, and lowest in primary forest at both local and landscape scales; over twice as many species and individuals were recorded in low-intensity agriculture than in primary forest. Bird communities in primary forests were distinct from those in all other land-use classes, but only 4 species were unique to primary forests. Low-, medium-, and high-intensity agriculture harbored 32 unique species. Of the species observed in primary forest, 80% had equal or greater abundance in low-intensity agricultural lands, underscoring the value of these lands in retaining diverse community assemblages at high densities in winter. Among disturbed landscapes, bird species richness and abundance declined as land-use intensity increased, especially in high-intensity pastures. Our results suggest that agricultural landscapes are important for most Himalayan bird species in winter. But agricultural intensification—especially increased grazing—will likely result in biodiversity losses. Given that forest reserves alone may inadequately conserve Himalayan birds in winter, comprehensive conservation strategies in the region must go beyond protecting intact primary forests and ensure that low-intensity agricultural lands are not extensively converted to high-intensity pastures.*

Keywords: agriculture, grazing, habitat disturbance, the Himalayas, land-use change, primary forest

La Importancia de las Tierras Agrícolas para las Aves del Himalaya en el Invierno

Resumen: *Los impactos del cambio de uso de suelo sobre la biodiversidad en el Himalaya son poco conocidos, a pesar de la deforestación extendida y la intensificación agrícola en esta región altamente biodiversa. Aunque los bosques primarios intactos albergan a muchas aves del Himalaya durante la época reproductiva, un gran número de especies de aves utilizan las tierras agrícolas durante el invierno. Valoramos cómo la riqueza, abundancia y composición de especies de aves del Himalaya durante el invierno son afectadas por la pérdida del bosque a partir de la agricultura y el pastoreo. Los censos de aves a lo largo de doce transectos de altitud dentro del bosque primario, de la agricultura de baja intensidad, de la agricultura de subsistencia mixta y de las zonas de pastoreo intensivo en invierno revelaron que la riqueza de especies de aves y la abundancia fueron mayores en la agricultura de baja intensidad y en la mixta, intermedias en las zonas de pastoreo, y más bajas en el bosque primario tanto en la escala local como la de paisaje; más del doble de especies y de individuos se registraron en la agricultura de baja intensidad que en el bosque primario. Las*

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comunidades de aves en el bosque primario fueron distintas de aquellas en todos los demás tipos de uso de suelo, pero sólo cuatro especies fueron únicas de los bosques primarios. La agricultura de intensidad baja, media y alta albergó 32 especies únicas. De las especies observadas en el bosque primario, el 80 % tuvo una abundancia igual o mayor en los suelos de baja intensidad agrícola, enfatizando el valor de estos suelos en la retención de ensamblajes diversos de comunidades a densidades altas durante el invierno. Entre los paisajes perturbados, la riqueza de especies y la abundancia declinaron conforme incrementó la intensidad del uso de suelo, especialmente en las pasturas de alta intensidad. Nuestros resultados sugieren que los paisajes agrícolas son importantes para la mayoría de las especies de aves del Himalaya durante el invierno; aunque la intensificación agrícola - especialmente el pastoreo incrementado - probablemente resultará en la pérdida de la biodiversidad. Dado que las reservas de bosques por sí solas pueden conservar inadecuadamente a las aves del Himalaya en invierno, las estrategias integrales de conservación en la región deben ir más allá de proteger los bosques primarios intactos y asegurar que los suelos de uso agrícola de baja intensidad no sean convertidos extensivamente a zonas de pastoreo de alta intensidad.

Palabras Clave: agricultura, bosque primario, cambio en el uso de suelo, las Himalayas, pastoreo, perturbación del hábitat

Introduction

The Himalayas are undergoing rapid deforestation (Pandit et al. 2007), yet this change has received surprisingly little attention from conservation scientists, despite this region being one of the most biodiverse places on Earth (Myers et al. 2000; Brooks et al. 2006). With over 10,000 plant species and nearly 1,000 bird species in the Himalayas, landscape conversion has the potential to affect a large number of species (Pandit et al. 2014). Fuelwood and fodder extraction and clearcutting for subsistence agriculture and pasture are the most pervasive drivers of forest loss in the region (Rao & Pant 2001; Lele & Joshi 2009; Puyravaud et al. 2010). India reports the largest volume of fuelwood removal of any country (over 300 million m³ annually since 2005) (FAO 2015a). Within India, the highest rates of forest loss are reported from Himalayan states and the adjacent hills regions (FSI 2015), and projected human population growth will only place further pressure on forests and forest resources.

Projections of total forest cover in the year 2100 based on current deforestation rates show a 65% reduction in forest area in the western Himalayas and a 38% reduction in the eastern Himalayas relative to 1970s levels (Pandit et al. 2007). As a result, some researchers predict that hundreds of endemic vascular plants and dozens of endemic vertebrate species will face extinction (Pandit et al. 2007). Reductions in Himalayan forest cover may also have consequences for biodiversity elsewhere due to, for example, increased flooding in neighboring lowland regions (Laurance 2007). Furthermore, rates of climate warming in the Himalayas are faster than the global average (Shrestha et al. 2012), and the future climatic suitability of key Himalayan reserves is expected to decline for many species (Bagchi et al. 2013), which would compound threats due to habitat loss.

The impact of agricultural expansion on biodiversity throughout the world has received much attention from scientists in recent years owing to the challenge of meet-

ing the food demands of growing human populations while conserving biodiversity (e.g., Tilman et al. 2001; Green et al. 2005; Phalan et al. 2011). With increasing isolation of protected landscapes due to an expanding agricultural matrix (DeFries et al. 2005), one approach to conserving biodiversity is to maximize or otherwise enhance the value of agricultural systems to wildlife (i.e., a land-sharing approach) (Green et al. 2005; Fischer et al. 2008). Agricultural and agroforest landscapes, although perhaps not as species rich as intact primary systems, can harbor considerable diversity (Daily et al. 2001; Edwards et al. 2011). Contrasting land-sparing approaches in which agricultural intensification is offset by enhanced forest protection elsewhere may not always be feasible (Fischer et al. 2011), such as in topographically complex landscapes like the Himalayas. As a result, there is pressing need to understand how biodiversity is affected by the conversion of intact primary forests to agricultural lands and pastures.

With nearly 10% of the world's bird species (Pandit et al. 2014), the Himalayas represent a critically important landscape for birds; many of these species are inadequately covered by the current system of protected areas in the region (Cantú-Salazar et al. 2013). Moreover, a growing number of studies indicate that intact forests in the Himalayas contain unique species assemblages and harbor a greater diversity of breeding birds relative to forest edges and the surrounding matrix (Brandt et al. 2013; Wood et al. 2015).

In the winter, however, the majority of Himalayan birds undertake short-distance elevational migrations, wintering at lower elevations within the mountains in regions where human population densities are highest and agriculture is rapidly expanding and intensifying (Grimmett et al. 1999). Although Himalayan agricultural systems may support diverse bird populations during winter (Laiolo 2004; Namgyel et al. 2008), the importance of different types of agricultural landscapes relative to intact forests for wintering birds in this region has not been assessed.

Furthermore, given the widespread human disturbance of Himalayan landscapes, it is essential to understand how wintering bird communities respond to varying degrees of agricultural intensification.

To assess how bird species richness, abundance, and community composition in the winter are affected by habitat conversion, we conducted bird surveys along 12 elevational transects in the western Himalayas in 4 dominant land-use types. Representing the typical progression of landscape conversion in the region and a gradient of land-use intensity, the 4 land-use types included intact primary forest, disturbed forest with patches of agriculture, mixed agriculture including terrace cultivation and orchards, and grazing pastures. By collecting detailed vegetation characteristics at all sites, we further examined how bird species richness and abundance related to changes in the vegetation structure resulting from habitat alteration.

Methods

Study Sites and Elevational Transects

We surveyed birds and habitat along elevational transects across 4 land-use types within Great Himalayan National Park (GHNP, 31.70°N, 77.50°E) and the adjacent human-dominated landscape (ecozone) in Himachal Pradesh, northern India, during the winter months of November and December 2013 (Fig. 1 & Supporting Information). Because we were unable to perform temporal replicate surveys over additional years due to financial constraints, we maximized spatial replication by establishing 12 distinct and continuous elevational transects and conducting repeated surveys along each transect. We established 9 transects in the ecozone between 1650 and 2700 m, which contained 3 disturbance types that together represented the major human-induced modifications to Himalayan landscapes. Three transects were located along mountainsides containing a mixture of community forest (retaining large, tall trees, often with a closed canopy) used for timber, fuelwood, and fodder extraction and scattered small agricultural plots (hereafter low intensity). Three transects were located along mountainsides with mixed agriculture, including crops (e.g., garlic, legumes, rice, and wheat), orchards (e.g., apple and pear), and occasional small wooded areas (with short, heavily lopped trees and an open canopy) used for fuelwood and fodder extraction (hereafter medium intensity). Three transects were located along mountainsides maintained by shepherds for grazing livestock. These transects were dominated by grasses, and there were few bushes or trees (hereafter high intensity). Within the national park, we established 3 transects in primary forest between 2000 and 2700 m (down to the lowest elevation possible in the national park) that originated in the Tirthan Valley and ascended opposing north- and

south-facing mountainsides (Figs. 1 & 2; Supporting Information). Irrespective of the land-use type, all transects covered similar broad-scale climate and habitat zones, including warm-temperate broadleaf and cool-temperate mixed coniferous forests.

Bird and Vegetation Surveys

We surveyed birds using a modified line-transect technique along existing trail networks. We surveyed each of the 12 transects 3 times throughout the winter season (2 morning surveys and 1 evening survey). We identified all birds by sight and sound and recorded the elevation, time, and count for all birds while walking at a slow, constant pace. The same observer conducted bird surveys along all transects to minimize detection bias due to the observer. We assigned all observed bird species a breeding-habitat status (i.e., forest vs. open country), migrant status (i.e., resident, elevational migrant, or winter visitor), and primary foraging guild following Grimmett et al. (1999).

We classified the disturbance type of each transect within the ecozone through a combination of visual assessment of land use from satellite imagery, through established local knowledge, and through personal observation during extensive field visits. We categorized the transects as low-, medium-, or high-intensity land-use types as described above. To determine how vegetation change arising from different types of disturbance affects the winter bird community, we quantified vegetation characteristics every 50 m of elevation along all survey transects. Within a 25-m radius of each point, we identified and counted all tree species ≥ 30 cm dbh (diameter breast height) to species, measured tree heights with a rangefinder, and calculated canopy cover with a densiometer. We identified all shrub and herbaceous species within 5 m of the point and combined the total number of species to calculate total understory species richness at the plot level.

Bird Abundance and Species Richness Analyses

We first tested for differences in the total abundance of all birds, forest birds, insectivorous birds, and granivorous birds between primary forest and each disturbance type with generalized linear models (GLMs) with Poisson error and a log link to accommodate count data. We controlled for variable survey effort (transect length) across sites. We defined a site as a 50-m elevational band on a particular transect to match our continuous bird observations to the spatial distribution of our vegetation sampling points (Supporting Information). We used raw counts as opposed to modeling abundances with variable detection probabilities because distance sampling along trails is often unreliable (Buckland et al. 1993) and small sample sizes for many rare species prohibited us from using

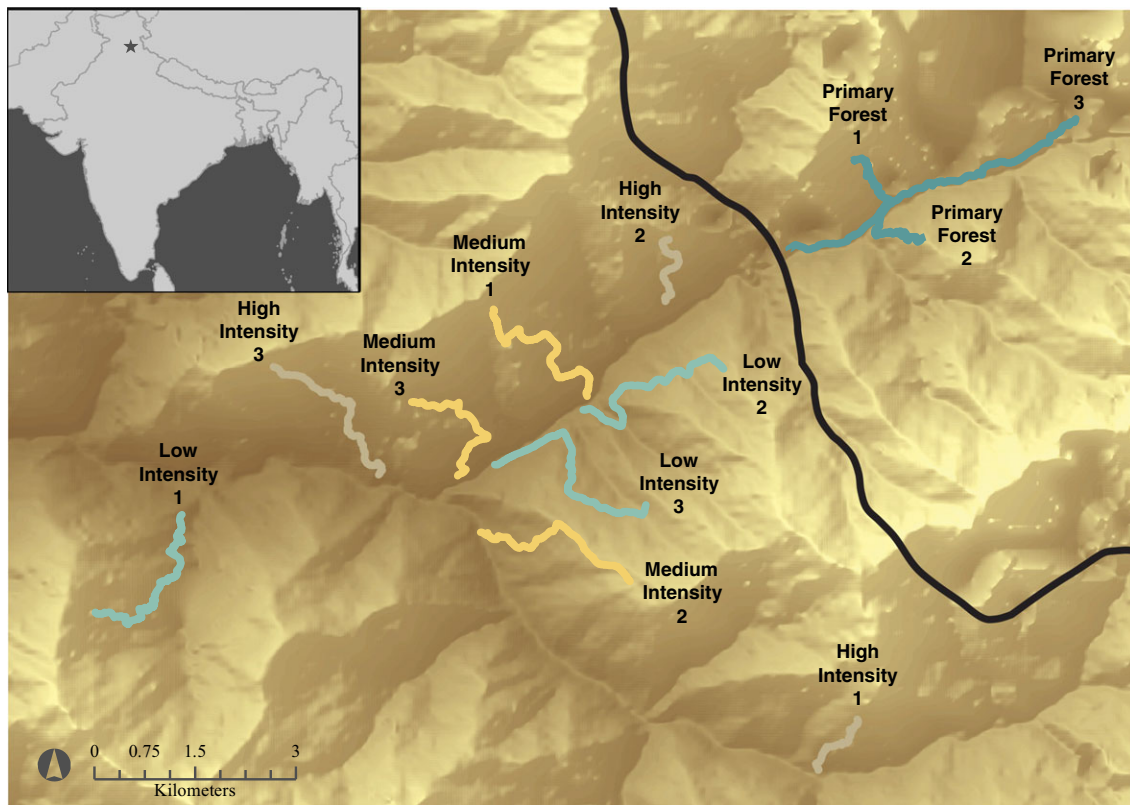


Figure 1. Map of the survey region, its position within India (inset), and the 12 transects surveyed (bold black line, Great Himalayan National Park boundary).

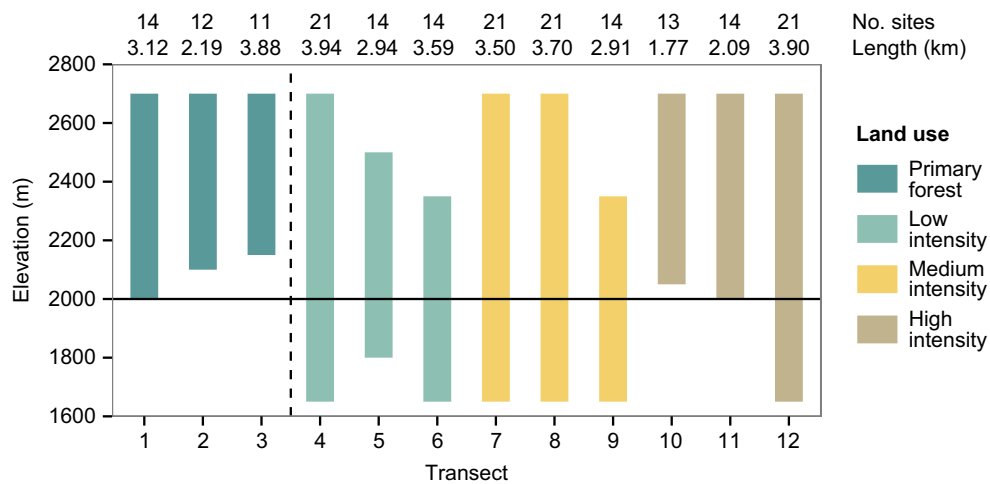


Figure 2. Elevational distributions of transects within 4 land-use types (above horizontal line, comparable portions of transects used in analyses including primary forest; right of vertical line, portions of transects used in analyses among disturbed landscapes). Transect numbers reflect those in Fig. 1. The number of sites reflects the number of points surveyed and the number of sites included in analyses of bird species richness and abundance.

repeated sampling methods such as N -mixture models. To enable direct and unbiased comparisons between our disturbed sites and intact sites, we first restricted the extent of our disturbed transects to include sites at comparable elevations (i.e., ≥ 2000 m) for analysis and then repeated the analyses by including sites at all ele-

vations (i.e., down to 1650 m) and limiting analyses to within disturbed land-use types only (Fig. 2).

We compared bird species richness between primary forest and each disturbance type at 2 spatial scales. Using presence-absence matrices for all species, we calculated the number of species within each site as defined

above and subsequently compared the site-level species richness among land-use types with GLMs with Poisson error and log link. We controlled for variable survey effort across sites. As above, we restricted analyses that included primary forest to sites at comparable elevations (see Fig. 2) and repeated our analyses with all disturbed sites when comparing among low-, medium-, and high-intensity sites only. Although our bird transects were established to minimize biases from spatial autocorrelation, we evaluated spatial autocorrelation by calculating Moran's I and evaluating the model residuals in correlograms to confirm the independence of plots and validate that species richness calculations were not affected by the spatial distribution of survey transects (Supporting Information). We repeated this process for analyses of species richness among sites at comparable elevations and for analyses among disturbed sites only.

We compared bird species richness patterns across land-use types by calculating total species richness within each land-use type with sample-based rarefaction curves (Colwell et al. 2012). We restricted our analyses to sites ≥ 2000 m to enable unbiased comparisons with primary forest. We first performed individual-based rarefaction to a standardized transect length of 100 m (removing 14 sites from the analysis that were <100 m long initially) as a way to control for variable transect lengths. We used abundance matrices for all species to perform sample-based rarefaction on the remaining sites. Following the same approach, we repeated rarefaction analyses across all sites strictly within disturbed land-use types.

Community Composition

We compared bird community composition in primary forest with composition in each disturbance type by calculating Bray-Curtis similarity indices for a presence-absence species matrix and using nonmetric multidimensional scaling (NMDS) to ordinate each survey site along 2 axes. To test for differences in community composition among land-use types, we performed pairwise perMANOVA tests (Anderson 2001). We repeated all ordination analyses with an abundance matrix, but results from these analyses were qualitatively similar to those with the presence-absence matrix, so only the latter is presented.

To test whether composition differences among land-use types were influenced by the spatial distribution of our survey transects, we conducted partial redundancy analysis (pRDA) (Legendre & Legendre 2012). We first transformed our species abundance matrix using Hellinger's distance, then used the resulting matrix as the response variable in a pRDA model with land-use type as the sole environmental predictor, conditioned on the latitude and longitude of our survey sites. We then assessed significance of the model with a permutation-based analysis of variance procedure with 1000 permutations. Finally, we used variable partitioning to parti-

tion the overall variance explained by the model into environmental, spatial, and joint components, which allowed us to assess the contribution of land-use type (adjusted R^2) only to the patterns of community composition across sites.

Population-Level Responses

We used vegetation characteristics recorded at each site to determine the potential mechanisms underlying differences in abundance and species richness among land-use types. We fit GLMs with all combinations of tree density, tree height, tree species richness, canopy cover, and understory species richness as predictors of site-level bird abundance and species richness. We controlled for variable survey effort across sites. We used an information-theoretic approach and compared models with Bayesian information criterion, which estimates the weight of evidence in support of a particular model while enforcing stricter penalties on overparameterized models (Burnham & Anderson 2002).

All analyses were performed in R (R Core Team 2014). Rarefaction analyses were performed in the iNEXT package (available from http://chao.stat.nthu.edu.tw/wordpress/software_download/). The NMDS ordination analyses, perMANOVA tests, and partial redundancy analyses were performed using the vegan package, and spatial autocorrelation analyses were performed using the ncf and ape packages.

Results

Bird Abundance and Species Richness

We recorded 128 bird species across all elevational transects (Supporting Information). Bird abundance in primary forest was significantly lower than in all other land-use types when controlling for transect length (GLM; $p < 0.001$) (Fig. 3a). When considering all birds, abundance was greatest in medium-intensity sites ($z_{4,139} = 16.453$, $p < 0.001$), followed by low-intensity sites ($z_{4,139} = 13.566$, $p < 0.001$) and high-intensity sites ($z_{4,139} = 9.173$, $p < 0.001$), and such patterns were consistent when incorporating all disturbed sites, although differences between medium- and low-intensity sites were only marginally significant ($z_{3,148} = 1.997$, $p = 0.046$).

At the scale of individual sampling points, bird species richness was greatest in medium-intensity sites (GLM; $z_{4,139} = 12.894$, $p < 0.001$) followed by low-intensity sites ($z_{4,139} = 10.478$, $p < 0.001$) and high-intensity sites ($z_{4,139} = 6.368$, $p < 0.001$) and lowest in primary forest after controlling for transect length (Fig. 3b). Tests of spatial autocorrelation through calculation of Moran's I indicated weak positive spatial autocorrelation of model residuals for analyses of species richness, including

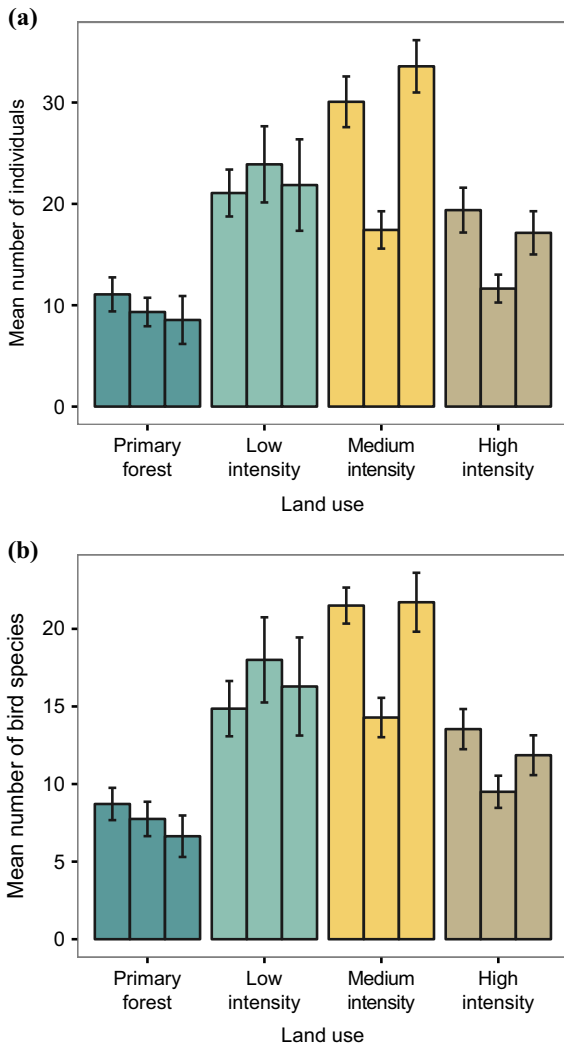


Figure 3. Mean and standard error of (a) bird abundance and (b) species richness per site (50-m elevational band of a given transect) across the 12 elevational transects within 4 land-use types in the Himalayas.

primary forest sites, and for analyses including only disturbed sites (Moran's I observed = 0.12, $p < 0.001$ for both analyses). Despite a modest signature of spatial autocorrelation, correlograms of model residuals indicated that sites were spatially independent at distances of 50 m for both analyses (Supporting Information), suggesting that observed differences in bird species richness among land-use types were largely not influenced by the spatial distribution of our surveyed sites.

Rarefaction analyses at the landscape scale also revealed that total species richness in primary forest was significantly lower than in all disturbance types and that total species richness was higher in low-intensity sites relative to medium- and high-intensity sites (Fig. 4). When restricting the sites for rarefaction analysis to those

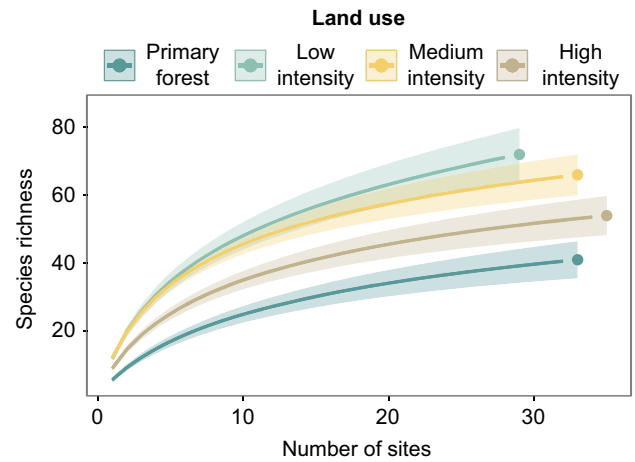


Figure 4. Sample-based rarefaction of bird species richness across 4 land-use types (shaded regions, 95% confidence intervals).

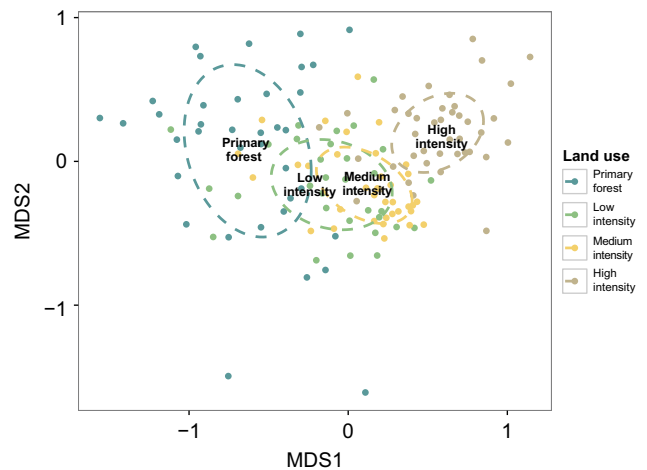


Figure 5. Nonmetric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity indices derived from species presences in 4 land-use types (stress = 0.21). Ellipsoids are centered at the mean MDS value of both axes per land use. Standard deviations determined the radius along each axis.

strictly within disturbed types but including the entire elevational gradient, species richness in medium- and low-intensity sites was greater than in high-intensity sites ($p < 0.001$), but we found no statistically significant difference in species richness between medium- and low-intensity sites ($p = 0.264$) at local or landscape scales (Supporting Information).

Community Composition

The NMDS ordination plots suggested strong community composition differences between primary forest and all disturbance types (Fig. 5). Pairwise perMANOVA

analyses testing for differences in species composition between primary forest and all disturbance types revealed distinct communities in primary forest versus high- ($R^2 = 0.25, p < 0.001$), medium- ($R^2 = 0.20, p < 0.001$), and low-intensity sites ($R^2 = 0.12, p < 0.001$). Medium- and low-intensity sites, while similar based on NMDS ordination plots (Fig. 5), were distinct based on perMANOVA analysis ($R^2 = 0.05, p < 0.001$). Species composition in high-intensity sites was distinct relative to medium- ($R^2 = 0.17, p < 0.001$) and low-intensity sites ($R^2 = 0.18, p < 0.001$).

Partial redundancy analysis revealed a significant effect of land-use type on community composition when accounting for the spatial distribution of survey sites ($F_{3,138} = 6.41, p < 0.001$). Land-use type explained 13.33% (adjusted R^2) of the overall variance in the data. Variance partitioning further revealed that the pure effect of land-use type accounted for 9.97% of the overall variance, and the pure effect of latitude and longitude (the conditioning variables) accounted for 0.73% of the overall variance (the joint effect of both explanatory variables accounted for 2.64% of the overall variance). This result indicates observed differences in community composition across the landscape predominately arose from inherent differences in land-use type, rather than from the spatial distribution of survey sites.

Of the 49 bird species recorded in primary forest, 10 were absent from low-intensity sites, 15 were absent from medium-intensity sites, and 23 were absent from high-intensity sites across comparable elevations (Fig. 6a & Supporting Information). Eighty percent of species found in primary forest either had greater abundance or showed no significant difference in abundance in low-intensity sites. The abundance of 66% of species found in primary forest was either higher or did not differ significantly in medium-intensity sites, and the abundance of 47% of such species was either higher or did not differ significantly in high-intensity sites (Fig. 6a & Supporting Information). Restricting our analyses to forest birds (see Methods) yielded results that were largely consistent with analyses for all birds (Fig. 6b). Insectivorous bird species declined across disturbance classes in similar proportions as all species combined, whereas granivorous birds showed proportionally larger declines (Figs. 6c & 6d). Notably, all land-use types held unique species: 5 species were recorded only in primary forest, 9 species only in low-intensity sites, 13 species only in medium-intensity sites, and 12 species only in high-intensity sites across transects at comparable elevations (Supporting Information).

Population-Level Responses

The model with greatest support in predicting both bird species richness and abundance included tree density, tree height, and tree species richness. Canopy cover was not included as an important predictor in the best performing species richness or abundance models (Support-

ing Information). Both bird species richness and abundance were significantly negatively related to tree density ($z_{4,139} = -3.016, p = 0.003$ and $z_{4,139} = -4.770, p < 0.001$, respectively) and tree height ($z_{4,139} = -5.183, p < 0.001$ and $z_{4,139} = -6.705, p < 0.001$, respectively) and significantly positively related to tree species richness ($z_{4,139} = 4.021, p < 0.001$ and $z_{4,139} = 4.914, p < 0.001$, respectively) after controlling for transect length.

Discussion

Although official reports by the Forest Survey of India document net reforestation in Himachal Pradesh (FSI 2015), previous estimates from satellite imagery reveal that natural forests in the state are, in fact, rapidly disappearing (Pandit et al. 2007; Puyravaud et al. 2010). Intact primary forests may be vital to Himalayan bird populations during breeding (Brandt et al. 2013), but we found that natural forest converted to low- and medium-intensity agriculture retained a substantial portion of the Himalayan bird community during winter and that this conversion negatively affected relatively few forest obligates and attracted nonforest species. Agricultural landscapes harbored greater species richness and abundance of birds in winter relative to primary forest at both local and landscape scales (Figs. 3 & 4). Some groups of bird species, such as Palearctic migrants wintering in the Himalayas, were rarely observed in primary forest and were most abundant in medium- and high-intensity sites (Supporting Information).

Moreover, agricultural landscapes maintained a substantial proportion of the winter bird community found in primary forest or otherwise considered forest dependent during the breeding season. Approximately half of the species recorded in primary forest did not differ in abundance among land-use types or their abundance was significantly higher, even in high-intensity sites (i.e., sites that were intensively grazed and supported very low tree densities and species richness) (Fig. 6b & Supporting Information). Previous studies have documented the potential importance of a variety of agricultural and agroforest landscapes for birds in tropical regions (Daily et al. 2001; Johnson et al. 2006; Edwards et al. 2011; Karp et al. 2012). For the majority of bird species in winter in the western Himalayas, our results were largely consistent with the notion that low- and medium-intensity agricultural landscapes can be neutral or even beneficial to many bird species during that season (Fig. 6a) and revealed that strict nature reserves protecting intact primary forests may not sufficiently conserve some forms of biodiversity, such as birds, throughout the year.

However, we found that within human-dominated Himalayan landscapes, intensifying agriculture by converting small-holder farms amidst forest to grazing pastures led to significant reductions in winter bird abundance

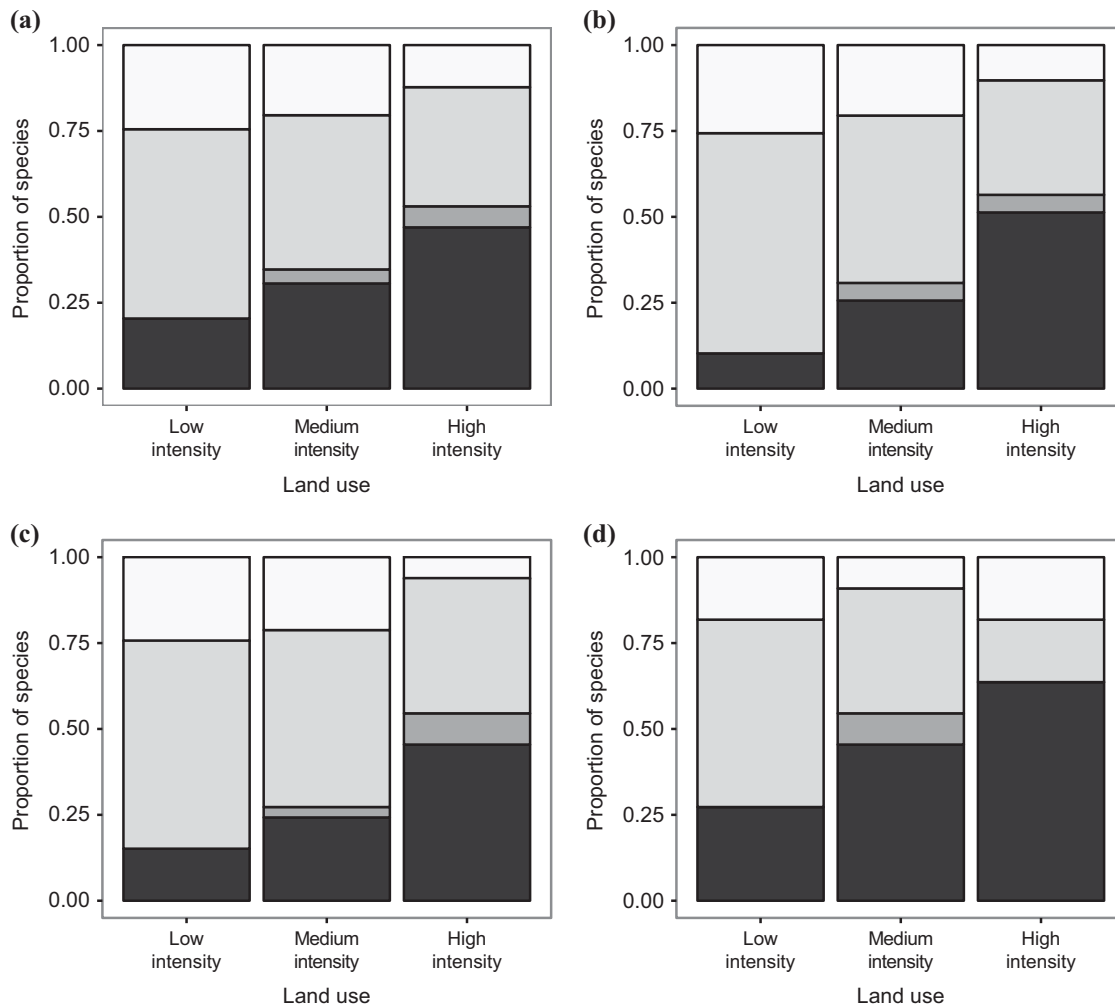


Figure 6. Proportion of 4 different groups of bird species in primary forest that were recorded in primary forest but were absent (black), were significantly lower (dark gray), did not differ significantly (light gray), and were significantly higher (white) in each land-use type: (a) all birds ($n = 49$), (b) forest birds ($n = 39$), (c) insectivorous birds ($n = 33$), and (d) granivorous birds ($n = 11$). See text and Methods for descriptions of habitat and foraging guild classifications for birds.

and species richness and significantly altered community composition, which led to homogenized bird communities. We found that bird species richness was significantly greater in low- and medium-intensity sites than in high-intensity sites at local and landscape scales (Supporting Information). As the level of intensification increased, community composition differed; there were relatively fewer forest-dependent species and relatively more open-country or generalist species (Supporting Information). Our analyses of bird species richness and abundance patterns in human-dominated landscapes as a function of vegetation characteristics indicated that lower bird species richness and abundance in high-intensity sites may primarily be driven by diminished tree species richness caused by grazing and grass cutting (Supporting Information). Retention of forest cover, even in the form of low-intensity agriculture within a forested matrix, could

alleviate both losses in overall bird species richness and losses of forest specialists that are often of more immediate conservation importance (Edwards et al. 2014).

We lacked empirical data to assess whether the abundance and species richness patterns we observed across land-use types during the winter persisted during the breeding period. Many North American breeding birds use agricultural landscapes when wintering in Central and South America but rely heavily on forests during the breeding season (Johnson et al. 2006; Holmes 2007). Over 80% of the birds we observed in the Himalayas undergo seasonal migrations (Grimmett et al. 1999; Supporting Information). Furthermore, with over 60% of these species breeding in forests (and the majority of summer visitors to the Himalayas also dependent on forests for breeding [Grimmett et al. 1999; Price et al. 2011; Supporting Information]), agricultural landscapes may revert

to relatively lower bird species richness and abundance in summer relative to primary forest when birds migrate to breed, which would underscore the importance of intact primary forest for reproduction and long-term population viability in Himalayan bird communities. This may be particularly true for 2 of the 4 threatened species in the region, Cheer Pheasant (*Catreus wallichii*) and Western Tragopan (*Tragopan melanocephalus*), which are known to be sensitive to grazing and forest conversion, respectively, even during winter (Gaston et al. 1983; Garson et al. 1992; Singh et al. 2011). Nevertheless, we found clear evidence that agricultural landscapes are important for the majority of Himalayan bird species during winter, a period that likely imposes climatic stress and resource limitation (Newton 1998).

Given the inherent limitations in the spatial and temporal resolution of our surveys, we did not assess the degree to which birds we observed in agricultural lands use forested areas during winter. Thus, our observations of forest species within agricultural lands could simply reflect opportunistic foraging in disturbed areas from nearby forest; many of these species perhaps depend on forests for roosting (Sekercioglu et al. 2007). Although we cannot rule out this possibility, our sampling design ensured that medium- and high-intensity sites were located at variable distances from primary forest, from approximately 1.5–6 km from primary forest edge (Fig. 1). Furthermore, of the 3 high-intensity transects we surveyed, we observed the lowest bird species richness and abundance on the transect closest to our primary forest sites (Figs. 1 & 3), which suggests that spillover or local movements of forest birds into agricultural lands from primary forest are unlikely to explain the differences in species richness and abundance we observed.

High human population growth and increasing demand for food will likely result in further conversion to agriculture, already the dominant land use in the region. Although our results suggest that low-intensity agriculture may be necessary for wintering bird populations in the western Himalayas, a holistic view of the effects of agricultural expansion in the region is necessary to ensure that populations of birds and other organisms are not imperiled with further landscape conversion. First, habitat conversion may pose more significant threats to bird species during the breeding season, so it is important to understand how birds are affected during this critical period. Second, western Himalayan birds may be more adaptable to conversion than birds from the eastern Himalayas, given their ecology and evolutionary histories (Price et al. 2011). A larger proportion of bird species in the western Himalayas originate from Palearctic regions and typically inhabit more open forested, temperate habitats than do eastern Himalayan birds, which are predominantly Indo-Malayan with life histories that reflect greater dependence on dense tropical forests (Price et al. 2011; Renner 2011). With these caveats in mind, our data sup-

port a dual conservation strategy involving both forests and agricultural lands for the western Himalayas.

However, were there to be a widespread shift from low-intensity and mixed subsistence agriculture to livestock grazing, the consequences for biodiversity could be devastating, resulting in a homogenized community of birds dominated by open-habitat species, similar to patterns observed in birds in intensive-agriculture areas in the Neotropics (Karp et al. 2012; Supporting Information). Livestock grazing in India has risen markedly over the past several decades, driven largely by increased production of cow and goat milk (roughly 700% and 900% increases, respectively) (FAO 2015b). Limiting the expansion of intensively grazed pastures or otherwise ensuring that grazing practices are intermixed with small-scale croplands in agricultural lands that retain some native vegetation may minimize negative biodiversity impacts in human-dominated Himalayan landscapes.

Effective conservation policies must take all of these factors into account, which will likely require contrasting approaches across different regions (e.g., eastern vs. western Himalayas), in different seasons (e.g., winter vs. summer), and for species with varying sensitivities to land-use change. We addressed one fundamental component concerning the conservation of bird species in the western Himalayas and conclude that low-intensity agricultural areas provide a vital refuge for the majority of Himalayan bird species during winter. Moreover, our results indicate that conservation measures that focus solely on preserving intact primary forests while allowing unrestricted expansion and intensification of agricultural lands may inadequately protect Himalayan bird communities during winter. A holistic conservation approach that best meets the needs of western Himalayan birds throughout the year should include preserving low-intensity agriculture in addition to large tracts of primary forest. Given the large human footprint on this landscape and its global importance for biodiversity conservation (Brooks et al. 2006; Pandit et al. 2014), retaining low-intensity agricultural lands and minimizing their conversion to intensive uses will be an important strategy for preventing biodiversity loss.

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Supporting Information

Habitat associations, foraging guilds, migratory statuses, and abundances of all recorded bird species in each land-use type (Appendix S1); generalized linear model output for predicting bird species richness and abundance (Appendix S2); photographic examples of elevational transects in each land-use type (Appendix S3); sample-based rarefaction of bird species richness within disturbed land-use types (Appendix S4); mean and standard errors for tree density, tree height, tree species richness, and herb and shrub species richness across land-use types (Appendix S5); proportions of species in habitat and association groupings across land-use types (Appendix S6); number of species across land-use types by migrant status (Appendix S7); nonmetric multidimensional scaling ordination plots of bird species and bird species richness (Appendix S8); and correlograms of bird species richness model residuals (Appendix S9) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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