



## Sacred forests are keystone structures for forest bird conservation in southwest China's Himalayan Mountains



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### ABSTRACT

Identifying and protecting “keystone structures” is essential to maintain biodiversity in an increasingly human-dominated world. Sacred forests, i.e. natural areas protected by local people for cultural or religious regions, may be keystone structures for forest birds in the Greater Himalayas, but there is limited understanding of their use by bird communities. We surveyed birds and their habitat in and adjacent to six Tibetan sacred forests in northwest Yunnan China, a biodiversity hotspot. Our goal was to understand the ecological and conservation role of these remnant forest patches for forest birds. We found that sacred forests supported a different bird community than the surrounding matrix, and had higher bird species richness at plot, patch, and landscape scales. While we encountered a homogeneous matrix bird community outside the sacred forests, the sacred forests themselves exhibited high heterogeneity, and supported at least two distinct bird communities. While bird community composition was primarily driven by the vegetation vertical structure, plots with the largest-diameter trees and native bamboo groves had the highest bird diversity, indicating that protecting forest ecosystems with old-growth characteristics is important for Himalayan forest birds. Finally, we found an increased bird use of the sacred forests and their edges during 2010, a severe drought year in Yunnan, indicating that sacred forests may serve as refuges during extreme weather years. Our results strongly indicate that sacred forests represent an important opportunity for Himalayan bird conservation because they protect a variety of habitat niches and increase bird diversity at multiple spatial scales.

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## 1. Introduction

As humans consume an ever-increasing proportion of the Earth's resources, biodiversity declines at an accelerating rate (Chapin et al., 2000; Foley et al., 2005), making the protection of “keystone structures”, i.e., discrete spatial features that maintain biodiversity at multiple spatial scales, ever more important (Belsky and Canham, 1994; Manning et al., 2006; Stagoll et al., 2012; Tews et al., 2004). For example, forest gaps, large trees, and temporary wetlands are keystone structures whose presence adds heterogeneity to the resources available in landscapes, facilitating greater species richness. The question is how to identify such keystone structures, and how to protect them.

Sacred forests, i.e., natural areas protected by local people for cultural or religious reasons (Dudley et al., 2009), may be keystone structures for biodiversity in traditional landscapes around the world. Sacred forests are numerous, dispersed across a broad range of topographic and micro-climatic conditions, and range in size from a single hectare to thousands of square kilometers (Ormsby, 2011). As such, they likely serve multiple ecological functions, including as corridors, refugia, and source habitats (Bhagwat and Rutte, 2006; Dudley et al., 2010). Sacred forests may be critical components of protected area networks (Verschuren et al., 2010), but we have little understanding of their potential role for biodiversity conservation, especially in the less-studied biodiversity hotspots.

The traditional land management systems that sustain sacred forests may create optimum conditions for species diversity at multiple spatial scales. For example, sacred forests are typically managed by communities (Dudley et al., 2009) and often experience a gradient of human disturbance (UNESCO-MAB, 2003), where a variety of organisms can utilize variable resource

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conditions (Belsky and Canham, 1994). In addition, sacred forests are typically embedded in landscapes with matrix habitats that are hospitable to at least some species, and thus conventional assumptions of patch size and fragmentation effects (MacArthur and Wilson, 1967) may not apply (Prugh et al., 2008). Furthermore, the edges between sacred forests and their matrix are often not abrupt barriers, but a gradient of disturbance to levels characteristic of the surrounding matrix. These edges may serve as “ecotones”, facilitating ecological interactions between the patch and the matrix, and offering supplementary resources not available in the core habitats (Ries et al., 2004). Despite their potential importance for species dispersal and persistence, we have little understanding of how sacred forests are influenced by patch size, edge effects, and interactions between patch and matrix habitats.

One region where sacred forests are relatively common are the Himalayan mountains (Barbhuiya et al., 2010; Luo et al., 2003; Mallarach, 2008; Salick et al., 2007; UNESCO-MAB, 2003; Xu et al., 2005). Several ethnic minority groups recognize sacred areas as part of their religion, including sacred beyuls (which protect entire valleys), sacred mountains (10s to 100s of km<sup>2</sup>), and village-level sacred forests (1–1000 ha). The Himalayan mountains also contain three biodiversity hotspots (Myers et al., 2000) and forest birds are of special conservation concern (Renner, 2011). The region exhibits high levels of bird diversity and endemism and ranks highest in global assessments of threatened bird species richness (Grenyer et al., 2006). Many forest bird species in the Greater Himalayas follow a Sino-Himalayan distribution (Renner, 2011; Renner and Rappole, 2011), which includes the Himalayan range, the mountains of southwest China, and the Qinghai Tibetan plateau (Fig. 1a). Forest degradation has accelerated throughout this region in recent decades (Brandt et al., 2012; Renner et al., 2007; Spehn et al., 2010), destroying bird habitats (Dumbacher et al., 2011). Sacred areas may be critical for bird conservation throughout this rapidly changing region, but their importance for Himalayan forest bird communities across multiple spatial extents is not well understood.

Our overarching objective was to understand the role of sacred forests for the conservation of Himalayan forest birds. We studied bird communities within and outside of Tibetan sacred forests in northwest Yunnan, China, with the following specific objectives:

1. Determine whether bird community composition and diversity is different within sacred forests compared to the surrounding matrix.
2. Identify the critical habitat characteristics structuring bird diversity, abundance, and community composition.
3. Investigate how patch size and edge habitats influence bird community composition, diversity and abundance patterns.

## 2. Methods

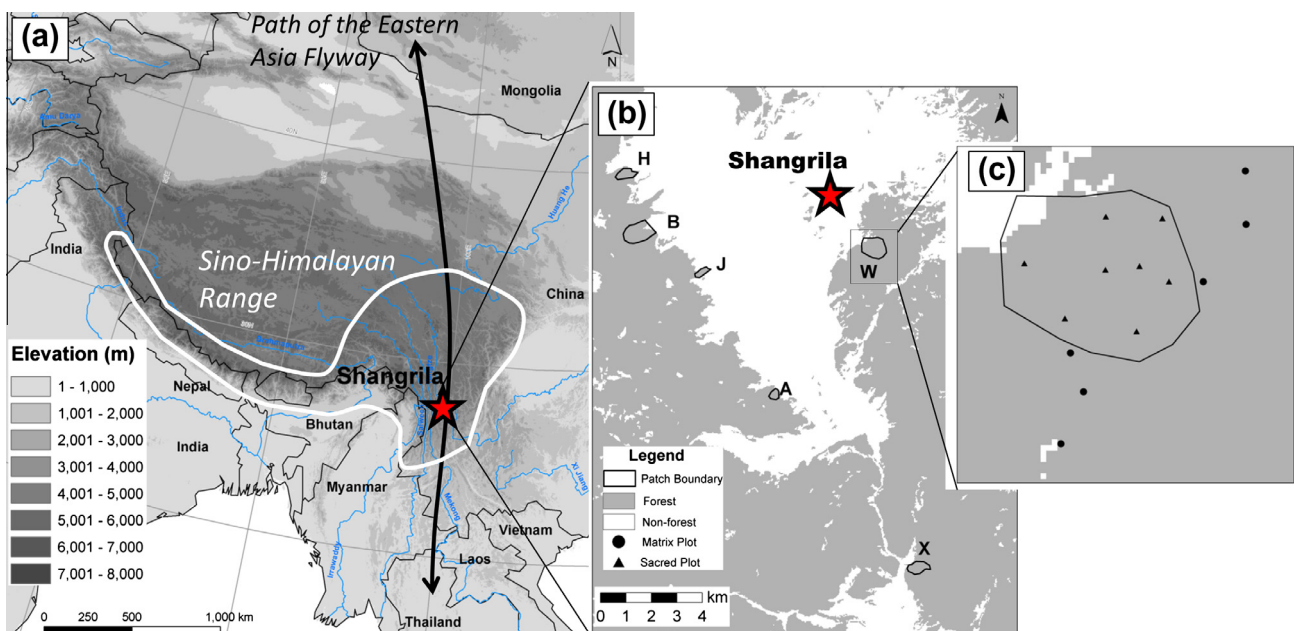
### 2.1. Study area

Our study area is in Shangrila, northwest Yunnan Province, China (Fig. 1a). Northwest Yunnan is a biodiversity hotspot in the Hengduan Mountains of the southeastern sub-Himalayan mountains, bordering Myanmar, Tibet and Sichuan Province. Three major rivers (the Yangtze, Mekong, and Salween) create steep gorges, with elevations ranging from 1800 to 6740 m, creating a large array of ecological niches in a relatively small area.

Northwest Yunnan has great importance for local, regional, and global bird diversity. First, it is a center of bird endemism (Lei et al., 2003). Second, it is part of the East Asian migratory flyway, providing important stop-over habitat for long-distance migrants (Cheng, 1987). Third, it lies at the confluence of the Palearctic, Himalayan, and Indo-Malay zoogeographic regions, and thus provides habitat for birds with distinct ecological and evolutionary histories (Renner, 2011).

Northwest Yunnan's avifauna is one the poorest understood on Earth (Renner and Rappole, 2011), and it is likely that forest birds face serious threats. Large expanses of northwest Yunnan's forests were clear-cut by state logging companies from the 1960s through the 1990s to fuel China's national development. Despite a ban on commercial logging in 1998 and heavy investment in reforestation and protected areas (Liu et al., 2008), old-growth forests continue to be logged and the ecological integrity of the new forests is unclear (Brandt et al., 2012; Xu, 2011).

Northwest Yunnan is home to several ethnic minority groups that recognize sacred areas as part of their religion (Xu et al., 2005). In particular, Tibetans have a complex sacred site system that includes large Tibetan sacred mountains (tens to hundreds



**Fig. 1.** (a) Location of Shangrila within the Greater Himalayan region, (b) the six sacred forest patches that were surveyed, and (c) sampling plots within and outside of sacred forests. Matrix plots were placed on transects at approximately 60, 260, and 510 m away from the edge of the sacred forest.

of square kilometers) and hundreds of smaller community-based sacred forests (1–1000 ha) at lower elevations (Luo et al., 2003; Shen et al., 2012). Vegetation communities in Tibetan sacred forest sites have higher vegetation species richness, diversity, and endemism than randomly selected non-sacred sites (Anderson et al., 2005), and larger and denser trees (Salick et al., 2007). However, nothing is known about the importance of Tibetan sacred forests for taxa other than plants.

## 2.2. Avifaunal sampling

We conducted bird point count surveys at six sacred forest sites that ranged in size from 13 to 75 ha (Fig. 1b). We surveyed a total of 62 plots, including 35 within the sacred forests, 9 edge plots (60 m away from the sacred forest boundary), and 18 matrix plots (260 and 520 m from the boundary) (Fig. 1c). Plots were placed at least 200 m apart, along walking paths when possible. At the plot center, we surveyed birds at least twice per year during the breeding season (May 18–June 30) in 2010 and 2011. Surveys consisted of 50-m radius, 10-min point counts following standardized methods for landscape ecology (Ralph et al., 1993), and included an estimate of distance to bird using a hand-held laser rangefinder (Buckland et al., 2001). Point counts were conducted by JSB. We assessed general characteristics of the breeding bird species we encountered, including (a) resident or migrant and (b) foraging guild, using the best available comprehensive resources for birds of this region (Cheng, 1987; MacKinnon and Phillipps, 2006; Rasmussen and Anderton, 2005) and our own field observations.

## 2.3. Habitat structure

Vegetation composition and structure was measured at each point-count station according to standardized protocols (Martin et al., 1997; Ralph et al., 1993) from June to August of 2010. Within each point-count station, we measured four 5-m radius subplots (Ralph et al., 1993). The initial sub-plot was located at the center of the point-count station, and the remaining three subplots were located 30-m away at 0°, 120° and 240°. Slope, aspect and basal area (using a 10- or 20-factor basal area per ft<sup>2</sup> prism) were measured at the center point of each subplot. Canopy coverage (using a densitometer) and foliage height diversity (in 0.3-m sub-sections) was measured at the north, east, south, and west edge of each of the four subplots. Visual estimates of percent coverage of different materials (e.g. woody shrub, coarse woody debris, leaf litter, etc.) for the sub-canopy layer (0.5–5 m) and the ground layer (0–0.5 m) were collected at each subplot. Finally, we recorded all species of trees and shrubs, and the heights and dbh of the three tallest and three largest-diameter trees, encountered in the entire 50-m radius plot.

## 2.4. Data analysis

### 2.4.1. Differences between sacred forest and matrix habitats

We estimated differences in detection probabilities among habitats, and between years based on our distance measurements and made density adjustments for those species for which we had sufficient observations (>75) in each year (Buckland et al., 2001). We lumped edge plots with matrix plots to estimate a species detection curve for sacred or non-sacred (i.e., edge and matrix plots) habitats because matrix and edge habitat characteristics were similar in bird detectability. There was a single species with sufficient observations in both 2010 and 2011 (Blyth's Leaf Warbler (*Phylloscopus reguloides*)), and an additional species with sufficient observations in 2010 only (Hume's Leaf Warbler (*Phylloscopus humei*)). Three models were used to fit the detection function (Buckland et al., 2001) and the

best model was selected using the Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002).

We compared bird diversity and abundance among habitat types and between years at three different spatial scales: plot, patch and landscape. At the plot scale, we compared raw values of observed bird species richness, Shannon index, and absolute abundance in sacred, matrix and edge habitats. Differences among habitat types were tested using a one-way analysis-of-variance (ANOVA) and pairwise comparisons (Tukey multiple comparisons of means). At the patch scale ( $n = 6$ ), we compared sacred and matrix/edge (lumped together for rarefaction) habitats using observed species richness, rarefied species richness, and rarefied Shannon index, all standardized by the number of individuals, derived from sample-based rarefaction curves constructed in EstimateS v.7 (Colwell, 2009). Differences at the patch scale were tested using paired two-sample student's *t*-tests. At the landscape scale, we calculated rarefied species richness, rarefied Shannon index, and estimated total species richness (using the Jackknife 1 estimator) (Colwell, 2009; González-Oreja et al., 2010). Patterns of bird diversity according to the Shannon Index were consistently similar to raw and rarefied species richness, and therefore only raw and rarefied species richness were reported here.

To determine whether bird species assemblages differed among habitats and sacred forests, we removed rare species (less than 3 observations per year) from our multivariate dataset and computed a Bray-Curtis similarity index on square root-transformed abundance data (Carr, 1997). We then used non-metric multidimensional scaling (NMDS) to create a graphical representation of the resemblance matrix (Kruskal, 1964). Bird assemblage differences among (a) habitats and (b) sacred forests were tested for using an analysis of similarity (ANOSIM). We used a Bonferroni adjusted alpha value for pairwise comparisons among the three habitats ( $p = 0.05/3 = 0.016$ ). NMDS and ANOSIM analyses were conducted using PRIMER v6 (Clarke and Gorley, 2006).

### 2.4.2. Habitat analysis

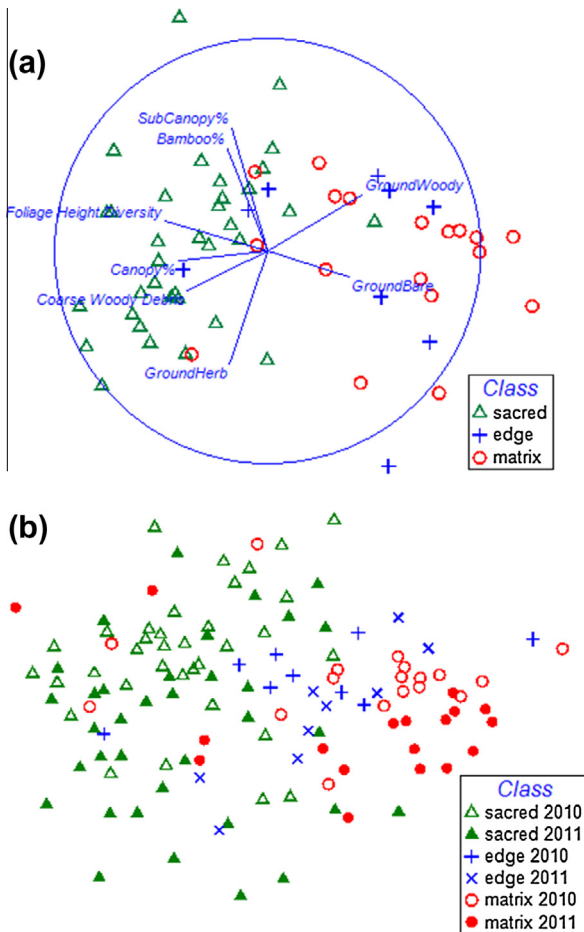
We used step-wise multiple linear regression to determine the most important environmental variables influencing bird diversity and abundance at the plot scale. The best model was selected using the Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). To investigate the importance of patch size on species richness, we calculated Pearson's correlations between patch size and raw species richness. These analyses were performed in the statistical package R version 2.8.1. To identify the most prominent habitat gradients and the most important variables driving those gradients, we performed principal components analysis (PCA, using PRIMER v6 (Clarke and Gorley, 2006)) on the habitat variables that were both uncorrelated and known to be important for bird communities according to the regression analysis. To understand the relationship between the prominent habitat gradients and bird community composition we performed canonical correspondence analysis (CCA in PC-ORD 6.04), which constrains habitat gradients by the bird species data.

## 3. Results

### 3.1. Differences between sacred forest and matrix habitats

#### 3.1.1. Habitat

The 62 plots captured a wide range of variability in vegetation disturbance, structure and species composition (see Appendix S1 in Supporting Information). PCA identified two prominent habitat gradients in our study area (Fig. 2a). The first axis (eigenvalue = 3.59, explaining 44.8% of the variance) corresponded to differences between sacred and matrix habitats, which had



**Fig. 2.** Multivariate analyses of (a) habitat gradients (PCA) and (b) bird community composition (NMDS).

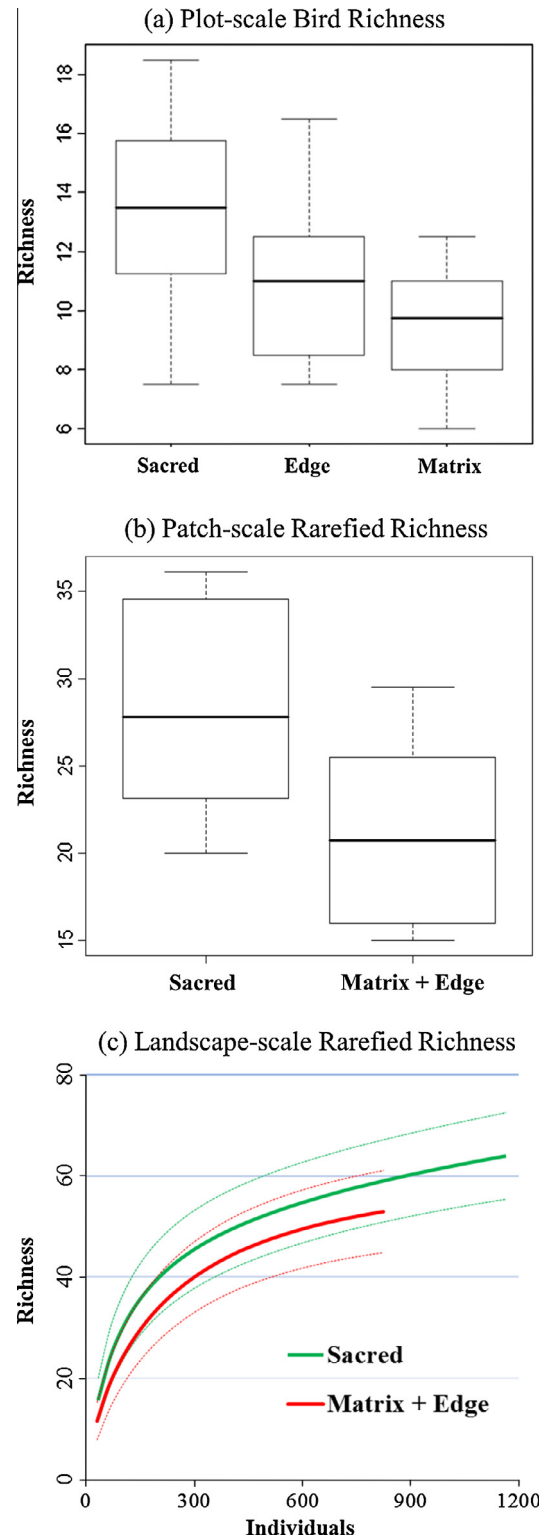
significantly different vegetation composition and structure in the canopy, sub-canopy and ground layers (see Appendix S2). The first axis had high vertical structure (foliage height diversity), canopy cover and coarse woody debris at low values on Axis 1, and high proportions of bare soil and multiple-stemmed woody vegetation in the ground layer (0–0.5 m) at high values on Axis 1. The second axis of the PCA (eigenvalue = 1.51, explaining 18.9% of the variance) represented a within-sacred forest gradient, with dense understory vegetation (i.e., high proportions of sub-canopy coverage and bamboo) corresponding to high values of Axis 2, while those with a more open understory (high herbaceous cover and coarse woody debris in the ground layer) corresponding to low values.

### 3.1.2. Birds

We observed a total of 81 species exhibiting breeding behavior (see Appendix S3), ranging from a few very common species (a total of 7 species detected >100 times) to several rarely-detected species (a total of 35 species observed 10 times or less). Detection probability was 5–21% higher in the matrix than in the sacred forests. Detection probability was 10–17% lower in 2010 than in 2011, and therefore we performed all analyses separately for the two years. We used raw counts for the statistical analyses because sample size was too low to estimate density for most species.

Species composition of the bird communities overlapped between the sacred, edge, and matrix habitats (Fig. 2b), but still exhibited statistically significant patterns (NMDS, 2D stress = 0.21, ANOSIM Global  $R = 0.254$ ,  $p = 0.001$ ). Edge and matrix plots shared

the same bird community ( $p = 0.51$ ), while sacred forest bird communities were distinct from edge ( $R = 0.227$ ,  $p = 0.005$ ) and matrix ( $R = 0.37$ ,  $p = 0.001$ ) communities. Furthermore, different sacred forests supported distinct bird assemblages. Species composition was significantly different in five of 15 pairwise comparisons (ANOSIM, Global  $R = 0.22$ ,  $p = 0.001$ ), indicating that the sacred for-



**Fig. 3.** Box plots of (a) plot-scale bird species richness, (b) patch-scale rarefied bird richness, and (c) rarefied species richness accumulation curves at the landscape scale (dotted lines are 95% confidence intervals).

ests as a whole provided habitat for more than one bird community.

We measured differences in bird species richness at three spatial scales. At the plot scale, mean species richness was higher in sacred forests (mean (SD) = 13.3 (3.1)) than in edge (mean = 11.1 (2.9),  $p = 0.084$ ) and matrix (mean = 9.64 (1.9),  $p < 0.001$ ) (Fig. 3a). Bird abundance was slightly higher in sacred than in edge or matrix, but these differences were not significant ( $p = 0.53$  and 0.33, respectively).

Since edge and matrix were always similar in terms of bird species composition and diversity, we aggregated edge and matrix plots into a single “matrix” class at the patch and landscape scales, which allowed us to build rarefaction curves and thereby adjust for differences in sampling effort and observed individuals. At the patch scale, sacred forest patches had higher mean rarefied species richness (mean (SD) = 28 (6.8)) than the matrix (mean = 21 (5.8)) ( $p < 0.001$ ) (Fig. 3b). At the landscape scale, bird species accumulated fastest in the sacred forest habitat (Fig. 3c) and rarefied species richness (rarefied to 824 individuals) was higher in the sacred (mean (SD) = 59 (4.1)) than the matrix (mean = 53 (4.1)).

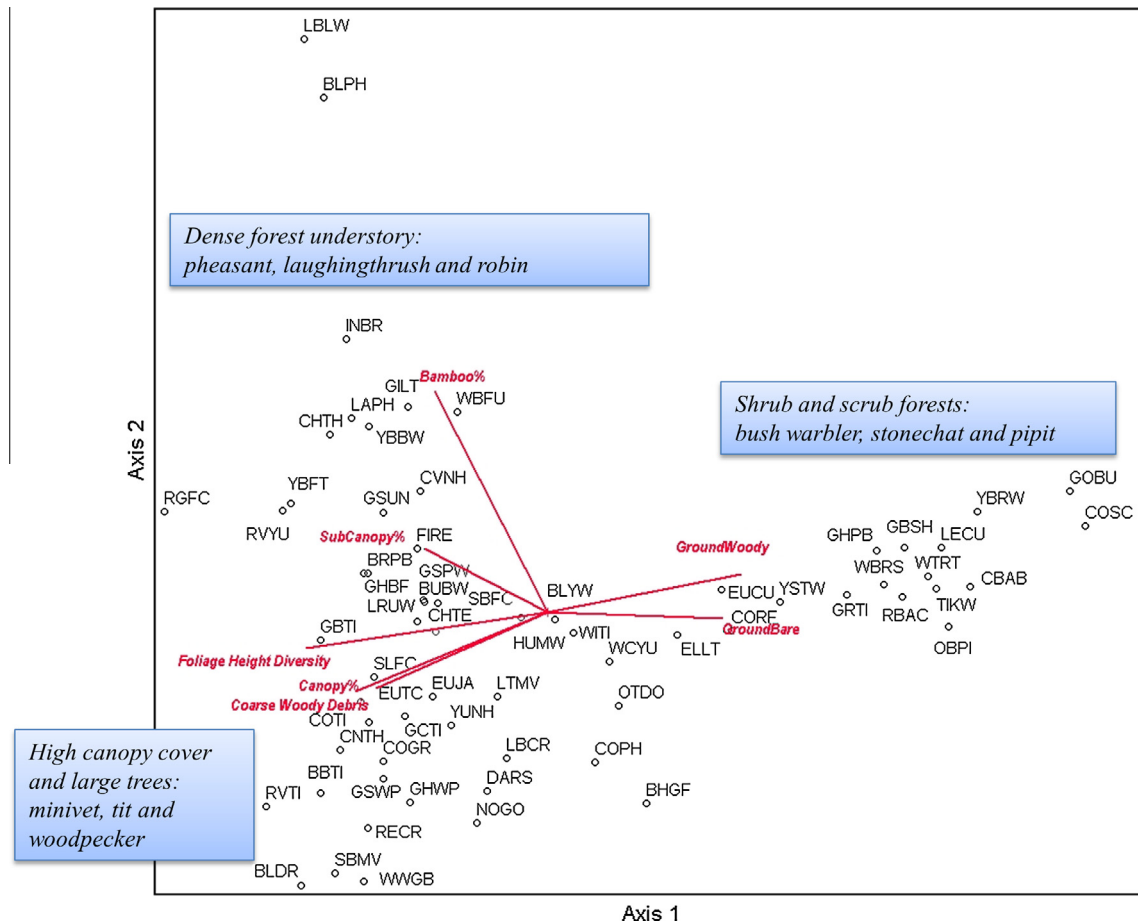
### 3.2. Habitat selection

Four variables were selected among the candidate variables in the stepwise regression (see Appendix S2) as important predictors of species richness: the diameter of the largest tree, percent bamboo, percent ground cover of coarse woody debris, and percent sapling cover (Stepwise Regression AIC = 112, Adj.  $R^2 = 0.46$ ,

$p < 0.0001$ ). In simple linear regression models to predict bird abundance, only one variable, the diameter of the largest tree, was a significant predictor of abundance (Adj.  $R^2 = 0.20$ ,  $p = 0.00018$ ).

While several common species (e.g., Hume’s and Blyth’s Leaf Warblers) were detected in all habitats, many species were clearly associated with either sacred forests or matrix. Thus, we assigned each species as “interior”, “edge/matrix”, or “generalist” according to their relative abundance (Appendix S3). Of the 81 species, 48 were interior species (2-fold higher abundance in sacred forest plots versus matrix or edge plots), 15 were edge/matrix species (2-fold higher abundance in matrix/edge plots versus sacred forest plots) and 18 were generalist species (<2-fold difference in abundance between the sacred and matrix/edge habitats).

The canonical correlation analysis indicated that habitat gradients and species composition were highly correlated (Axis 1 Pearson’s  $r > 0.95$ , Axis 2 Pearson’s  $r = 0.718$ , Fig. 4). Axis 1 (Eigenvalue = 0.480, explaining 14% of the variance in the species data) captured a gradient between birds associated with the matrix habitats at high values (e.g., White-bellied Redstart (*Hodgsonius phaenicuroides*), White-tailed Rubythroat (*Luscinia pectoralis*), and Common Stonechat (*Saxicola torquata*)), and those associated with the sacred forests at low values (e.g., Mrs Gould’s Sunbird (*Aethopyga gouldiae*), Blood Pheasant (*Ithaginis cruentus*), Chinese Thrush (*Turdus mupinensis*), Grey-crested Tit (*Pyrrhula erythaca*), and Giant Laughingthrush (*Garrulax maximus*). Foliage height diversity had the highest correlation with Axis 1 ( $r = -0.525$ ), indicating that it explained the highest variance in the species data. Axis 2



**Fig. 4.** Canonical Correspondence Analysis demonstrates that Foliage Height Diversity was the main characteristic structuring bird communities along Axis 1, while Axis 2 showed the separation between two distinct sacred forest bird communities. Bird species indicated with 4-letter species code. Full species names can be found in Appendix S3.

(Eigenvalue = 0.114, explaining 3.3% of the variation in the species data) captured a gradient of within-sacred forest habitats, and birds associated with dense understory cover (e.g., Giant Laughingthrush, Lady Amherst's Pheasant (*Chrysolophus amherstiae*), and Yellowish-bellied Bush Warbler (*Cettia acanthizoides*)) had high values of Axis 2, while birds associated with large trees, high canopy cover and coarse woody debris (e.g., Yunnan Nuthatch (*Sitta yunnanensis*), Great Spotted Woodpecker (*Dendrocopos major*), and several tit species) had low values.

### 3.3. Edge effects and patch-matrix interactions

To investigate whether edges influenced bird diversity patterns, we regressed bird richness against distance from the edge of a sacred forest. Within sacred forest patches, species richness increased with a plot's distance to the edge of the sacred forest patch ( $R^2 = 0.11$ ,  $p = 0.06$ ). For the matrix, we found the opposite relationship. Matrix bird diversity was highest at the edge, but decreased with distance from the sacred forest ( $R^2 = 0.17$ ,  $p = 0.03$ ).

The correlation between patch size and bird species richness was positive and significant for patch size and raw species richness in the sacred forest patches ( $r = 0.79$ ,  $p = 0.03$ ) and in the matrix plots associated with each sacred forest patch ( $r = 0.80$ ,  $p = 0.05$ ). However, when standardizing for sample effort and number of

individuals, the correlations between patch size and rarefied species richness were not significant.

### 3.4. Differences between 2010 versus 2011

We encountered significantly more birds in 2010 than in 2011 ( $p < 0.001$ ) in all three habitats (sacred, matrix, and edge). There were a total of 15 species (including Greenish Warbler (*Phylloscopus trochiloides*), Bar-tailed Treecreeper (*Certhia himalayana*) and Grey-chinned Minivet (*Pericrocotus solaris*)) that were observed in 2010 but not 2011, and another 9 species (including Lady Amherst's Pheasant, Chinese Thrush, Giant Laughingthrush, and Chestnut-vented Nuthatch (*Sitta nagaensis*)) that were observed in both years, but were considerably ( $>2x$ ) more abundant in 2010 than 2011 (Appendix 3). Plot-scale bird richness was significantly higher in 2010 than in 2011 in sacred and edge, but not in matrix (Fig. 5a). Estimated total species richness curves indicated that species accumulated at the same rate in both years in both the matrix and sacred habitats, but species accumulated at a much faster rate in edge habitats in 2010 versus 2011 (Fig. 5b).

## 4. Discussion

### 4.1. Sacred forests as keystone structures

Our results indicated that Tibetan sacred forests conserved some characteristics of old-growth forests, and thus protected unique forest bird communities in the Chinese Himalayan mountains. In addition, sacred forests had the highest bird diversity of all habitats at multiple spatial scales and in both years. Since detection probabilities were considerably lower in the sacred forests compared to their matrix, it is likely that our estimates of differences are conservative, and that sacred forests are even more important than indicated by the raw data.

Sacred forests exhibited several characteristics of keystone structures (Tews et al., 2004). First, sacred forests maintained higher bird and vegetation diversity despite being small in proportion to the adjacent matrix habitats that make up the majority of the Shangrila landscape. Second, the bird diversity was not dependent on a particular tree species or forest community, but instead associated with structural characteristics that increased habitat heterogeneity. Finally, the positive relationship between habitat heterogeneity and bird diversity was consistent across multiple spatial scales.

Keystone structures maintain biodiversity because of both within-patch and between-patch heterogeneity. The Tibetan sacred forests that we studied have been protected from clear-cut logging, but do experience a range of human disturbance, including occasional selective logging, non-timber forest product (NTFP) collection, and grazing. Thus, they are structurally complex and composed of a mixture of successional and old-growth forests. This within-patch heterogeneity is important to create an environment where a variety of organisms can utilize the variable resource conditions of the patch (Belsky and Canham, 1994).

In terms of between-forest heterogeneity, although the sacred forests were relatively close to each other ( $<20$  km) and at similar elevation (3200–3800 m), they contained a variety of habitat niches due to micro-topographic and micro-climatic variability. In contrast, the surrounding matrix, which has been subject to a range of high-intensity subsistence land-use pressures including logging, non-timber forest resource collection, and grazing, exhibited a relatively homogeneous matrix habitat. As a result, while the matrix habitats had a single, homogeneous bird community, sacred forests supported a wider range of bird species, and two distinct sacred forest bird communities.

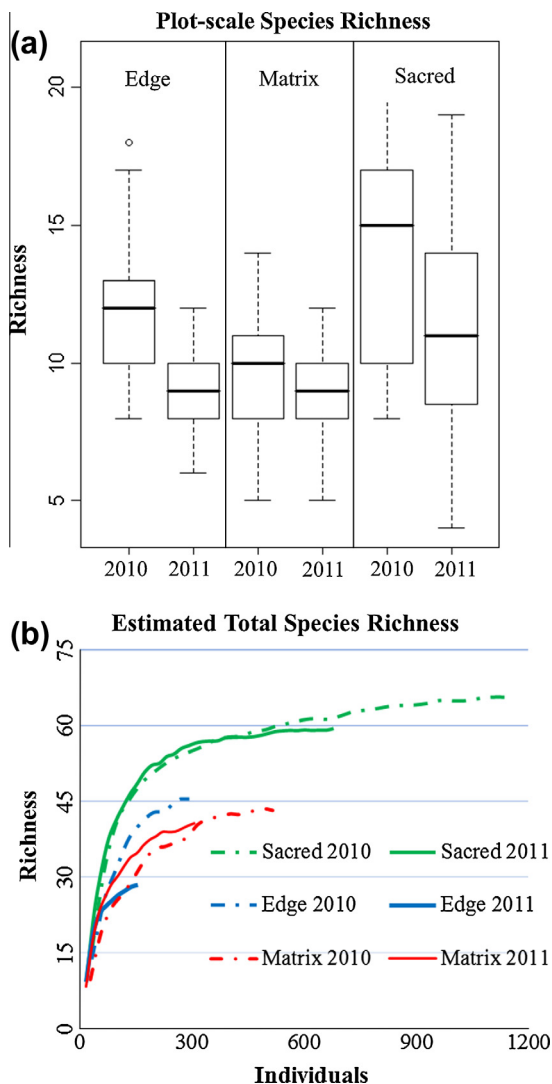


Fig. 5. Inter-annual variability in (a) plot-scale species richness and (b) estimated total species richness at the landscape scale.

#### 4.2. Habitat selection of old-growth forest characteristics

Our results indicated the importance of mature forest ecosystems over secondary or disturbed forest habitats. The relatively large range in vertical complexity (i.e., foliage height diversity, MacArthur & MacArthur, 1961) of our survey plots was the main characteristic structuring bird species composition, while old-growth trees, bamboo groves and coarse woody debris were the most important factors determining high species richness and abundance. In some ecosystems, bird diversity peaks in secondary growth stages (Keller et al., 2003; Schieck and Song, 2006), while in other ecosystems, primary forests support unique, high-diversity bird communities (Barlow et al., 2007; Ding et al., 2008). Old-growth forests, including large trees and bamboo groves (a native understory component), have been heavily exploited for both subsistence and commercial use in this region (Brandt et al., 2012; Xu, 2011). Our results suggest that the protection of forests that retain old-growth characteristics should be a high priority for forest bird conservation in this biodiversity hotspot.

Bird diversity at the plot scale was also positively associated with high proportions of sapling cover. Post-logging tree regeneration in the matrix is limited due to logging practices that leave no mature trees as sources for natural regeneration, and due to grazing which destroys any seedlings and saplings which do grow, allowing shrub and scrub-forest communities to persist for decades following forest clearing (Xu, 2011). Land management practices that encourage tree regeneration in the matrix would likely benefit forest bird communities.

#### 4.3. Influence of edge habitats and patch size on bird community patterns

In some ecosystems, edges serve as an ecotone, providing supplementary resources that are not present in the core or matrix habitats, resulting in relatively high species richness and abundance and distinct species assemblages along edges (Ries et al., 2004). Surprisingly, our results suggested that sacred forest edges were not a distinct habitat, but rather an intermediate and overlapping zone between sacred and matrix habitats. In addition, species richness increased moving deeper into the core of the sacred forests, indicating that interior forests contained higher quality habitat than edges.

Thus, large remnant sacred forest patches are especially important for birds in our study area. Generally speaking, the larger the patch the higher the ratio of core forest to edge habitats (Turner et al., 2001). Furthermore, while even the smallest sacred forest patch that we surveyed (13 h) had a bird community that was distinct from – and more diverse than – the surrounding matrix, large patches supported more bird species, likely because they contained more habitat niches (MacArthur and Wilson, 1967) and supported more individual birds (More Individuals Hypothesis (Srivastava and Lawton, 1998)).

#### 4.4. Differences between 2010 versus 2011

We found clear inter-annual differences in bird presence, abundance, and richness. Bird abundance was higher in all habitats in 2010. In sacred and edge plots we also encountered higher bird diversity in 2010, and the edge habitat had a higher rate of species accumulation. Yunnan province as a whole experienced a severe drought in 2010, receiving 60% less rainfall than normal during the 6 months leading up to the 2010 breeding season (Qiu, 2010). The nearest weather station (Zhongdian weather station of the National Meteorological Administration of China) received 11.3 mm of precipitation in the first 6 months of 2010, which is slightly below the average (11.9 mm (SD = 2.22)) precipitation re-

ceived in the first 6 months of every year from 1990 to 2010. The typical effect of a drought is to reduce bird abundance and diversity in some habitats while other habitats act as refugia (Albright et al., 2010). Our results indicated that sacred forests, and especially their edges, may serve as refuges during extreme weather years.

Our data did not indicate that species with different migratory strategies or foraging preferences benefited differently from the refuge effect of sacred forests. Of the 24 species that were more abundant in 2010, 15 were resident species (63%), identical to the proportion of all resident breeding species recorded in the study (51 of 81, 63%). Species from insectivore, omnivore, bole gleaner and granivore guilds all experienced considerable (>2x) decreases in abundance from 2010 to 2011.

#### 4.5. Conclusions and management implications

Our results suggest that sacred forests are a keystone structure for forest birds in northwest Yunnan, and, potentially, throughout the Himalayas. Faced with rapid land use and climate change (Brandt et al., 2013), effective conservation in Yunnan Province requires reserve networks that cover the entire range of elevations and aspects (Wu et al., 2010). However, establishing large, contiguous protected areas is challenging in this densely inhabited landscape. Our study suggests that sacred forests provide an existing network of native vegetation patches that protect a variety of habitat niches, maintain biodiversity at multiple spatial scales, and may even function as refugia during extreme weather years.

China's protected area system has expanded greatly in recent years, adding 1500 nature reserves nationwide. In northwest Yunnan, 15 national protected areas (nature reserves, scenic areas and national parks) have been created since the 1980s, and several more are pending. Protected areas are larger than sacred forests, but are typically in remote areas and at higher elevations. Sacred forests could form the backbone of an expanded protected area network because they are closer to the centers of human land use, and represent lower-elevation forests.

Protected areas throughout China have struggled to implement effective management (Zhou and Grumbine, 2011). In northwest Yunnan, they have destroyed existing traditional management systems without replacing them with effective alternatives, leading to serious environmental degradation (Bo et al., 2003; Harkness, 1998; Tang et al., 2006; Xu et al., 2005; Xu and Melick, 2007; Xu and Wilkes, 2004; Yang et al., 2004; Zhou and Grumbine, 2011). Sacred forests, on the other hand, have proven to be effective and resilient in a wide range of temporal and geographic contexts in southwest China (Anderson et al., 2005; Luo et al., 2003; Shen et al., 2012). As such, they may not only be key components of protected area networks, but also may offer insights on how to improve protected area effectiveness.

We propose several steps towards the incorporation of sacred forests into official conservation strategies. First, sacred forests should be included in systematic conservation planning assessments (Zhang et al., 2012) to understand the distribution, extent, and conservation value of sacred forests at the regional scale. Second, sacred forests could be designated officially as a protected area. However, this may not be desirable from the community perspective, as it leads to a loss in legal ownership and property rights (Bhagwat and Rutte, 2006). Alternatively, a new type of protected area could be created, "sacred forest", in which a community's legal ownership and property rights remain, or are potentially even strengthened. For example, sacred forests could be off-limits for threatening activities (e.g. road-building, dams) that villages themselves are not likely to engage in.

A critical question is whether, in the face of rapid social change, sacred forests will persist on the landscape and continue to fulfill

their keystone role for conservation. Therefore, a final priority is to better understand the cultural beliefs and institutional arrangements underlying sacred forests. Sacred forests do not exist primarily for conservation, and fit neither communal nor privatized paradigms of land management (Rutte, 2011). Although in the past, sacred forests have proven to be remarkably resilient to social change (Dudley et al., 2009), cultural assimilation is currently leading to their degradation (Rutte, 2011). For example, as tourism expands, communities are beginning to exploit sacred forests for commercial use as touristic destinations, leading to a fundamental change in their meaning, management and ecological function (Barbhuiya et al., 2010). Incorporating sacred forests into protected area networks will inevitably lead to trade-offs between culture, economics, legal rights, and conservation. Engaging communities in dialogs about these trade-offs is a key component to successful, long-term integration of sacred areas into official conservation strategies.

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### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.06.014>.

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