

Habitat–occupancy associations and tree-species use patterns by breeding birds in Tibetan sacred forests

Eric M. Wood · Jodi S. Brandt · Anna M. Pidgeon · Volker C. Radeloff

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Abstract Himalayan forests are undergoing rapid changes due to population growth and economic development and their associated bird communities are among the most threatened and least-studied on earth. In the Chinese Himalaya, traditionally managed Tibetan sacred forests are keystone structures for forest bird conservation. Yet, it remains unclear which fine-scale habitat characteristics of the sacred forests are best associated with Himalayan forest bird species. Our goal here was to quantify the relationship between forest habitat characteristics and bird communities in Tibetan sacred forests to understand habitat associations of common forest birds in the Chinese Himalaya. In 2010 and 2011, we conducted bird point counts and habitat surveys at 62, 50-m radius, sample points distributed within and adjacent to six Tibetan sacred forests in northwest Yunnan, China. From this data, we constructed habitat–occupancy relationship models for 35 bird species and documented tree-use patterns of 14 common arboreal foraging bird species. Our modeling results revealed that large diameter trees and heterogeneity in vertical vegetation structure were the most important habitat characteristics, and were positively associated with occupancy of 63 % of the study bird species. Furthermore, we found that occupancy of eight bird species of conservation concern was related to specific thresholds of forest integrity characteristics. For example, predicted occupancy of three of eight species was

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E. M. Wood · J. S. Brandt · A. M. Pidgeon · V. C. Radeloff
SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630
Linden Drive, Madison, WI 53706, USA

E. M. Wood (✉)
Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA
e-mail: emwood@wisc.edu

J. S. Brandt
Environmental Studies Program, Dartmouth College, 6182 Steele Hall, Hanover, NH, USA

high in forested habitats with >15 % bamboo cover and was greatly reduced when bare ground cover exceeded 5 %. We found that bird species foraged on pine (*Pinus densata*, 58 % more than it was available) and poplar (*Populus davidiana*, 41 %) in higher proportion to their availability, but that foraging success was highest on fir (*Abies* spp.), oak (*Quercus* spp.), willow (*Salix* spp.) and Chinese Larch (*Larix potaninii*). Our findings suggest that, although conservation is not a primary management goal of Tibetan sacred forests, these lands harbor critical habitat features for forest breeding birds of the Chinese Himalaya.

Keywords Breeding birds · China · Foraging · Habitat selection · Himalaya · Yunnan

Introduction

Himalayan montane forest ecosystems, which occur in a narrow band from southern China to Central India, are among the richest (Grenyer et al. 2006), most threatened (Somveille et al. 2013), and least studied forests on earth (Renner 2011). Their broad distribution, and steep elevational gradients create a diversity of forested habitats with a variety of ecological niches, which in turn support exceptionally high biodiversity and complex evolutionary histories (Price et al. 2006; Renner 2011). The primary threats to these forests are rapid population growth, cultural change, and economic development (Renner et al. 2007; Brandt et al. 2012), all of which have led to accelerated rates of land use change and destruction of natural habitats (Dumbacher et al. 2011; Brandt et al. 2012).

Changes in land use are threatening the region's biodiversity. Himalayan forest bird communities, in particular, are of conservation concern (Renner 2011), because many endemic species within the region are largely dependent on primary forest ecosystems. Land use change within Himalayan montane habitats has disproportionately negative effects on bird communities, because the adaptive response of species associated with these habitats is restricted (Norbu et al. 2013). Thus, Himalayan forest bird communities likely face challenges in adapting to primary forest disturbance and loss (Chettri et al. 2005; Norbu et al. 2013), which is occurring at a rapid rate in the region (Brandt et al. 2012).

A major challenge for the conservation of Himalayan forest bird communities is to identify forest management strategies that maintain viable habitat conditions. Unlike many developing regions of the world, where population density was historically sparse and intensive ecosystem management uncommon, the Himalayan region has a long and rich history of forest management. The Himalaya has been densely inhabited by indigenous people who, for centuries, have used traditional land use practices and community-based institutions to manage their forests sustainably (Shen et al. 2012). In recent decades, governments have invested substantially in efforts to conserve and restore forest ecosystems throughout the region, through imposing logging restrictions, designating protected areas, payment for ecosystem services policies, ecotourism development, and reforestation programs (Liu et al. 2008; Tambe et al. 2011). Thus, at the same time that Himalayan forests are under growing threat, the traditional forest management activities and newly formed conservation institutions present an opportunity to integrate bird habitat considerations into the stewardship of forested habitats.

In Yunnan Province of southwest China, Tibetan sacred forests are remnant patches under traditional forms of forest management (Shen et al. 2012; Allendorf et al. 2014).

According to Tibetan cultural beliefs, forests that are deemed sacred are protected from logging, hunting, and extensive subsistence use (Wang et al. 2012). However, the majority of sacred forests exhibit a gradient of human disturbance, and contain a mix of mature and successional vegetation creating a mosaic of forest habitat types that support a more diverse avian community than adjacent degraded habitats (Brandt et al. 2013b). Despite their importance as forest bird breeding habitat, little is known about which habitat characteristics of Tibetan sacred forests are associated with bird occupancy.

Our overarching goal was to shed light on the importance of indigenous forest management practices in Tibetan sacred forests by identifying essential habitat associations of forest breeding birds, focusing on species of conservation concern. In addition to our focus on Tibetan sacred forests, we designed our analysis to provide valuable forest management information for the broader Chinese Himalaya region. We had two specific objectives. First, to understand which characteristics of the Tibetan sacred forests and adjacent habitats are more strongly associated with forest breeding birds, we fit occupancy models for 35 bird species, eight of which are International Union for Conservation of Nature (IUCN) species of conservation concern. Second, to inform management of common Himalayan tree species of forested habitats, we characterized arboreal bird foraging patterns.

Materials and methods

Study site

We collected data on habitat characteristics, tree composition, bird occupancy, and bird use of trees in Tibetan sacred forests, and their associated neighboring degraded habitats, distributed throughout the Shangrila region, northwest (NW) Yunnan Province, China (Fig. 1a). NW Yunnan is a biodiversity hotspot situated within the Three Parallel Rivers drainage (Myers et al. 2000). NW Yunnan is still relatively undeveloped but experiencing rapid economic growth and land use change. Local peoples continue to practice subsistence-based agriculture and pastoralism, but since the 1970s, NW Yunnan has undergone major changes due to national policies aimed at fostering both economic development and environmental protection. These policies stimulated rapid infrastructure development, immigration of culturally-dominant Han Chinese, tourism, new protected areas, and changes in land use (Yang et al. 2004; Xu and Wilkes 2004). In addition, NW Yunnan is experiencing accelerated climate change, which is resulting in dramatic ecosystem shifts (Brandt et al. 2013a).

Many forest bird species in the Shangrila region of Yunnan 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. The Sino-Himalayan region is particularly important for bird conservation. It has among the highest rates globally of threatened migratory species, narrow-range migratory species, total species richness, and total threatened species (Somveille et al. 2013). Within the region, Tibetan sacred forests are renowned as keystone structures for biodiversity preservation (Anderson et al. 2005; Brandt et al. 2013b). In addition to harboring high bird species richness (Brandt et al. 2013b), Tibetan sacred forests also have higher tree richness and larger trees than surrounding landscapes (Salick et al. 2007).

We studied six Tibetan sacred forests (hereafter sacred forests) ranging in size from 13 to 62 ha, and six adjacent degraded habitats (hereafter referred to as matrix habitats) (Fig. 1b). We gathered information on sacred forest boundaries from local people, and

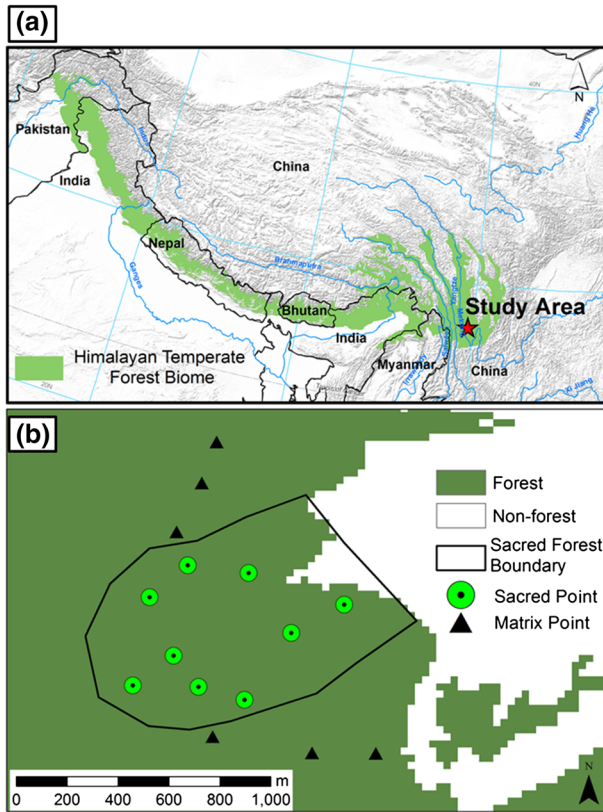


Fig. 1 **a** Location of study area in Shangrila, northwest Yunnan Province, China, **b** the distribution of sample points within and outside of one of the sacred forest patches

marked the perimeter of each forest using a GPS unit. We surveyed a total of 62 sample points, including 35 sacred and 27 matrix sample points. We placed sacred forest sample points at least 200 m apart, and along walking paths when possible. We used a haphazard sampling design because in many sacred forests, interior vegetation was dense and difficult to penetrate. Although our sampling design may have introduced small bias in our surveys, we felt this was an acceptable trade-off allowing for more visits to sample points per day, and thus a broader sample of the avian community. We placed matrix sample points at regular distances (60, 260 and 520 m) from the sacred forest edge (Fig. 1b). To explore patterns of spatial autocorrelation among sample points, we fit semivariograms of the residuals of the total bird species richness of each sample point from 2010 and 2011 (Legendre and Fortin 1989). We detected no patterns of spatial autocorrelation in any of our six regions, and thus considered data from each sample point as independent (Online Resource Fig. A).

Habitat characteristic data

We measured habitat characteristic data at each sample point from June to August of 2010 using standardized breeding bird survey protocols (Martin et al. 1997). Within each point-

count station, we measured vegetation in four 5-m radius sub-plots. We established a 5-m radius sub-plot at the center of the sample point, and three sub-plots, 30-m from the sample point center point at 0°, 120° and 240°. In each sub-plot, we measured stem density (using a 10- or 20-factor basal area per ft² prism), tree canopy cover (using a densiometer), and foliage height diversity (in 0.3-m sub-sections). We also made ocular cover estimates of the sub-canopy layer (0.5 to 5-m), including true shrubs, tree shrubs (i.e., sapling trees within the sub-canopy layer, <10 cm diameter-at-breast height, dbh), and bamboo, and the ground layer (0 to 0.5-m), as well as cover of leaf litter, moss, bare ground, and total live herbaceous materials (i.e., grasses and sedges). Furthermore, we measured litter depth at four random locations within each sub-plot, and counted cone density (i.e., fallen conifer cones) within the sub-plot. After concluding sub-plot measurements, we recorded the dbh of the three largest-diameter trees encountered in the 50-m radius sample point. We averaged all sub-plot and tree dbh data to estimate sample-point totals of the habitat characteristics. We also included elevation, which we measured at the center of each sample point with a GPS unit, and the categorical value of sacred forest or matrix habitat, which captures the habitat-type of a sample point. We used the categorical habitat classification variable to determine the association of bird species with the traditionally managed sacred forests.

Habitat structure is an important cue birds use to select habitat during the breeding season (Cody 1981). Thus, eleven of the twelve habitat characteristic variables that we included for analysis were designed to quantify a range of habitat structure attributes at the ground, shrub, and tree layers. We included six habitat characteristics at the ground layer including % cover of bare ground, which is a composite variable of % cover of soil and ground lichen, moss, and leaf litter cover, litter depth, density of conifer cones on the ground, which we use as a proxy for resource availability for conifer seed-eating birds, and live herbaceous cover. We included three habitat characteristics at the sub-canopy layer, including % cover of bamboo, true shrubs (shrub), and tree shrubs, and three habitat characteristics at the tree layer including, stem density, foliage-height diversity (FHD), and the average dbh of the three largest trees within a sample point (hereafter largest tree dbh). Prior to analysis, we checked for collinearity among the habitat characteristics. To do so, we constructed a Spearman's rank correlation matrix. We found that the majority of habitat characteristics were weakly to moderately correlated (absolute Spearman's correlation coefficients = 0.03–0.64) although half of the pair-wise comparisons were significant (Online Resource Table B). However, because we did not detect any strong correlations we included the twelve habitat characteristics, in addition to elevation, and the categorical habitat classification variable, for all avian habitat–occupancy analyses.

To determine if habitat characteristics were significantly different between sacred forests and matrix habitats, we used a Wilcoxon rank-sum test and a significance level of p value <0.05. Only % bare ground cover was significantly higher in matrix habitats, and % bamboo cover was higher in sacred forests, though not significantly (Online Resource Fig. C). All other habitat characteristics were significantly higher in sacred forests (Online Resource Fig. C).

Avian point counts

We conducted standardized, 10-min, 50-m radius avian point counts at the 62 sample points from late March to late-June in 2010 and 2011 at each sample point to characterize the breeding avian community (Ralph et al. 1995). We surveyed sample points two times in each season. J. S. Brandt collected all point count data in 2010, and 59 % of the data in

2011. E.M. Wood collected the other 41 % of point count data in 2011. Both observers were trained and proficient in identifying the region's birds by sight and sound. We began point counts at sunrise and continued for approximately 3 h if weather conditions were acceptable (i.e., low wind and no rain). We used laser rangefinders to estimate distances to detected birds, and we only included birds detected within the 50-m radius sample point boundary in analyses. From our point count data, we selected 35 bird species with sufficient data (null detection from occupancy analysis >0.15 , see statistical analysis section below), and that were common either in sacred forests or matrix habitats (Table 1). We combined data for Blood (*Ithaginis cruentus*) and Lady Amherst's Pheasant (*Chrysolophus amherstiae*) because we had low detections of both birds. However, the birds are similar morphologically and ecologically, and are of high conservation concern, and we detected them in similar forested habitats. Of the 35 species, eight are listed by the IUCN as Species of Conservation Concern (Table 1), and because of this we placed special emphasis on the results from an occupancy analysis of these species. Populations of seven species, including Blood and Lady Amherst's Pheasant (grouped as a single species for analysis purposes), Yellowish-bellied Bush-Warbler (*Cettia acanthizoides*), Indian Blue Robin (*Luscinia brunnea*), Giant Laughingthrush (*Garrulax maximus*), Elliot's Laughingthrush (*Garrulax ellioti*), Rufous-vented Tit (*Periparus rubidiventris whistleri*), and Chestnut-vented Nuthatch (*Sitta nagaensis*) are suspected to be in decline, but there is currently not enough data to support designation (The IUCN Red List of Threatened Species 2013). Yunnan Nuthatch (*Sitta yunnanensis*) is designated as a near threatened species (The IUCN Red List of Threatened Species 2013).

Tree availability measurements

To quantify the availability of trees as foraging substrates for birds in sacred forests, we used the point-center quarter method. The point-center quarter method is a plotless technique first developed by botanists to randomly sample the composition of trees indicative of vegetation communities (Cottam and Curtis 1956). Ornithologists adopted the method as a measure of the availability of trees as foraging substrates to birds (Holmes and Robinson 1981). Unlike the habitat characteristic and avian point count data, we only collected tree availability and bird-tree use data within sacred forest boundaries because there were few trees in the adjacent matrix habitats. To determine point-center quarter sampling plots, we used a systematic sampling design where we placed transects, in an east–west direction, and separated by 100 m, within the boundaries of a sacred forest patch. On each transect, we established point-center quarter sampling plots, also separated by 100 m. All point-center quarter plots were at least 50 m from the boundary of sacred forests. We offset the point-center quarter sampling stations from adjacent transects by 50 m to adequately capture differences in tree composition based on slope and aspect, soil composition, elevation, and microclimates. At each point-center quarter sampling station, we recorded species and measured dbh. From this, we calculated (1) frequency: the number of point-center quarter sampling stations in which a given tree species was found divided by the total number of point-center quarter sampling stations, (2) density: the total number of individuals tallied for a given tree species divided by the total area of all sacred forest patches, and (3) dominance: the sum of the basal area of a tree species (from all point-center quarter sampling stations) divided by the total area of all sacred forest patches (Mitchell 2001). The basal area is the cross-sectional area an individual tree covers at breast-height, and we calculated this by converting our dbh measurement to radius ($\text{dbh}/2$), and then using the equation: $\text{area} = \pi r^2$. We then calculated the relative values of each of

Table 1 Common and scientific names, naive (raw), and modeled (ψ) habitat occupancy (\pm se), and null detection probability $p(\cdot)$ in 2010 and 2011 (\pm se), for 35 study birds in Tibetan sacred forests, and surrounding habitats, in northwest Yunnan, China

Common name	Scientific name	Naive	ψ	2010 p	2011 p
<i>Sacred forest affiliates</i>					
Blood and Lady Amherst's Pheasant ^a	<i>Ithaginis cruentus & Chrysolophus amherstiae</i>	0.19	0.41 \pm 0.19	0.18 \pm 0.10	0.12 \pm 0.07
Long-tailed Minivet ^a ^{n=7, 372}	<i>Pericrocotus ethologus</i>	0.35	0.72 \pm 0.23	0.17 \pm 0.07	0.15 \pm 0.06
Chinese Thrush	<i>Turdus mupinensis</i>	0.35	0.61 \pm 0.16	0.19 \pm 0.04	0.12 \pm 0.03
Chestnut-headed Tesia	<i>Tesia castaneocoronata</i>	0.10	0.12 \pm 0.05	0.27 \pm 0.13	0.41 \pm 0.16
Yellowish-bellied Bush-Warbler ^a	<i>Certhia acanthizoides</i>	0.29	0.31 \pm 0.06	0.58 \pm 0.09	0.45 \pm 0.09
Buff-barred Warbler ^a ^{n=19, 858}	<i>Phylloscopus pulcher</i>	0.59	0.70 \pm 0.09	0.48 \pm 0.07	0.25 \pm 0.05
Lemon-rumped Warbler ^a ^{n=26, 1208}	<i>Phylloscopus proregulus</i>	0.63	0.71 \pm 0.07	0.46 \pm 0.06	0.39 \pm 0.06
Hume's Leaf-Warbler ^a ^{n=43, 1818}	<i>Phylloscopus humei</i>	0.81	0.82 \pm 0.05	0.79 \pm 0.04	0.57 \pm 0.05
Large-billed Leaf-Warbler	<i>Phylloscopus magnirostris</i>	0.11	0.12 \pm 0.04	0.77 \pm 0.12	0.42 \pm 0.13
Bianchi's Warbler	<i>Seicercus valentini</i>	0.68	0.68 \pm 0.06	0.72 \pm 0.05	0.68 \pm 0.05
Slaty-backed Flycatcher	<i>Ficedula hodgsonii</i>	0.52	0.55 \pm 0.08	0.54 \pm 0.08	0.45 \pm 0.07
Slaty Blue Flycatcher	<i>Ficedula tricolor</i>	0.39	0.47 \pm 0.08	0.42 \pm 0.08	0.28 \pm 0.07
Indian Blue Robin ^a	<i>Luscinia brunnea</i>	0.23	0.26 \pm 0.07	0.45 \pm 0.11	0.34 \pm 0.09
Yellow-bellied Fantail	<i>Rhipidura hypoxantha</i>	0.03	0.03 \pm 0.02	0.49 \pm 0.25	0.74 \pm 0.23
Giant Laughingthrush ^a	<i>Garrulax maximus</i>	0.24	0.43 \pm 0.15	0.23 \pm 0.09	0.15 \pm 0.07
Black-browed Bushiti ^a ^{n=40, 1716}	<i>Aegithalos bonvaloti</i>	0.21	0.39 \pm 0.15	0.21 \pm 0.10	0.15 \pm 0.07
Coal Tit ^a ^{n=23, 1375}	<i>Periparus ater</i>	0.40	0.55 \pm 0.11	0.30 \pm 0.07	0.26 \pm 0.07
Rufous-vented Tit ^a ^{n=25, 968}	<i>Periparus rubidiventris whistleri</i>	0.19	0.33 \pm 0.13	0.27 \pm 0.12	0.12 \pm 0.07
Gray-crested Tit ^a ^{n=22, 974}	<i>Pyrrhula erythaca</i>	0.31	0.50 \pm 0.14	0.21 \pm 0.08	0.21 \pm 0.07
Chestnut-vented Nuthatch ^a	<i>Sitta nagaensis</i>	0.18	0.25 \pm 0.08	0.39 \pm 0.13	0.13 \pm 0.07
Yunnan Nuthatch ^a ^{n,n=6, 237}	<i>Sitta yunnanensis</i>	0.18	0.26 \pm 0.09	0.31 \pm 0.12	0.19 \pm 0.09
Mrs Gould's Sunbird	<i>Aethopyga gouldiae</i>	0.47	0.73 \pm 0.15	0.27 \pm 0.07	0.19 \pm 0.05
Gray-headed Bullfinch	<i>Pyrrhula erythaca</i>	0.42	0.68 \pm 0.15	0.24 \pm 0.07	0.19 \pm 0.06

Table 1 continued

Common name	Scientific name	Naïve	ψ	2010 p	2011 p
<i>Matrix habitat affiliates</i>					
Ring-necked Pheasant	<i>Phasianus colchicus</i>	0.10	0.13 ± 0.06	0.37 ± 0.17	0.20 ± 0.12
Oriental Turtle Dove	<i>Streptopelia orientalis</i>	0.37	0.52 ± 0.11	0.27 ± 0.07	0.27 ± 0.07
Olive-backed Pipit	<i>Anthus hodgsoni</i>	0.10	0.11 ± 0.05	0.43 ± 0.16	0.36 ± 0.15
Tickell's Leaf-Warbler	<i>Phylloscopus affinis</i>	0.31	0.34 ± 0.07	0.45 ± 0.09	0.44 ± 0.09
Yellow-streaked Warbler	<i>Phylloscopus armandii</i>	0.50	0.56 ± 0.08	0.23 ± 0.05	0.57 ± 0.07
White-tailed Rubythroat	<i>Luscinia pectoralis</i>	0.23	0.24 ± 0.06	0.65 ± 0.10	0.45 ± 0.10
White-bellied Redstart	<i>Hodgsonius phaenicuroides</i>	0.34	0.34 ± 0.06	0.68 ± 0.07	0.66 ± 0.08
Siberian Stonechat	<i>Saxicola maurus</i>	0.08	0.09 ± 0.04	0.53 ± 0.18	0.26 ± 0.14
Elliot's Laughingthrush ^a	<i>Garrulax elliotii</i>	0.77	0.85 ± 0.06	0.60 ± 0.06	0.28 ± 0.05
White-collared Yuhina ^{a/10, 230}	<i>Yuhina diademata</i>	0.34	0.49 ± 0.12	0.28 ± 0.08	0.23 ± 0.07
Gray-backed shrike	<i>Lanius tephronotus</i>	0.21	0.31 ± 0.10	0.26 ± 0.10	0.24 ± 0.09
Common Rosefinch	<i>Carpodacus erythrinus</i>	0.68	0.69 ± 0.06	0.70 ± 0.50	0.54 ± 0.06

Birds with superscript number indicate (1) number of foraging observations and (2) the cumulative number of seconds birds were observed foraging. We grouped bird species that were positively associated with either sacred forests or matrix habitats based on modeled occupancy associations (see Online Resources for detailed occupancy models for each species)

^a International Union for Conservation of Nature (IUCN) species of concern

the three measurements by dividing the value of a given tree species by the same respective measurement for all tree species together. We calculated the relative importance value of tree species using the formula: relative importance value = relative frequency + relative density + relative dominance, divided by three (Cottam and Curtis 1956). The relative importance value represents the relative availability of each tree species as foraging substrate for bird species (Table 2) (Holmes and Robinson 1981; Gabbe et al. 2002; Wood et al. 2012). We quantified the importance of seven tree species, and three tree groups that were difficult to identify in the field (Table 2).

Avian tree use and foraging success

To explore tree species use patterns by breeding birds, we collected foraging data from late-May to late June in 2011, which encompasses the breeding period for many species in Yunnan forests (Brandt et al. 2013b). Between sunrise and noon, we proceeded along each tree-availability transect and actively searched for foraging flocks of bird species observed to use trees as foraging substrates. E.M Wood collected 88 % of the foraging observation data, and J.S. Brandt collected the other 12 %. We made all observations within the boundaries of a sacred forest patch, >50 m from the edge, in order to quantify foraging behavior of birds on interior forest trees rather than early successional trees common on the edges of the sacred forests. Although we detected 30 bird species using trees in our study area, we only had sufficient data (>5 observations) to analyze use patterns of 14 species, which we refer to as focal species (Tables 1 and 3). Although our sample sizes for three of the 14 species were low (<10), we opted to include these species in analyses to provide information for as many foraging birds as possible. We collected avian foraging data on an additional four species, which we did not include in our occupancy analysis. These were Rufous-vented Yuhina (*Yuhina occipitalis*, $n = 8$ foraging observations, 311 s observed foraging), Willow Tit (*Poecile montanus*, $n = 15$, 465 s), Blyth's Leaf-warbler (*Phylloscopus reguloides*, $n = 53$, 2,368 s), and Red Crossbill (*Loxia curvirostra*, $n = 14$, 276 s). Once we detected a focal species, we followed and documented the individual's activities and movements for as long as possible up to 5 min within the boundaries of a study stand using standardized methods (Remsen and Robinson 1990). Both EWM and JSB trained extensively together in this survey methodology to ensure that their activity tallies concurred. It was easier to acquire foraging data on some tree species than others due to lower stature and less dense foliage. However, we were careful to only observing foraging bird behavior when birds were in clear view. After acquiring foraging behavior data for a bird, we either moved to another individual in the immediate area, or moved back to the tree-availability transect in search of another focal species. To avoid auto-correlated foraging data, we only recorded data on a focal species that was at least 200 m from a previous detection of the same species. We observed most bird species using multiple trees during a foraging observation. In analyzing tree use versus availability, we used only data from the first tree at which a bird was observed actively attacking a prey item to control for any effects of individual bird foraging preferences (Holmes and Robinson 1981). For our analysis of foraging success among tree species, we included foraging data from all trees of a given species to understand differences in foraging success by both individual and different birds (Wood et al. 2012). We used a digital recorder with a built in timer (Sony ICD-PX720 Digital Voice Recorder) to record the following data, which we later transcribed at the field-station: bird species, tree species, number of perch changes (hops, walks, flights, and shuffles), and type of attack (leaf glean, bark glean, flower glean, cone glean, flush-chase, hover, and sally).

Table 2 Common and scientific name and relative importance value (IV), frequency, dominance and density of ten tree species (or groups of species) among Tibetan sacred forests

Common name	Scientific name	IV	Frequency	Dominance	Density
George's Fir	<i>Abies georgei</i>	2.21	2.08	2.52	2.02
Maple species	<i>Acer</i> spp.	3.19	4.17	2.39	3.02
Chinese Paper Birch	<i>Betula albo-sinensis</i>	3.93	4.17	3.84	3.78
Himalayan Birch	<i>Betula utilis</i>	17.77	22.40	10.26	20.65
Chinese Larch	<i>Larix potaninii</i>	14.67	16.67	11.46	15.87
Spruce species	<i>Picea</i> spp.	31.36	18.75	53.93	21.41
Sikang Pine	<i>Pinus densata</i>	9.33	8.85	5.53	13.60
Chinese Aspen	<i>Populus davidiana</i>	2.28	3.65	0.42	2.77
Evergreen Oak species	<i>Quercus</i> spp.	12.36	14.58	8.63	13.85
Willow species	<i>Salix</i> spp.	2.91	4.69	1.02	3.02

Table 3 Common name, four-letter code, number of foraging observations with cumulative number of seconds birds were observed foraging in superscript, and Chi square goodness-of-fit test results comparing observed with expected frequency of tree-use by fourteen breeding focal bird species in Tibetan sacred forests

Common name	Code	<i>n</i>	df	χ^2	<i>p</i> value	PI
Long-tailed Minivet	LTMI	7 ³⁷²	9	102.0	<0.01	80.13
Buff-barred Warbler	BUBW	19 ⁸⁵⁸	9	55.5	<0.01	68.61
Lemon-rumped Warbler	LRUW	26 ¹²⁰⁸	9	70.5	<0.01	43.54
Hume's Leaf-Warbler	HULW	43 ¹⁸¹⁸	9	109.3	<0.01	79.27
Blyth's Leaf-Warbler	BLLW	53 ²³⁶⁸	9	57.7	<0.01	48.07
Rufous-vented Yuhina	RVYU	8 ³¹¹	9	103.3	<0.01	100.29
White-collared Yuhina	WCYU	10 ²³⁰	9	65.3	<0.01	62.71
Black-browed Bushtit	BBBT	40 ¹⁷¹⁶	9	86.1	<0.01	96.84
Willow Tit	WITI	15 ⁴⁶⁵	9	165.6	<0.01	135.19
Coal Tit	COTI	23 ¹³⁷⁵	9	152.8	<0.01	91.14
Rufous-vented Tit	RVTI	25 ⁹⁶⁸	9	130.0	<0.01	89.48
Gray-crested Tit	GCTI	22 ⁹⁷⁴	9	84.4	<0.01	62.94
Yunnan Nuthatch	YUNU	6 ²³⁷	9	99.1	<0.01	156.63
Red Crossbill	RECR	14 ²⁷⁶	9	155.6	<0.01	89.29

We also show the preference-index (PI), which is a measure of selectivity. A higher PI value indicates higher tree-preference

Statistical analysis

To account for variability in species detectability, which is common in bird surveys, we calculated the probability of sample-point occupancy, ψ (Ψ), adjusted for detection probability (p) (MacKenzie et al. 2006). We did not include bird species in this analysis that were either too common (Blyth's Leaf-warbler) or too rare (Willow Tit) during our point count surveys because the common birds were predicted to occupy all sample points

and the estimates for rarer birds were unreliable (MacKenzie et al. 2006). We used a detection probability threshold of 0.15 because occupancy estimates calculated from bird species with low detection probabilities are not reliable (Table 1) (MacKenzie et al. 2006). However, in some cases, such as for the Blood and Lady Amherst's Pheasant, the Chinese Thrush (*Turdus mupinensis*), and the Rufous-vented Tit (*Periparus rubidiventris whistleri*), we relaxed this rule to provide much needed habitat–occupancy relationship information for as many bird species as possible from our study area (Table 1). We used the history of detection and non-detection of a given bird to fit a single-season, single-species model. Because detection probability can vary greatly among years, we calculated the within-year null detection probability based on the two counts in 2010 and the two counts in 2011 for each species. Doing this allowed for us to model a unique detection function for an individual species within each year. We used this design matrix to calculate detection probabilities, from which we calculated the sample-point specific probabilities of occupancy (MacKenzie et al. 2006).

We further explored relationships between habitat characteristics and bird species occupancy of sacred forests and the adjacent matrix habitats. Using a similar detection model, in which we again varied detection by year, we calculated occupancy of each bird species as a function of each of the fourteen habitat characteristics. Including the null model, we fit 15 models for each of the 35 bird species, totaling 525 models (see Online Resource Tables D.1 to D.35). We used an information theoretic approach, and we adjusted the Akaike's Information Criterion (AIC) values to the corrected AIC (AIC_c) to account for modest sample sizes. To rank models, we calculated the model likelihood, which is the probability of the model given the data, and the delta AIC_c (ΔAIC_c), which is a measure of each model relative to the best model with values <2 indicating a competitive model (Burnham and Anderson 2002). Additionally, to understand variable importance, we calculated the AIC_c model weight (w_i). We fit single-variable models rather than more complex multi-variable models in order to provide baseline information on habitat occupancy patterns for bird species in sacred forests and matrix habitats, and because we had no a priori hypotheses about associations of bird species with multiple habitat characteristics. We assessed model fit to the data by computing a goodness-of-fit bootstrap test using 1,000 bootstraps on the best supported model (MacKenzie and Bailey 2004). The bootstrapping routine compares the structure of the observed best-model to a randomly generated model (1,000 pseudo-random numbers from 0 to 1) (MacKenzie and Bailey 2004). If there was significant evidence of lack of best-model fit due to over-dispersed data ($\hat{c} > 1.0$), we calculated the Quasi- AIC_c , which is the AIC_c adjusted by a factor of the \hat{c} -value (MacKenzie et al. 2006). We performed all occupancy analyses using program PRESENCE (Hines 2006).

To understand tree foraging selectivity by focal species, we tested whether tree species were used as foraging substrates in higher proportion than they were available in sacred forests. To do so, we used a Chi square goodness-of-fit test to compare observed use-versus expected use-frequencies for each focal species (Holmes and Robinson 1981). To obtain expected use-frequencies, we multiplied tree importance values by the total number of observations of all focal species on each tree species (Gabbe et al. 2002). The seven tree species, and three groups of trees, each had an importance value percentage >2.2 %, which indicated they were common enough to be used as foraging substrates by birds of interest of our study (Wood et al. 2012).

To quantify tree-species preferences of focal species, we calculated preference and aversion values (Holmes and Robinson 1981). Preference and aversion values are a measure of tree foraging selectivity with higher values indicating preference and lower

values aversion (Holmes and Robinson 1981). We calculated preference and aversion values by taking the difference of the relative percent use by focal species and the relative importance percentage of a given tree species, or tree group. Additionally, we calculated the preference-index (PI) for each focal species. The PI is a measure of a bird's foraging selectivity and is the sum of the absolute values of the percent difference between observed and importance values for all tree species, or tree groups (Holmes and Robinson 1981).

To determine avian foraging success on tree species or tree groups, we calculated an attack-index. The attack-index is the total number of attacks per minute by all focal species for a particular tree or tree group, divided by the total number of searches per minute (Wood et al. 2012). A higher attack-index on a given tree species or tree group indicated birds had greater foraging success. We limited our calculations to birds that we observed foraging for >30 s. If a focal species used multiple trees during a foraging observation, we used foraging data from each tree species, or tree group, to calculate the tree species- or tree group-specific attack-index. To quantify if foraging success varied among tree species we used a Kruskal–Wallis test, with tree species, or tree group, as the treatment. The Kruskal–Wallis test was significant ($H_8 = 41.18$, p value = < 0.01). Therefore, we calculated a non-parametric multiple comparisons test, based on relative contrast effects, using nparcomp (Konietschke 2011), in the R statistical software package (R Development Core Team 2012) to determine differences in foraging success among tree species, or tree groups. We used a Bonferroni adjusted p value = $0.05/36 = 0.001$ to assess significance.

Results

We found that 23 bird species were associated with sacred forests habitats and 12 species with matrix habitats (Table 1). Of the eight species of conservation concern, seven were positively associated with sacred forests, and only Elliot's Laughingthrush was positively associated with matrix habitat. The average detection probabilities for birds associated with sacred forests were 0.39 and 0.30, in 2010 and 2011 respectively, whereas these probabilities were 0.45 and 0.38 in 2010 and 2011 for birds associated with matrix habitats (Table 1). The average occupancy estimate for the 23 sacred forests bird species of 0.46 was a 26 % increase from the naïve (raw) occupancy of 0.34. In contrast, the average occupancy estimate for the 12 bird species associated with matrix habitats was 0.39, which was a 14 % increase from the naïve occupancy of 0.34.

Our modeling exercise revealed much needed occupancy–habitat associations for the 35 species of our study (Online Resource Tables D.1–D.35). The 23 sacred forest affiliates were positively associated with habitat characteristics of sacred forests such as the largest tree dbh, FHD, and % cover of leaf litter, bamboo, and moss, and negatively associated with the dominant habitat characteristic of matrix habitats, % cover of bare ground (Fig. 2). The 12 species associated with matrix habitats had nearly opposite associations with the same habitat characteristics. The only exception to these patterns was for the largest tree dbh, with which matrix birds had an apparently neutral association, presumably because there were few trees in the matrix habitats. There were apparent habitat occupancy thresholds for six of the eight species of conservation concern (Fig. 3, Online Resource Fig. E). Overall, we found that the majority of species were positively associated with core habitat characteristics of sacred forests (Online Resource Tables D.1–D.35). Generally, these associations were strongly positive for FHD, stem density, the largest tree dbh, and % leaf litter and bamboo cover, and negative for % bare ground cover. More specifically, during fieldwork for a parallel study (Brandt et al. 2013b), we noticed that six of the eight

species of conservation concern all forage and breed in the understory (the exceptions being the Chestnut-vented Nuthatch and Yunnan Nuthatch). We also found this to be the case based on the occupancy modeling analysis, where six of the understory-affiliated species were strongly associated with ground cover variables (Fig. 3). For example, occupancy greatly increased at sites where cover of bamboo and leaf litter was >15 %. The Yunnan Nuthatch is an arboreal forager, and the ground cover variables were not as important in determining habitat occupancy for this species (Fig. 3). The exception was leaf-litter cover, an indicator of deciduous tree canopy, which is likely an important foraging substrate for this species. One of the 8 species of conservation concern, the Elliot's Laughingthrush consistently displayed similar habitat occupancy thresholds patterns, though in the opposite direction (i.e., occupancy increased where cover of bamboo and leaf litter was low). We found the Elliot's Laughingthrush in both sacred forests and matrix habitats (personal observation), and the threshold patterns indicate tolerance of this species to forest habitat degradation (Fig. 3).

We recorded 311 foraging observations of the fourteen focal species, totaling 219 min and 35 s (Table 3). Spruce tree species (*Picea* spp.) were the most important trees (i.e., highest relative importance value) within sacred forests (31.36 %), followed by Himalayan Birch (*Betula utilis*, 17.77 %), and Chinese Larch (*Larix potaninii*, 14.67 %) (Table 2). Tree species with lower importance values included George's Fir (*Abies georgei*, 2.21 %), Chinese Aspen (*Populus davidiana*, 2.28 %), and Willow species (*Salix* spp., 2.28 %) (Table 2). The focal species were highly selective in their tree use. Among the broad groups of focal species, Tits (including Bushtit, five species) and Warblers (including Leaf-Warblers, four species) made up the bulk of our observations. We documented 141 observations of foraging Warblers for 104 min and 12 s, which was 48 % of our total foraging observation time, and 125 observations of foraging Tits for 91 min and 38 s, which totaled 42 % of our observations. In general, the Warblers were less selective in their tree use patterns (PI = 59.87) than the Tits (PI = 95.12). The Yunnan Nuthatch was the most selective forager (PI = 256.63), often preferring *Pinus densata* and *Picea* spp. (Table 4). However, the low amount of foraging data for this species (six observations totaling 2 % of observation time), likely influenced this result. Other species that we found to be highly selective foragers were Willow Tit (PI = 135.19) and Rufous-vented Yuhina (PI = 100.29) (Table 3). Willow Tit preferred *Betula utilis* and *Populus davidiana*, whereas Rufous-vented Yuhina preferred *Picea* spp., *Quercus* spp. and *Abies georgei* (Table 4). However, as was the case for Yunnan Nuthatch, we recorded low numbers of foraging observations for the Rufous-vented Yuhina, which possibly influenced the calculated foraging selectivity values for this species.

Certain tree species were used by the focal bird species in higher proportion than they were available as foraging substrates in sacred forests (Fig. 4). Seven of fourteen focal species preferred *Pinus densata*, which was used 58 % more than it was available in sacred forests (Table 4, Fig. 4). Other tree species, or groups of trees, that were preferred as foraging substrates included *Populus davidiana* (41 % more than it was available), *Quercus* spp. (11 %), *Larix potaninii* (8 %), and *Abies georgei* (3 %) (Fig. 4). On the other hand, we also detected broad patterns of tree species, or groups of trees, that were avoided by birds as foraging substrates. These included *Betula albo-sinensis* (used 61 % less than it was available), *Acer* spp. (39 % less), *Picea* spp. (31 % less), and *Betula utilis* (23 % less) (Fig. 4).

A closer examination of foraging success of focal species among trees, or groups of trees, revealed contrasting conclusions to the use versus availability analysis (Fig. 5). Although *Pinus densata* was used in the highest proportion relative to its availability

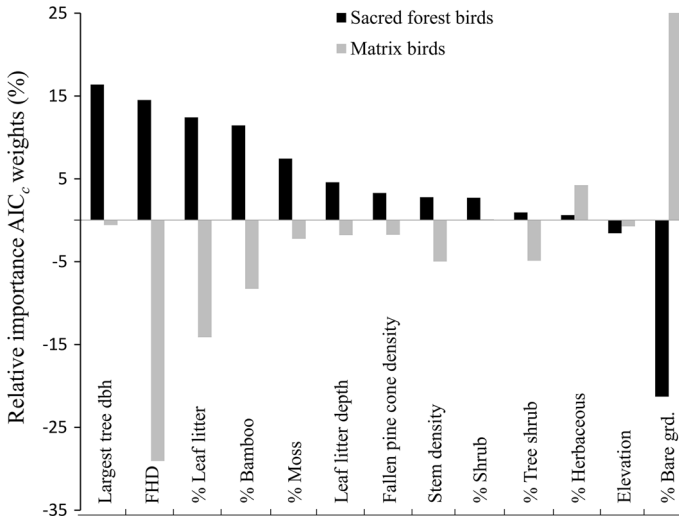


Fig. 2 Relative importance values of thirteen covariates used to model occupancy patterns of 35 bird species within and adjacent (matrix) to Tibetan Sacred Forests, NW Yunnan Province, China. We grouped bird species by two categories: (1) species positively associated with sacred forests (sacred forest birds, $n = 23$), and (2) species negatively associated with sacred forests (Matrix birds, $n = 12$). We calculated relative importance values as the summed AIC_c weights for a particular covariate for all species within a bird group (i.e., sacred forest or matrix), divided by the total AIC_c weights for all covariates for a bird group. The positive and negative values represent the coefficient direction of the collection of models for either the sacred forest or the matrix bird groups. If a covariate was both positively and negatively correlated for a collection of birds within a group (i.e., sacred forest or matrix habitat affiliates), we took the combined positive or negative relative AIC_c weights to describe the occupancy–habitat relationships for a bird group

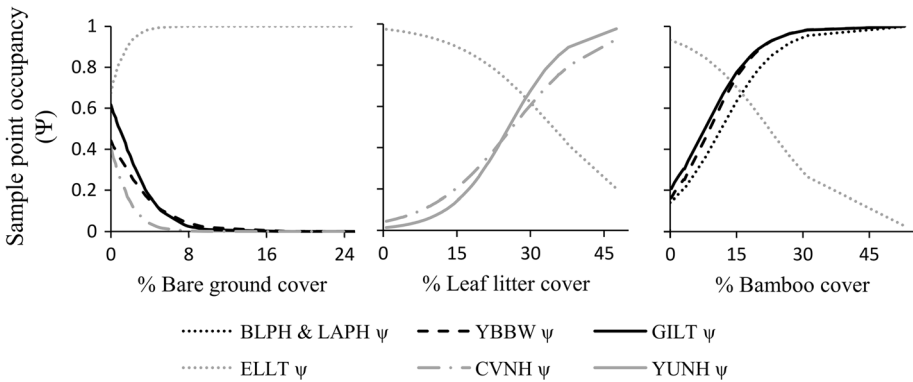


Fig. 3 Relationships of predicted sample-point occupancy (Ψ) for six bird species with three habitat characteristics representing the ground and sub-canopy layer. We only plotted predicted occupancy curves for covariates that had considerable model support ($\Delta AIC_c < 2$). *BLPH & LAPH* Blood and Lady Amherst’s Pheasant, *YBBW* Yellowish-bellied Bush Warbler, *GILT* Giant Laughingthrush, *ELLT* Elliot’s Laughingthrush, *CVNH* Chestnut-vented Nuthatch, *YUNH* Yunnan Nuthatch

among all trees in sacred forests (Fig. 4), birds had comparably lower foraging success on this tree species. Similarly, *Populus davidiana* was also used in higher proportion than its availability (Fig. 4), but bird foraging success was lower than all other tree species

Table 4 Tree-species preference (positive) and aversion (negative) values, which are a measure of tree foraging selectivity, for 14 breeding bird species in Tibetan sacred forests

Tree species	LTMI	BUBW	LRUW	HULW	BLLW	RVYU	WCYU	BBBT	WITI	COTI	RVTI	GCTI	YUNU	RECR
<i>Abies georgei</i>	-2.21	13.58	1.64	-2.21	-0.32	10.29	-2.21	0.29	-2.21	-2.21	-2.21	2.34	-2.21	-2.21
<i>Acer</i> spp.	-3.19	-3.19	4.50	-3.19	2.47	-3.19	-3.19	-3.19	-3.19	-3.19	-3.19	-3.19	-3.19	-3.19
<i>Betula albo-sinensis</i>	-3.93	-3.93	-3.93	-3.93	-0.16	8.57	6.07	-3.93	-3.93	-3.93	-3.93	-3.93	-3.93	-3.93
<i>Betula utilis</i>	-3.48	3.28	-10.08	3.16	4.87	-17.77	12.23	-12.77	35.56	-17.77	-17.77	-8.68	-17.77	-17.77
<i>Larix potaninii</i>	-0.38	6.39	4.57	13.24	-3.34	-14.67	5.33	-2.17	-14.67	11.42	1.33	-5.57	-14.67	6.76
<i>Picea</i> spp.	40.07	-15.57	3.25	-19.73	-10.61	18.64	-1.36	-26.36	-31.36	-5.28	-15.36	5.00	-31.36	18.64
<i>Pinus densata</i>	-9.33	-9.33	-5.48	23.23	11.43	-9.33	-9.33	25.67	-9.33	34.15	6.67	22.49	74.01	19.24
<i>Populus davidiana</i>	-2.28	-2.28	-2.28	-2.28	5.27	-2.28	7.72	2.72	31.05	-2.28	-2.28	-2.28	-2.28	-2.28
<i>Quercus</i> spp.	-12.36	3.43	3.03	-7.71	-6.70	12.64	-12.36	17.64	0.98	-8.01	35.64	-7.81	4.31	-12.36
<i>Salix</i> spp.	-2.91	7.62	4.78	-0.58	-2.91	-2.91	-2.91	2.09	-2.91	-2.91	1.09	1.64	-2.91	-2.91

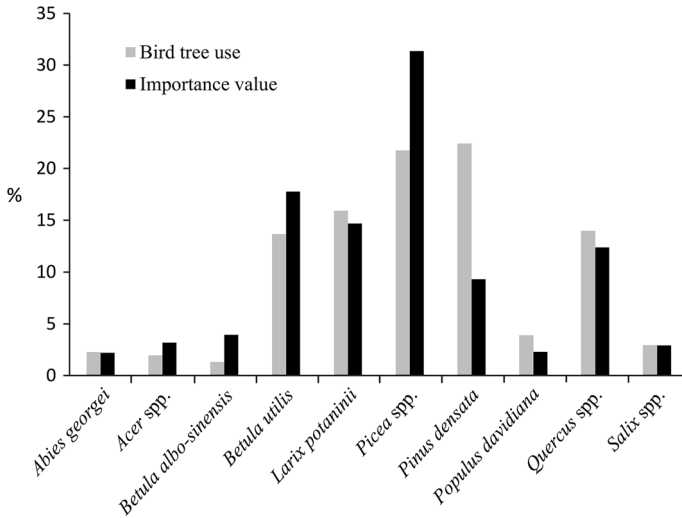


Fig. 4 Relative importance values of tree species, which is a measure of a tree's availability as foraging substrate to birds, and the proportional use of each tree species by fourteen arboreal foraging breeding birds in 2011

(Fig. 5). We found that bird species foraging on *Quercus* spp. and *Salix* spp. had the highest foraging success among all trees, or groups of trees. Bird foraging success on tree species of these two groups was significantly higher than all other trees except for *Larix potaninii* and *Abies georgei*. Bird foraging success on *Abies georgei* appeared high. However, we only documented seven bird foraging observations on this tree species, and this low sample size meant that we found no significant differences in foraging success for *Abies georgei* compared with other trees (Fig. 5).

Discussion

We found that Tibetan sacred forests promote habitat characteristics such as large trees, heterogeneous vertical vegetation structure, and high cover of leaf litter, bamboo, and moss, all of which were positively associated with habitat occupancy of forest bird species of conservation concern. We found that 23 bird species were associated with sacred forests and 12 species with degraded habitats adjacent to the forests. Of the eight species of conservation concern, seven were positively associated with sacred forests. In the face of widespread change throughout China, our findings suggest the traditionally managed Tibetan sacred forests harbor critical habitat features for breeding forest birds of the region, and increase our understanding of the important role of sacred forests for biodiversity conservation.

Globally, indigenous communities have developed and adapted forest management practices primarily as a strategy for procuring or preserving resources or for cultural customs (Wiersum 1997). In some cases, the protection offered by such forest management strategies is beneficial for biodiversity (Porter-Bolland et al. 2012). For example, in tropical forests throughout the world, community managed forests are often similar, or possibly even more effective, than federal protected areas in reducing deforestation

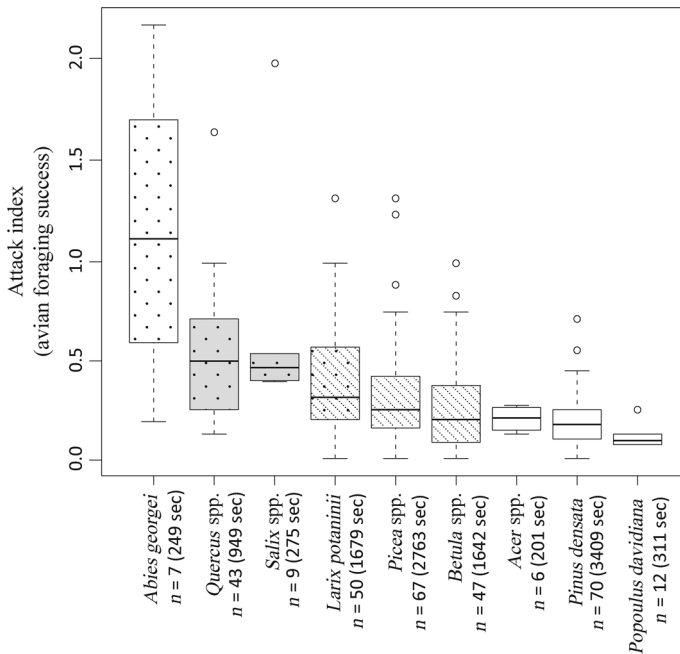


Fig. 5 Summary of the attack index, which is calculated as the total attacks by a bird species divided by the total search maneuvers, scaled per minute, for nine tree species or a tree group (e.g., *Acer* spp.) in Tibetan sacred forests. A higher attack index indicates a higher success rate of birds finding prey on a given tree species of tree group. We display the number of foraging observations and the cumulative number of seconds we observed birds foraging per tree species or tree group. Boxes with different colors, or patterns, differ significantly based on a Kruskal–Wallis test with nonparametric multiple comparisons procedure with a Bonferroni adjusted p value $0.05/36 = 0.001$. We grouped *Betula albo-sinensis* with *Betula utilis* due to low number of cumulative seconds birds were observed foraging in *Betula albo-sinensis*

(Porter-Bolland et al. 2012). However, in the case of sacred forests, which are set aside for cultural or spiritual practices, biodiversity conservation may not be a central goal of the forest management (Bhagwat and Rutte 2006; Allendorf et al. 2014). Nevertheless, sacred forests can be important for species of high cultural significance, such as the White-eared Pheasant (*Crossoptilon crossoptilon*) (Wang et al. 2012). Furthermore, in our previous study, we found forest breeding bird richness was higher in Tibetan sacred forests than adjacent non-sacred forest habitats (Brandt et al. 2013b). Yet, Wang et al. (2012) caution that as cultural norms shift and development accelerates, the conservation benefit of Tibetan sacred forests may be in jeopardy. Furthermore, it is unclear whether Tibetan sacred forest should be directly integrated into broader conservation plans since these forest are typically set aside to provide cultural rather than biological significance (Allendorf et al. 2014). However, our results support prior studies that found that Tibetan sacred forests do indeed harbor important habitat characteristics that are associated with forest breeding bird occupancy, including resources beneficial for several species of conservation concern (Porter-Bolland et al. 2012; Wang et al. 2012).

Our findings support other studies in the region that also documented the importance of structural characteristics and tree heterogeneity for forest breeding bird communities (Chettri et al. 2005; Ding et al. 2008). For example, in Himalayan forests in Sikkim, India,

bird species richness is positively related with tree species diversity (Chettri et al. 2005). Similarly, along a gradient from bamboo grasslands to spruce forests in the mountains of Taiwan, bird communities were positively associated with higher vertical structure, which was more common in late successional spruce forests (Ding et al. 2008). Our findings in Tibetan sacred forests build on the work in India, and Taiwan, in that breeding birds were associated with similar structural variables, which are likely indicators of important nesting and foraging substrates. Furthermore, the tree-foraging patterns that we observed for 14 common arboreal species indicated that high diversity of tree species is likely necessary to provide sufficient resources throughout the breeding period. Although local Tibetan communities did not set aside sacred forests for biodiversity preservation, our results highlight the importance of the traditional forest management, which preserves forest characteristics similar to remnant conditions and are associated with a diverse bird community.

In addition to the importance of sacred forests to the forest bird breeding community as a whole, our results also shed light on key habitat associations between species of conservation concern and specific habitat characteristics. Six of the eight species of conservation concern that we studied were understory birds, and our findings illuminate the high importance of cover of bamboo and leaf litter and the negative effects of bare ground cover. Bamboo is heavily used by local people for subsistence. While bamboo was prevalent as an understory component in four of our six sacred forests, bamboo was absent outside their boundaries. Likewise, leaf litter, associated with deciduous tree cover, was relatively low outside of sacred forests, but our results indicate this may be an important foraging substrate for birds within sacred forests. Bare ground cover, a prominent feature outside of sacred forests but not within, was negatively associated with birds of conservation concern. Our tree species foraging analysis also revealed important clues to the importance of tree diversity, which is a component of Tibetan sacred forest. Our findings are also likely relevant at a broader scale, where core components of natural forests of this region—bamboo, large trees, and heterogeneity in vertical structure and tree composition—are not only important for the broad group of forest breeding birds, but also Himalayan forest bird species of conservation concern.

Conclusions

Although bird conservation is not a primary goal of Tibetan sacred forest management, our findings indicate they do provide important habitat for breeding birds. Our results suggest that forest management practices of the Chinese Himalaya should promote structural and floristic heterogeneity, including managing for multi-age, multi-species forest communities. A common component of Tibetan sacred forests are large, old, trees, which was one of the most important factors associated with breeding bird occupancy, and suggests caution in managing for single-age forest stands. Bamboo is a critical habitat element for several of the bird species that we studied (e.g., Yellowish-bellied Bush Warbler), and is also an important resource for Tibetans. Thus, managing for bamboo, as an understory component of diverse forests will be beneficial for both local communities as well as breeding birds. The occupancy thresholds that we found for bird species of conservation concern indicate their sensitivity to relatively low levels of logging and grazing intensity. However, we note that bird species respond variably to these factors, indicating that sacred forests, which offer a gradient of disturbance and forest conditions, provide suitable resources for many breeding bird species. Furthermore, while some species of trees were more highly preferred

as foraging substrates by breeding birds, other tree species provide conditions, such as greater food accessibility, that lead to higher foraging success rates. This highlights the importance of promoting tree heterogeneity in order to provide necessary resources for a variety of arboreal foraging forest birds.

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