Building a conservation evidence base for the Critically Endangered Blue-crowned Laughingthrush *Pterorhinus courtoisi*

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Declaration of Authorship

I, Rosalind Gleave, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated. Contributions made by others in the form of data collection, analysis and other guidance are indicated clearly.

Signed:

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Abstract

Understanding why species have restricted ranges is important to developing a conservation evidence base. The Blue-crowned Laughingthrush *Pterorhinus courtoisi* (BCLT) is a Critically Endangered passerine with an officially recorded population of c.320 birds found in northeast Jiangxi Province, China. It occurs in colonial, cooperative breeding groups close to villages and agricultural habitat, making it difficult to understand why it is not more widespread across other human-modified landscapes in China, and scant evidence exists explaining why the species is restricted to a small area or why the population remains small.

I combined, contrasted and analysed existing data, including two independently collected monitoring datasets, and citizen science data. Results showed the BCLT population may be 42.8% higher and occupy more breeding sites than previously believed. A species distribution model (SDM) showed BCLT occurrence is linked to annual temperature range, precipitation during the breeding season and land cover. I also conducted systematic interviews across the BCLT range at 39 villages. Results revealed two villages where BCLT may breed (but not officially recorded), the first evidence of recent trapping of the BCLT in southeast China, and regions which should be prioritised for conservation efforts. I also found an association between BCLT breeding sites and local landscape changes.

Previous research into BCLT habitat associations have compared relatively few breeding sites and not accounted for the wider mixed agricultural mosaic. I quantified habitat preferences with resource selection functions across 39 villages, comparing the home range and nest site scales. Nesting sites were significantly more likely to contain large broadleaved trees or stands of bamboo, fir or mixed forest, and be on flatter slopes. This supports past work linking BCLT to mature broadleaved trees, but also nuances past assumptions about BCLT nesting habitat.

To understand influences on range at the landscape scale, I compared seven SDM model algorithms and two pseudo-absence methods, using a land cover map with eight types, and k-fold cross validation. I showed that BCLT occurrence is linked to precipitation during the breeding season and in landscapes with higher tea plantation. This may be related to the

presence of mature trees and non-crop vegetation in tea plantations across the study region, with implications for landscape policy.

Table of Contents

List of Tables and Figures

Chapter 1

Chapter 2

museum, (c) and (d) both murals drawn by local schoolchildren of Blue-crowned Laughingthrush, close to their best-known breeding site.

Figure 3. Diagram of **(a)** a square habitat survey quadrat. Each quadrat is centred around a specific tree, and the diameter at breast height (DBH) and species of each tree over 2m high was taken. The approximate percentage (to the nearest 5%) was given for each of a set of land cover types within the quadrat; **(b)** a circular survey boundary around each survey village or settlement. Fifteen quadrats would be randomly generated within each circle. Second order analyses compare circles as survey units (with quadrats replicated within each unit, and third order analyses compare the individual quadrats as nesting or non-nesting quadrats, regardless of circular boundary.

Table 1. Model algorithms available in *biomod2*.

Chapter 3

Figure 1. Blue-crowned Laughingthrush occurrence records from annual census (blue), eBird.org (yellow) and the lead author's own opportunistic sightings in the field in 2018 and 2019 (black). Records are distributed across three counties in Jiangxi and Anhui provinces, China.

Figure 2. Locations of Blue-crowned Laughingthrush breeding sites based on census data from both HFQ and ZWW (dots show number of sites as surveyed, including geographically separate locations combined together). Yellow dots show censused breeding sites surveyed by both observer groups, blue dots surveyed by HFQ only, and grey dots by ZWW only.

Figure 3. Blue-crowned Laughingthrush census count data broken down by individual breeding site, from years 2000-2017. Yellow dots shows counts by HFQ, blue dots show counts by ZWW.

Figure 4. Overall Blue-crowned Laughingthrush numbers when datasets from HFQ and ZWW data were pooled to fill in gaps (left-hand y axis). The higher value from either set of counts was taken, and data from any overlooked breeding sites were included. The right-hand y axis shows number of occupied breeding sites per year. Grey bars show the total number of individuals, and black dots show the number of occupied sites.

Figure 5. Summary of the marginal effect of year generated by a ZIP GAMM between 2000 and 2017 based on survey data from all 16 Blue-crowned Laughingthrush breeding sites, showing the estimated effect of year on log abundance. The shaded area represents the 95% credible interval. The dotted line runs through the y intercept at zero; above shows an increasing trend, below a decreasing trend.

Table 1. Relative contributions of the highest contributing environmental variables to the Maxent model for the Blue-crowned Laughingthrush.

Figure 6. Representation of the Maxent model for the Blue-crowned Laughingthrush, showing a cumulative output that predicts suitable conditions above a threshold in an approximate

range of 1-20 (yellow-orange). Warmer colours indicate areas with better predicted conditions. The red polygon indicates the known range of subspecies *P. courtoisi*, and red dots indicate the last reported locations of *P. c. simoaensis*.

Supporting Information

Table S1. The integration of the site labelling systems developed by HFQ and ZWW, the corresponding names of the villages where breeding sites were located, and a new numbering system developed for my own analysis.

Table S2. All WorldClim bioclimatic variables not included in the Blue-crowned Laughingthrush species distribution model.

Table S3. Environmental and bioclimatic variables used in Blue-crowned Laughingthrush species distribution modelling.

Figure S1. Correlation plot of all candidate numerical covariates for inclusion in Maxent model.

Figure S2. Correlation plot of all final numerical covariates for inclusion in Maxent model.

Figure S3. Probability of observing Blue-crowned Laughingthrush at any given breeding site, per year. Red lines show the probability per site, averaged over time. Black dots show years in which presence or absence of breeding Blue-crowned Laughingthrush were detected.

Table S1A. Model outputs for the frequentist poisson GAMM.

Figure S2A. The standardised number of Blue-crowned Laughingthrushes predicted to be counted between 2000 and 2017 by a GAMM based on survey results from eight breeding sites. Shaded areas represent the 95% confidence interval for predicted values. Actual standardised count data are also given for each monitoring site included in the model.

Figure S3A. Blue-crowned Laughingthrush population trend over time (2000-2017) as estimated by a frequentist GAMM.

Table S4. Total bird counts from Years 2012-2017 for all breeding sites combined; total counts for all sites and years where both observer groups had made counts.

Figure S4. Proportion of occupied to counted breeding sites during each year of the Blue-crowned Laughingthrush census, 2000-2017. Bars are calculated on the following bases: black bars are where site counts were not performed (as the observers observed Blue-crowned Laughingthrushes but were unsure of breeding activity) are classed as ‘NA’ values, and therefore not treated as ‘counted’. Grey bars are these same site counts classed as ‘0’ (rather than NA) and therefore treated as ‘counted’ sites.

Figure S5. Univariate response curves from Maxent model for (a) annual temperature range (b) land cover, (c) precipitation of the wettest quarter and (d) elevation.

Figure S6. Jackknife tests of variable importance for final Maxent model, showing (a) training gain (b) test gain and (c) AUC on test data.

Chapter 4

Figure 1. The distribution of sampled villages depicted as coloured circles. Shaded areas cover the counties of Wuyuan, Dexing, Leping (Jiangxi Province) and Xiuning (Anhui Province). Thick black lines demark the boundaries between provinces. The polygons show the Extent of Occurrence (EOO) drawn around known Blue-crowned Laughingthrush breeding sites, the Minimum Convex Polygon (MCP) drawn around all known Blue-crowned Laughingthrush sightings (including those from eBird), and the outer polygon shows the 25km buffer region around the MCP.

Table 1. Global and reduced GLMMs for investigating Blue-crowned Laughingthrush sighting responses in relation to habitat change and human threat covariates. Model specification uses R notation.

Figure 2. Proportion of respondents who recognised each of five local bird species by either photograph or standard common name.

Figure 3. Spatial distribution of sampled villages, showing the proportion of respondents who recognised Blue-crowned Laughingthrush that last saw the species in (a) the breeding season (spring/summer) or (b) the non-breeding season (autumn/winter). Pink = breeding villages, blue = control villages.

Figure 4. Spatial distribution of sampled villages, showing proportion of respondents who reported seeing different-sized flocks in breeding (pink) and control (blue) villages. (a) 'small' flocks, (b) 'medium' flocks, (c) 'large' flocks, (d) 'very large' flocks.

Figure 5. Percentage of respondents reporting a change in different land use types around their home villages during their lifetime in (a) breeding villages and (b) control villages. Blue bars show an overall percentage of people reporting an increase in a land type, and pink bars show an overall decrease.

Figure 6. Locations where Blue-crowned Laughingthrushes have been reported as being caught (blue squares) and where Blue-crowned Laughingthrushes were sighted by at least one respondent during the breeding season (spring–summer) between 2014–2019 (green circles). Villages are shown in groups, with some physically close pairs of villages grouped together as one. Polygons and names indicate Chinese counties.

Figure 7. Interval plot showing the 90% credible intervals (CI, represented by black horizontal lines) for the posterior distribution of each factor level, in relation to **(a) whether respondents had seen a Blue-crowned Laughingthrush** or **(b) whether respondents had seen Blue-crowned Laughingthrush within the previous 18 months.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Plot displays the optimal candidate models. Variables in the model are: road building, and awareness of people catching Blue-crowned Laughingthrush.

Table 2. Outputs from a series of univariate Bayesian GLMs for breeding vs control villages, and EOO vs buffer villages. Variables where the 95% credible interval (CI) range does not overlap with zero represent the equivalent of statistically significant.

Supplementary Information

Figure S1. English language copy of the final questionnaire used during data collection in June-July 2019.

Figure S2. Bird species images used in the questionnaire.

Figure S3. Flock sizes used in questionnaire.

Table S1. Questionnaire data processing protocol, listing examples of main response types and how these are processed/standardised.

Figure S4. Multiple Correspondence Analysis (MCA) (a) scree plot showing the percentage variance explained by each MCA dimension and (b) the correlation between each variable and MCA principal dimensions 1 and 2.

Table S2. All variables considered for inclusion in final models. Black ticks show variables *a priori* included in final full models.

Table S3. Demographic characteristics of interview respondents.

Figure S5. Number of respondents who recognised the Blue-crowned Laughingthrush by either its name, an image or a sound recording of the birds calling.

Figure S6. Proportion of respondents reporting the year they last saw a Blue-crowned Laughingthrush.

Table S4. Changes in land types around respondent home villages: overall percentage of respondent reporting (a) an increase or decrease, and (b) no change/absence of land types.

Table S5. General types of birds, reasons for catching or killing, and methods for catching and killing birds.

Table S6. Leave-One-Out Cross Validation differences between Expected Log Pointwise Predictive Density (ELPD) scores and Standard Error scores of the 'Seen BCLT' and 'Recently seen BCLT' GLMMs. Moment matching was performed on the LOO cross validation for values with a pareto k value of > 0.7, which indicates outlier observations which have a disproportionate effect on the model and make estimating out-of-sample accuracy difficult. '_gp' denotes a Gaussian process model. Optimal models highlighted in bold.

Figure S7. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each factor level, in relation to **whether respondents had seen a Blue-crowned Laughingthrush**. Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. **Plot displays the third most optimal candidate model (within -2.7 ELPD).** Variables in the model are: vegetable garden change, *fengshu*i forest change, awareness of people catching Blue-crowned Laughingthrush, bush/scrub change, and bamboo forest change.

Figure S8. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each factor level, in relation to **whether respondents had recently seen a Blue-crowned Laughingthrush**. Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. **Plot displays the second most optimal candidate model (within -0.4 ELPD).** Variables in the model are: types of birds caught, change in tea plantation.

Table S7. Outputs for breeding model variations, and the EOO models.

Chapter 5

Figure 1. Map showing the distribution of sampled villages, depicted as coloured circles. Shaded areas cover the counties of Wuyuan, Dexing, Leping (Jiangxi Province) and Xiuning (Anhui Province). Thick black lines demark the boundaries between provinces. The polygons show the Extent of Occurrence (EOO) drawn around known Blue-crowned Laughingthrush breeding sites, the Minimum Convex Polygon (MCP) drawn around all known Blue-crowned Laughingthrush sightings (including those from eBird), and the outer polygon shows the 25km buffer region around the MCP.

Table 1. Response variables (*) and covariates used in resource selection models for the Blue-crowned Laughingthrush**.**

Table 2. All full model and candidate sub-model resource selection functions for the Blue-crowned Laughingthrush. Model specification uses R notation.

Table 3. The most commonly occurring tree species found within 585 survey quadrats within villages formerly or currently containing breeding Blue-crowned Laughingthrush colonies, and control villages.

Figure 2. Interval plot showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a village was in the EOO.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship with villages in the EOO if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the second most optimal candidate model (*submodel 1*).

Figure 3. Interval plot showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a village was a breeding site.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to breeding sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the optimal candidate model (*submodel 2*).

Figure 4. Interval plot showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a survey quadrat was ever a nesting site.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to nesting sites if the CI is to the right of plot, and

negative if they are to the left of the plot. Plot displays the optimal candidate model (*global model, random intercept only*).

Figure 5. Interval plots showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a village was a) a breeding site or b) within the EOO** based on remote sensing land cover data**.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to a breeding or EOO site if the CI is to the right of plot, and negative if they are to the left of the plot.

Supplementary Information

Figure S1. Principal Components Analysis plot of Dimensions 1 and 2 of land cover type percentages.

Figure S2. Principal Components Analysis plot showing total contribution of land cover type percentages to Dimensions 1 and 2.

Figure S3. Correlation plot of all candidate numerical covariates for inclusion in generalised linear mixed models.

Table S1. The full set of potential predictor variables, with descriptions and reasons given for their inclusion. A subset of these will be included in the final analyses. An 'x' symbol is given for predictor variables which are being considered for each response variable, based on the outcomes of exploratory analyses.

Table S2. Leave-One-Out Cross Validation outputs for GLMMs. Shows the difference in Expected Log Pointwise Predictive Density (ELPD) and difference in Standard Error between candidate sub-models and full models.

Table S3. Generalised linear mixed model estimates and credible interval range (full models).

Table S4. Generalised linear mixed model estimates and credible interval range (optimal models).

Figure S4. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each predictor, in relation to **whether a village was ever a breeding site (2nd order analysis; 2019 breeding sites only).** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to Blue-crowned Laughingthrush breeding sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays *submodel 1*.

Figure S5. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each predictor, in relation to **whether a village was ever a breeding site (where the two villages where past breeding is unsure, are classed as breeding).** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to Blue-crowned Laughingthrush breeding sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the optimal candidate model.

Table S5. Mean user's, producer's and balanced accuracy (%) of random forest supervised classification of eight land cover types.

Chapter 6

Figure 1. Range map for the Blue-crowned Laughingthrush, showing coordinates of all presence locations used for fitting species distribution models. Extent extends from 499910,709850 to 3090200,3400080 UTM (117.20, 118.50 to 28.50,29.80 lat/long). The rectangular box demarcates the area from which pseudo-absence locations were drawn for modelling, and for which current simulations were projected. The lines radiating from the Blue-crowned Laughingthrushes' range centre show the three segments of the map used for leave-one-out cross-validation of models. Provincial and county borders are plotted using the 'GADM' dataset available via the *raster* package in R (Hijmans and van Etten 2012). Not all presence points are visible as separate.

Table 1. Blue-crowned Laughingthrush SDM AUC scores for all variables, with all presence/pseudo-absence data included and also using segmented k-fold models. The two best model algorithms for each pseudo-absence method, as identified by k-fold analysis, are highlighted in bold.

Figure 2. Delta AUC scores for each variable from the two best-fitting model algorithms based on k-fold analysis AUC scores, for a) convex hull method models, and b) presence point method models. Each point represents one of the bioclimatic predictor variables used in the models.

Figure 3. Response curves of Blue-crowned Laughingthrush occurrence records to each variable, using a) the convex hull method, and b) presence point method. FDA = blue, GLM = red, Maxent = green, MARS = turquoise. Land cover values correspond as follows: **broadleaf forest = 0.00, vegetable garden = 0.14, other forest = 0.28, tea plantation = 0.42, rice paddy = 0.57, bush/scrub = 0.71, settlement/road = 0.85, water = 1.00**. Values are decimals due to the raster conversion process.

Figure 4. Projections for all model algorithms using a). the hull-based method and b). presence point based method. Projections are unavailable for the FDA models.

Supplementary Information

Figure S1. Example field survey sheet used to collect ground-truthed data for remote sensing image classification.

Table S1. Land cover categories, their definitions, and quantities of data points per category from a field survey in May 2019. Data collected are intended to classify remote sensing imagery.

Figure S2. Methods of generating pseudo-absence points (two types of buffer): (a) convex-hull based and (b) presence-point based.

Figure S3. Correlation plot of the final numerical environmental variables chosen for inclusion in the species distribution model. Land cover is excluded as it is categorical.

Figure S4. Correlation plot all environmental variables considered for inclusion in the species distribution models.

Table S2. Environmental predictor variables included in the species distribution model.

Table S3. Mean user's, producer's and balanced accuracy (%) of random forest supervised classification of eight land cover types.

Figure S5. AUC estimates with 95% CIs, from models using all data. (a) hull-based method and (b) presence-based method.

Figure S6. Tea plantations surrounded by mature trees and other non-crop vegetation at Blue-crowned Laughingthrush breeding sites and other sites in Wuyuan and Xiuning counties.

Publications and other contributions

Publications

Chapter 3 is prepared as a manuscript to *Global Ecology and Conservation*

Chapter 4 is prepared as a manuscript to *People and Nature*

Chapter 5 is prepared as a manuscript to *Diversity and Distributions*

Chapter 6 is prepared as a manuscript to *Animal Conservation*

Co-author contributions

I made the lead contribution to all chapters, including all aspects of study design, data collection, data analysis and interpretation, and writing.

Sarah Papworth, Samuel Turvey and Steve Portugal provided comments and guidance on all aspects of this work in their capacity as academic supervisors, and gave comments and editorial suggestions on drafts.

Chapter 3: Weiwei Zhang, Tao Liu, Yingyu Su, Bai Mo and Fenqi He collected data. Laura Gardner facilitated data collection and gave input into study design.

Chapter 4: Weiwei Zhang provided guidance on design. David Bauman provided guidance on analysis. Yikang Liu, Xiaojin Cheng and Zhiming Cao collected data.

Chapter 5: David Bauman provided guidance on analysis. Yurong Yu collected data.

Chapter 6: Andrew Bladon provided guidance on design and analysis.

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ZSL Annual Science Symposium (2019, 2020; presentation)

British Ecological Society Annual Meetings (2020, 2021; speed talk and poster)

ZSL Speed Talk (2020)

Co-chaired session for ZSL Social Science Working Group (2020)

Definitions

AOO – Area of Occupancy, defined as 'the area within its 'extent of occurrence' which is occupied by a taxon, excluding cases of vagrancy. The measure reflects the fact that a taxon will not usually occur throughout the area of its extent of occurrence, which may contain unsuitable or unoccupied habitats' (IUCN 2012).

ANN – Artificial Neural Network

AUC – Area Under the Curve

BRT – Boosted Regression Tree

CART – Classification and Regression Tree

Chinese Cultural Revolution – A socio-political revolution in China that took place between 1966 and 1976. It was marked by the violent removal of societal aspects deemed as bourgeois or superstitious (Coggins 2012).

CI – Credible Interval

DBH – Diameter at Breast Height

EAZA – European Association of Zoos and Aquaria

eBird – eBird.org is the world's largest biodiversity-related citizen science project, documenting georeferenced bird sightings across the globe, with more than 100 million bird sightings contributed each year.

ELPD – Expected Log Pointwise Predictive Density

EOO – Extent of Occurrence, defined as 'the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy' (IUCN 2012).

EVI – Enhanced Vegetation Index

FDA – Flexible Discriminant Analysis

***Fengshui* forests –** Patches of mature forest grown deliberately close to villages in China, particularly across southern China. They form part of ancient, cultural beliefs around maintaining energy flow in the land and harmony between earth and the cosmos (Coggins 2003).

GAM – Generalised Additive Model

GBM – Generalised Boosting Model

GLMM – Generalised Linear Mixed Model

Great Leap Forward – Period in Chinese history between 1958 and 1961 characterized by rapid industrialisation and deforestation of large swathes of the country, including the loss of fengshui forests (Coggins 2012).

INLA – Integrated Nested Laplace Approximation

IUCN – International Union for the Conservation of Nature

Landsat – Landsat is a moderate spatial-resolution satellite program run by the National Aeronautics and Space Administration (NASA), representing the longest continuous global record of the Earth's surface, running since the early 1970s.

LEK – Local Ecological Knowledge

LOOCV – Leave-One-Out Cross Validation

MARS – Multiple Adaptive Regression Splines

Maxent – Machine-learning software used for modelling species niches and distributions; it is a portmanteau of 'maximum entropy'.

MCA – Multiple Correspondence Analysis

NASA-MODIS/Terra – MODIS stands for 'Moderate Resolution Imaging Spectroradiometer'; it is a remote sensor aboard the Terra satellite, collecting satellite imagery which are available for free. The Terra satellite has been in operation since 1999.

NDVI – Normalized Difference Vegetation Index

NGO - Non-Governmental Organisation

NUTS – No-U-Turn Sampler, an algorithm for Bayesian model updating used by Bayesian platform Stan.

PCA - Principal Component Analysis

QGIS – Free and open source geographic information system programme.

RF – Random Forest

ROC – Receiver Operating Curve

RSF – Resource Selection Function

SAFE Project – Stability of Altered Forest Ecosystems Project

SDM – Species Distribution Model

SRTM – Shuttle Radar Topography Mission

USGS – The United States Geological Survey

WikiAves – Citizen science website for birdwatchers in Brazil

WorldClim – Database of high spatial resolution global bioclimate data.

Xeno Canto – Online archive of bird audio recordings from around the world, available for free.

ZIP GAMM – Zero-Inflated Poisson Generalised Additive Mixed Model

ZGAP – Zoological Society for the Conservation of Species and Populations

1. Introduction

1.1 Restricted geographic ranges as a correlate of extinction risk

With biodiversity loss occurring at an alarming rate (IPBES, 2019), extinction risk and drivers have been increasingly studied to understand where these declines may be mitigated (Brook, Sodhi and Bradshaw, 2008). Four distinct processes were initially identified as responsible for the decline and ultimate extinction of species, known as the 'Evil Quartet' (Diamond, 1989): habitat loss, overexploitation, introduced species and secondary extinctions (subsequent extinctions following the extinction of a species, where dependencies exist between species). More recently, understanding of extinction drivers has grown more nuanced with acknowledgement of the roles also played by disease, climate change and stochastic factors (Carroll, 2007; Brook, Sodhi and Bradshaw, 2008). In addition, research has expanded to consider extrinsic factors both separately to, and in synergy with, intrinsic biological traits associated with increased risk, such as slow life history, low population density and high trophic level, with extinctions occurring non-randomly across taxa, determined phylogenetically (Purvis *et al.*, 2000; Higgins, Bond and Pickett, 2001; Fagan and Holmes, 2006). Frequently, species declines are a result of multiple extrinsic and intrinsic drivers acting synergistically to amplify the rate at which such declines occur (Brook, Sodhi and Bradshaw, 2008), with extinction drivers disproportionately affecting geographically restricted, locally uncommon species (Dickman, Pimm and Cardillo, 2006). For example, it is believed that habitat loss, secondary extinctions and introduced species together have been the cause of significant decline in many pollinator species worldwide (Potts *et al.*, 2010). Climate change also exacerbates other extrinsic drivers such as habitat loss (Jetz, Wilcove and Dobson, 2007) or disease (Pounds *et al.*, 2006). However, while extinction processes, both intrinsic and extrinsic, are important to understand, it is of more pressing concern in practical conservation management to understand current extinction risk to individual species.

When assessing the overall threat of extinction to a species, a restricted geographic range is considered a key factor (Mace *et al.*, 2008). Restricted geographic range size constitutes Criterion B of the IUCN Red List Categories and Criteria (IUCN, 2012), one of five criteria (A-E) on which species' threat status are judged. In addition to range size, the Red List factors into its assessments the decline rate of a population and population size as part of a quantitative, criterion-based process (Mace *et al.*, 2008). The thresholds as defined by the IUCN (2012) for restricted geographic ranges under the Red List threatened categories are given in **Table 1**.

Table 1. Area thresholds for 'Extent of Occurrence' (EOO) and 'Area of Occupancy' (AOO) for the three Red List Threatened categories as defined by the IUCN (2012).

Threat Category	Geographic range
Critically Endangered	EOO less than 100 km^2, AOO less than 10 km^2
Endangered	EOO less than 5,000 km^2, AOO less than 500 km^2
Vulnerable	EOO less than 20,000 km^2, AOO less than 2,000 km^2

Along with the interaction between small geographic range size and extinction risk, species with small ranges also tend to have slow life history, low population density and high trophic level (Purvis *et al.*, 2000), which are characteristics associated with risk. However, a restricted range alone does not necessarily imply a high level of threat (Gaston, 1994). When small range is associated with other risk factors such as a small population size, fragmentation, high rates of decline and other indicators of risk (all of which have a strong evidence base within theoretical and empirical studies), range restriction does indeed qualify as a strong indicator (Mace *et al.*, 2008). Islands are by their nature small and/or restricted in size, thus island species are perceived as being at higher risk of extinction, with half of the 724 recorded animal extinctions in the last 400 years occurring on islands, especially for birds (Mulongoy *et al.*, 2006). Proportionally fewer island species with ranges between 1,000 and 100,000km^2 are considered threatened, however, when compared to similar continental species with equivalent range sizes (Manne, Brooks and Pimm, 1999). This is thought to be because island species tend to be locally common compared to their range restricted mainland counterparts.

Restricted geographic range sizes are underpinned by many different biotic and abiotic processes (Gaston 2003). These processes do, however, form something of a continuum. On one end, 'naturally' range restricted taxa may exist as relics from the last Ice Age glaciation (e.g. Saimaa ringed seal, *Phoca hispida saimensis*, Sipilä, 2003) or represent habitat specialists (e.g. Charco Palma Pupfish, *Cyprinodon veronicae*, Valdes Gonzales 2019). An example of a more extreme habitat specialist is *Nymphaea thermarum*; now Extinct In The Wild, this water lily had adapted to life in a single hot spring in Rwanda (Fischer *et al.*, 2019). Another example of a 'naturally' restricted range is the Critically Endangered Iriomote cat *Prionailurus bengalensis iriomotensis*, an island endemic, with a naturally small range of 284 km^2 (Izawa and Doi 2015). These examples illustrate how some species can occupy tiny ranges regardless of human impacts. However, many other species are not naturally range restricted, but have ranges restrictions mediated by people.

In contrast to naturally small ranges, some species formerly occupied a large area but now have a heavily reduced range as a result of human activities. The widespread but now Critically Endangered Yellow-breasted Bunting *Emberiza aureola* (BirdLife International 2017), for example, once bred across the northern Palearctic from north-west Europe through far eastern Asia. This bird has recently undergone a steep decline and is now thought to have disappeared from Belarus, Finland, Ukraine and parts of Russia, largely as a result of hunting (BirdLife International 2017). The range is thought to have retracted by at least 5,000 km between 1980 and 2013 (Kamp *et al.*, 2015). Further down the human-driven end of the continuum, the Endangered Ethiopian Bush-crow *Zavattariornis stresemanni* was found to persist only in an area stretching just 160 km from north to south, and 100 km from east to west. The species requires a specific climate envelope with suitable human-modified vegetation (BirdLife International 2021; Donald *et al.*, 2012), so is restricted by a blend of human-driven and natural factors. Donald *et al.* (2012) posited that prior to human agricultural systems in the region some 8,000 years ago, the climate envelope may have been larger and the open areas the species currently relies upon may have occurred naturally. Other species with restricted ranges are considered 'refugee species', where current ranges occupy not optimal habitat, as previously thought, but suboptimal habitat where they persist away from hunting or predation. One such example is the Lord Howe Island Woodhen *Tricholimnas sylvestris*, which originally bred on coastal flats, and became restricted to montane areas to prevent predation by feral pigs (Miller and Mullette, 1985). Such examples highlight the complex and differing factors that can regulate restricted ranges, and why isolating their causes has a bearing on how to approach conserving these species.

Assessing whether a species' range is restricted naturally or by human activities is, therefore, critical for understanding the species' level of threat. Understanding levels of threat allows appropriately planned conservation measures to be designed and targeted at the drivers of extinction, as conservation is intended for threatened, not unthreatened species (IUCN 2012). As with *Nymphaea thermarum,* some species naturally occur in a small area. In this case it would be inappropriate to channel conservation funds into expanding its range, as its threats are of a different nature (Juffe 2010). In contrast, the Hainan Gibbon *Nomascus hainanus* was once widespread across lowland forest on Hainan Island, but is now confined to a single population found within a 15km^2 intact forest fragment, thus restricted entirely by human impacts (Chan et al. 2005; Zhou *et al.*, 2005; Zhang *et al.*, 2010). These gibbons, therefore, are species that are strong contenders for conservation actions through potential expansions of their current range, to approximate their historical distribution. Similarly, Echo Parakeets from the island of Mauritius 'were once widespread in the native forests' (Jones, 1980, p. 351), but deforestation began after colonisation in the 1600s and by 1980, 2% of the island was covered by native vegetation and the parakeets were restricted to a small patch of forest.

The precise factors leading to a restricted range are not always straightforward to determine. For example, the Takahe's (*Notornis mantelli*) native habitat was the subject of lengthy debate. On the New Zealand mainland it occupies isolated alpine habitats; and Mills, Lavers and Lee (1984) determined that the Takahe is a habitat specialist and native to alpine regions with a range reduced by late Pleistocene expansion of forests. This was challenged by (Bunin and Jamieson, 1995) who concluded that the Takahe had been native to lowland streams and forest margins, with numbers initially declining due to habitat destruction some 800-1000 years ago.

1.1.1 Proximate vs ultimate factors

Species may decline due to ultimate factors (such as habitat loss) which are then exacerbated by proximate factors (such as disease and stochastic factors) (Hernández *et al.*, 2013). For example, the Echo Parakeet (*Psittacula echo*) of Mauritius saw its native habitat destroyed by European settlers after their arrival in the 17th century (Jones, 1980). Once the population was heavily diminished and restricted to the remaining native forest, this became vulnerable to factors such as cyclones, as well as competitive interactions with Ring-necked Parakeets (*Psittacula krameria*). Another island species, the Lord Howe Woodhen, also fell into decline following the arrival of European settlers, but was gradually driven to the most remote mountain regions through predation by introduced feral pigs (Miller and Mullette, 1985). The population dropped to just 10 breeding pairs, at which point it was vulnerable to extinction through high adult mortality. After large-scale extinction drivers reduced the Woodhen population to being small and vulnerable, proximate factors such as storms and normal predation events had a magnified effect on the remaining individuals (Caughley, 1994).

1.2 Species range research techniques

The conservation needs of any given species can be clarified through understanding influences on its geographic range and population size, by combining and analysing environmental factors and extinction drivers. Typically, current research aims to determine if a species' current range is determined naturally, or has been modified by anthropogenic factors. To achieve this, it should be established if factors such as habitat loss (at various spatial scales), or overexploitation, contributed to the present range; additionally, it should be determined if past ranges used to be larger (Chatterjee, Tse and Turvey, 2012; Chen *et al.*, 2018; Yang *et al.*, 2018). A challenge faced is a lack of past evidence of range: the Echo Parakeet was described in eyewitness accounts from the 1870s (Jones, 1980) and the Hainan gibbon has historic records of its distribution dating back to 1688 (Zhou *et al.*, 2005). Despite this challenge, past geographic ranges are important to establish, as these can indicate how 'natural' a species' current range is (Jones, 1980), and can be deduced with both historical records (Ali *et al.*, 2017; Chen *et al.*, 2018) and subfossil data (Bunin and Jamieson, 1995).

However, the approach often used to understand species' ranges includes combining systematic surveys of threatened species with remote sensing data and/or ground-truthed habitat surveys (Jones, Linsley and Marsden, 1995; Jeganathan *et al.*, 2004; Dechner, 2011; Peck *et al.*, 2011; Donald *et al.*, 2012; De Lima *et al.*, 2016) which can track a species' ecological niche, or land cover changes over time. For example, for the hirola (*Beatragus hunteri*), an antelope with population declines since the 1970s, Ali *et al.* (2017) combined ground survey data and aerial surveys with a classified land map, and compared the species' decline with changes in tree cover revealing the mechanisms driving sustained low populations of this ungulate. Direct ecological observations can also inform nesting or feeding behaviour, which can explain ranges on smaller spatial scales (Oppel *et al.*, 2004; Oppel *et al.*, 2004; Walker, Cahill and Marsden, 2005; Ni *et al.*, 2018)

Increasingly, studies have also begun incorporating the knowledge of the local people - local ecological knowledge (LEK) - taken from interviews, to aid in determining species distributions and both current and historical threats (Menon *et al.*, 2010; Turvey *et al.*, 2010; Ravaloharimanitra *et al.*, 2011; Nash, Wong and Turvey, 2016). LEK can provide novel insights into conservation parameters, such as information on threats or past range not detected by standard ecological techniques. One example is research performed on the Critically

Endangered cao vit gibbon (*Nomascus nasutus*), rediscovered in 2002 in northern Vietnam (La *et al.*, 2002) and again in southern China (Chan *et al.*, 2008). Fan *et al.* (2011) interviewed local elders to piece together forest and other land-use changes that had occurred within living memory. This revealed changing local levels of timber extraction throughout the 20th century, constant clearing of land for agriculture, as well as mass-production of charcoal in the gibbon habitat from the mid-1990s until 2005; this information was relevant to understand the specific unsustainable threat processes that had contributed to the species' decline and small population size. Locals suggested that at least two gibbon groups disappeared during the charcoal-making period (Fan *et al.*, 2011).

1.2.1 The importance of spatial scales

When studying ecological relationships in reference to species' ranges, it is important to consider these at different spatial scales, such as regional/landscape, species' home ranges or nest sites, across which biotic and abiotic factors may influence ranges in different ways (Jones, 1980; Lockyer *et al.*, 2015). Varying from fine to coarse scale, measurements may reveal different habitat associations (Fattebert *et al.*, 2018) or different food availability (Sherley *et al.*, 2017) for species; for example, different scales reveal varying impacts of organic farming (Gabriel *et al.*, 2010). Different ecological patterns occur over multiple spatial scales, for example, microclimate over fine spatial scales and tree communities over larger spatial scales (Ewers *et al.*, 2011). These varying patterns may also affect range restricted species: if it is not understood how factors change or shift in importance across scales, key factors determining range restriction may be missed. For example, human activity and food availability were the best predictors of habitat selection at finer spatial scales for the Cross River Gorilla (*Gorilla gorilla diehli*), helping explain why the species has a fragmented distribution (Sawyer and Brashares, 2013).

1.3 The conservation crisis across China

China is recognised as one of the most biologically diverse countries: according to Xie *et al.* (2015) it ranks eighth of the world's top 12 megadiverse countries, despite being located mainly away from the tropics, with 6,347 species of vertebrate (14% of global species) and over 30,000 higher plants (10% of global species). Whilst China has been heavily populated by humans for millenia, there have been intensifying landscape changes occurring over the past 400 or so years (Elvin 2004). Large population increases and mass migration took place in South China from 1700 onwards, and huge areas of forest were converted to cultivated land in southern China (Marks 1998), culminating in parts of Guangdong and Guangxi provinces experiencing severe fuelwood shortages in the early 19th century. These changes coincided with the decline or loss of many species within the same region and time period, including megafauna such as tigers and elephants, and smaller taxa such as giant centipedes. Across China more broadly, range restrictions have occurred for once common and widely distributed species, such as pangolins (Yang *et al.*, 2018), gibbons (Chatterjee, Tse and Turvey, 2012), and snub-nosed monkeys (Li, Pan and Oxnard, 2002). All now have highly restricted ranges: for example, snub-nosed monkeys were once distributed across 11 Chinese provinces, and were abundant around the Yangtze River, but as of 2002, only five extant populations remained at high elevations (Li, Pan and Oxnard, 2002). Many of these species are now confined to mountainous habitat, as lower-elevational habitats were more accessible to expanding human populations and so were historically converted into agricultural land to a greater degree, with current ranges not necessarily representing optimal habitat (Nüchel *et al.*, 2018; Kerley *et al.*, 2020). In tandem with expanding human populations and habitat loss, wildlife exploitation exacerbated many of these declines. For example, trade in wild animal products was encouraged by the government for sale at Foreign Trade Stations between 1950s–1980s (Coggins 2017). Additionally, species such as Chinese Pangolin (*Manis pentadactyla*) have been substantially reduced due to demand for their parts**,** with the species now classed as Critically Endangered on the IUCN Red List and with a heavily contracted distribution (Yang *et al.*, 2018). Similarly, heavy trapping pressure across the East Asian Flyway in China for the Yellow-breasted Bunting (*Emberiza aureola*) led to a dramatic population decline and range contraction (Kamp *et al.*, 2015).

1.4 Asian songbird crisis

An ancient culture of bird keeping and rapid human population growth during the 20th century has led to a songbird crisis across Southeast Asia (Sykes, 2017), with Indonesia at the epicentre, where it has gained the most attention (Nijman *et al.*, 2021). In South-East Asia, over 1,000 wild bird species are traded as caged birds, including species of Laughingthrush, Mynas, Bulbuls, and Leafbirds (Lee *et al.*, 2016) amongst numerous other taxa. Trapping of wild birds heavily affects at least 26 globally threatened species in Indonesia alone**,** and 36 Asian songbirds were assessed as threated on the IUCN Red List as of 2022 (BirdLife International 2022). The recognised plight of a few species including the Blue-crowned Laughingthrush (*Pterorhinus courtoisi*), Bali Myna (*Leucopsar rothschildi*) and Javan Green Magpie (*Cissa thalassina*) led concerned conservationists and zoos to form the EAZA 'Threatened Songbirds of Asia Working Group' (Collar *et al.*, 2012), which became the Threatened Asian Songbird Alliance in 2015 (Sykes, 2017). The phenomenon is now dubbed the 'Asian Songbird Crisis' (Lee *et al.*, 2016; Shepherd and Cassey, 2017). In China, wildlife, for example the Chinese Hwamei (*Garrulax canorus*; Dai and Zhang, 2017; Shepherd *et al.*, 2020) is traded as a pet or caged bird. Bird and pet markets have been recorded in many cities across China, e.g. Guiyang, Beijing, Guangzhou, Kunming and Shenyang (Zhang, Hua and Sun, 2008; Huo *et al.*, 2009; Dai and Zhang, 2017; Cheng, 2019; Fiennes *et al.*, 2021), and the country was one of the main exporters of birds between 1998-2007 (Nijman, 2010). However, wild animal trade monitoring in China is weak, making assessment of the extent of the trade and impacts on species difficult (Zhang, Hua and Sun, 2008), and overall knowledge of the extent of Chinese wildlife trade, including the pet songbird trade, is very low (Fiennes *et al.*, 2021).

1.5 *Fengshui* forests

Fengshui forests (*fengshuilin*) are patches of mature broadleaved or coniferous trees found close to villages, in many instances representing remnants of native subtropical forest. Found across southern China, *fengshui* forests have high cultural and spiritual importance, representing the achievement of harmony between earth and the cosmos for rural communities and affecting traditional village spatial planning (Coggins, 2003). They also perform more functional 'ecosystem services' roles, such as preventing soil erosion, acting as wind barriers, and providing non-timber forest products such as medicinal plants (Zheng *et al.*, 2009; Coggins *et al.*, 2018). They can exist as individual trees (*fengshuishu*) situated within villages, through to more substantial stands of trees many hectares in size (Coggins, 2003). *Fengshui* forest presence has been identified through Chinese scientific literature and fieldwork surveys across China, in seven provinces across southern China and one further north, in Shandong (**Figure 1**). These stretch from Yunnan in the west to Anhui, Jiangxi and Fujian in the east, and may exist in as many as 14 provinces (Chen *et al.*, 2018)**.**

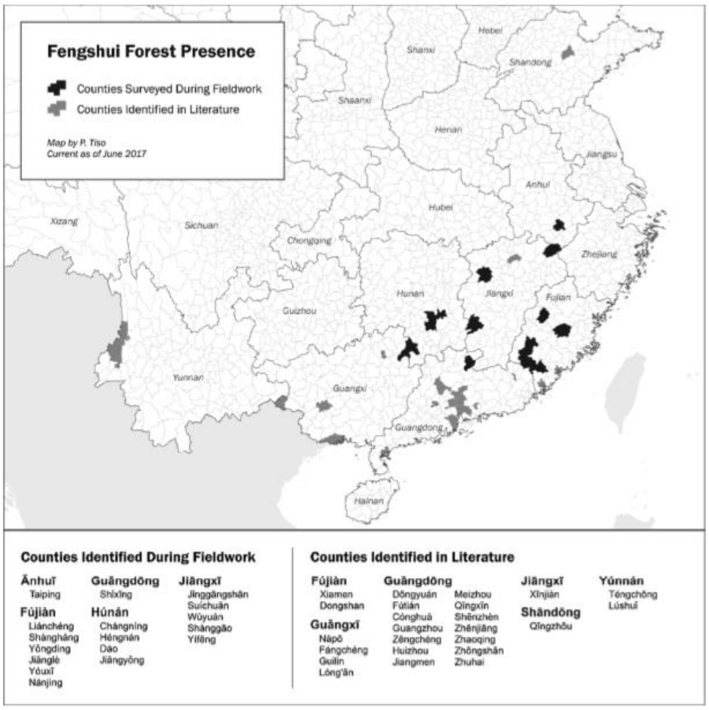

Figure 1. Counties in China identified by both fieldwork (in black) and literature (in grey) as containing *fengshui* forests. Province and county names and listed below the map. Figure taken from Chen *et al.* 2018.

Viewed as 'feudal superstition' and representing a source of valuable timber, many *fengshui* forests were destroyed during Chairman Mao's political reign (1949– 1976) (Coggins, 2003). This particularly occurred during the Great Leap Forward (1958-1961) and the Cultural Revolution (1966-1976). In fact, Tang *et al.* (2012) found the current existence of *fengshui* woods positively correlates with increasing distance from urban areas. In more remote areas, local people were reportedly able to persuade government officials that the trees were in fact 'scenic forests', providing protection from the wind, preventing soil erosion, and giving shade during field labour (Coggins, 2003). The fact that they received such strong civil protection during this period of political upheaval demonstrates their high cultural importance to local people. *Fengshui* forests often exist in landscapes otherwise dominated by fir and bamboo plantations which lack the floral diversity of the former subtropical forest, the habitat which once covered much of southern China (**Figure 2**). *Fengshui* forests in Fujian Province have been shown to harbour rare and threatened tree species such as Chinese hemlock (*Tsuga longibracteata*) and Chinese yew (*Taxus chinensis*) (Coggins, 2003). A recent review of *fengshui* forest research across Chinese language literature (Chen *et al.*, 2018) found that *fengshui* forests have demonstrably higher tree species diversity than other types of secondary forests or plantations.

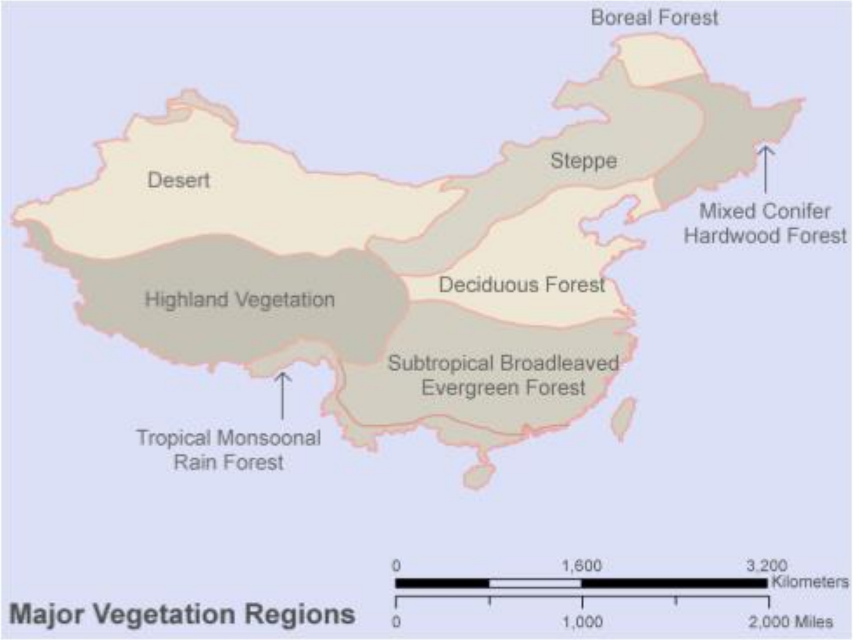

Figure 2. Map of the original vegetation regions covering China. Much of southern China was dominated by subtropical broadleaved evergreen forest. Figure taken from Coggins *et al.* 2012.

These native forest patches today face threats from market forces, dwindling adherence to traditional belief systems and urbanisation (Coggins, 2003). Wuyuan County, Jiangxi Province in China leads a new approach towards *fengshui* forests in China, with the local government affording state protection to many, designating them ‘small protected areas’ or ‘*baohu xiaoqu*’ (**Figure 3**; Hong *et al.* 2003; Wilkinson *et al*. 2004). This system has now been rolled out at the provincial level in Jiangxi (C. Coggins 2018, personal communication).

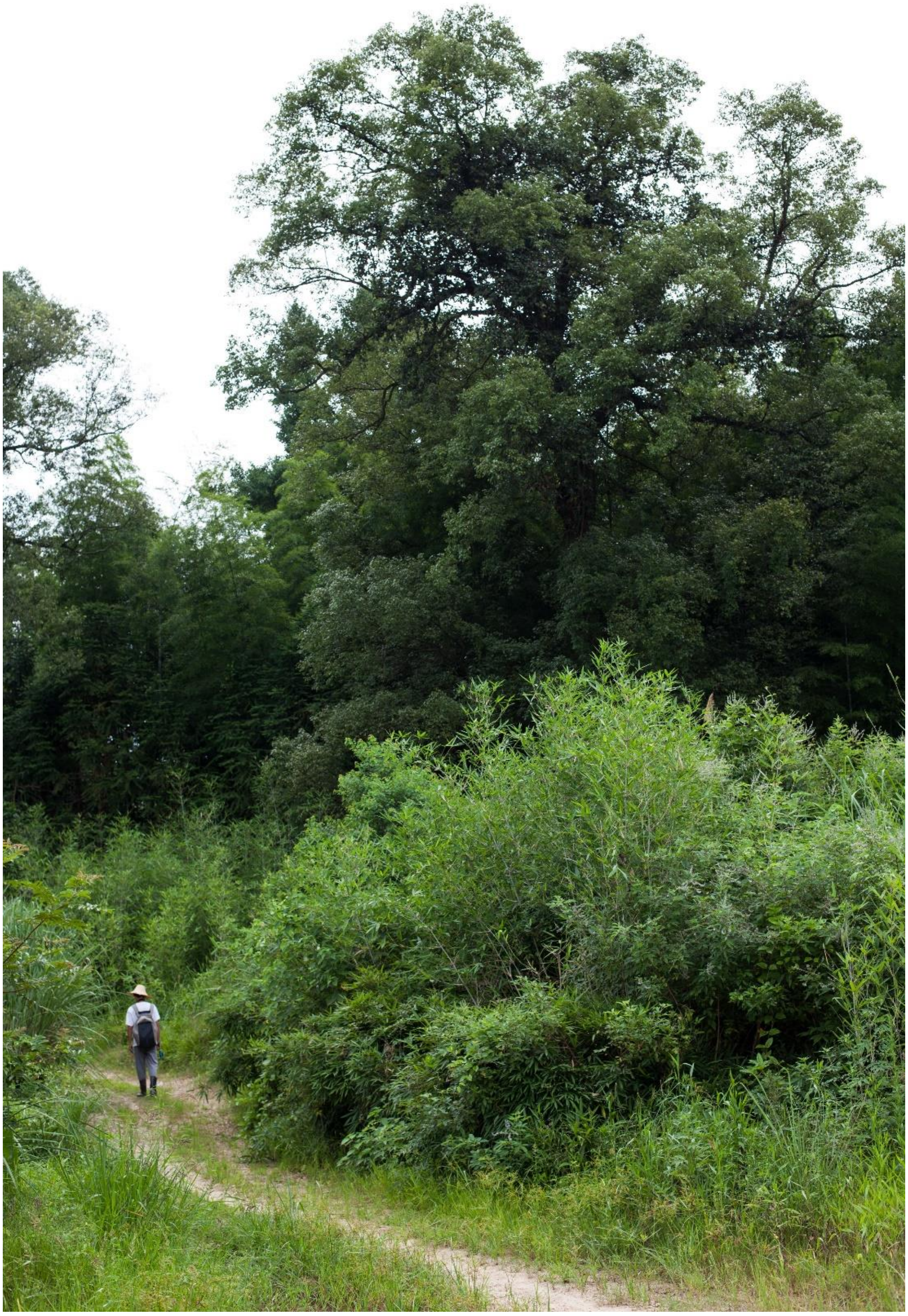

Figure 3. *Fengshui* forest from Wuyuan County, Jiangxi Province (Rosalind Gleave).

1.6 Contemporary rural landscapes in China

Many studies have highlighted the importance of landscape heterogeneity, or mixed-mosaics in agricultural landscapes, in supporting biodiversity (Fuller, Hinsley and Swetnam, 2004; Gabriel *et al.*, 2010; Fahrig *et al.*, 2011), with agricultural intensification in Europe strongly linked to declines in bird communities (Donald, Green and Heath, 2001). In China, this importance is no different, with richness and abundance of bird communities explained by quantities and heterogeneity of non-crop vegetation (Li *et al.*, 2020). Landscapes across rural Asia commonly feature densely populated and intensively managed 'village landscapes' (Ellis, 2004) which are composed of agroecosystems, forests and settlements for local income and usage (**Figure 4**). In China, however, these rural landscapes have experienced a shift from traditional to modern farming practices, which have been driven by both technical developments and political reforms from the late 1970s onwards, with a transition from integrative approaches such as intercropping and rice-fish systems, which supported reasonably high biodiversity levels, to a loss of landscape heterogeneity and increase of synthetic fertilisers and pesticides (Liu, Duan and Yu, 2013). Similarly, a comparison of land use at two villages on the Yangtze river plain between 1955 and 1977 showed large changes, relatable to national-level agricultural policies (Baudry, Yu and Liewan, 1999), with a loss of wetlands and increase in rice paddy fields. Urbanisation has also driven dramatic land use changes over recent decades. Between 1984-2012, urban land space increased by 1.53%, and loss of ecological land-space was highest in eastern China around Jiangsu and Zhejiang provinces (Wang, He and Lin, 2018). Overall, changes over the past 100 years to the rural landscape across China have been significant, and are likely to continue to be in the future.

Figure 4. Heterogenous vegetation in cropland around a village in Wuyuan County, Jiangxi Province (Rosalind Gleave).

1.7 The Blue-crowned Laughingthrush

The Blue-crowned Laughingthrush is a Critically Endangered colonially-breeding passerine, with its remaining known breeding populations restricted to northern Jiangxi Province, China. Its estimated Extent of Occurrence (EOO) is approximately 610 km^2 (BirdLife International 2017) which is sufficiently small to qualify this species as threatened under the IUCN's Red List framework (IUCN 2012). Its estimated Area of Occupancy (AOO), however, is unknown. Within this range, breeding populations are highly fragmented, with approximately only 13 known breeding sites in recent history (L. Gardner 2018, personal communication), and its population of mature individuals is considered in decline, altogether qualifying it for Critically Endangered status under criterion C2a (i,ii) (BirdLife International 2018). C2a (i) is 'no subpopulation estimated to contain more than 50 mature individuals' and (ii) is 'at least 90% of mature individuals in one subpopulation' (IUCN 2012). This is due to the Blue-crowned Laughingthrushes' small population size and overall decline, coupled with small, fluctuating subpopulations. The species has, since the late 1980s, been a topic of recurring discussion and study. Below, I outline what is currently known about Blue-crowned Laughingthrushes including their taxonomy, locations, breeding habitat requirements, behaviour, possible threats and past conservation actions.

1.7.1 Existing information on the Blue-crowned Laughingthrush

1.7.1.1 *Taxonomy*

The Blue-crowned Laughingthrush species is part of the family Leiotrichidae (Laughingthrushes and allies). This entire family previously sat within Timaliidae (Asian babblers), and there is no sexual dimorphism (Collar, 2006). Individuals are about 24.0 cm in total body length (23.8 – 24.6 cm) (Long *et al.* 2004), with an average mass of 40-50 g for captive birds (L. Gardner 2018, personal communication) (Collar, Robson and Sharpe, 2019). When first discovered from two skins collected in September 1919, in Wuyuan County, Jiangxi Province (**Figure 5**) (Menegaux 1923), *Pterorhinus courtoisi* was recognised as a distinct species (under the genus *Garrulax*); however, this was subsequently revised and the Blue-crowned Laughinghthrushes described from Wuyuan in 1919 were for many years considered a subspecies of the relatively common Yellow-throated Laughingthrush *Pterorhinus galbanus* (Berlioz 1930). The nominate form of this latter species was found in India and Myanmar (**Figure 5**). During this period Blue-crowned Laughinghthrushes were more commonly referred to as 'Courtois's Laughingthrush' (**Figure 6**). A second subspecies was described from specimens collected during 1956 in Simao district, Yunnan Province, China, called *Garrulax galbanus simaoensis* (**Figure 5**) (Cheng and Tang 1982). Following several birds turning up in consignments of mixed wild birds in Europe (Long *et al.*, 2004; Pasini *et al.*, 2004) there was renewed interest in the two Chinese subspecies. Based on morphometric scoring, *Pterorhinus courtoisi courtoisi* and *Pterorhinus courtoisi simaoensis* were eventually split from *Pterorhinus galbanus* and renamed the 'Blue-crowned Laughingthrush' (Collar 2006). Genetic work conducted between 2004-2007 did not give support for the separation of *P. courtoisi* and *P. simaoensis* from *P. galbanus* based on mitochondrial CO1 gene sequencing (Dunning 2007); however, recent analysis of four nuclear genes did give support for independence of *P. courtoisi* from *P. galbanus* on a genetic basis (Liu 2019).

The Yellow-throated Laughingthrush was first listed as endangered in the Red List of Chinese Species Volume 1 (Wang and Xie, 2004); then subsequently, as the Blue-crowned

Laughingthrush, it was listed as critically endangered in the Red List of Chinese Species Volume 2 (Wang and Xie, 2009). No reports were made of Blue-crowned Laughingthrushes as having been seen in the wild by any ornithologist or birdwatcher following collection of the type specimens in 1919. After wild Blue-crowned Laughingthrushes turned up in captive bird collections in Europe, however, concern for this species grew and many attempts to locate wild populations were made during the 1990s, funded by zoo consortium ZGAP, finally locating a breeding population in 2000 (Hong *et al.* 2003).

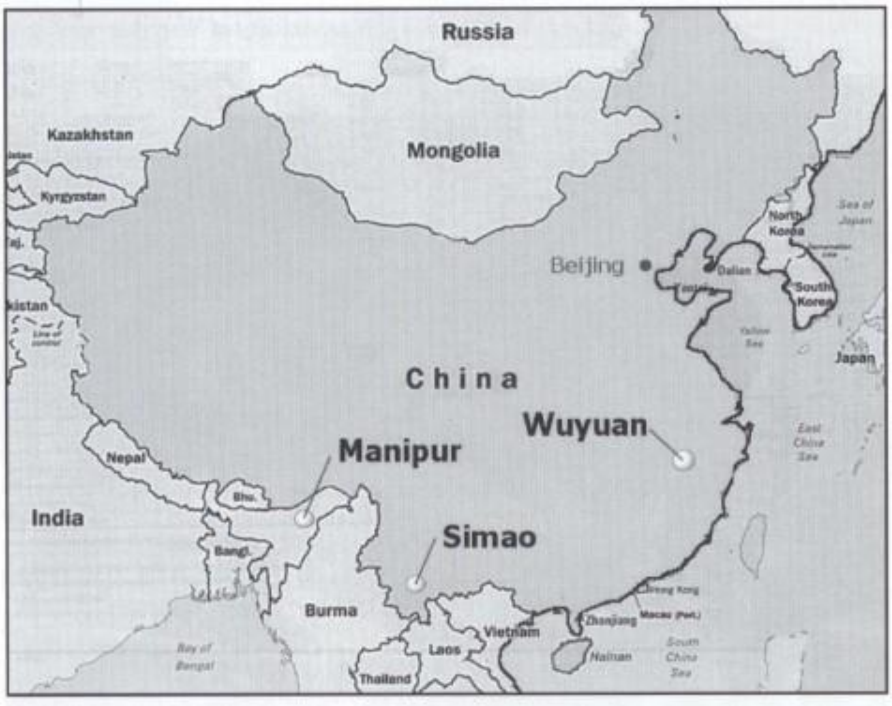

Figure 5. Map showing type localities of *Pterorhinus galbanus* (Manipur, India), *Pterorhinus courtoisi simaoensis* (Simao, China) and *Pterorhinus courtoisi courtoisi* (Wuyuan, China). Taken from Wilkinson *et al.* 2004.

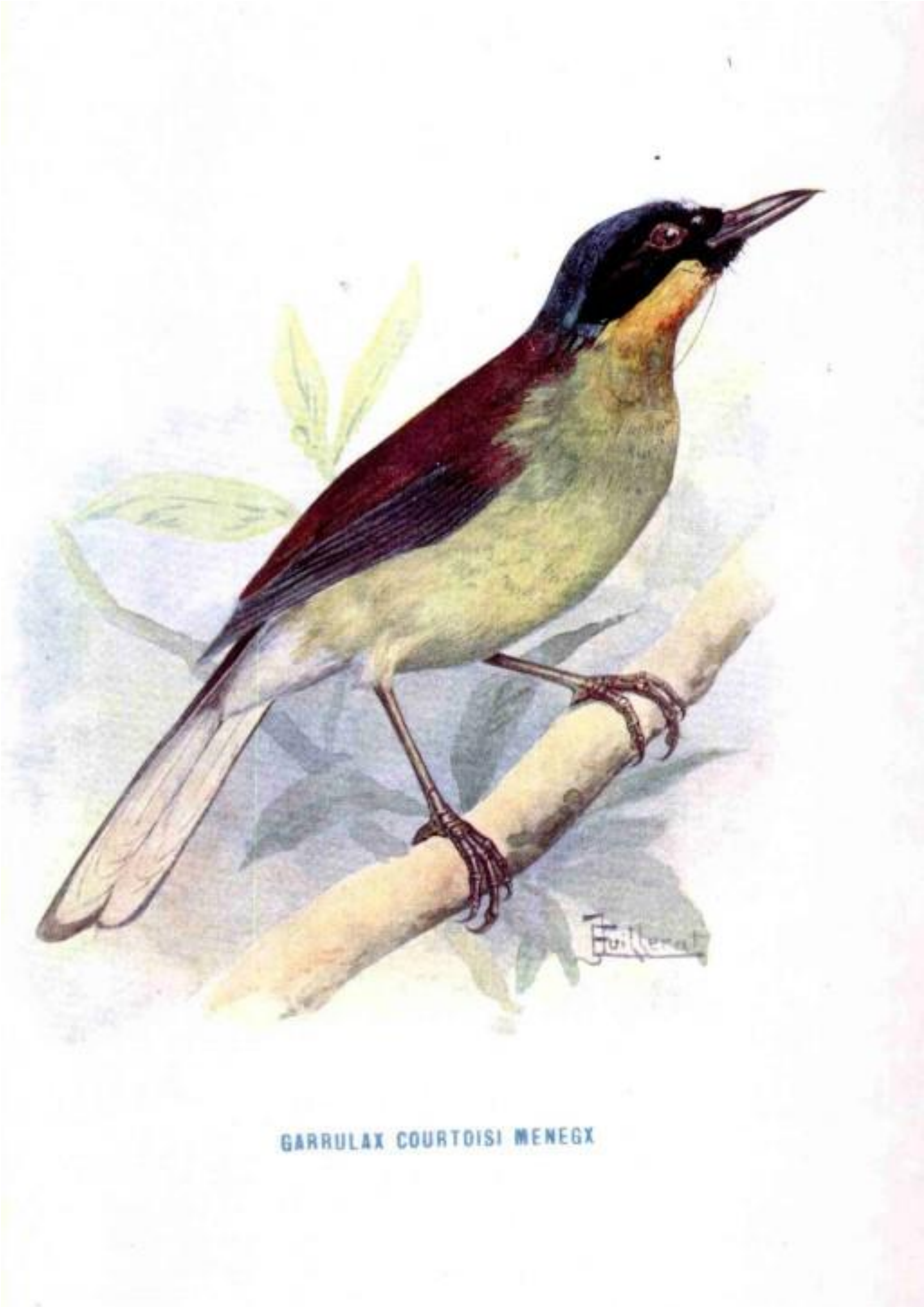

Figure 6. Colour plate of the Blue-crowned Laughingthrush, *Pterorhinus courtoisi*. Taken from Menegaux (1923).

1.7.1.2 *Locations*

Today, *P. c. courtoisi* breeds in northern Jiangxi Province; *P. c. simaoensis* was briefly sighted in Yunnan Province in 2005 (Richardson 2005) but since appears to have been extirpated after more than a decade of failed searches for a remnant population (He *et al.*, 2017). The landscape in Wuyuan, Jiangxi is described by He (1994) and Richardson (2005) as consisting of non-native conifer plantation, bamboo plantation and secondary sub-tropical forest growing on the low hillsides. In addition, small stands of large, mature, broadleaved trees grow on hillsides or flank rivers (**Figure 7**). Intensive agriculture is present in the valleys consisting of rice paddies, oilseed rape, tea plantations and vegetable gardens.

Figure 7. Typical Wuyuan County landscape (Rosalind Gleave).

1.7.1.3 *Breeding sites*

Much of the information to date about Blue-crowned Laughingthrush feeding behaviour and breeding site selection exists in grey literature rather than peer-reviewed articles. These include field reports from NGOs such as Hong Kong Bird Watching Society and Durrell Wildlife

Conservation Trust, as well as annual field report and census counts by Prof. Fenqi He of the Chinese National Academy of Sciences. Unstructured observations are provided in a series of Chinese-language papers on feeding and breeding behaviour (He and Xi 2002; Hong *et al.*, 2006; Liao *et al.*, 2007; Liu *et al.*, 2016). Few systematic or structured observations have been made that are subject to any statistical analysis, with the exception of Zhang *et al.* (2017), Huang *et al.*, (2018) and Liu *et al.*, (2020). Most reports or studies on the Blue-crowned Laughingthrush are on the Wuyuan population; a small number of sources mention only anecdotal data from Simao, Yunnan (He, 1994; Wilkinson *et al.* 2004).

Most reports or studies on the Blue-crowned Laughingthrushes concur with each others' primary findings. Blue-crowned Laughingthrush breeding sites are reported as being close to rivers and human habitation (Richardson 2005) and below 100 m elevation (Hong *et al.* 2004, Wilkinson *et al.* 2004). Blue-crowned Laughingthrushes are reported as staying in their breeding sites from April to July (Yu 2003, Zhang *et al.* 2017). Arrival time at these sites is influenced by the weather, with birds arriving earlier in a warmer spring. Departure from the breeding sites is reported as synchronous (Yu 2003) or as a few days after the young have fledged (Zhang *et al.*, 2017). The species has appeared to show a strong, though not necessarily exclusive, breeding site association with stands of *fengshui* forests (Hong *et al.* 2003; Yu 2003; Liao *et al.*, 2007). Hong et al. (2003) commented that 'it is interesting to speculate whether the subspecies has evolved some form of obligate relationship with human settlements during the breeding season, or whether their current breeding sites are simply a consequence of the fact that the only large, old trees now left occur around villages'. These forest stands are known to have deep cultural value and have been locally protected for centuries (Coggins, 2003).

Tree species selected for nesting are varied. Nesting trees are predominantly mentioned as subtropical broadleaf species, including Chinese Sweet Gum (*Liquidambar formosana*) (Richardson 2005; Hong *et al.*, 2006; Liao *et al.*, 2007; Zhang *et al.*, 2017; Huang *et al.*, 2018), Camphor (*Cinnamomum camphora*) (Richardson 2005; Hong *et al.*, 2006; Liao *et al.*, 2007; Zhang *et al.*, 2017), Chinese Ash (*Pterocarya stenoptera*) (Liao *et al.*, 2007; Zhang *et al.*, 2017, Huang *et al.*, 2018), Chinkapin (*Castanopsis sclerophylla*) (Hong *et al.*, 2006) and Hackberry (*Celtis sinensis*) (Richardson 2005; Zhang *et al.*, 2017; Huang *et al.*, 2018). Other tree types recorded as used for nesting include Bamboo (*Phyllostachys heterocycla*) (Hong *et al.*, 2006;

Zhang *et al.*, 2017), fruit trees (Richardson 2005; He *et al.*, 2017), conifers (He and Xi 2002; Richardson 2005; He *et al.*, 2017), Sweet Osmanthus (*Osmanthus fragrans*) (Richardson 2005; Wilkinson *et al.*, 2004; Zhang *et al.*, 2017) and palms (*Trachycarpus fortunei*) (He *et al.*, 2017), although nesting in these trees is reported as being less common.

Wilkinson *et al.* (2004) gave Blue-crowned Laughingthrush nest heights as normally being 4-15 m from the ground. Yu (2003) and Hong *et al.* (2003) both described the birds as nesting in large, ancient trees, and He *et al.* (2017) and Huang *et al.* (2018) described the birds as nesting in tall trees. Richardson (2005) corroborated these findings, with nest heights described as 3-16 m and a consistent association with large, mature trees. However, He et al. (2017) mentioned occasionally finding nests only 1.5 m from the ground. Blue-crowned Laughingthrushes were observed by Liao *et al.* (2007) as roosting away from the nesting sites (excepting those adults brooding eggs), in dense secondary broadleaf forests or shrubs between 100 – 950m from the nests.

Blue-crowned Laughingthrushes are often found breeding in colonies of between 10-80+ birds (F. He 2018, personal communication). Birds have occasionally been observed feeding chicks from other pairs (Yu 2003). Cooperative breeding behaviour was reported by Richardson (2005) and Wilkinson *et al.* (2004, 2010) with pairs within colonies breeding simultaneously, and having helpers at the nest. Cooperative breeding behaviour was further studied in captive birds (Liu *et al.*, 2016), finding that all adult birds participated in brooding, despite not all males having the opportunity to mate with females. Breeding success data are scarce, with scant data available from Jiangxi Agricultural University: three to four eggs are typically laid in each clutch and nesting success rates are as high as 80-90% (W. Zhang 2018, personal communication). It is clear Blue-crowned Laughingthrushes breed colonially, mostly in tall, broadleaved trees, close to human settlements; what is not clear is whether this constitutes an obligate breeding habitat.

1.7.1.4 *Behaviour*

Behaviourally, Blue-crowned Laughingthrushes are described in anecdotal field observation by Yu (2003) as gregarious, and typically active around the upper storey of *fengshui* woods, making frequent contact calls whilst foraging. Yu (2003) stated that during different surveys, the birds foraged both under the woodland canopy and close to the ground. Others reported the canopy layer was used most often from April to June, with a peak in May (Liu *et al.*, 2020). The birds have also been observed feeding on insect larvae caught from a tree trunk, and on fruits (**Figure 8**). Non-systematic feeding observations were carried out by Richardson (2005), describing the birds as foraging for 'small larvae, flies, moths and small wild fruits'. This author also observed that insect supplies seemed plentiful near water and human waste. Foraging for invertebrate prey becomes reportedly more important when feeding chicks (W. Zhang 2018, personal communication) a strategy common to many bird species (Wilson *et al.*, 1999; Anderson, 2006).

Figure 8. Blue-crowned Laughingthrush foraging for invertebrates (Rosalind Gleave).

Blue-crowned Laughingthrush have been described as foraging in vegetable gardens (Richardson 2005; Hong *et al.*, 2006; Liao *et al.*, 2007; He *et al.*, 2017; Liu *et al.*, 2020), tea gardens (Hong *et al.*, 2006; Liao *et al.*, 2007), shrubs and bushes (Liao *et al.*, 2007) and rice paddies (Richardson 2005). A recent study by Liu *et al.* (2020) investigated habitat use with radio telemetry, tagging a total of 17 birds. They found woodland was significantly preferred by Blue-crowned Laughingthrush, and that shrub/grass areas and vegetable plots were used relatively more than other habitats (including residential areas, other farmland, water and sandy beaches) except woodland. Collectively these observations indicate that Blue-crowned Laughingthrushes utilise a wide variety of food sources and prey items, and are unlikely to be extreme habitat or diet specialists, though they do show preferences for areas of woodland, vegetable plots and scrub.

1.7.1.5 *Threats*

Numerous threats to the Blue-crowned Laughingthrush have been reported since its rediscovery in the wild. These threats comprise both the risk of extinction to the Blue-crowned Laughingthrush population in the absence of targeted conservation measures, as well as stochastic events which affect its long-term persistence. It is possible that Blue-crowned Laughingthrushes were also once much more widespread, given the populations of *P.courtoisi* and *P.c. simaoensis* are each other’s closest relatives, and would in theory have once had greater connectivity; therefore, their numbers may have declined widely due to broad-scale factors. Thus, in their present situation, with a very small population, they are particularly vulnerable to proximate threats such as local human disturbance and flooding.

In terms of overexploitation, the subspecies *Pterorhinus courtoisi simaoensis* from Yunnan Province is thought to have become locally extinct through trapping for the bird trade (He 1994): over 400 birds are estimated to have been taken from the wild between 1987 - 1992, based on interviews with local trappers in Yunnan and Guangxi provinces (Wilkinson and He 2010). Referring to the Wuyuan subspecies *Pterorhinus courtoisi courtoisi*, Yu (2003) commented that ‘even small-scale trapping which focuses on the breeding site of the Laughing Thrush could completely extirpate the only known population’. According to local stakeholders, bird trapping activity is thought to be largely restricted to the Blue-crowned Laughingthrush population once found in Yunnan Province, with no current evidence of trapping in Jiangxi (Wilkinson *et al.*, 2004; Wilkinson and He, 2010) although two individual birds from a market in Hong Kong were traced back to Wuyuan (Yu 2003). Past or present trapping in Wuyuan has not been investigated in the field. Past occurrence of trapping in general is supported by the fact that the Blue-crowned Laughingthrush was rediscovered by encountering individuals through the international bird market (Yu 2003). Certainly, poaching to fuel the songbird trade remains a widespread issue across Asia, where wild songbird keeping is embedded in the culture.

Habitat loss may be playing a role in restricting Blue-crowned Laughingthrush population size and/or range, and certainly the species does appear to be selective over breeding sites; however, robust evidence for habitat loss representing an ultimate cause of decline is lacking. The Blue-crowned Laughingthrush's association with the Wuyuan landscape, which has been described as 70% forested and possessing large, old trees near villages (Hong *et al.*, 2003), points to a potential combination of factors which may be missing in other parts of southern China; however, the landscape in Wuyuan is also overall similar to other agricultural rural landscapes across other parts of southern and eastern China (Ellis, 2004). In the last known locality of *Pterorhinus courtoisi simaoensis*, Wilkinson *et al.* (2004) described the area as having depleted natural habitat, with few remaining trees.

Large-scale habitat destruction has taken place across much of southern China in the last two millennia, with vast replacement of original forests for plantations of chiefly fir, pine and bamboo between 1000-1700 CE across much of Jiangxi, Anhui and Zhejiang provinces and surrounding regions (Miller 2020). Later, massive population growth and land reclamation, with removal and continual suppression of large areas of former forest, occurred in southern China between the 17th and 19th centuries (Marks 1998), with this pattern culminating in widespread severe timber shortages across China by the 18th and 19th centuries (Elvin 2004). There was a concomitant loss or severe range reduction of many animal species including snub-nosed monkeys (*Rhinopithecus*) (Li, Pan and Oxnard, 2002), gibbons (Turvey, Crees and Di Fonzo, 2015), Asian elephants (*Elephas maximus*), Peacocks Elvin (2004) and South China tiger (*Panthera tigris amoyensis*) (Marks 1998); many of these declines were also accompanied by aggressive or targeted hunting.

In terms of other extinction drivers, there is no evidence to support the idea that introduced species and secondary extinctions may be playing a role in Blue-crowned Laughingthrush decline. Other threats have been described as directly human-mediated, with urban development and associated disturbance having already caused breeding site abandonment (Wilkinson and Gardner, 2011; He *et al.*, 2017), through processes including river channel repair, highway construction, and housing construction. Wuyuan has been promoted as a popular destination for Chinese domestic tourists since the late 1990s, building its brand as 'the most beautiful countryside in China' (Zhou, 2014, p. 228). This has seen ongoing development of holiday resorts in the county (Yu 2003). Tourists are also drawn to the area in spring by mass blooms of rapeseed flowers, which for this reason are supported by local authorities (Fu *et al.*, 2016), with unknown impacts on local wildlife. Increasing visits by wildlife photographers have even led to the abandonment of individual Blue-crowned Laughingthrush nests (Zhang *et al.*, 2017). Increased traffic flow stemming from tourism development next to a breeding site was also observed to cause a change in Blue-crowned Laughingthrush behaviour, and road building and urban development are considered responsible for destruction of nesting habitat and disturbance for one or more breeding sites (Wilkinson and Gardner, 2011; He *et al*., 2017). Although no other explicit record of tourist development has been shown to negatively impact Blue-crowned Laughingthrushes, the area is promoted as a tourist region with many plans for resorts near Wuyuan Town (Yu 2003). Indeed, I witnessed the construction of multiple tourist resorts throughout the region during field visits in 2018 and 2019, and the landscape appears to be changing rapidly (R. Gleave, pers. obs.). Without proper planning, this activity could well pose a serious future threat. There appears to be a tension between environmental protection and economic development in the region, mirroring similar situations in national parks and other protected areas across China (Wang *et al.*, 2012).

Stochastic events have also been implicated in affecting Blue-crowned Laughingthrush populations. For example, the most recent of these is flooding along the Le'An river, along which many Blue-crowned Laughingthrush breeding sites are found, which is thought to have caused Blue-crowned Laughingthrush to abandon a breeding site (F. He 2019, personal communication). Southern China experiences seasonal flooding each year, but 2017 saw catastrophic flooding which heavily damaged multiple Blue-crowned Laughingthrush breeding sites (FloodList 2017; L. Gardner 2018, personal communication). Another example is bird killing by local children (Yu 2003), and predation has been observed by Chinese Goshawks (*Accipiter soloensis*) and squirrels (Yu 2003), and with both Red-billed Blue Magpies (*Urocissa erythrorhyncha*) and Pallas' squirrels (*Callosciurus erythraeus*) being described as having aggressive interactions with the Blue-crowned Laughingthrushes at one breeding site (Richardson 2005).

1.7.1.6 *Conservation action*

A few key conservation actions have been taken for the Blue-crowned Laughingthrush. In terms of policy and/or legislation, the most notable is the creation of 'Mini Protected Areas' in Wuyuan County (Hong *et al.*, 2003; Wilkinson *et al*., 2004). Some of these overlap with known Blue-crowned Laughingthrush breeding sites, also protecting habitat for many other bird species (Hong *et al.*, 2003). However, more recently, calls have been made for China to cover gaps in national protected areas which do not cover all Blue-crowned Laughingthrush breeding sites (Li *et al.*, 2021). At the national level, Blue-crowned Laughingthrush received no official state protection until 2020, when it was added to China's list of protected animals under the highest protection, Class I (Ministry of Agriculture and Rural Affairs of the People's Republic of China 2021); this list had been largely unchanged since 1988 (China Dialogue 2020), before the species' 'rediscovery'.

On the ground, education work with local people in Wuyuan has taken place by raising public awareness of birds, as well as engaging students in bird conservation, with a particular focus on the Blue-crowned Laughingthrush (HKBWS 2011). Several talks on Blue-crowned Laughingthrush were also delivered to schoolchildren at an event at Caomen Primary School in May 2019 (near a well-known Blue-crowned Laughingthrush breeding site) by Panji Zheng, Daochang Liu, Rosa Gleave and Yikang Liu (**Figure 9**).

Figure 9. Rosa Gleave and Yikang Liu deliver a talk to primary schoolchildren at Caomen School as part of the international day of biodiversity, run by Wuyuan County Wildlife Protection Society.

Zhang *et al.* (2017) identified that disturbance from photographers was causing Blue-crowned Laughingthrushes at their Shimen island breeding site to nest higher up in trees compared to less disturbed sites. Visitors to Shimen island are now required to procure a research permit before entering the island, which prevents most photographers from entry. Photographers are now in effect restricted from photographing, except from the opposite riverbank from the main nesting area (R. Gleave personal observation).

1.7.1.7 *Knowledge gaps*

Although much information has been gathered on Blue-crowned Laughingthrush basic biology, ecology and threats since its rediscovery, there are still many key unanswered questions on this rare bird. The Blue-crowned Laughingthrush's geographic range, habitat and elevation when first discovered in 1919 is unknown; the type specimen of *Pterorhinus courtoisi* came with no information about its location beyond "Ouyuen" (Wuyuan), the county in which it is still found (Menegaux 1923). All other specimens are thought to come from subspecies *Pterorhinus courtoisi simaoensis* via a limited number of wild, or many captive, animals, and so very little is known about the habitat that Blue-crowned Laughingthrushes occupied when first discovered. Additionally, it is unclear whether there are key biotic or abiotic differences between Blue-crowned Laughingthrush breeding sites and non-breeding sites. Richardson (2005) observed that breeding sites may not necessarily be optimal or specifically chosen. The Blue-crowned Laughingthrushes in Wuyuan may represent remnants of a species that once bred more widely, with breeding sites instead chosen through site fidelity (Greenwood, 1980; Brown, Roche and Brown, 2017) or even lack of suitable sites (Miller and Mullette, 1985).

For the Blue-crowned Laughingthrush, information on its range prior to its formal scientific discovery in 1923 is strikingly absent. Studies on primate declines (Li, Pan and Oxnard, 2002; Turvey, Crees and Di Fonzo, 2015) give insight into general social and environmental changes across southern China during the last 400 years which may help understand the past scenario for Blue-crowned Laughingthrushes. Rapidly increasing human population densities, the expansion of cultivation and an increase in hunting is linked to fragmented and isolated populations of monkeys and gibbons, and these patterns could conceivably also be linked to the decline of other Chinese species.

If Blue-crowned Laughingthrushes are occupying a range that is neither ancestral nor optimal (in some way restricted by the actions of people), there may be any combination of the following factors. First, a positive association on any scale with habitats that are the climax vegetation type for the region, which in southern China may include, but are not restricted to, subtropical broadleaf forest (**Figure 2**) or scrub. Second, outside of their current range there may be past records, either written (in the form of gazeteer records or otherwise) or as part of local ecological knowledge (LEK), of habitat alteration and high human population levels, that are higher than within their range. If, however, the Blue-crowned Laughingthrushes' current range is ecologically 'natural', there could be differences between the landscape within their range and the landscape outside, due to differences in habitat that are not ecologically altered or mediated by humans: for example, an association with specific regionally endemic tree species or a natural climatic envelope, and an absence of other human-driven limiting factors.

1.7.1.8 *Non-breeding season*

A key unknown in Blue-crowned Laughingthrush ecology is where the species occurs outside of its breeding season each year (He and Xi 2002; Yu 2003; Hong *et al.*, 2003; Wilkinson *et al.*, 2004; Zhang *et al.*, 2017). As potential threats during this period could have an important bearing on population dynamics, this gap in knowledge is important to fill. Anecdotal reports suggest that the species might overwinter in secondary forests in the Wuyuan region (He 1994; Yu 2003; Wilkinson *et al*., 2004; He *et al*., 2017). All suggestions are based on verbal reports of sightings in winter by local people (**Table 2**).

Richardson (2005) also put forward that this may be the case. To this end, Richardson (2005) reported attempts in 2004 to attach a tracker device to two birds, hoping to record their movements post-breeding season, but this ultimately failed. They then planned to track at least 10 individuals in July 2005; however, there is no available report on whether this took place, or what the outcome was. Since then, no further attempts to track the birds beyond breeding sites have been mentioned in the literature. It is recognised as an important requirement; however as strong political and practical sensitivities exist around such invasive work on a Critically Endangered species in mainland China this information would be best obtained through more indirect means such as social surveys.

Table 2. Anecdotal reports of Blue-crowned Laughingthrush sightings from during the non-breeding season.

Date of non-breeding season report	Location given	Number of birds	Source
Winter 1991	Longshancun	4-5	He (1994)
Winter 1991	Kongcuncun	4-5	He (1994)
Winter 1991	Daijia	4-5	He (1994)
8 November 1997	Dawu, Changkeng & Dongwu around the Beilei Valley	2	Wilkinson *et al.* (2004)
December 2002	Wuyuan County	A few	Yu (2003)

1.7.1.9 *Relationship to fengshui forests*

As discussed earlier, Blue-crowned Laughingthrushes have intriguingly shown a strong positive relationship between their breeding sites and local '*fengshui* forests' (Yu 2003, Hong *et al.*, 2003, Hong *et al.*, 2006). These appear, at least superficially, to represent key breeding habitat for the species. This association surprised even the team of researchers who rediscovered the species in the wild, who stated: 'In fact, although we had thought we had surveyed all the potential habitats available for this laughingthrush in Wuyuan County in previous years, we failed to find any trace of the bird. However, while we were counting and identifying the large, old trees occurring around villages in 2000, the bird was suddenly and very surprisingly, right in front of us!' (Hong *et al.*, 2003). Given this strong, but anecdotal, association between stands of *fengshui* forest and Blue-crowned Laughingthrush breeding sites, it is important to quantify this potential relationship in helping to make landscape-level decisions about land management to benefit the Blue-crowned Laughingthrush in the future. As such, a deeper understanding of the past and current cultural value of these sites may be crucial to securing the long-term persistence of these birds in the Chinese landscape, which is undergoing rapid changes.

1.7.1.10 *Involvement in the Global Species Management Plan*

The Blue-crowned Laughingthrush has been in captivity since the late 1980s. The captive European population has been officially managed by Laura Gardner (formerly of ZSL London Zoo, now based at Wildwood Trust) since 2002-2003, annually publishing the European Studbook; this was approved as an International Studbook in 2012 (WAZA 2022). In 2015, the studbook was promoted to the status of European Endangered Species Programme (EEP), and as of 2018, the EEP population comprised 171 individuals in 39 member institutions (including ZSL London and Whipsnade zoos), plus four private members. The Asian zoos (including Nanchang Zoo in mainland China, which manages a population of the Wuyuan subspecies only) housed 39 birds across three institutions (WAZA 2022). The initiative is referred to as the Global Species Management Plan (GSMP), which convenes annually to manage the international captive breeding programme and share knowledge regarding optimal rearing of Blue-crowned Laughingthrush, but also liaises with Chinese partners in Wuyuan regarding *in-situ* Blue-crowned Laughingthrush conservation. Until 2017, the GSMP coordinated funding of annual census counts performed by Prof Fenqi He, as well as negotiating the renewal of a Memorandum of Understanding with the Wuyuan County Forestry Bureau (also referred to as Jiangxi Wuyuan National Forest Bird Nature Reserve Management Office). This PhD reports to and feeds into the *in-situ* conservation plans of the GSMP, and is part-funded by several of its member institutions.

1.7.1.11 *Collaboration with Jiangxi Agricultural University*

This PhD project collaborates, in addition to the above relationships, with a research group led by Dr Weiwei Zhang at Jiangxi Agricultural University, based in Nanchang, Jiangxi Province. Dr Zhang carries out annual research projects alongside undergraduate and graduate students on Blue-crowned Laughingthrushes, including annual census counts, surveys of breeding success and predation experiments. Dr Zhang has supported my research throughout the project, giving input into my study design, helping with logistics and hosting me at Jiangxi Agricultural University.

1.8 Thesis aims and overview

Chapter 2 details background information on the main study site at Wuyuan County, Jiangxi Province, including its geography, environmental history, avifauna and the ongoing impact of tourism. A discussion of methodological approaches taken throughout the research is also given here.

Chapter 3 collates and integrates all pre-existing information on the Blue-crowned Laughingthrush, carrying out analyses to better understand consistencies of independent counts over time, their long-term population trend, and biotic and abiotic factors across southern China associated with their spatial distribution. This aimed to help identify other potential unknown sites where the species might occur. A comparison of surveyed sites between independent observer groups was also conducted.

Chapter 4 examines local ecological knowledge of local landscape change, recognition of Blue-crowned Laughingthrush, and potential threats to this species and other birds. We also assess how known information on the Blue-crowned Laughingthrush compares to local knowledge. The aim was to associate landscape changes with Blue-crowned Laughingthrush presence and absence, better understand threats to the species, and explore whether this information could help identify priority areas for conservation of the species.

Chapter 5 focusses on habitat selection of the Blue-crowned Laughingthrush at the breeding site and nesting site scales. This was with the aim of characterising breeding or nesting sites versus control sites, and better understanding whether the species is restricted by local-scale habitat selection.

Chapter 6 investigates more robust species distribution modelling of the Blue-crowned Laughingthrush, through comparison of multiple model algorithms, rigorous validation and inclusion of a fine-scale land cover map based on past reported Blue-crowned Laughingthrush habitat associations. This aimed to help elucidate whether the species' range is restricted by bioclimatic or abiotic factors at a coarse scale.

Chapter 7 discusses the wider implications of the findings detailed in Chapters 3-6 through contextualisation within regional and global settings, and gives recommendations for future avenues of research.

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2. Introduction to Study Site and General Methods

"The most beautiful countryside in China" – Chen Fuli

In this chapter, I present a short history, geography, and ecology of the study region, Wuyuan County in Jiangxi Province, China, and surrounding regions, of relevance to the Blue-crowned Laughingthrush. I then give detail on general methods used for later chapters, mostly **Chapters 5** and **6** but also **3** and **4.**

2.1 The Study Region

2.1.1 Wuyuan County

Breeding locations of the Blue-crowned Laughingthrush have, to date, only ever been recorded in Wuyuan and Dexing counties, Jiangxi Province, China (**Figure 1**). The fieldwork for this project was undertaken in northeast Jiangxi Province and southern Anhui Province, China. Wuyuan County, Jiangxi Province (coordinates 29°01′~29°34′N and 117°22′—118°12′E) is central to this research, as it is given as the location of the type specimen for the Blue-crowned Laughingthrush from 1919, and where the Blue-crowned Laughingthrush was 'rediscovered' in the wild (Menegaux 1923). It has an area of 2,947.51 km^2 (Shi 2017) and a population of 360,000 (He *et al.*, 2014). Wuyuan's northern section is connected to the Huangshan mountains via the Wulong mountains, and its southern section to the Hauiyu and Wuyi mountains (Huang *et al.*, 2018). Wuyuan County contains many rivers, chiefly the Le'An, which is a tributary of the Rao. The Le'An originates from the Dayu and Wulong mountains in the north of Wuyuan County, and has many tributaries scattered across Wuyuan (Huang *et al.*, 2018).

In terms of climate, Wuyuan County is located within the subtropical region, and is humid and warm, with a relative humidity of 83% (He *et al.*, 2014) and four distinct seasons. It has an average annual precipitation of 1330.3 mm, average annual temperature of 17.7°C, an extreme high temperature of 41.0°C and an extreme low of -11.0°C (He *et al.*, 2014). The rainy season occurs from April to July, accounting for 61% of the annual rainfall, and sees frequent flooding (Huang *et al.*, 2018). The landscape is dominated by hills and mountains (He *et al.*, 2014), with mountain peaks in the north of Wuyuan reaching 800-1600m, and in the central and southern parts of county reaching 200-500m, but with an overall average elevation of 100-150m (Huang *et al.*, 2018). The county is estimated to have a forest coverage rate of 82.0%, with 48.0% of the forest area constituting native broadleaved forests (Hong *et al.*, 2006). In terms of agriculture, Wuyuan County produces green and chrysanthemum tea, oilseed rape (the last two attracting tourists to the region with their yellow flowers in spring; Zhou, 2014), rice, vegetables and commercial forestry (Richardson 2005).

Figure 1. Map of the core study area, Wuyuan County, Jiangxi Province, and surrounding counties in Jiangxi, Anhui and Zhejiang provinces. Thick black lines show provincial boundaries. UTM coordinates given.

2.1.2 Avifauna of Wuyuan

Wuyuan County has a reputation for being popular with birders, who are particularly drawn by species such as the Blue-crowned Laughingthrush, Pied Falconet (*Microhierax melanoleucos*) and Mandarin Duck (*Aix galericulata*). Wuyuan also supports many bird species in general, with records of 302 species belonging to 63 families (He *et al.*, 2014), and with 51 of those species belonging to the first and second order list of national protected species (Shi 2017). It straddles two biogeographic realms (Palearctic and Indo-Malayan) and is located along the East Asian bird migration route (He *et al.*, 2014). Yu (2003) recorded 111 species during a short visit, mostly from surveying *fengshui* forest and secondary woodland, noting Wuyuan as one of the best areas for birds in southern China. Richardson (2005) reported seeing 27 bird species at Blue-crowned Laughingthrush breeding sites in Wuyuan, including three species of Woodpecker, Silver Pheasant (*Lophura nycthemera*) and Dollarbird (*Eurystomus orientalis*). Internationally, parts of Wuyuan County are designated as a Key Biodiversity Area (Key Biodiversity Area Partnership 2022) and an Alliance for Zero Extinction site (Alliance for Zero Extinction 2022) due to populations of the Blue-crowned Laughingthrush and the Scaly-sided Merganser (*Mergus squamatus*).

2.1.3 Environmental History of Wuyuan

Wuyuan County was part of Huizhou Prefecture from the Tang dynasty (740 CE), becoming part of Jiangxi Province after 1949 (Zhang, Long and Zhao, 2019). Huizhou was at the epicentre of forestry practices which developed from the 11th to the 18th centuries in southern China, where hundreds of thousands of hectares of subtropical broadleaf forest were gradually clear-cut and replaced with hand-planted, often single species plantations of Chinese fir (*Cunninghamia lanceolata*) and bamboo, designated as taxable ‘forest’ acreage (Miller, 2020). Wuyuan had 46% of its land recorded as taxable forest in 1315 (Miller, 2020). Patterns of forest have changed across China over time, with a low of 8.6% forest coverage in 1949, which increased to 20% in 2012, although about a third of this is thought to be conifer plantation (Coggins *et al.*, 2012).

According to Hong *et al.* (2006), until the 1950s Wuyuan was: ‘still full of mountains with big trees and clear streams, and vegetation was dominated by typical mid-subtropical evergreen broad-leaved forests'. After this, much of these forests were cleared and replaced with conifer plantation forests dominated by pine and fir. Different logging bans were in place in Wuyuan during the 1980s-1990s to stem 'natural' forest loss (Hong *et al.*, 2006). In addition to a loss of native forests in the hills, there was a loss of *fengshui* forest in Wuyuan in the 1950s and 1960s during the Great Leap Forward and Cultural Revolution, with records of state-ordered *fengshui* forest loss in various villages across Wuyuan (Coggins, unpublished data).

2.1.3.1 *Mini protected areas in Wuyuan*

From 1993, the Wuyuan County Government began designating the traditionally preserved village *fengshui* forests as 'small protected areas' (*baohu xiaoqu*). As of December 2005, the county had 119 *fengshui* forest reserves (Shi 2017; Huang *et al.*, 2018). Some of these overlap with Blue-crowned Laughingthrush breeding sites (Wilkinson *et al.*, 2004).

2.1.3.2 *History of Blue-crowned Laughingthrush breeding sites*

Histories are not available for all known Blue-crowned Laughingthrush breeding sites, but information is available for some. For example, Zhongyun was a breeding site within a government administrative compound. This was originally called the 'Qilin Pavilion' (Wu Family Ancestral Hall) and was surrounded by ancient trees, then later demolished during the 20th century to make the government compound. Only a handful of the original trees remain (Hong *et al.*, 2006). Another, Taibai, lost 'scenic' (*fengshui*) forests to the expansion of residential buildings and vegetable plots (Hong *et al.*, 2006).

2.1.3.3 *Blue-crowned Laughingthrush Local Education*

The Blue-crowned Laughingthrush today is a feature of local education. It is part of a major exhibit at the local wetland museum in Wuyuan Town, the main town of Wuyuan County (**Figure 2a,b**), and has been drawn by local schoolchildren on a series of murals near to a key breeding site (**Figure 2c,d**).

Figure 2. (a) Sign featuring the Blue-crowned Laughingthrush at the wetland museum in Wuyuan Town, (b) detail from an artwork on the Blue-crowned Laughingthrush at the wetland museum, (c) and (d) both murals drawn by local schoolchildren of Blue-crowned Laughingthrush, close to their best-known breeding site.

2.1.4 Tourism in Wuyuan

Wuyuan County has been a famous domestic tourism destination in China since the late 1990s. During the 1980s, several films and TV shows showed Wuyuan as having beautiful scenery, generating growing interest in the county. Then, in 1993, photographer Chen Fuli held an exhibition in Hong Kong showcasing 'most beautiful countryside in China - Wuyuan' (Zhou, 2014). After this, the tourism industry in Wuyuan was more formally cemented, establishing a tourism bureau in 1998. In 2013, the county received up to 1000 million visitors (Zhou, 2014). The county has thus generally been a focus of investment and commercialization for the tourist industry leading to ongoing development works such as building tourist resorts and road infrastructure (Zhang, Long and Zhao, 2019). Some of these have already impacted or potentially impacted Blue-crowned Laughingthrush breeding sites, for example road construction at Hexi, and highway construction at Shimen (He *et al.*, 2017). More recently, modification of riparian forest habitat took place at Majia, a former Blue-crowned Laughingthrush breeding site, in 2019. Ground vegetation was cleared to make way for series of upmarket hotel cottages, but the nearby *fengshui* forest trees were retained as part of the aesthetic appeal of the site (R. Gleave *pers. obs*.). This could potentially alter the habitat sufficiently to deter future breeding of Blue-crowned Laughingthrushes. However, this breeding site had not been used by Blue-crowned Laughingthrush since 2001 by this point (F. He 2019, personal communication).

2.2 General Methods

2.2.1 Research journey

My journey began with a BSc in Biology (2005-2008), followed by several years of working to save up the substantial funds needed to carry out voluntary work as a research assistant on Ludwig's Bustard (*Neotis ludwigii*) in South Africa (2011) and then carry out an MSc in Conservation Science at Imperial College London (2012-2013). My MSc research took place at the SAFE project, a large-scale ecological experiment in Malaysian Borneo investigating changes in ecological processes at different spatial scales when tropical rainforest is converted to oil palm plantation, leaving behind forest fragments. My work focussed on the removal rates of seeds from the forest floor across a disturbance gradient, from old growth forest to secondary forest to oil palm plantation, comparing the relative input from vertebrates (i.e. rodents) to invertebrates (i.e. ants). This work was published as part of a larger paper in 2015, in *Nature Communications*. Whilst in Malaysia, I was hospitalised with an unknown, but severe illness, and on my return to the UK my digestive health was severely and possibly permanently altered.

Following this MSc, I worked at a medical non-profit while volunteering on the committee for Bristol Nature Network and for Avon Wildlife Trust (2014-2016). After unsuccessfully applying for a PhD, I joined BirdLife International (2016-2018) as their Partner Relations Officer, then also Conservation Evidence (2017-2018) as acting Managing Editor of their journal. At BirdLife I worked alongside Dr Nigel Collar who became my mentor and nurtured my ongoing wish to carry out a PhD. Quite by chance, this Blue-crowned Laughingthrush PhD became available, which I mentioned to Nigel - who it turned out had a very long-term involvement with the Blue-crowned Laughingthrush, even splitting it taxonomically from the Yellow-throated Laughingthrush into a single species in 2006. I began the PhD in 2018, and carried out a scoping trip to Wuyuan in the same year. During this scoping trip, I met my Chinese collaborators at Jiangxi Agricultural University, and familiarised myself with a number of Blue-crowned Laughingthrush breeding sites. I carried out my first full field season in 2019. I had secured funding from the Association of Zoos and Aquariums for a second field season in 2020; however, I was unable to carry this out due to the COVID-19 pandemic. However, I had luckily collected a large amount of data in 2019, enabling me to perform analyses for my research questions. Although, had I been able to collect further data, I could have expanded my geographic coverage for **Chapters 4** and **5**, visiting other surrounding counties in China. I was also unable to conduct interviews or habitat surveys at a new breeding site, which I was only made aware of on my return from China, as well as at one last eBird location.

The chronic health condition I developed during my MSc fieldwork has still not gone, and affects every aspect of my life and day to day tasks, including throughout my PhD. However, I have been taking on additional work throughout my PhD to fund my private treatment, including as a facilitator on an MSc course for the Royal Veterinary College, a teaching assistant at Royal Holloway, an event volunteer at London Zoo, and at a food market, which has developed my personal and professional growth in other ways. I have researched and implemented strict lifestyle changes which, alongside treatment, have resulted in large improvements in my health, especially when comparing the beginning of my PhD to now, which I consider the second biggest achievement in the last four years, only after this thesis.

2.2.2 Data collection

My research has involved a variety of data types and analyses, which are designed to complement one another.

Chapter 3 focussed on pre-existing Blue-crowned Laughingthrush data, so used existing monitoring data, data available from online citizen science websites, and freely available online remote sensing data that did not depend on any field-based data collection. I searched and/or approached the following citizen science data sources: eBird, Xeno Canto, HBW Alive and Oriental Bird Images. I asked Terry Townshend and Chinese collaborators about Chinese equivalents; however, they were unable to give me any suggestions. Despite this, I did by chance discover Bird Report, a Chinese website. Only eBird had location information that a) contained sufficiently precise metadata to provide accurate locations and b) were novel locations, not well-known breeding sites. Other data obtained were from Google Earth Engine (via USGS), Remap-App and WorldClim.

Chapter 4's data were collected by a team of two undergraduate and postgraduate students from Jiangxi Agricultural University, a high school student from Nanchang, and fifteen local high school students from Wuyuan and Dexing counties, who had all recently completed their *gaokao* (final) examination and were aged 18 or over. These assistants were spread unevenly across two months of data collection, and all were volunteers. Interview pilots were conducted with two volunteer assistants. All assistants were trained in interview methods and were initially supervised by a more experienced assistant once newly trained. Data were collected in June and July 2019.

Chapter 5's data were collected by a local high school student, a postgraduate volunteer, a high school student from Nanchang, and me. I piloted habitat survey techniques at some of same villages where **Chapter 4** pilots took place. Assistants were trained in habitat survey methods and supervised by me. Data were collected in June and July 2019.

Chapter 6 used ground-truthed land cover data collected by an undergraduate at Jiangxi Agricultural university, a high school student from Nanchang and me, working in a pair along stretches of quiet road, using an e-bike as transport. These data were used to validate land cover classification in Google Earth Engine. I also used the Blue-crowned Laughingthrush location data used in **Chapter 3**, as well as many of the same remote sensing data sources (Google Earth Engine and WorldClim). Data were collected in April - May 2019.

2.2.3 Interviews

Social science methods can deliver distinct benefits compared to standard ecological techniques (Turvey *et al.*, 2014; Nash, Wong and Turvey, 2016). Questionnaire surveys are likely the most broadly used method to gather social data in conservation, as they can be adapted to different contexts and cultures (Newing 2011). They can be standardised, allowing comparison among large numbers of participants across large geographical areas, and permitting quantitative analysis (Newing 2011), and can also be delivered face to face in cases of illiteracy. However, they are sensitive to the precise wording of questions, and may lack the ability to obtain a more in-depth understanding of issues (Newing 2011).

Piloting the questionnaires for the Blue-crowned Laughingthrush took place in seven villages in Wuyuan County, with a total of 40 interviews, carried out by two research assistants. Both assistants were trained on interview techniques beforehand, and I created a protocol document for future assistants based on lessons learned through this piloting process. Pilot villages were different to those included in final sampling design to ensure we were not repeating interviews with the same participants. The main issue raised by piloting was that many of the older respondents (>70 years old) could only speak the local *Wuyuanhua* dialect, not Mandarin (standard simplified Chinese). Unless addressed, this may have impacted the sample of people we were able to interview, missing older residents. The solution to this was to recruit high school students from the local area as volunteers, many of whom were able to speak fluent *Wuyuanhua*. Also, it is possible that respondents' more exaggerated claims of seeing Blue-crowned Laughingthrush (such as 'all year round, every day') were given more often when I was present for interviews, plus I tended to attract larger groups of people which interfered with the interviewing process. To counter this, I was not present for any interviews, instead collecting habitat data in the same village at the same time. Questions on last Blue-crowned Laughingthrush encounters were placed before questions on threats to birds, which may affect subsequent threat-related answers, if participants perceived the bird to be special in some way. I chose to do so as I was more concerned about Blue-crowned Laughingthrush identification, recall, and likelihood of volunteering information on sensitive behaviours being negatively affected if questions were placed the other way around.

All interview questions were translated by a research assistant and checked by another native Chinese speaker. All research assistants except one were from Jiangxi Province. No census information is available in China so I could not carry out probability sampling in selecting respondents, instead sampling by walking through villages and nearby farmland and encountering people at 'random'. Data collection had a cross-sectional study design, with the sample aiming to represent the population of the study area (Newing 2011).

2.2.4 Ethical considerations for working with human subjects

Ethical approval was obtained from the Royal Holloway, University of London ethics committee (reference no. 1536-2019-02-21-16-10-PEBA015). Prior to commencing interviews in villages, approval was also sought from village leaders. For each respondent, my assistants and I gave an opening statement explaining the purpose of the research: we stated we were from Jiangxi Agricultural University, conducting a study on the birds and landscape of that region, and that we wanted to learn more about the local environment from them. I obtained free, prior and informed consent from each respondent, and all respondents were assured their answers were anonymous and that they could stop the interview at any time. At the start of interviews, our assistants reassured respondents that there were no incorrect answers, that we just wanted to hear about their experiences, and always gave the option of 'don't know' answers. Research assistants introduced themselves as local students, and this positionality (aided further by involving high school students from the local area) helped respondents feel comfortable giving us information. Respondents were unwilling to give interviews at a small number of villages, where we were informed that local governments had either acted in an exploitative manner towards them or failed to act when they voiced their concerns over local issues. However, respondents at most villages were very welcoming and open in their readiness to be interviewed and their responses. In fact, in general, respondents did not appear reluctant to share potentially sensitive information on bird trapping during the pilot survey or main interviews.

Permission was granted by the relevant local government office (Jiangxi Wuyuan National Forest Bird Nature Reserve Management Office), with full transparency given over methods (they were shown a copy of the questionnaire). The government office gave us logistical support, including a local driver and contact with local schools as a source of volunteer assistants. However, no local officials joined any interviews, to prevent influencing responses. No raw data to the individual or village level was or will be shared with authorities, to protect participants; data will be shared with authorities as summary reports only. Finally, research assistants that contributed significant amounts of data collection are included as co-authors, and all others will be appropriately acknowledged (Brittain *et al.*, 2020).

2.2.5 Habitat data

The study of avian habitat use and selection has been studied for many years (Grinnell, 1904; Svärdson, 1949). Earlier theories were dominated by models correlating aspects of habitat and species abundance. These later became models involving density dependence ('ideal-free distribution' and 'ideal-despotic distribution' models; Fretwell and Lucas 1969; Fretwell 1972), then later into studies that factor, for example, how landscape structure can influence how 'ideal' or 'free' animals are while selecting habitats across landscapes (Karr and Freemark, 1983; Petit and Petit, 1996). The conceptual frameworks and terminology of researchers can be inconsistent in terms of 1). the meaning of habitat use vs selection, 2). contextualisation of outputs in terms of behaviour, and 3). the scale or order of the study. I will address 1). and 3). below.

2.2.5.1 *Habitat use and selection: definitions*

Habitats can be thought of as 'regions in environmental space' (Hirzel and Le Lay, 2008) made up of different environmental variables. These variables may be dynamic or static, and positively or negatively related to use. *Habitat use* is defined as 'the way in which an individual or species uses habitats to meet its life history needs' (Block and Brennan, 1993, cited in Jones, 2001, p. 557) and describes the actual distribution of individuals' across habitats (Hutto, 1985). It can also be defined as 'the quantity of that [habitat] component utilized by the consumer in a fixed period of time' (Johnson, 1980, p. 66). *Habitat selection* is 'a hierarchical process of behavioural responses which may result in the disproportionate use of habitats to influence survival and fitness of individuals' (Hutto, 1985; Block and Brennan, 1993, cited in Jones, 2001, p. 557). It is also thought of as the 'process in which an animal chooses that component [habitat]' (Johnson, 1980, p. 66), with use being considered selective if the habitat use is disproportionate to availability. Also, patterns of habitat use are considered 'the end result of habitat selection processes' (Jones, 2001, p. 557). A key implicit assumption of *habitat preference* studies is that all habitat within an available region is equally accessible, with habitat 'selection' and 'preference' terms often used synonymously (Beyer *et al.*, 2010). Beyer *et al.* (2010) also used selection as a species' behaviour in choosing a habitat, with preference trying to quantify selection given a habitat unit's availability; but this does not automatically reflect the underlying process. *Selection* also has 'a connotation of understanding complex behavioural and environmental processes' (Jones, 2001, p. 557).

There are two main ways that habitat selection is tested for breeding birds with territorial systems (Jones, 2001):

1). Comparing used with unused habitat, where 'used' is habitat currently occupied by the study species

2). Comparing used with available habitats, where 'available' is all habitat in a specific area, including the habitat currently in use by the study species

Johnson (1980) considered the used/unused habitat comparison as less informative than the used/available comparison. Logistic models can be used to estimate the probability of use for used/unused comparisons, creating a 'resource selection probability function' (Manly *et al.*, 2002). However, a species' absence from a given habitat does not automatically imply avoidance of the habitat, as many nonhabitat-related factors can influence habitat selection in birds. For example, population demographics and density can have big effects on whether habitats are used or not (Wiens, 1989; Haila *et al.*, 1996, cited in Jones, 2001, p. 558). Used/available tests are preferable as they facilitate inferences about choice. However, this can be an issue as habitat availability measures are very difficult; availability means the accessibility of resources and habitat, as well as the amount (Wiens, 1989; Hall *et al.*, 1997, cited in Jones, 2001, p. 558).

2.2.6 Modelling techniques

In terms of modelling these testing frameworks, for used/unused samples, logistic models can be used to estimate the probability of use. Outputs from this are referred to as a 'Resource Selection Probability Function' (Manly *et al.*, 2002). Resource Selection Functions (RSFs) are defined as any function that is proportional to the probability of the use of a resource unit by an organism (Manly *et al.*, 2002). For used/available samples, exponential models are often used to evaluate 'the relative probability of use' (Johnson *et al.*, 2006, cited in Beyer *et al.*, 2010, p. 2248) and fitted using logistic regression (Manly *et al.*, 2002).

Generalised linear mixed models (GLMMs) can accommodate several data issues: bias from unequal sample sizes, variation in preference among individuals of a species, and lack of independence in location data that is temporally correlated (Gillies *et al.*, 2006; Hebblewhite and Merrill, 2008; Fieberg *et al.*, 2009, 2010; McLoughlin *et al.*, 2010). However, the sampling design of available habitat has ramifications for the interpretation of these models. There is some debate around the appropriateness of using logistic (binomial) regression to estimate RSFs from use/availability data. For example, Keating and Cherry (2004) claim that logistic regression is often misapplied when modelling habitat selection, in terms of issues with interpretation and sampling design. According to them, there are three main sampling designs:

- **Random** (e.g. if nests are common and easily seen, choose random trees in a forest and record both characteristics and whether tree contains a nest)
- **Case-control** (e.g. if nests are uncommon but easily seen, to ensure the final sample has adequate number of nest trees)
- **Use-availability** (if only presence can be determined reliably, and nests are cryptic)

The key differences between these sampling designs is as follows, using trees and nests in a forest as an analogy: a random design gives a sample that contains nest and non-nest trees in approximate proportion to their occurrence in the forest; case-control gives a sample of nest and non-nest trees, but the relative proportions of each are determined by the researcher, and might not reflect the underlying population; use-availability gives a random sample of nest trees, and a second random sample taken from all trees in the forest, but it is not known if the trees in the second sample contained nests.

Case-control sampling is best evaluated in terms of odds ratios, which can be difficult to interpret in the context of a given problem. Odds ratios can be interpreted as an RSF, but only an approximation, with validity resting on the assumptions that probability of use is small for all habitats. If this goes above 0.10, the probability of use will be over-estimated (Zhang and Kai, 1998).

2.2.6.1 *Spatial scales*

Spatial and temporal scales influence how availability of habitat is perceived (Orians and Wittenberber, 1991, cited in Jones, 2001, p. 558). Johnson (1980) defined four orders of habitat selection that acknowledge its hierarchical nature and provides a useful empirical framework for habitat studies. The natural ordering of habitat selection processes are defined by Johnson (1980) as follows:

- 1st order selection: the geographic range of a species
- 2nd order selection: the home range of an individual organism, or a social group or colony
- 3rd order selection: how various habitat components are used within the home range
- 4th order selection: if 3rd order selection denotes a feeding site, then the foraging of food items from those available gives the 4th order scale

In my research, **Chapter 5** looks at second and third order habitat selection of the BCLT, while **Chapters 3** and **6** looks at first order selection. My second and third order sampling design made use of quadrats randomly distributed within larger circular sampling units around each village or settlement (**Figure 3**).

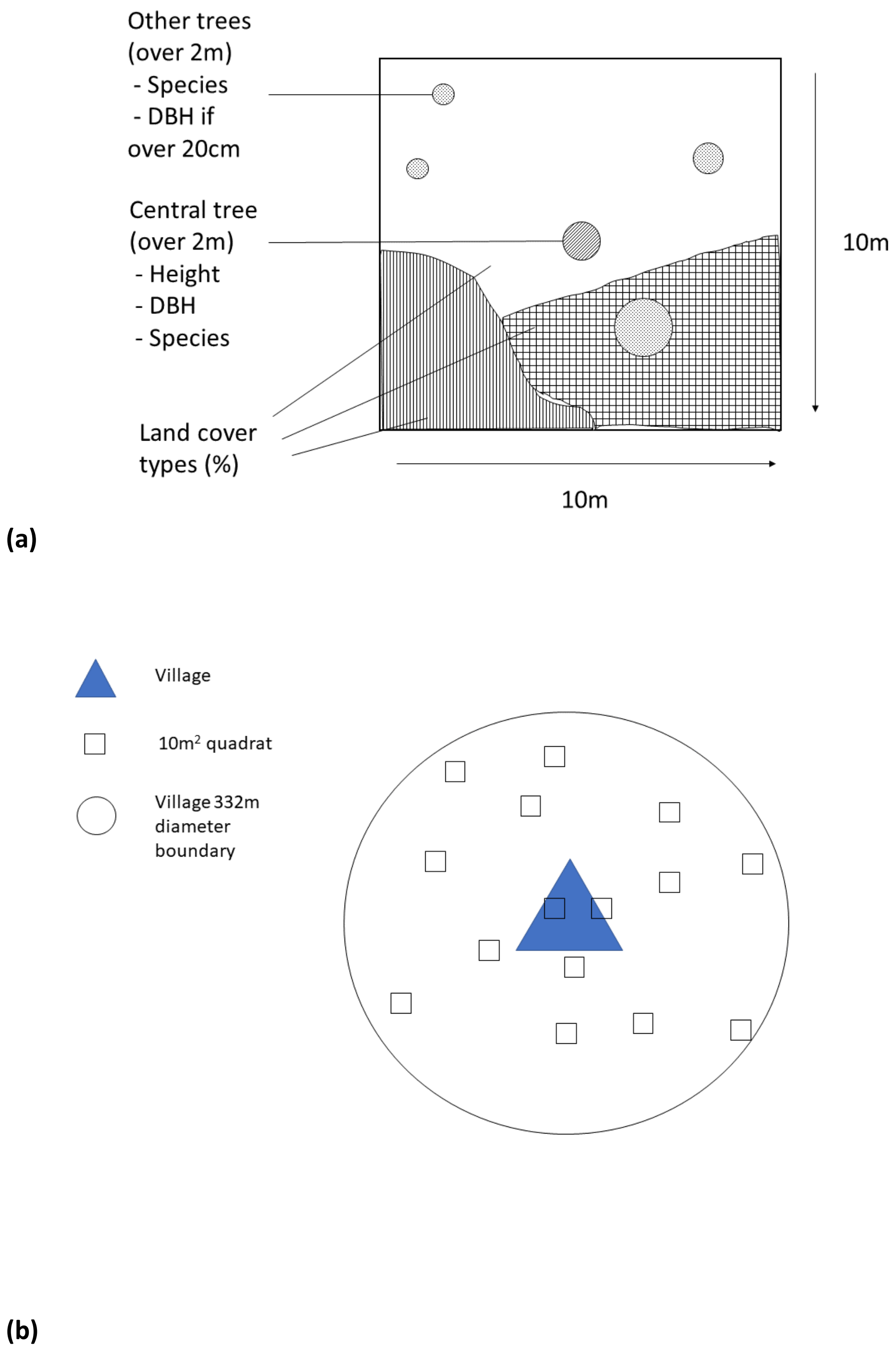

Figure 3. Diagram of **(a)** a square habitat survey quadrat. Each quadrat is centred around a specific tree, and the diameter at breast height (DBH) and species of each tree over 2m high was taken. The approximate percentage (to the nearest 5%) was given for each of a set of land cover types within the quadrat; **(b)** a circular survey boundary around each survey village or settlement. Fifteen quadrats were randomly generated within each circle. Second order analyses compare circles as survey units (with quadrats replicated within each unit, and third order analyses compare the individual quadrats as nesting or non-nesting quadrats, regardless of circular boundary.

2.2.7 Remote-sensing data

To date, no research has been performed on distribution of the Blue-crowned Laughingthrush at the landscape scale. First, I looked at its distribution using pre-existing information, without visiting the field for ground-truthed data, using a simple land cover map and with a single model algorithm, Maxent (**Chapter 3**). Next, I used field data collected in China to build a more complex land cover map, which complements habitat analyses performed at smaller spatial scales (**Chapter 5**) to use in a more robust species distribution model procedure (**Chapter 6**).

2.2.7.1 *WorldClim climatic data*

A set of 19 bioclimatic variables are available from the WorldClim website. These were developed to represent the kinds of seasonal trends relevant to the physiological constraints of different species and are widely used for species distribution modelling. The variables are averaged between the years 1970-2000 (Fick and Hijmans, 2017). I downloaded the highest resolution available (30 arc seconds), and all 19 variables, and checked collinearity separately across my two study extents for **Chapters 3** and **6**.

2.2.7.2 *Elevation*

Digital elevation data are available through Google Earth Engine via the Shuttle Radar Topography Mission, provided by NASA (SRTM; Farr *et al.*, 2007). SRTM was flown aboard the space shuttle Endeavour between February 11-22nd, 2000, and represents a near-global set of land elevations. I used the V3 product, which has a resolution of 1 arc-second (approximately 30m).

2.2.7.3 *Vegetation indices*

Vegetation indices are designed to enhance sensitivity to characteristics of vegetation in remote sensing, whilst reducing factors such as atmospheric effects and soil reflectance (Fang and Liang, 2014). Two of the most commonly used indices are Normalised Difference Vegetation Index (NDVI; Rouse *et al.*, 1974) and Enhanced Vegetation Index (EVI; Liu and Huete, 1995). NDVI enhances the contrast between soil and vegetation, and EVI was developed to optimize the signal in regions with high biomass or dense vegetation, hence its use for our study in subtropical China.

2.2.7.4 *Land cover*

Habitats can be mapped through categories of land cover and can be derived from pre-made maps or through customised land classification procedures. Both land cover and vegetation indices were derived from Landsat 8 Surface Reflectance imagery (**Chapter 3**) and Sentinel-2 (**Chapter 6**), through the Google Earth Engine platform (**Chapter 3 and 6**) and the Remap App tool for land cover (**Chapter 3**). Landsat 8 is 30m resolution, with five visible and near-infrared spectral bands, and two thermal infrared bands. Sentinel-2 is 10m resolution with three visible spectral bands, three red edge, one near-infrared and two short-wave infrared bands (Aschbacher and Milagro-Pérez, 2012).

As fitting SDMs to a large number of environmental predictors can give misleading outcomes, it is best to avoid this by defining a small number of predictors which are likely to be biologically relevant to the species in question (Peace-Higgins and Green, 2014).

2.2.8 Land classification methods

Classifications are used to quantify landscape features for different types of analysis. They involve taking imagery of a defined area, deciding on a classification scheme (defining the classes), collecting training and validation data, classifying the imagery, then assessing classification accuracy. The objective in my case is to better understand the relationship between Blue-crowned Laughingthrush occurrences or range and different types of habitat or land cover, through use of a land cover map in a species distribution model. Automated classification methods use computer algorithms to classify pixels. Automated classification methods fall into two categories: supervised and unsupervised. Unsupervised methods do not require training data: users specify the number of classes they want to identify and the algorithm divides the pixels by spectral information alone, into clusters of similar pixels. These are typically used for exploratory analyses. In recent years, machine learning algorithms have gained popularity as they do not require *a priori* information and are robust to large feature spaces, plus they can combine categorical with continuous data (Wegmann *et al.*, 2016).

2.2.8.1 *Supervised classification*

Supervised classification is defined by Wegmann *et al.* (2016) as follows: supervised classifiers use training data which are sample pixels of the classes to be classified. The algorithm uses these pixels to 'learn' the characteristics of those classes from their predictor values and uses that knowledge to classify all unlabelled pixels. Predictor values can be spectral bands as well as Vegetation Indices. I am using a supervised algorithm as I want to classify specific, pre-determined land cover types, and have prior knowledge of my study landscape as well as ground-truthed validation data.

2.2.8.2 *Types of supervised classifier algorithm available in Google Earth Engine*

Classification and Regression Trees (CART) (Breiman *et al.*, 1984): involves construction of a decision tree: a cascading system of asking questions of the data based on spectral values until the most probable class is reached. However, there are disadvantages to using a single tree, including some inaccuracies with new data.

Maximum Entropy (Maxent) (Berger, Della Pietra and Della Pietra, 1996): is a machine learning algorithm, which is often employed when users have relatively little training data compared to the number of variables they have. Maxent attempts to find the best probability distribution that satisfies various constraints. It also selects the probability distribution with the highest amount of entropy possible.

Minimum Distance (Wacker and Landgrebe, 1972): determines the mean of all the different classes. When classifying a new pixel, it works out which mean reflectance value for each land cover class is closest. The algorithm can cause issues as it does not consider the shape and distribution of groups of land cover data. However, this can be corrected through using Mahalanobis distance which corrects for data distribution.

Support Vector Machine (SVM) (Burges, 1998): tries to find the optimal line in feature space that separates the different classes, by maximising or equalising the distance between the two closest observations. The machine part creates new dimensions to separate more complex classes (through transformations, such as squaring axes), but also classifies through regressions. Users need to specify which type of SVM to use, as well as what kernel to use to split classes (the default is linear, and other options include polynomial, sigmoid etc.).

Random Forest (RF) (Breiman, 2001): involves multiple tree classifiers. It incorporates a factor of randomness into its decision making. Each decision tree contains a random component, and when new pixels are classified, it is done so by all of the decision trees in the 'forest'. The class that the most trees predict is selected for that pixel.

NaiveBayes (Kononenko, 1991; Hand and Yu, 2001): determines the odds of pixels having a certain value and being assigned a certain land cover class. It then compares the probabilities of all the variables for being part of the different classes. It assumes that features are conditionally independent of one another.

I selected RF for my land cover classification, and compared its performance to CART, due to their relative ease of use without specifying optimal parameters based on *a priori* knowledge (unlike SVM - https://developers.google.com/earth-engine/guides/classification). Also, these methods are non-parametric so less sensitive to the distribution of input data (Friedl and Brodley, 1997). CART and RF have previously been shown to perform highest for classification of other habitat types in Landsat imagery (Lee *et al.*, 2016).

2.2.9 Species Distribution Modelling

Species distribution modelling was used to describe the climate and habitat associations of the Blue-crowned Laughingthrush at the landscape scale in **Chapter 3** and **Chapter 6**. For Chapter 6, I used the R package *biomod2* (Thuiller *et al.*, 2009). All model algorithms available for *biomod2* are given in **Table 1**.

2.2.9.1 *Modelling techniques*

Table 1. Model algorithms available in *biomod2*.

Biomod2 name (*abbr*)	**Other name (*abbr*)**	**Data**	**Type**	**Reference**	**Use in chapter? Y/N**
Generalised Linear Model (GLM)	NA	Presence/Absence	Statistical, Regression	McCullagh and Nelder (1989)	Y
Generalised Additive Model (GAM)	NA	Presence/Absence	Statistical, Regression	Hastie and Tibshirani (1990), Yee and Mitchell (1991)	Y
Generalised Boosting Model (GBM)	Boosted Regression Trees (BRT)	Presence/Absence	Machine learning	Ridgeway (1999)	Y
Classification Tree Analysis (CTA)	Decision Tree Analysis (DT), Regression Tree Analysis (RTA)	Presence/Absence	Machine learning	Breiman *et al.* (1984)	N
Artificial Neural Networks (ANN)	NA	Presence/Absence	Machine learning	Ripley (1996)	N
Surface Range Envelope (SRE)	BIOCLIM	Presence only	Profile matching	Busby (1991)	N
Flexible Discriminant Analysis (FDA)	Mixture Discriminant Analysis (MDA)	Presence/Absence	Statistical	Hastie *et al.* (1994)	Y
Multiple Adaptive Regression Splines (MARS)	NA	Presence/Absence	Statistical, Regression	Friedman (1991)	Y
Random Forest (RF)	NA	Presence/Absence	Machine learning	Breiman (2001)	Y
Maximum Entropy (Maxent.Phillips)	NA	Presence/Background	Machine learning	Phillips *et al.* (2006)	Y
Maximum Entropy (Maxent.Phillips.2)	NA	Presence/Background	Machine learning	Phillips *et al.* (2006)	N

2.2.9.2 *Short description of each model type*

2.2.9.2.1 *Generalised Linear Model (GLM)*

GLMs have been used extensively as SDMs due to their good statistical foundation and capability in modelling ecological relationships (Austin, 2002) with multiple predictors. They fit parametric terms with a combination of linear, quadratic and/or cubic terms, and use a link function to describe how the mean of the response variable (Y) depends on linear predictors, and a variance function describing how Y's variance depends on its mean (Franklin 2009). GLMs can be fitted to presence/absence, count or ordinal data. Logistic regression is the most common form of GLM in SDMs using presence-absence data.

2.2.9.2.2 *Generalised Additive Model (GAM)*

GAMs use non-parametric, data-defined smoothers, fitting non-linear relationships between predictors and response (Elith *et al.*, 2006; Franklin 2009), with the coefficients of a GLM replaced by a smoothing function. They are more capable of modelling complex shapes of ecological responses than GLMs. Spatial predictions are made by importing new data (entire GIS datasets, with values for every pixel), predicting using existing software, and exporting the results as a GIS map (Franklin 2009). However, GAMs cannot be used to calculate species responses in terms of tolerance or optimums (Hirzel *et al.*, 2002) and as they are additive, it is difficult to add interaction terms. Despite this, they usually out-perform GLMs in SDMs (Meynard and Quinn, 2007), but GAMs often do not make accurate predictions outside of the ranges of the predictors upon which they are built (Pearce-Higgins and Green 2014).

2.2.9.2.3 *Multiple Adaptive Regression Splines (MARS)*

MARS is viewed as a generalization of stepwise linear regression, suitable to problems with many predictor variables, or as a modified regression tree approach (Franklin 2009). Its use of piecewise splines gives it a similarity to GAMs (Franklin 2009), and its coefficients are estimated for sections of the model between inflection points (knots) along the range of a predictor. Initially, a large model is fit, which is then pruned (made less complex) by iteratively removing basis functions which add the least to model fit. MARS is computationally fast for large and complex datasets, and more straightforward for spatial prediction than GAMs.

However, local variations in the data can bias results, leading to a loss of predictive power when extrapolating to new data (Franklin 2009).

2.2.9.2.4 *Generalised Boosting Model (GBM) & Classification Tree Analysis (CTA)*

GBMs, also known as Boosted Regression Trees (BRT), are a type of Decision Tree (DT). Decision tree models aim to partition, or divide, data into homogenous sub-groups (nodes) based on thresholds within ranges of predictor variable values, according to different classes or response variables (Franklin 2009). This occurs as three stages: 1). tree growing, 2). tree stopping and 3). tree pruning (Olden, Lawler and Poff, 2008). GBMs deal well with categorical predictors, interactions and threshold responses; however, they can also be unstable and have lower prediction accuracy than other methods, so new methods have been developed to counter this. BRTs create DTs many times (e.g. 30-80) without pruning and performing model averaging on the results, known as 'bagging'. 'Boosting' then refers to how each observation does not have equal weighting but instead has a higher probability of selection if it was misclassified by previous models (Ridgeway, 1999). A portion of the data are held 'out of each sample' and used to evaluate the model. GBMs are unique among ensemble tree models as they are sequential.

2.2.9.2.5 *Random Forests (RF)*

RFs are another type of decision tree 'bagging' that builds many de-correlated trees, which are then averaged (Hastie *et al.*, 2009). Many trees are developed from data subsets, as before, but now each split in the tree model is then developed with a random subset of the predictor variables. Many trees (500-2000) are grown without pruning, and then these predictions are averaged. Again, a test sample is held back for assessing model error, and variable importance.

2.2.9.2.6 *Artificial Neural Networks (ANN)*

Neural networks are large family of models based on the derivation of new, composite variables which are linear combinations of predictor variables; these then model the response as a non-linear (often logistic or sigmoidal) function of these composite variables, within a 'hidden layer'. They are, in essence, non-linear statistical models (Hastie *et al.*, 2001). ANNs are two-stage classification/regression models. For classifying *k* classes, there are *k* units in the output layer: for species occurrence (single class), then there is one unit in the output layer. Overfitting these models is prevented through limiting the number of iterations during the estimation procedure through cross-validation. Experience is needed to estimate these models: the user must decide the starting values for weights, number of hidden layers and other parameters. ANNs can be more difficult to operate than other modelling methods for SDMs, and have a steep learning curve.

2.2.9.2.7 *Maximum Entropy (Maxent)*

Maximum entropy is the principle from information theory/statistical mechanics that probability distributions with maximum entropy (the most spread out and closest to uniform), subject to known constraints, is the best approximation of an unknown distribution. This is because it makes no assumptions about unknowns, and agrees with everything that is known. In SDMs, the estimated distribution is derived from the multivariate distributions of habitat conditions that are associated spatially with species occurrence records. When applied to presence only data, Maxent has a higher predictive accuracy than other methods in comparisons, and it was designed for presence only data and to overcome issues with small, undesigned samples (Franklin 2009).

2.2.9.2.8 *Surface Range Envelope (SRE)*

SRE, also known as BIOCLIM, was one of the first species distribution modelling software systems. It creates a minimum rectilinear envelope around all presences (or 95% of them) giving a binary classification of suitable/unsuitable habitat (Franklin 2009). SRE is simple and recently used for applications such as planning species reintroductions (Pearce and Lindenmayer, 1998) and determining potential distributions of widespread species (Zhao *et al.*, 2006).

For my research, I left out three modelling techniques, as these are considered unlikely to improve the results, based on the available literature: **SRE (BIOCLIM)** due to its weaker performance (Elith *et al.*, 2006); **ANN,** as it is not easily interpretable, requires experience to fit effectively, and is disconnected from the underlying biological mechanisms (Franklin 2009); and **CTA,** as both BRT and RF show improvements on a single decision tree modelling process (Franklin 2009; Prasad, Iverson and Liaw, 2006).

2.2.9.3 *Model evaluation*

The available Blue-crowned Laughingthrush location data are not necessarily fully representative of its prevalence in the environment: there is likely to be some bias towards where the species is already known to occur, resulting in uneven field data collection with biased sampling across the known range. Therefore, to assess model performance, a model metric is required which is insensitive to species prevalence. Area Under the Curve (AUC) of the receiver-operating characteristic (ROC) is a measure of prediction accuracy (Hanley and McNeil, 1982) that is independent of a single threshold; conversely, threshold-dependent measures are sensitive to species prevalence (Franklin 2009). AUC typically indicates the proportion of time that a random selection from the positive (true positive or sensitivity) group will score higher than a random selection from the negative (false positive or 1-specificity) group (Fielding and Bell, 1997). However, for my dataset, which is composed of presence and pseudo-absences, AUC must be interpreted as the probability that a model scores a random presence site higher than a random background site (Phillips *et al.*, 2009). AUC values of >0.9 indicate good model performance, 0.5-0.7 moderate performance, and <0.5 poor performance (Franklin 2009).

As I had a small amount of location data available for the Blue-crowned Laughingthrush, I was unable to use 'out-of-sample', independent validation data. However, other techniques exist to instead partition sample data into 'training' and 'test' samples. These include bootstrapping (sampling, with replacement), jack-knifing (*n* – 1 partitions, used for training) and k-fold partitioning (*k* – 1 partitions, pooled for testing). These approaches all experience trade-offs between model accuracy (large training samples) and lower variance in the estimate of error (large testing samples), which can be overcome using repeated instances of model partitioning and fitting (Fielding and Bell, 1997). Training and test points are typically randomly assigned per model run; however, this approach is associated with the risk of spatial autocorrelation (Pearce-Higgins and Green 2014), as it may select training and testing locations that are geographically close together.

I used the approach carried out by Bladon *et al.* (2019, 2021), partitioning my presence and pseudo-absence data into radial partitions. I chose three partitions due to the small number of available species presence records, and spread these spatially across my study region to achieve an equal number of points per partition, but resulting in very different numbers of pseudoabsences. Panels were created by splitting the study area from the Blue-crowned Laughingthrush range centre. The range centre was based on the simple mean and the x and y coordinates of all presence records; this showed less bias towards more distant, northern records than a range centre based on the geodesic centroid of the convex hull around all records, or a geodesic centroid of different sized cells. I started from due north and split the area into roughly equal partitions, then adjusted these until presence locations were distributed as equally per partition as possible.

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3. Re-writing the baseline: integrating monitoring and citizen science data to guide conservation for the Blue-crowned Laughingthrush *Pterorhinus courtoisi*

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3.1 Abstract

Evidence is needed to develop and monitor appropriate conservation actions, with key components of baseline data including population trends, and factors explaining spatial distribution. However, although important for developing an evidence base, monitoring data are often not collected using standardized protocols, and might be unable to track population trends accurately. Blue-crowned Laughingthrushes (BCLT; *Pterorhinus courtoisi*) are a Critically Endangered colonially breeding passerine found only in southeastern China, but there is little understanding of their true population trends or why their breeding range is highly restricted. By combining, contrasting and analysing two independently collected monitoring datasets from 2000-2017, we gained important new insight into BCLT population trends, and bioclimatic and abiotic influences on their spatial distribution. We found that the long-term BCLT population trend has not changed significantly over time, and that the total population in 2017 may be 42.8% higher than previously thought. Independent counts at the same sites showed minimal observer differences, but only 60% of known breeding sites were monitored by both sets of observers. Breeding site occupancy increased over time, although this may be due to changes in survey effort. A species distribution model using both monitoring data and independently available citizen science data indicates that BCLT presence is associated with annual temperature ranges between 30-34°C, elevation between 0-400m, and mean precipitation of 600-1000mm in the wettest quarter (impacting the BCLT during their breeding season). The model also identifies suitable regions outside the known BCLT breeding range that should be surveyed for additional breeding sites. Our results show that integrating and analysing multiple sources of pre-existing data on threatened species can provide key information into their long-term population trends and better understanding of their environmental requirements.

Keywords: Maxent, SDM, citizen science, monitoring, population trend, laughingthrush, *Pterorhinus courtoisi*, China

3.2 Introduction

Evidence in conservation is required for developing effective management frameworks, and for avoiding unwanted outcomes from interventions (Sutherland *et al.*, 2004, McCarthy & Possingham, 2007; Nichols & Williams, 2006; Travers et al., 2019). However, threatened species are often poorly understood and lack robust baseline data on population size and dynamics, distribution, and/or threats from which to design effective conservation action. Accurate characterisation of population trends is especially important for the management of threatened species (Joseph *et al.*, 2006), with inaccurate estimates potentially limiting the ability to determine the effectiveness of management actions (Wiest et al. 2018). These inaccuracies can lead to inappropriate assessment within metrics such as the Red List Index (Connors *et al.*, 2014; Fox *et al.*, 2019), or even potentially allowing species to decline or become extinct before effective conservation responses can be implemented (Collar 1998). Understanding the factors that underpin spatial distributions of threatened species is also crucial to developing appropriate conservation actions, especially for highly range-restricted species; these can be caused by drivers as wide-ranging as climate, habitat specialisms, habitat loss or overexploitation (Jones, Linsley and Marsden, 1995; Zhou *et al.*, 2005; Donald *et al.*, 2012; Monadjem *et al.*, 2019; Colyn *et al.*, 2020).

Many long-term monitoring programmes have been established with the goal of accurate population trend detection (Durant *et al.*, 2007, Sauer *et al*. 2013). Effective long-term monitoring programmes should have clear objectives and consistent methods, address defined questions, and possess adaptive sampling designs capable of detecting change (Field *et al.*, 2007; Lovett *et al.*, 2007). For some threatened species, long-term monitoring datasets may already exist in the form of unpublished grey literature, such as government or consultant reports and student projects, forming valuable and potentially untapped resources (Awan, Buner and Kingdon 2015). However, monitoring data are frequently collected within frameworks lacking one or many of the above traits (Reynolds, Thompson and Russell, 2011; Lindenmayer *et al.*, 2012). Studies that do not follow recommended requirements can result in limited or biased data which are unusable, have low statistical power, or contain inaccurately perceived trends (Field *et al.*, 2007). A lack of statistical power can be particularly critical when dealing with threatened species with already low numbers. With a rigorous analytical process, it can often be possible to detect underlying ecological signals in such datasets that can feed back into and refine monitoring protocols (Field *et al.*, 2007; Holland *et al.*, 2012). However, few studies have yet employed rigorous analytical approaches when trying to interpret non-systematically collected monitoring data for species of conservation concern.

Spatial presence data may also be available for threatened species from multiple sources, including both published scientific sources and grey literature. Presence data can be modelled alongside environmental data to understand species' niches or distributions at a variety of spatial scales (Elith and Leathwick, 2009). Species Distribution Models (SDMs) have been a common tool in recent decades for understanding the determinants of restricted species ranges (Araújo & Guisan 2006), and can use readily available remote sensing data (Bradley & Fleishman 2008). SDMs extrapolate species distribution information both spatially and temporally, investigating which environmental variables (e.g. bioclimatic or land cover) correlate with species presence. Important applications for SDMs include providing explanations for the causal determinants of a species' range (Rodríguez *et al.* 2007), as well as predicting current or future distributions (Hamazaki, 2002; Menon *et al.*, 2010; Bladon *et al.*, 2021).

However, whereas larger sample sizes ($n \geq 50$) have a positive effect on SDM accuracy (Hernandez *et al.*, 2006), threatened species can suffer from limited data from which to estimate distributions or environmental associations (Chen *et al.*, 2018). To maximise model accuracy through increased sample size and geographic coverage, monitoring datasets can be supplemented with secondary data available from sources such as citizen science activities (Tulloch *et al.*, 2013; Lees and Martin, 2015; Tiago, Pereira and Capinha, 2017). Citizen science data have many potential benefits, including new records of rare species (Bonney *et al.*, 2009; Dickinson, Zuckerberg and Bonter, 2010) and large datasets over broad geographic areas (Tulloch *et al.*, 2013), but can also be affected by low estimate precision (Snäll *et al.*, 2011), uneven survey effort, errors within records (Robertson, Cumming and Erasmus, 2010), and taxonomic misidentification (Tiago, Pereira and Capinha, 2017). However, despite these potential issues with data integrity, citizen science data can generate usable predictions for species distributions (Coxen *et al.*, 2017; Tiago, Pereira and Capinha, 2017); and combining data from citizen science projects with other data sources has revealed a range of novel conservation insights for many threatened species (Lees and Martin, 2015; Lees, 2016; Giovos *et al.*, 2018; Yang *et al.*, 2018; Giovos *et al.*, 2019).

A species that would benefit from critical assessment of existing data sources is the Blue-crowned Laughingthrush (BCLT; *Pterorhinus courtoisi*), a brightly coloured passerine with an extremely restricted breeding range. The only known extant population breeds in northern Jiangxi Province, China (He *et al.* 2017) and its historical distribution is unknown (Wilkinson *et al.* 2004), as its type specimen was collected from a locality within its current limited range (Menegaux 1923). A second population known from Yunnan Province, usually recognised as the separate subspecies *P. courtoisi simaoensis* (although see Collar *et al.* 2019), is now regarded as extirpated (Wilkinson and He 2010; He *et al.* 2017). As BCLT breed next to villages and agricultural habitat (Richardson 2005; He *et al.* 2017), it is unclear why the species is not more widespread across other human-occupied and modified landscapes in southern and central China (Ellis, 2004). The BCLT is Critically Endangered (BirdLife International 2018) with a maximum estimated population size of 348 individuals at five known breeding sites in 2017 (He *et al.* 2017, BirdLife International 2018). Its Red List status is precautionary, based upon the species having a small, fragmented known range, and a very small population that may still be in decline (BirdLife International 2018). While the species has only ever been recorded breeding in northeast Jiangxi, the possibility of overlooked breeding sites does exist (Hong *et al.* 2006; BirdLife International 2018).

Long-term monitoring data on spatial and temporal BCLT population dynamics have been collected since 2000, with two independent survey datasets available from different teams. Additional opportunistic BCLT observations are also available from a citizen science database (eBird.org). However, these data have not yet been integrated or assessed within a robust quantitative analytical framework, and previous assessments of BCLT population trends have been based on simple plots of raw data. Furthermore, there have been no studies on BCLT landscape-scale biotic and abiotic requirements associated with these available presence records, with ecological investigations limited to small-scale studies of breeding sites (Zhang *et al.*, 2017; Huang *et al.* 2018; Liu *et al.*, 2020). This limited assessment of available data represents a possible barrier to understanding the species' biology and ecology, thus hindering the possibility of developing a successful implementation plan for population recovery. A better understanding of BCLT population trends and ecological requirements could also be used to inform a more robust Red List assessment for the species.

This study investigates whether combining and contrasting different pre-existing data sources and analytical approaches has the potential to contribute to effective conservation management of the BCLT, through: (a) establishing a better understanding of its long-term population trends; (b) establishing a better understanding of its biotic and abiotic requirements at the landscape scale, based on its breeding range; and (c) identifying other potential locations to search for previously unknown breeding sites. Our findings provide a strengthened evidence-base for this poorly-known species, and also provide a template for maximising the information-content of other highly threatened populations through critical evaluation of existing sources.

3.3 Methods

3.3.1 Datasets

3.3.1.1 *Census datasets*

The Jiangxi population of BCLT is only known from two adjacent counties in northeastern Jiangxi Province, China (**Figure 1**): Wuyuan County (29°14’53”N, 117°51’43”’E) and Dexing County (28°55’50”N, 117°35’41”E). Two BCLT census datasets are available for these counties: (1) dataset collected by Fenqi He (henceforth ‘HFQ’) in 2000-2017; (2) dataset collected by Weiwei Zhang (henceforth ‘ZWW’) and her MSc students in 2012-2017. Both observer groups performed counts at 12 breeding sites.

The HFQ dataset was collected through annual field visits during the BCLT breeding season (between April and July) (Yu 2003; Zhang *et al.*, 2017; Liu *et al.*, 2020). For the first few years of the census, a core area around sites 1-3 (**Table S1, Supplementary Information**) was surveyed, as the principal focus of the researchers was on BCLT breeding ecology. During *c*.2006-2007, a wider search was performed for new breeding sites at locations within Wuyuan and Dexing counties and in adjacent regions of southern Anhui and western Zhejiang provinces considered to contain potentially suitable habitat (**Figure 1**). In subsequent years, the same sites in Wuyuan and Dexing counties were surveyed, with additional areas also surveyed each year; HFQ searched for nine breeding colonies each year, and searched for new sites if these colony were not located where they had previously been found. HFQ looked actively for new breeding sites and discovered new locations across a wide area, but did not record sites that are very close to other known ones, possibly because search effort stopped after nine colonies were identified. BCLT breeding colonies were detected near the start of the breeding season both visually and acoustically, as they have distinctive contact calls that are easy to distinguish in the field (F. He, 2019, personal communication). Once breeding sites were confirmed, counts were made of all adult birds present at the site; counts were performed at this time of year because BCLT flocks tend to move between trees or vegetation patches as a single group at the beginning of the breeding season, flying in a 'follow the leader' formation that facilitates more precise counts (F. He 2019, personal communication). A subsequent visit to these sites was also typically made later in the breeding season, to re-confirm that the birds were indeed breeding based on the location of active nests.

The ZWW dataset was collected by checking for the presence of breeding birds at all past BCLT breeding sites known to the research group, by visually looking for nests. Searches also took place on an annual basis between April and July. Sites surveyed each year were based on sites previously discovered by HFQ; no potential new breeding sites were systematically checked or monitored, although opportunistic checks were made of sites if BCLT were heard in passing. This observer group did not actively searching for new colonies but instead typically spent longer periods in small geographical areas, increasing the likelihood that new local sites could be discovered opportunistically.

Neither set of bird counts were conducted following a standardised survey methodology. In each dataset, the sum of the counts from each site was treated as a total population count (a census) for each year, or absolute numbers of individuals, rather than a sample. No birds possessed colour rings or other ways to mark or recognise individuals. The census datasets were georeferenced to the scale of specific villages within or adjacent to which BCLT were recorded as breeding, providing presence-only data. No data are available on survey effort, detectability, absence of birds from all visited sites during any survey years, or specific survey dates for each annual survey. These datasets were integrated by holding discussions with each observer group to ascertain exact locations, then developing a new numbering system (**Table S1, Supplementary Information**).

3.3.1.2 *Citizen science data*

We collated all georeferenced BCLT location records available on www.eBird.org. eBird is a global data portal for birdwatchers to input their bird sightings to the benefit of researchers (eBird 2019). We interpreted all records as accurate identifications, as the BCLT is a highly distinctive species that is difficult for reasonably competent birdwatchers to confuse with other locally occurring species. A request was made to eBird for sensitive and protected location data from the online platform, recovered records of 41 BCLT sightings; these were predominantly from Wuyuan County, with a single sighting reported in southern Anhui Province (**Figure. 1**). Records at all locations dated from 2008-2018, and were all recorded during the BCLT breeding season (April to June); however, as these are past records, we cannot confirm whether these individuals were observed at breeding sites or were passing through the landscape.

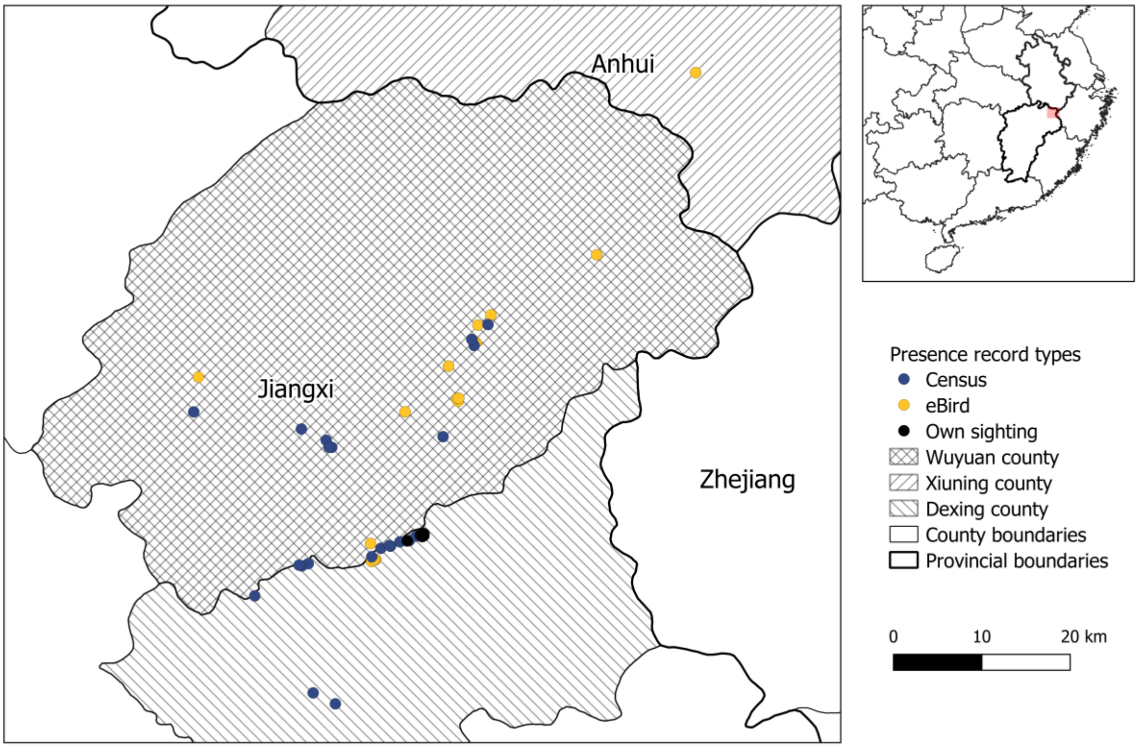

Figure 1. Blue-crowned Laughingthrush occurrence records from annual census (blue), eBird.org (yellow) and the lead author's own opportunistic sightings in the field in 2018 and 2019 (black). Records are distributed across three counties in Jiangxi and Anhui provinces, China.

3.3.1.3 *Opportunistic sightings*

Six sightings of BCLT away from known breeding sites were made by R. Gleave during June 2018 and July 2019. All were localities based along the Le'An river in Wuyuan and Dexing counties (29.107-29.108, 117.80-117.82).

3.3.1.4 *Environmental layers*

Administrative provincial and county boundaries were downloaded from WorldMap (available at http://worldmap.harvard.edu/chinamap/; Guan *et al.* 2012). Nineteen bioclimatic variables were obtained from the WorldClim global climate database (http://www.worldclim.org/; **Supplementary Information, Table S2 & S3**) (Fick and Hijmans, 2017). To avoid model overfitting, raster layers were clipped to the study extent (96.164, 124.289, 21.462, 31.099) in QGIS, and 2,000 random points were generated in a shapefile of the same extent. Values were extracted from each raster layer using the 'Point Sampling Tool' plugin, which were saved to CSV format, then checked for collinearity within the *corrplot* package in R (Wei & Simko 2021). Variables were excluded that had a coefficient of correlation >0.7 (Green 1979; **Supplementary Information, Figure S1 & S2**). As including higher numbers of predictors can lead to misleading correlations, it is better practice to identify a small number of predictors which are likely to have relevance to the study species (Pearce-Higgins and Green 2014). Five bioclimatic variables that were not strongly intercorrelated were selected for inclusion in models (annual mean diurnal range, annual temperature range, mean temperature of wettest quarter, precipitation seasonality and precipitation of wettest quarter; **Table S3, Figures S1 & S1; Supplementary Information**), which represent indices of temperature and precipitation either annually or during the BCLT breeding season.

Land cover classifications were obtained using the Re-Map App land tool (available at https://remap-app.org/; Murray *et al.* 2017), which combines Landsat imagery and Google Earth Engine technology. Users can manually select pixels from pre-processed Landsat images according to self-selected and generated categories, which are then used by the tool's algorithm to classify land types. Land cover types classified for our study area were forest, agriculture, human settlement and water. Exposed rock in mountainous areas (which represent remote areas relatively unaltered by human activity and surrounded by forest) was classified as forest to prevent it from being classified as human settlement; however, this formed a minimal proportion of the study area.

Elevation data were generated from NASA Shuttle Radar Topography Mission (SRTM) Digital Elevation imagery at a resolution of 1 arc-second (approximately 30m) using Google Earth Engine (Gorelick *et al.* 2017). Imagery was clipped to the study extent. NDVI was generated from USGS Landsat 8 Collection 1 Tier 1 Top of Atmosphere Reflectance imagery, also using Google Earth Engine. NDVI data were also calculated in Google Earth Engine (see **Additional Methods, Supplementary Information**).

3.3.2 Population Trend Analysis

BCLT population trends were investigated using the two census datasets. Median values of the census data were taken where data were presented as range of values (e.g. 40-50). If the median was a fraction, the lower integer of the two possible values was taken (e.g. if the median value was 44.5, the value would be taken as 44). All values were treated as conservative; for example, where '70+' was given, this value was treated as '70'. Any '?' values, where BCLT were detected at a site but the observer was unsure if the birds were breeding, were treated as 'NA' values.

The mean and standard error of differences between census counts were calculated (comparing identical sites within identical years) to measure precision between datasets. A simple linear model of the differences was used to explore differences between the two sets of count data, with difference between survey counts modelled as a function of breeding site and year. The two datasets were then pooled together to fill any gaps in surveying. Where observer groups showed a difference between counts at a given site and year, the highest count was used; data were never summed together for this purpose. Separate and pooled survey counts and breeding site occupancy were then plotted over time.

Analysis of BCLT population trends over time were then carried out on the combined dataset using R version 4.0.2 (R Core Team, 2020). Exploratory plots of BCLT population counts suggested that temporal trends may not be linear, so additive models were used as they permit the modelling of non-linear relationships (Wood, 2006). A random intercept for the site variable was also included in analyses as recommended by Harrison *et al.* (2018), to account for non-independent error structures generated by repeated measures at the same breeding sites.

A Bayesian zero-inflated poisson generalised additive mixed model (ZIP GAMM) was built in order to model data from all 15 breeding sites (as defined by census surveys). Data exploration showed that data contained a high proportion of zeros (65%), with an uneven percentage of zeros from year to year (14-71%). ZIP models are a form of hurdle model, which model 'true' zeros (when habitat is unsuitable) versus 'false' zeros (due to observer or animal error, i.e. when observers failed to detect birds, or when birds were not present at the time of survey but would typically be present; Zuur 2014). BCLT are rare, colonial breeders with an uneven dispersion across the study area (He *et al.*, 2017), and thus they will not necessarily occupy all suitable breeding habitat, meaning that the dataset is expected to contain a high proportion of zeros. The ZIP GAMM was fitted using the Bayesian inference framework Integrated Nested Laplace Approximation (INLA; Rue, Martino & Chopin 2009). We used the ZIP term 'zeroinflatedpoisson1' family, which uses all observations of the response variable in the model (not just those over 0). The mean probability across years of recording birds at any individual site was 61%; this value was fairly consistent across most sites (**Figure S3, Supplementary Information**), and so the model used a constant zero probability parameter. Default priors were used.

Model equation: Bird_count ~ Intercept + s(Year) + (1|Site) (count part of the model)

Bird_count ~ Intercept + Year (binary part of the model)

A separate frequentist GAMM was also fitted to the data (see **Frequentist GAMM, Supplementary Information**).

3.3.3 Species Distribution Modelling

Species distribution modelling was conducted using Maxent v 3.4.0 (Maximum Entropy; (Bonney *et al.*, 2009, Phillips *et al.* 2006, Phillips 2017) to understand which environmental variables show a relationship with BCLT presence. Maxent is a machine-learning method suitable for use with presence only data and performs well even with low sample sizes (Phillips, Anderson and Shapire, 2006; Papeş and Gaubert, 2007). Model performance of SDMs is known to decrease quickly for sample sizes below 20 (Stockwell and Peterson, 2002), so we combined the existing census data (21 locations) with 41 georeferenced BCLT records from eBird with sufficiently accurate metadata for inclusion in the SDM, with our own additional opportunistic field observations from the 2018 and 2019 breeding seasons (six additional locations); this gave a sample of 68 records. There is no risk of including duplicate records within this analysis, as Maxent automatically removes spatial duplications from within the same grid cell (Phillips 2017), in this case approximately 1km x 1km, the smallest sampled resolution of our environmental input layers.

Environmental rasters were re-projected to the projection system long/lat, WGS 84, and extended to the same geographic extent (96.164, 124.289, 21.462, 31.099), using NA values to fill in any gaps. This extent was chosen to cover southern China south of the Yangtze River, and inclusive of the former known range of *P. courtoisi simaoensis* in Yunnan. All rasters were extended to the same resolution, using the BIO2 (annual temperature range) raster as the reference layer (resolution: 30 arc seconds, or 1km x 1km) to reduce computation/processing time. All datasets were then re-extended to ensure they were not influenced by sampling, and were written as ASCII files.

Geographic distribution of the BCLT was related to the seven environmental variables by fitting an SDM model to the presence data in Maxent, and generating 10,000 background points (the default value). Due to high cloud cover over the area containing BCLT presence points, the NDVI layer was removed as it was unable to contribute sufficient data points to the model. All variables were continuous except for land cover (categorical). The model was set to a cumulative output, with a random test percentage of 25% and a regularization multiplier of one. A jackknife test was run to measure which variables were most important to the model. The ability of the model to discriminate between occupied and unoccupied regions was estimated from the area under the curve (AUC) of the receiving operator characteristic (Fielding & Bell, 1997; Phillips, Anderson and Shapire, 2006). Model fit was assessed from the regularised training gain.

3.4 Results

3.4.1 Combination and comparison of census counts

Both sets of survey observers independently surveyed 12 BCLT breeding sites. As each group used different naming or labelling systems, the two sets of breeding sites seemed superficially to be identical. Some of these surveyed breeding sites contain spatially separated locations which have been combined together for census counts, as they were considered by observers as part of the same breeding colony. However, we found that when the two datasets were integrated, they in fact covered a total of 15 known BCLT breeding sites, with nine that overlapped between both sets of observers, and six (three per group) that were only known by a single observer group (**Figure 2**). HFQ exclusively surveyed sites 4, 12 and 13, two of which are relatively distant from other breeding sites. ZWW exclusively surveyed sites 14, 15 and 16, all of which are relatively close to other breeding sites (they are in villages adjacent to previously known breeding sites; **Figure 2**). In total, these datasets together included 19 spatially separate breeding locations (**Figure 1**); several breeding sites reported by both HFQ

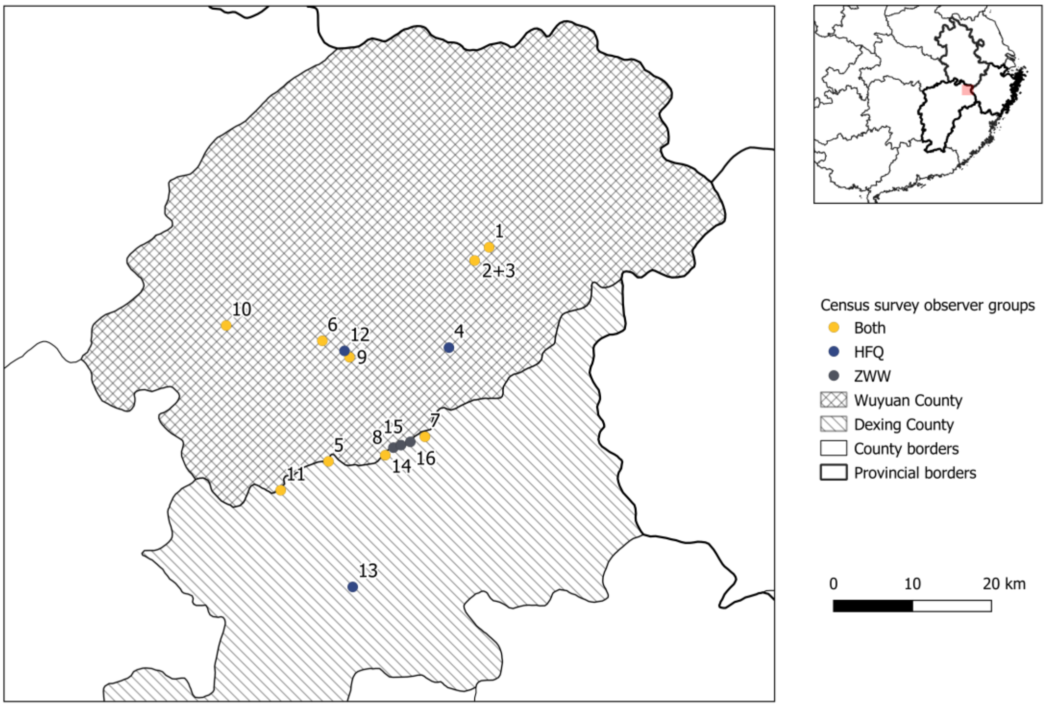

Figure 2. Locations of Blue-crowned Laughingthrush breeding sites based on census data from both HFQ and ZWW (dots show number of sites as surveyed, including geographically separate locations combined together). Yellow dots show censused breeding sites surveyed by both observer groups, blue dots surveyed by HFQ only, and grey dots by ZWW only.

or ZWW (2+3, 7, 9, 13; **Figure 1**) actually comprise more than one village located close together.

There is a negligible difference in overall counts per site and per year made between the two observer groups between 2012-2017 (mean = -0.06, SE = 2.72). Most counts by each group were identical, with some small differences and few larger differences between counts (**Figure 3**). ZWW's and HFQ's mean counts were 40.37 and 40.31 respectively (**Table S4, Supplementary Information**). There were no significant differences between survey counts at any sites except Site 7, where ZWW's and HFQ's mean counts were 94.5 and 73.0, respectively, based on a simple linear model (Adjusted R^2 = 0.008, p=0.05, df = 31). This difference in counts is likely to be due to ZWW's observer group discovering an additional breeding site at an adjacent village close to site 7, but including these counts as part of site 7 rather than as a separate breeding site (W. Zhang 2018, personal communication).

Markedly different trends are apparent when population trends are broken down by individual breeding sites (**Figure 3**). Consistent breeding populations are a feature of some sites (sites 2+3, 5, 7 and 8), whereas other sites contain either seemingly transient populations (site 4, 6) or insufficient prior history to reconstruct temporal patterns (sites 10-16).

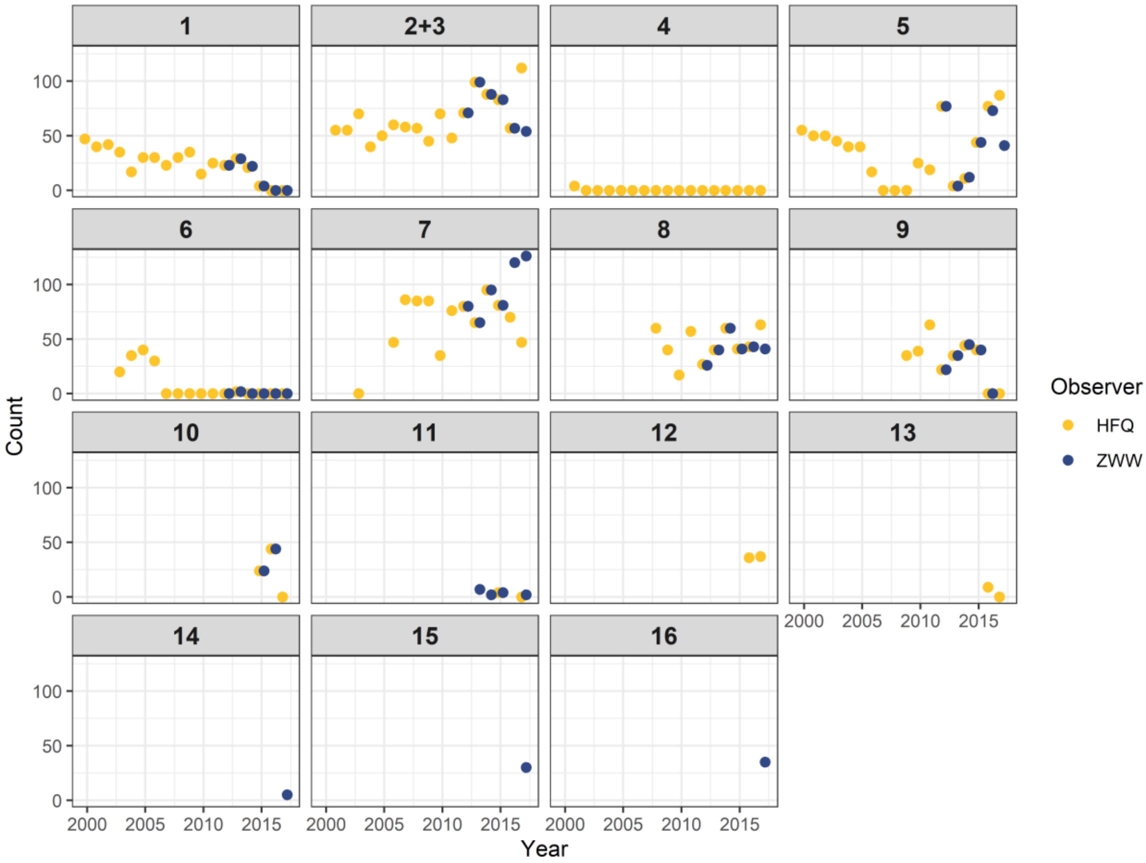

Figure 3. Blue-crowned Laughingthrush census count data broken down by individual breeding site, from years 2000-2017. Yellow dots shows counts by HFQ, blue dots show counts by ZWW.

The raw data from the pooled datasets show an increasing positive trend over time, suggesting an overall increase in population size (**Figure 4**). The number of occupied breeding sites also increased over time (**Figure 4**), from two breeding sites in 2000 to nine breeding sites occupied by 2017. However, these increases may represent changes in survey effort rather than a genuine trend, as more sites were surveyed in 2017 than 2007 (**Figure S4, Supplementary Information**). Pooled data suggest the population could be as high as 497 individuals across all nine occupied breeding sites in 2017, although it is possible that some birds might have travelled between sites and were double counted.

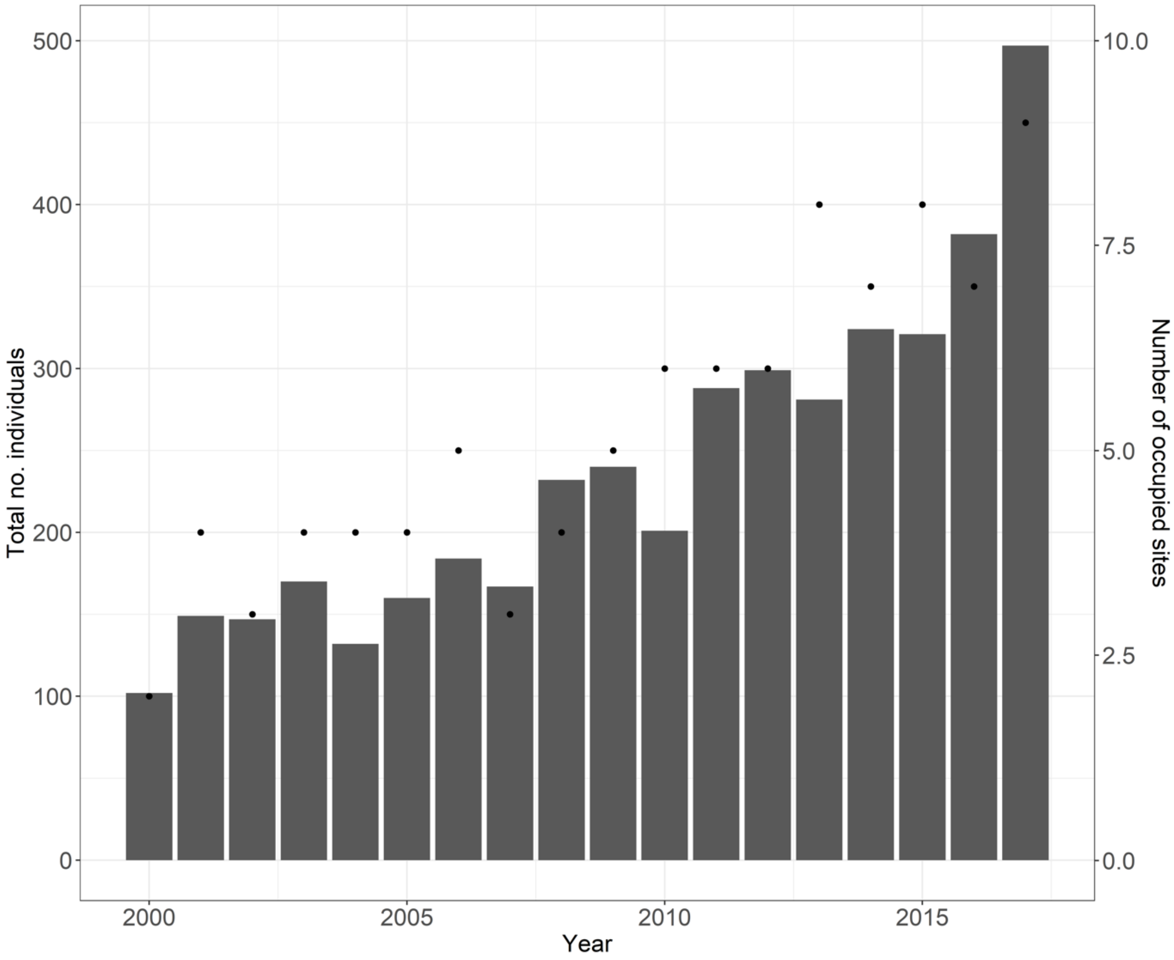

Figure 4. Overall Blue-crowned Laughingthrush numbers when datasets from HFQ and ZWW data were pooled to fill in gaps (left-hand y axis). The higher value from either set of counts was taken, and data from any overlooked breeding sites were included. The right-hand y axis shows number of occupied breeding sites per year. Grey bars show the total number of individuals, and black dots show the number of occupied sites.

3.4.2 Population trend over time

3.4.2.1 *Bayesian ZIP GAMM*

The mean values from the Bayesian ZIP GAMM also show little overall change in BCLT abundance over time from 2000 to 2017 (**Figure 5)**. The ZIP GAMM shows an increasing trend in log abundance due to year during the early survey period (2000-2003), followed by a varying but overall decreasing trend (2004-2014) and then a steeply increasing trend (2015-2017). The ZIP GAMM fits better to observed values in later years compared to earlier years, with a narrower 95% credible interval (**Figure 5).**

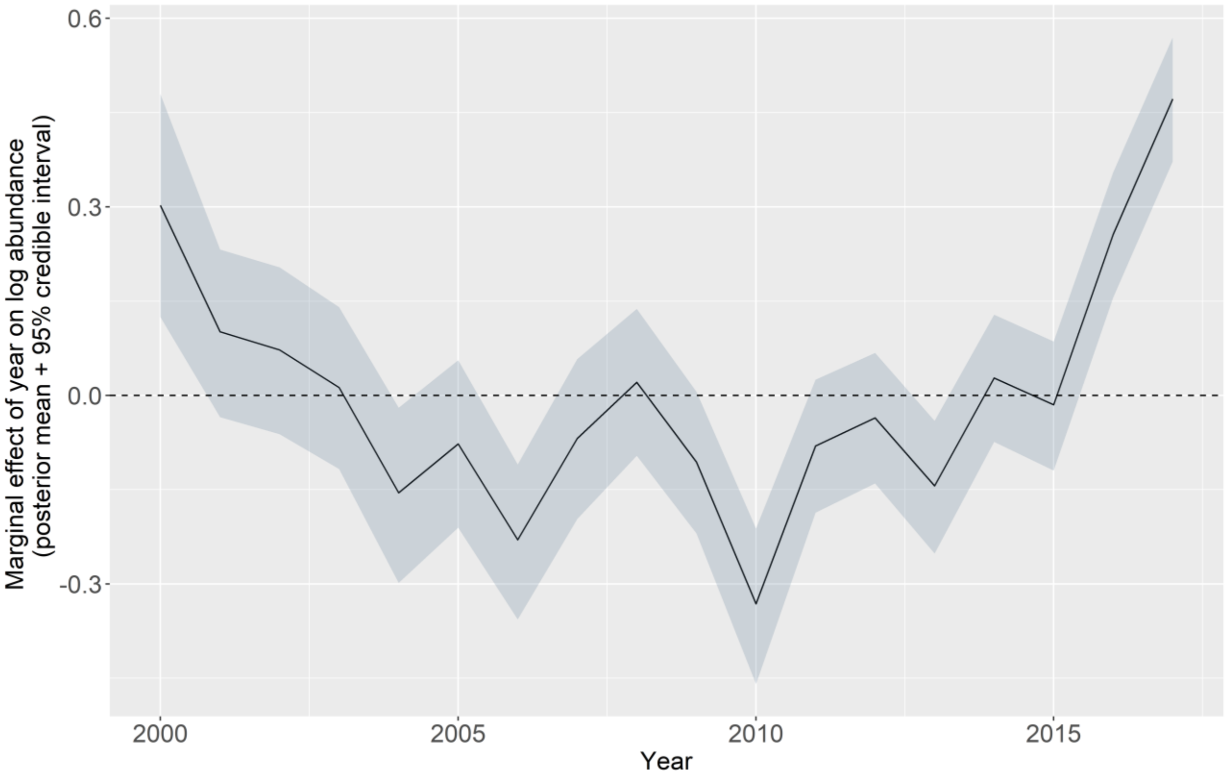

Figure 5. Summary of the marginal effect of year generated by a ZIP GAMM between 2000 and 2017 based on survey data from all 16 Blue-crowned Laughingthrush breeding sites, showing the estimated effect of year on log abundance. The shaded area represents the 95% credible interval. The dotted line runs through the y intercept at zero; above shows an increasing trend, below a decreasing trend.

3.4.3 Species Distribution Model

Following removal of duplicates, the Maxent model was built using 28 BCLT point localities, (many of the eBird points were duplicate locations from well-known breeding sites). AUC was 0.999 (**Table 1**) indicating excellent model fit. In the model, the four variables making the highest contributions to the model were annual temperature range, land cover, precipitation of the wettest quarter and elevation, which collectively made a 95.8% relative contribution to the model (based on individual increases in training gain made by each variable). The other three variables made contributions as follows: mean temperature of the wettest quarter (4.3%), and precipitation seasonality and annual mean diurnal range did not contribute to the model (0.0%). Annual temperature range was the predictor with by far the highest permutation importance (**Table 1**), with the response curve from the univariate model suggesting a high likelihood of occurrence with annual temperature ranges between 30-34°C, below which the likelihood of occurrence dropped close to zero (**Figure S5, Supplementary Information**). BCLT also have a higher likelihood of occurrence in areas with a mean precipitation of 600-1000mm during the wettest part of the year, which occurs during the BCLT's breeding season, and at elevations between 0-400m, above which the likelihood of occurrence dropped close to zero. Land cover had a high relative contribution, however did not give a land type with higher predicted occurrence. The variable with highest gain (training data only) when used in isolation was land cover, indicating that this variable contained the most useful information by itself. This relationship inverted to a negative gain when used with test data only (**Figure S6, Supplementary Information**).

In the Maxent model, areas of moderate likelihood of BCLT occurrence (threshold >1.6) are present in Jiangxi, Anhui, Zhejiang, Fujian, Hunan and Hubei provinces **(Figure 6**). All of Yunnan Province, including the location of the extirpated *P. c. simaoensis* population, showed no predicted conditions of occurrence (**Figure 6**). The AUC statistic for the test data was 0.995 (SD = 0.001), suggesting that the model has a good measure of separability so can distinguish between areas with and without BCLT. The difference in AUC between training and testing data was 0.004, suggesting minimal overfitting. The model's prediction is statistically significant at all given cumulative thresholds (p<0.001), meaning that test points perform better than a random prediction with the same fractional predicted area.

Table 1. Relative contributions of the highest contributing environmental variables to the Maxent model for the Blue-crowned Laughingthrush.

	% Contribution	**Permutation importance**
Model 1 (AUC = 0.999, regularised training gain = 4.880)		
BIO7 (Annual Temperature Range)	31.8	22.7
Land Cover (Forest, Human settlement, Agriculture, Water)	28.4	0.0
BIO16 (Precipitation of Wettest Quarter)	22.3	9.3
Elevation	13.3	52.3
BIO8 (Mean Temperature of Wettest Quarter)	4.3	15.7
BIO15 (Precipitation Seasonality)	0.0	0.0
BIO2 (Annual Mean Diurnal Range)	0.0	0.0

Table shows the contributions to the final model made by each variable. Two measures of model contribution are given for each variable: % contribution is estimated heuristically from the variable's contribution to the model, and dependent on the path selected for the model run. Permutation importance is the estimated random permutation of the values of each variable among both presence and background training points, then measuring the resulting decrease in training AUC. This value is only dependent on the final model, not the path, with a large value indicating high reliance on that variable. Values for both measures are given as percentages.

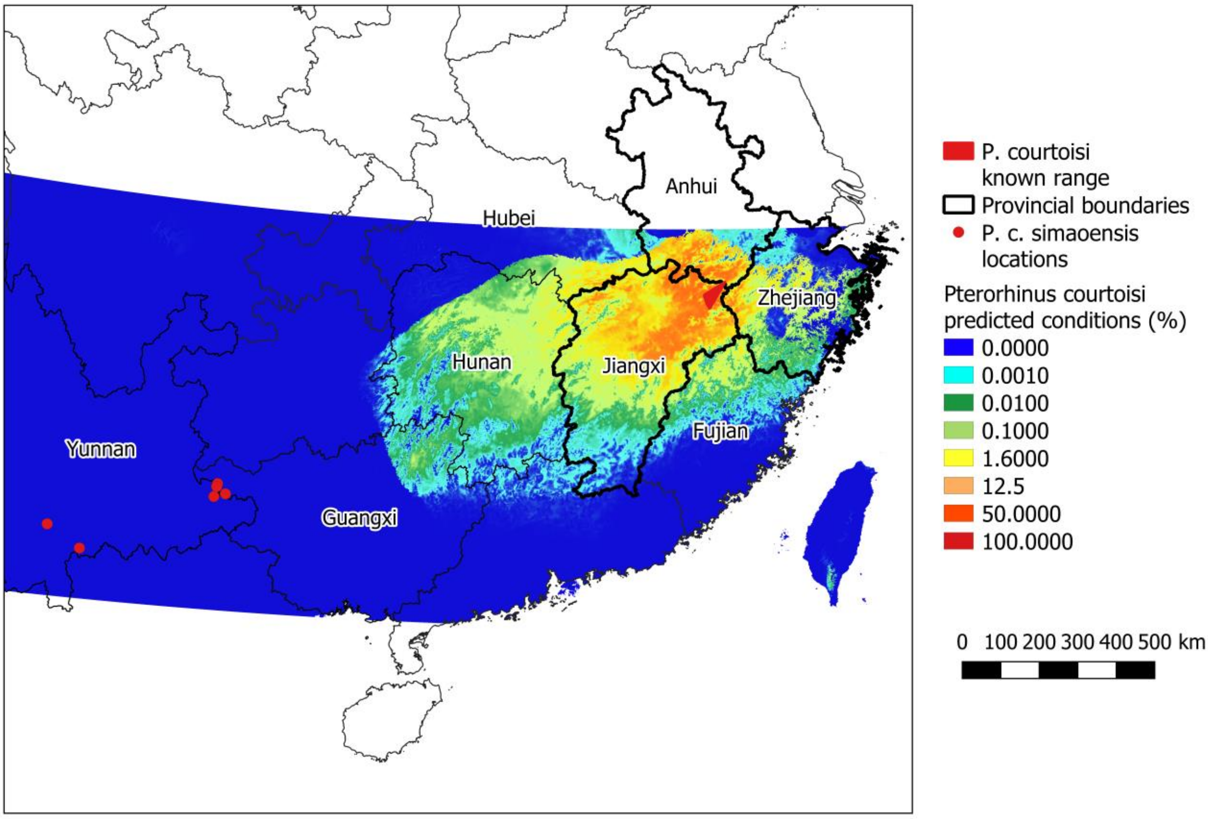

Figure 6. Representation of the Maxent model for the Blue-crowned Laughingthrush, showing a cumulative output that predicts suitable conditions above a threshold in an approximate range of 1-20 (yellow-orange). Warmer colours indicate areas with better predicted conditions. The red polygon indicates the known range of subspecies *P. courtoisi*, and red dots indicate the last reported locations of *P. c. simoaensis*.

3.5 Discussion

This study is the first rigorous assessment of all known presence and population data collected to date on the Blue-crowned Laughingthrush. Our findings underline the importance of combining and investigating the information-content of all available data sources for threatened species to strengthen conservation knowledge-bases and identify knowledge gaps (Mogensen *et al.*, 2021), and to not make assumptions about whether independently collected datasets are duplicates or identical. Importantly, this approach reveals that the BCLT population may be as much as 42.8% higher than the highest previous population estimate of 348 birds, which was based on just one of the datasets (He *et al.* 2017).

A comparison of the two existing long-term monitoring datasets for the BCLT shows that not all occupied breeding sites were surveyed over the 2000-2017 monitoring period: neither observer group counted all active breeding sites in each year, with 40% of the total number of sites only known to each single group of observers. Our analysis shows that where identical breeding sites were surveyed by the two observer groups, relatively consistent counts were made, as shown by the lack of statistically significant differences between most overlapping portions of the two datasets. The increase in occupied breeding sites per year may superficially indicate an ongoing population increase for the species, however, it can be unwise to interpret data at face value in this manner, as this pattern could also be explained as a function of observer groups discovering new breeding sites, either through increased survey effort or opportunistically. We ultimately cannot test between these hypotheses due to the lack of associated data on survey effort. Overall, in view of the high proportion of sites known only to single observer groups, it is reasonably likely that other undiscovered breeding sites may also exist, and may have been active during the recent census period. Indeed, a flock of 43 BCLTs was spotted but not found breeding in 2007 (He *et al.* 2017). These findings highlight that existing census data should be interpreted as a minimum estimate or underestimate of the current global BCLT population, thus raising a cautious note of optimism for the status of the species.

The ZIP GAMM analysis indicated little overall change in BCLT population trend over time, although there was evidence for an increasing trend in later years, when more breeding sites were located. However, it is still uncertain whether this trend represents a true population recovery. While the ZIP GAMM modelled 'true' and 'false' zeros (absences at breeding sites), and captures the effect of differences between sites, the increasing trend quantified in later years may partly be an artefact of ZWW discovering more breeding sites during that period, in effect increasing survey effort. The IUCN assessment for the species, which is based only upon HFQ's census data, considers the species to have a 'decreasing' trend based on the number of mature individuals, and infers a past population decline 'owing to low productivity and the threat of building developments to several colonies' (BirdLife International 2018). However, merging the two existing census datasets suggests a maximum count that appears to increase over time, reaching 497 individuals in 2017. This count could meet the threshold for downlisting the species to Endangered on the Red List based on the current assessment criterion C2a(i,ii): the existing Critically Endangered status is based on the 'very small, fragmented known range and extremely small known population which is likely to be declining owing to a number of threats' (BirdLife International 2018). However, our data suggests a possible stable or increasing population trend (IUCN 2012) and the discovery of additional breeding sites, which could justify downlisting. However, caution is recommended in retaining the existing Red List status assessment until the nature or severity of anthropogenic threats are better known, as has been recommended for other threatened species in similar situations (Shaw *et al.*, 2016), as well as the implementation of a new survey protocol which more clearly distinguishes between true population trends and an artefact of survey effort.

Combining data sources and exposing them to rigorous analysis has previously been used to uncover potential new sites for threatened species (Menon *et al.*, 2010; Giovos *et al.*, 2018; Giovos *et al.*, 2019), understand their landscape-scale environmental requirements (Bladon *et al.*, 2018), and even determine unknown migration and movement patterns (Lees and Martin, 2015; Lees, 2016). Using location data from existing monitoring datasets, citizen science sources and opportunistically collected field data, we found evidence that there may be large regions of potentially suitable habitat for BCLT across southern China. As analysis of available monitoring data provides evidence of 'overlooked' breeding sites, other nearby regions outside their current known range may therefore be appropriate to survey for possibly unknown BCLT breeding colonies. Potential BCLT habitat is identified in much of northern and central Jiangxi, as well as western Zhejiang, southern Anhui and Hubei, and small parts of northern Fujian provinces, suggesting that more of these regions could be focused on for exploratory searches for BCLT. In addition, combining and contrasting independently collected monitoring datasets, if available, can reveal new population trends and overall abundance. Our findings that additional breeding sites were not counted has implications for data biases: for example, site-selection bias, which can exaggerate the rate of species declines (Fournier, White and Heard, 2019).

The species' key requirements at the landscape scale are moderate annual temperature ranges, moderate rainfall during the breeding season and low elevation (31.8%, 22.3% and 13.3% contributions to the model, respectively). This may suggest the BCLT is more likely to breed in landscapes at lower elevation and in areas that are alternately both wetter and drier, and with greater and lesser extremes of temperature than surrounding landscapes. Low elevation may be linked to the BCLT breeding near lowland villages and rivers (Richardson 2005), and the breeding season temperature and rainfall values may reflect either a specific climate envelope, or the conditions found across Wuyuan and surrounding areas, which are defined by ecological barriers to the north and south in the Huangshan and Wuyi mountains, respectively (Hong *et al.* 2006). Land cover was also an important determinant of habitat suitability (28.4% contribution), although its impact on model performance is somewhat contradictory: it had a negative test gain, meaning that the model performs better without inclusion of this variable, but the model without it also had decreased gain, suggesting that land cover contains more information that is not present in other variables. One possible explanation for this apparent contradiction is that BCLT tend to be found in close proximity to villages within the species' breeding range; however, there are no BCLT data associated with the many villages outside its range, countering model predictions.

A potential limitation of this study is that as available BCLT occurrence data cover an extremely narrow geographic range, the high AUC statistic obtained for our model may partially be an artefact of this spatial restriction, and does not necessarily indicate that the model has a good fit to the data (Phillips 2017). In addition, this model is predictive of the data available for the current-day range of the BCLT; therefore it does not necessarily represent a fundamental ecological niche, and may instead represent only those environmental conditions associated with locations where individuals have managed to survive. These are wider issues that potentially affect all SDM studies for highly range-restricted species (Zhou *et al.*, 2005; Fisher, 2011; Chatterjee, Tse and Turvey, 2012; Kerley *et al.*, 2020). SDMs often assume that occupied habitat represents a set of optimal conditions for a given species (Hirzel and Le Lay, 2008); however, remnant surviving populations of many species might instead occupy ecologically suboptimal habitat where human pressures are reduced, and where they have become 'refugee' species (e.g. European bison *Bison bonasus*, Hainan gibbon *Nomascus hainanus*, Lord Howe Woodhen *Tricholimnas sylvestris*; (Miller and Mullette, 1985; Caughley, 1994; Zhou *et al.*, 2005; Cromsigt, Kerley and Kowalczyk, 2012; Turvey, Crees and Di Fonzo, 2015). In our model, the locations where *P. c. simaoensis* was last reported from Yunnan Province are predicted to have low likelihood of occurrence, suggesting that either this subspecies was capable of tolerating different conditions, or that the surviving population in Jiangxi Province represents an incomplete snapshot of the species' fundamental niche. It might therefore be appropriate to interpret our SDM as indicating a minimum estimate of where suitable BCLT habitat might occur. Furthermore, Maxent relies on making accurate predictions through unbiased sampling data (Dudík, Schapire & Phillips, 2005); however, our data were not sampled systematically and so are likely to contain biases in their representation of suitable environmental conditions for the species. Nevertheless, as our primary aim was to prioritise regions outside the BCLT's known breeding range for future searches, rather than to characterise its precise ecological niche, our findings remain useful within this context. Whereas this study uses a single SDM approach, SDM outputs from different modelling approaches have been shown to be highly variable (Pearson *et al.*, 2006; Buisson *et al.*, 2010; Bladon *et al.*, 2018), and comparing multiple SDMs in the future will be important to gain the most robust inferences about potential BCLT range.

Although our analyses were able to provide new insights into BCLT population size and trends, we strongly recommend standardising future BCLT surveys, and in particular recording all absences, survey effort and dates, and estimating detectability and other sources of bias, as this will allow a robust assessment of true population change in the future. Attempting to measure an annual 'true census' for the BCLT should form a part of ongoing monitoring efforts, as this is a rare and threatened bird species with a restricted range (Sutherland, Newton and Green, 2004); our analyses show the influence of new sites on inferred population trends, so that capturing all breeding sites in a survey would give more reliable estimates. Census and sampling approaches could be combined in future under a carefully designed sampling strategy, censusing a core area and sampling areas outside of the known range (Sutherland, Newton and Green, 2004). We also support future searches for more BCLT breeding sites and presence locations in general, and recording all instances of finding them (not just breeding sites), as this will aid future efforts to understand the species' distribution in relation to environmental changes or any conservation efforts. In our analysis, a simple metric of land cover containing four classes was shown to be an important variable; however, land cover patterns across southern China are complex and varied (Frolking *et al.*, 1999; Liu, Duan and Yu, 2013; Zhou, Lee and Goodale, 2018), and so we also recommend looking in finer detail at land cover types to predict BCLT occurrence across the Chinese landscape.

Our investigative approaches demonstrate the conservation utility of even incomplete and biased monitoring datasets which were not explicitly collected for quantitative analysis. These benefits are especially strong when multiple datasets are combined, allowing identification of data gaps and overlap. However, our findings also highlight the need to use analyses which account for variation between sites (hierarchical models, mixed effects) and are capable of handling high levels of zero-inflation. Bayesian analysis using a ZIP GAMM was a good approach for handling the data, as this can incorporate data for all sites and revealed a complete population trend, giving additional benefits in comparison to the approach used by Holland *et al.* (2012). In a similar study, Carvalho *et al.* (2020) were able to better model zero-inflated aphid population data using a Bayesian approach in comparison to a frequentist GAM. We also recommend checking citizen science data (local or global) as a source of location data for SDMs. Our findings suggest that for other species with limited available distribution records or monitoring data, it may be possible to locate informative citizen science data, which can provide important new ecological insights such as augmenting the extent of known ranges. This supports other work such as Bradsworth *et al.* (2017) and Biddle *et al.* (2021) in demonstrating the potential importance of combining monitoring and citizen science records in understanding species distributions. Indeed, species of particular interest to the public (e.g. visually attractive and uncommon birds such as the BCLT) are more likely to be reported in citizen science datasets than more common species (Geldmann *et al.*, 2016). Citizen science datasets are commonly used in conservation assessments in UK, Europe, Australia and North America (Snäll *et al.*, 2011; Bradsworth *et al.*, 2017; Coxen *et al.*, 2017; Fattebert *et al.*, 2018; Rose, Halstead and Fisher, 2020), and have been used increasingly in the Global South (Lees and Martin, 2015; Biddle *et al.*, 2021), however this is a relatively novel approach in China (Duan *et al.*, 2020). Birdwatching is a growing pursuit in China (Walther and White, 2018), and any resulting citizen science represents an underutilised resource in this and similar countries, where baseline census data on many threatened bird species remains relatively poor.

In this study, combining and analysing different existing monitoring datasets and building SDMs both support the need to search for more BCLT breeding sites, and to re-design standardised monitoring protocols with quantitative modelling in mind. Our findings also support the need to reassess the BCLT's Red List status once a broader systematic survey of the species has been performed, and all ongoing anthropogenic threats have been determined. Finally, future work should carry out multiple SDMs for the BCLT on more complex land cover data. More widely, this case study shows the value of contrasting and combining all available datasets for threatened species and using analytic approaches capable of modelling all monitoring sites, to potentially re-write species' baselines without the need for further field-based data collection. This approach can achieve a better understanding of long-term population trends and biotic requirements at the landscape scale, help to identify sites for potential future surveys, and identify existing data gaps and where existing data collection practices have room for improvement.

3.6 References

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Supplementary Information

Table S1. The integration of the site labelling systems developed by HFQ and ZWW, the corresponding names of the villages where breeding sites were located, and a new numbering system developed for my own analysis.

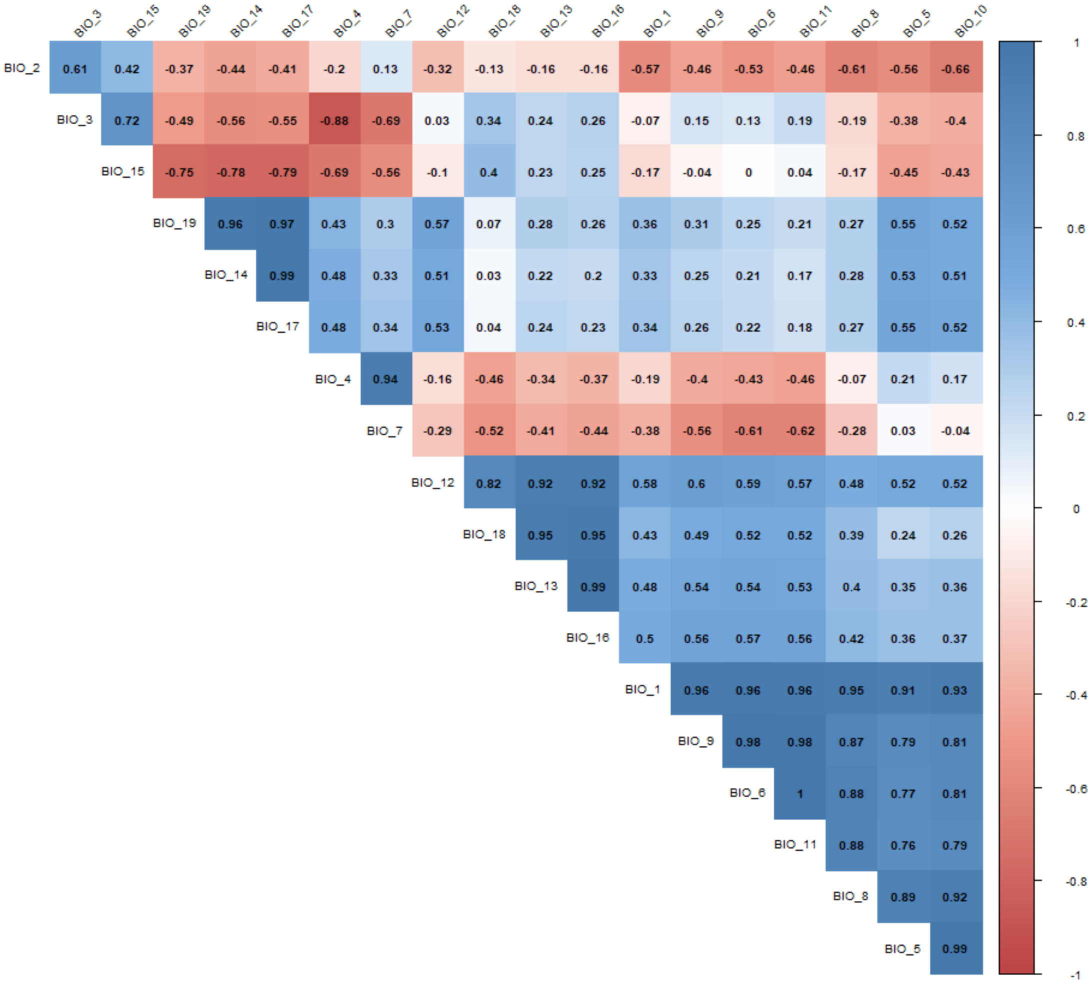
HFQ_Label	ZWW_Label	New_Label
1	A	1
2_3	B	2+3
4	NA	4
5	C	5
6	D	6
7	E	7
8	F	8
9	G	9
10	H	10
11	I	11
12	NA	12
13	NA	13
NA	J	14
NA	K	15
NA	L	16

Table S2. All WorldClim bioclimatic variables not included in the Blue-crowned Laughingthrush species distribution model.

Variable name	Variable meaning	Variable source
BIO1	Annual Mean Temperature	WorldClim.org
BIO3	Isothermality (quantifying how large the day-to-night temperatures oscillate relative to annual oscillations)	WorldClim.org
BIO4	Temperature Seasonality	WorldClim.org
BIO5	Max Temperature of Warmest Month	WorldClim.org
BIO6	Min Temperature of Coldest Month	WorldClim.org
BIO9	Mean Temperature of Driest Quarter	WorldClim.org
BIO10	Mean Temperature of Warmest Quarter	WorldClim.org
BIO11	Mean Temperature of Coldest Quarter	WorldClim.org
BIO12	Annual Precipitation	WorldClim.org
BIO13	Precipitation of Wettest Month	WorldClim.org
BIO14	Precipitation of Driest Month	WorldClim.org
BIO17	Precipitation of Driest Quarter	WorldClim.org
BIO18	Precipitation of Warmest Quarter	WorldClim.org
BIO19	Precipitation of Coldest Quarter	WorldClim.org

Table S3. Environmental and bioclimatic variables used in Blue-crowned Laughingthrush species distribution modelling.

Variable name	Variable meaning	Variable source
BIO2	Annual Mean Diurnal Range (the mean of the monthly temperature ranges)	WorldClim.org
BIO7	Annual Temperature Range	WorldClim.org
BIO8	Mean Temperature of Wettest Quarter	WorldClim.org
BIO15	Precipitation Seasonality (measure of the variation in monthly precipitation totals over the course of the year)	WorldClim.org
BIO16	Precipitation of Wettest Quarter	WorldClim.org
DEM	Digital Elevation Model. Elevation in metres	Google Earth Engine (via USGS)
NDVI	Normalised Difference Vegetation Index of Landsat 8 imagery	Google Earth Engine (via USGS)
Land cover classification	Classification of Landsat 8 imagery into four land cover types: forest, water, human settlement, agricultural land	Re-map App.org



	BIO_3	BIO_15	BIO_19	BIO_14	BIO_17	BIO_4	BIO_7	BIO_12	BIO_18	BIO_13	BIO_16	BIO_1	BIO_9	BIO_6	BIO_11	BIO_8	BIO_5	BIO_10
BIO_2	0.61	0.42	-0.37	-0.44	-0.41	-0.2	0.13	-0.32	-0.13	-0.16	-0.16	-0.57	-0.46	-0.53	-0.46	-0.61	-0.56	-0.66
BIO_3		0.72	-0.49	-0.56	-0.55	-0.88	-0.69	0.03	0.34	0.24	0.26	-0.07	0.15	0.13	0.19	-0.19	-0.38	-0.4
BIO_15			-0.75	-0.78	-0.79	-0.69	-0.56	-0.1	0.4	0.23	0.25	-0.17	-0.04	0	0.04	-0.17	-0.45	-0.43
BIO_19				0.96	0.97	0.43	0.3	0.57	0.07	0.28	0.26	0.36	0.31	0.25	0.21	0.27	0.55	0.52
BIO_14					0.99	0.48	0.33	0.51	0.03	0.22	0.2	0.33	0.25	0.21	0.17	0.28	0.53	0.51
BIO_17						0.48	0.34	0.53	0.04	0.24	0.23	0.34	0.26	0.22	0.18	0.27	0.55	0.52
BIO_4							0.94	-0.16	-0.46	-0.34	-0.37	-0.19	-0.4	-0.43	-0.46	-0.07	0.21	0.17
BIO_7								-0.29	-0.52	-0.41	-0.44	-0.38	-0.56	-0.61	-0.62	-0.28	0.03	-0.04
BIO_12									0.82	0.92	0.92	0.58	0.6	0.59	0.57	0.48	0.52	0.52
BIO_18										0.95	0.95	0.43	0.49	0.52	0.52	0.39	0.24	0.26
BIO_13											0.99	0.48	0.54	0.54	0.53	0.4	0.35	0.36
BIO_16												0.5	0.56	0.57	0.56	0.42	0.36	0.37
BIO_1													0.96	0.96	0.96	0.95	0.91	0.93
BIO_9														0.98	0.98	0.87	0.79	0.81
BIO_6															1	0.88	0.77	0.81
BIO_11																0.88	0.76	0.79
BIO_8																	0.89	0.92
BIO_5																		0.99

Figure S1. Correlation plot of all candidate numerical covariates for inclusion in Maxent model.

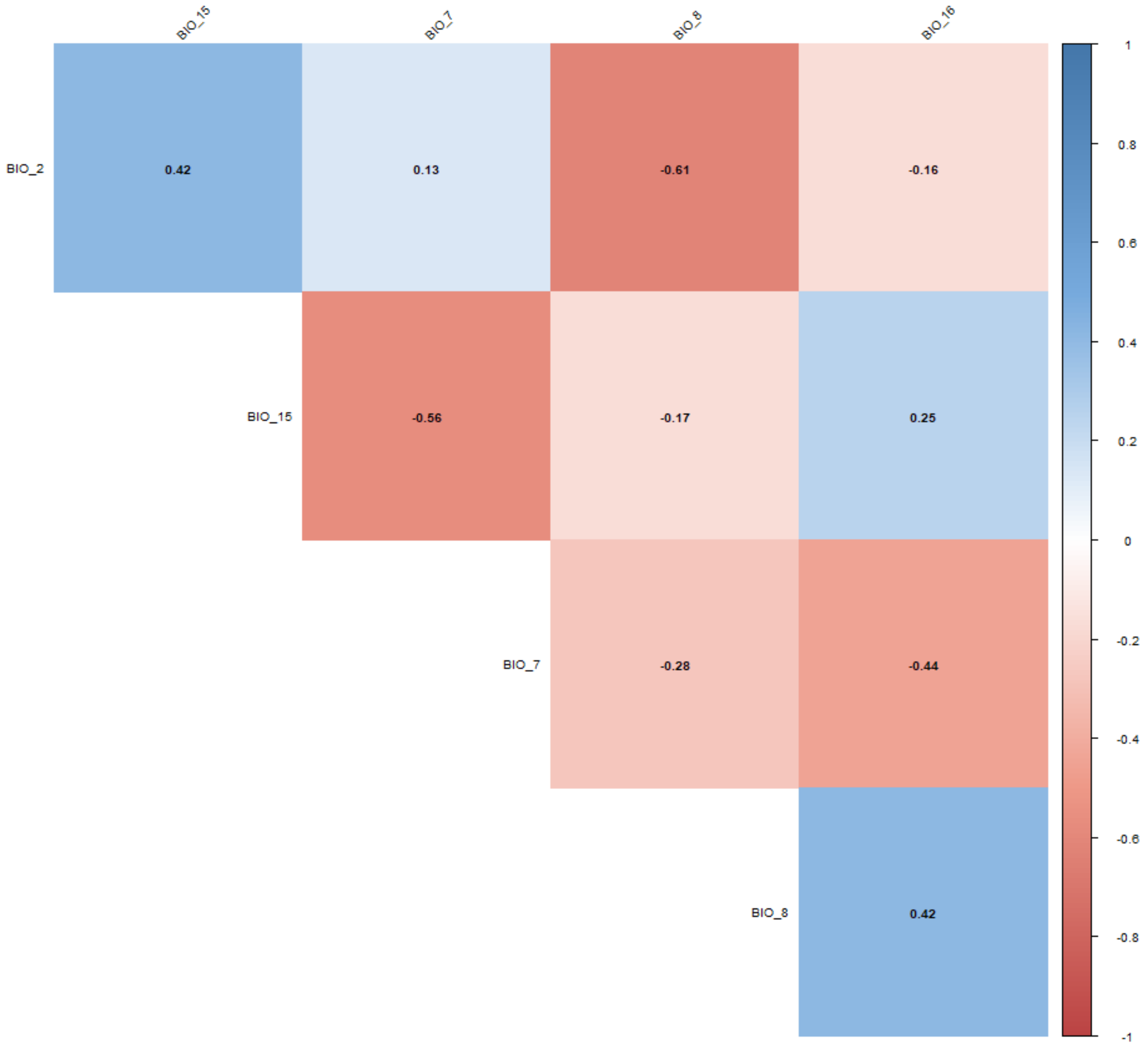


Figure S2. Correlation plot of all final numerical covariates for inclusion in Maxent model.

Additional Methods

Citizen science data sources

The audio recording website Xeno Canto also provided data on bird sightings; however, the location metadata was too imprecise for inclusion in the model. Other websites checked included HBW Alive, Bird Report (Chinese website) and Oriental Bird Images. However, images of BCLT on these sites were all from the two best known breeding sites or are of captive birds in zoos, thus not adding to the pool of unique locations in the wild.

NDVI processing

In Google Earth Engine, images were filtered by spatial area, and temporally between 1 February and 1 September 2019, to represent the BCLT breeding season but also allow a wider time window to identify the least cloudy images. Images were filtered to include only those with cloud cover of 40% or less; they were built into a composite using a maximum value function, and cloud and cloud shadow was removed using a cloud mask function. NVDI was then calculated from the data. Additional pre-processing was avoided due to the likelihood of introducing additional biases to the data (Young *et al.*, 2017).

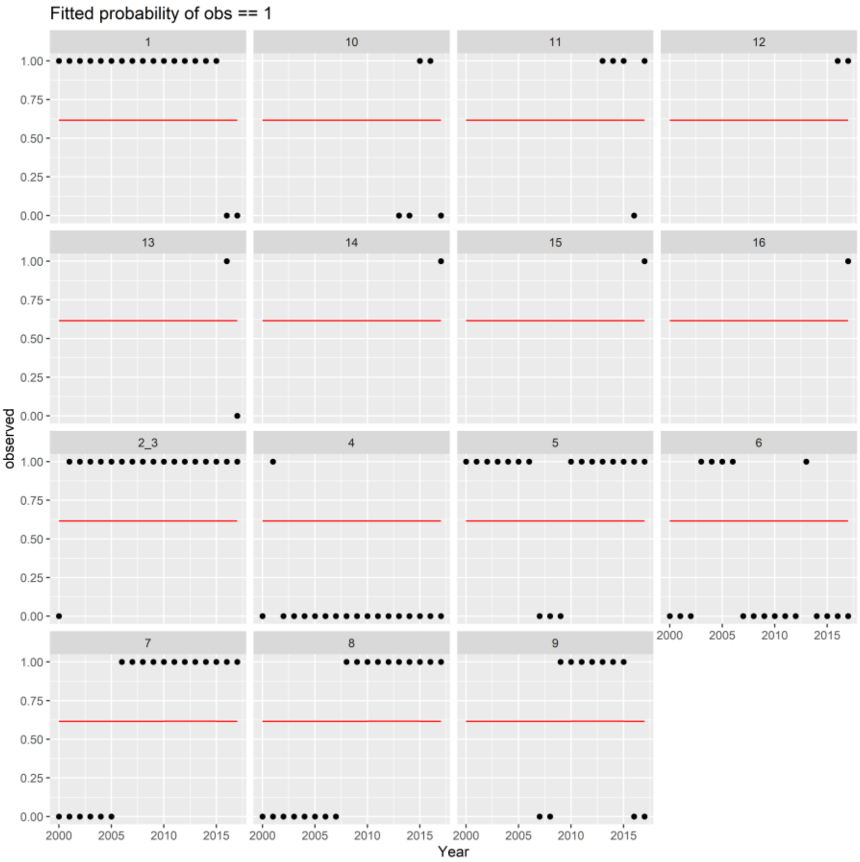
Frequentist GAMM

Relative abundance of BCLT over time was modelled using a frequentist generalised additive mixed model (GAMM). Due to irregular sampling of breeding sites over time, it was necessary to only include sites where at least four mostly consecutive years of surveying had been conducted (i.e. there were no gaps of >1 years between surveys). This method was adapted from Holland et al., (2012) and fitted using the *mgcv* package (Wood 2006). Eight breeding sites met these criteria for inclusion in the analysis. Year of survey was included as the sole fixed covariate, and was fitted with a smoothing function to allow non-linear changes in population over time. Site was included as a random intercept in the model, as more than five sites were included and this provided sufficient factor levels (Harrison et al., 2018).

Model equation: Bird_count ~ s(Year) + (1|Site)

An initial model, fitted with a Poisson error distribution, showed clear heterogeneity within the model residuals, so response counts were standardised following the methods of Holland et al., (2012) and Zuur *et al.*, (2009). Each time series was broken down by site, then the mean was subtracted and divided by the standard deviation to scale data into the same range without removing temporal trends. This approach generated a continuous numeric variable with a Gaussian distribution.

Figure S3. Probability of observing Blue-crowned Laughingthrush at any given breeding site, per year. Red lines show the probability per site, averaged over time. Black dots show years in which presence or absence of breeding Blue-crowned Laughingthrush were detected.



Frequentist GAMM

Year of survey was not significantly related to the standardised number of individuals counted at eight breeding sites from 2000 to 2017 (p = 0.49) (**Table S1A**), suggesting that relative BCLT abundance has not changed overall during this monitoring period. Predicted values from the frequentist GAMM suggest a slight overall decline in the BCLT population over this period (**Figure S2A**). In contrast, the smoother curve shows an increasing trend during the early survey period (2000-2005), a subsequent decreasing trend (2006-2014), and then another slight increase (2015-2017) (**Figure S3A**).

Table S1A. Model outputs for the frequentist poisson GAMM.

Model	**Explanatory variable**	**e.d.f.**	**F**	**p-value**
Change through time	S(Year)	1	0.465	0.497

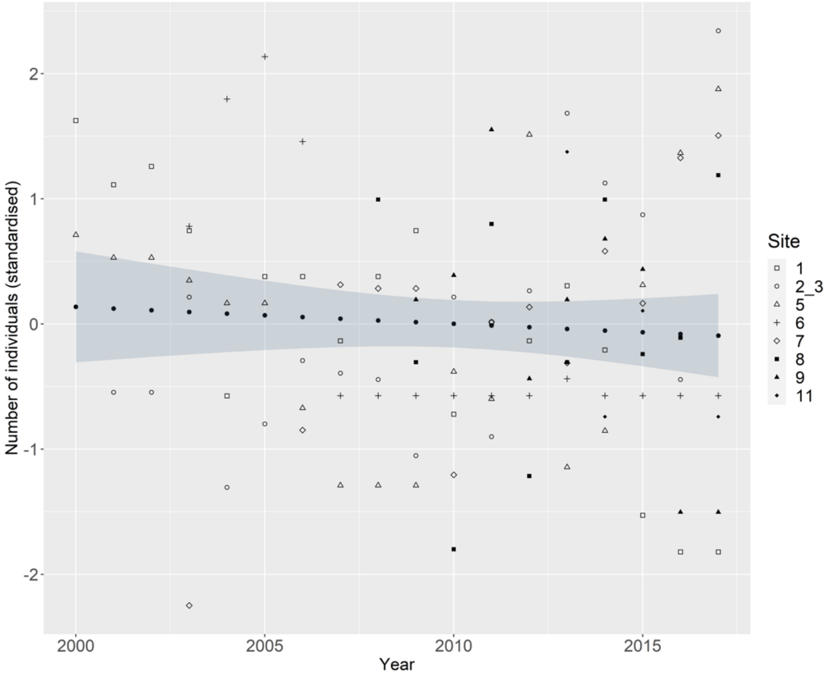


Figure S2A. The standardised number of Blue-crowned Laughingthrushes predicted to be counted between 2000 and 2017 by a GAMM based on survey results from eight breeding sites. Shaded areas represent the 95% confidence interval for predicted values. Actual standardised count data are also given for each monitoring site included in the model.

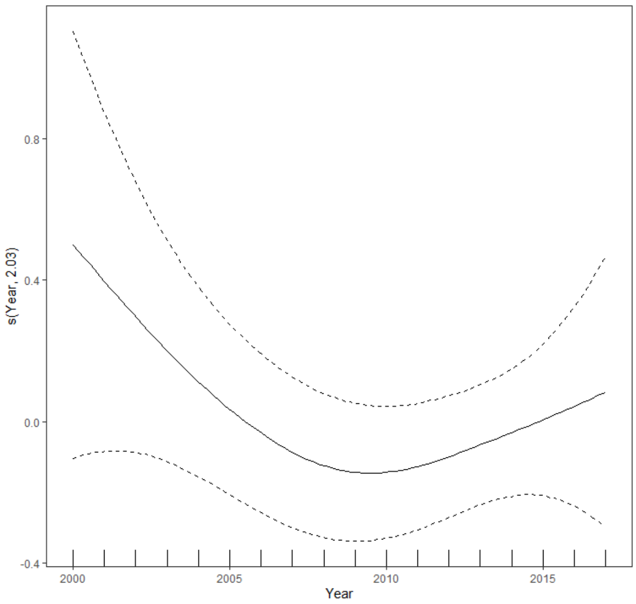


Figure S3A. Blue-crowned Laughingthrush population trend over time (2000-2017) as estimated by a frequentist GAMM.

Differences between ZIP GAMM and frequentist GAMM

The two population trend analyses show similar results, with both indicating little overall change in BCLT population trend. The GAMM showed a slight, non-significant overall decreasing trend, but this analysis was only able to use data from 50% of breeding sites, so has a limited ability to capture full population dynamics. In contrast, the ZIP GAMM includes all known breeding sites and is thus more likely to represent the most accurate trend, showing a more pronounced increasing trend in later years, when more breeding sites were located.

Table S4. Total bird counts from Years 2012-2017 for all breeding sites combined; total counts for all sites and years where both observer groups had made counts.

	HFQ	**ZWW**
Total BCLT counts	1,814	1,817
Mean of counts	40.31	40.37

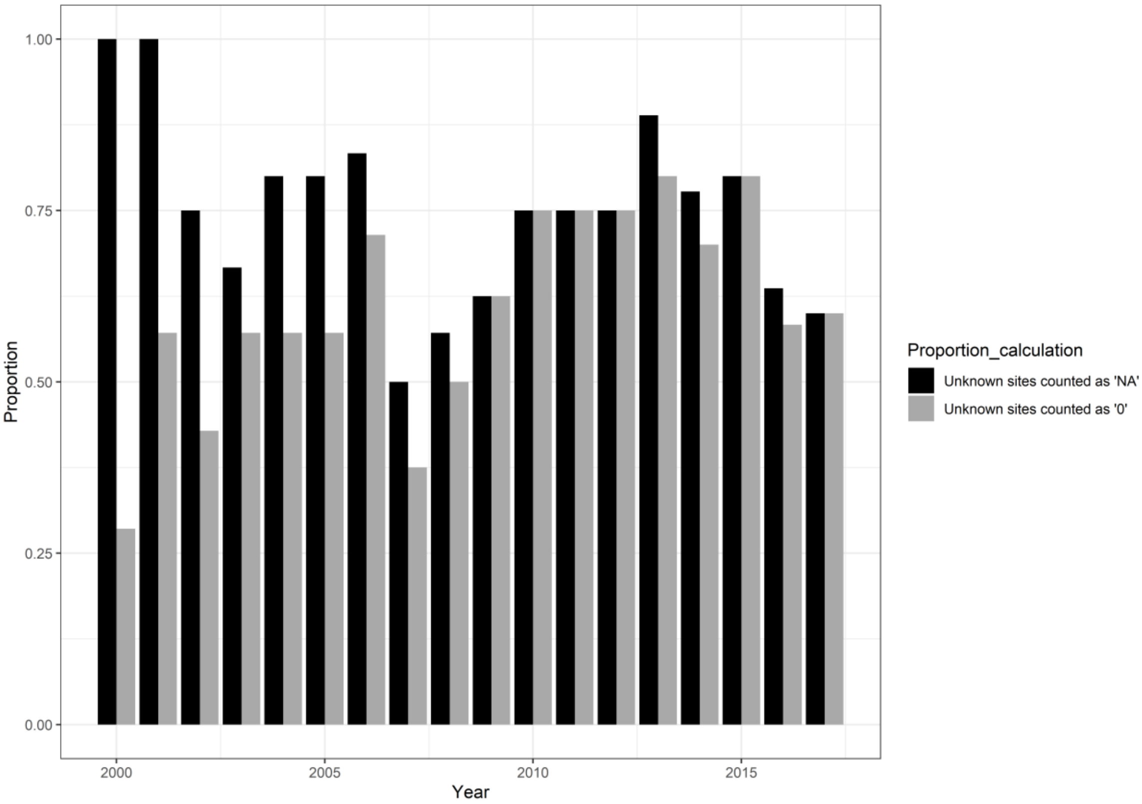
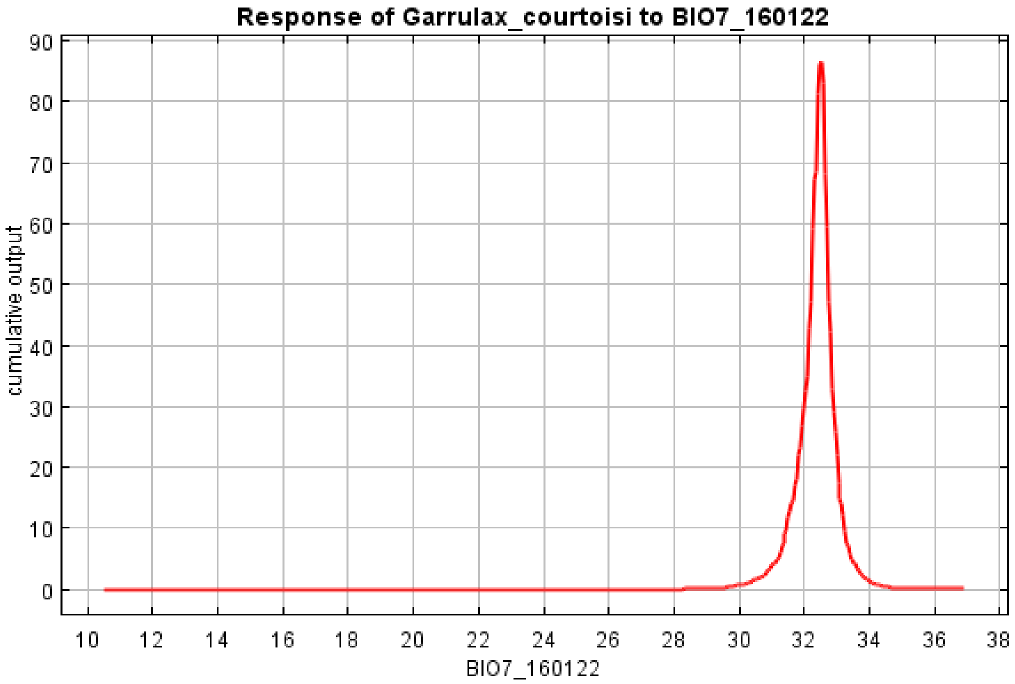
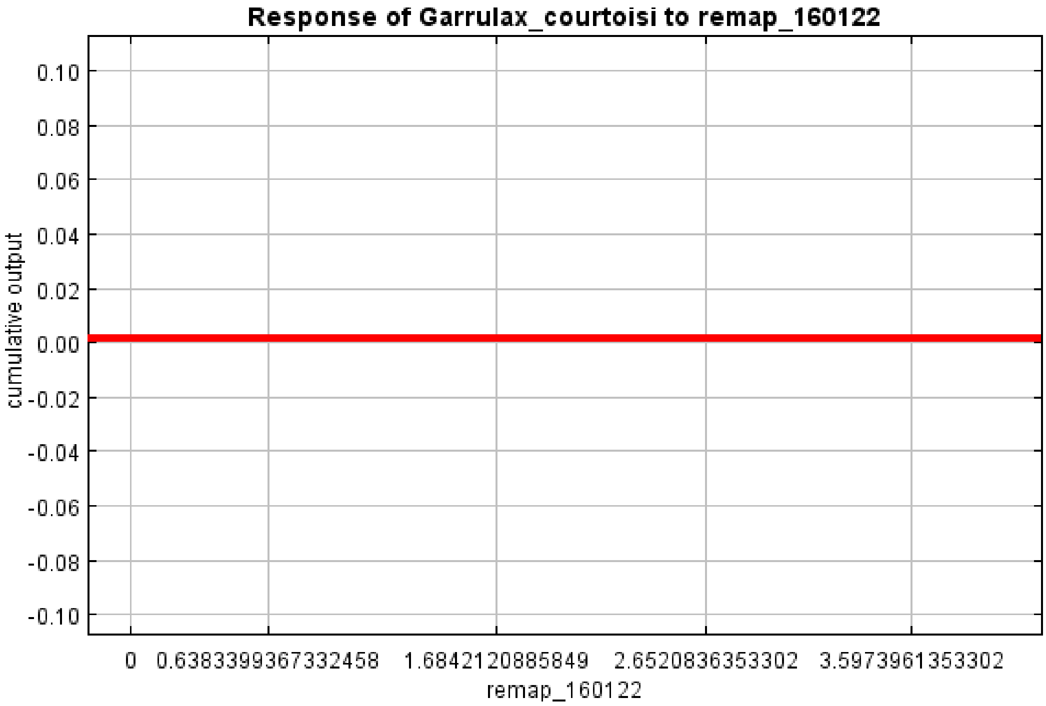


Figure S4. Proportion of occupied to counted breeding sites during each year of the Blue-crowned Laughingthrush census, 2000-2017. Bars are calculated on the following bases: black bars are where site counts were not performed (as the observers observed Blue-crowned Laughingthrushes but were unsure of breeding activity) are classed as 'NA' values, and therefore not treated as 'counted'. Grey bars are these same site counts classed as '0' (rather than NA) and therefore treated as 'counted' sites.

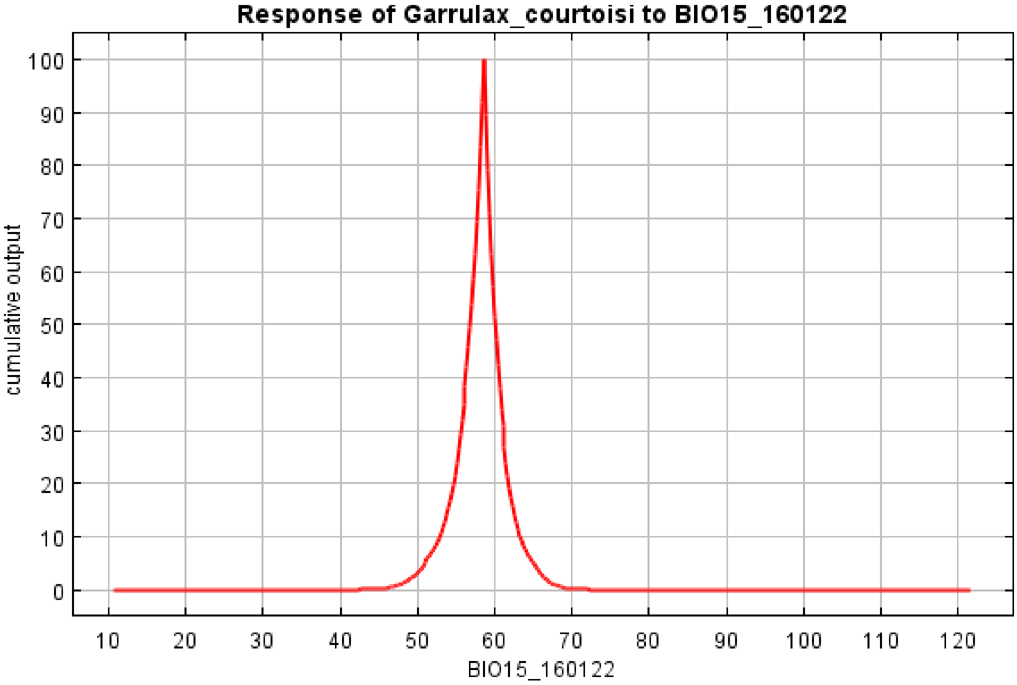
(a)


Response of Garrulax_courtoisi to BIO7_160122
cumulative output
90
80
70
60
50
40
30
20
10
0
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
BIO7_160122

(b)


Response of Garrulax_courtoisi to remap_160122
cumulative output
0.10
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
0
0.6383399367332458
1.6842120885849
2.6520836353302
3.5973961353302
remap_160122

(c)



(d)

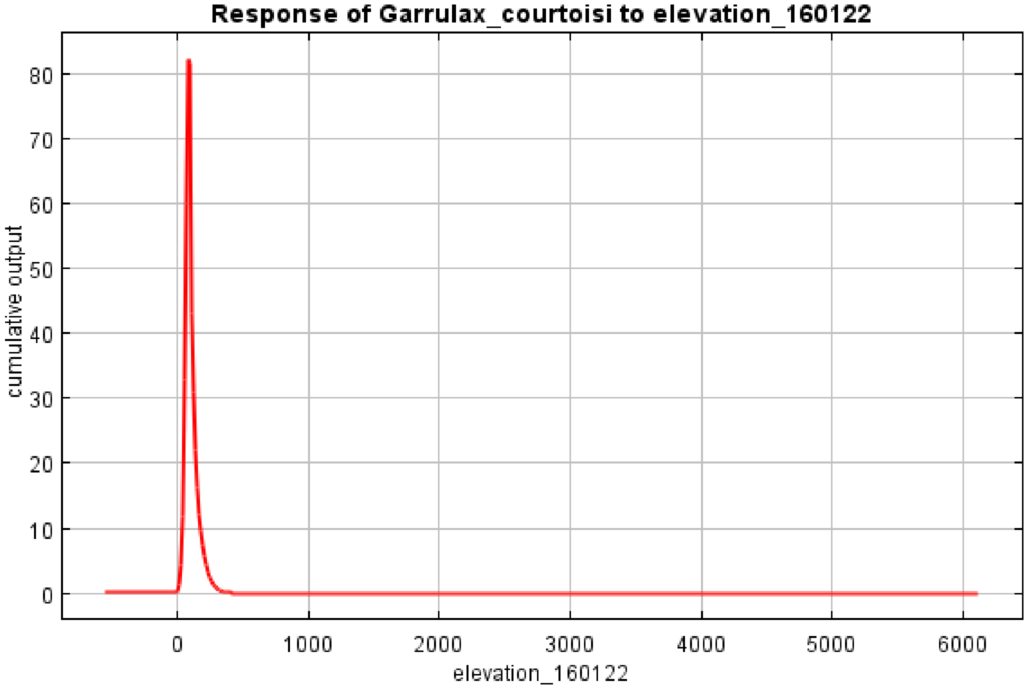


Figure S5. Univariate response curves from Maxent model for (a) annual temperature range (b) land cover, (c) precipitation of the wettest quarter and (d) elevation.

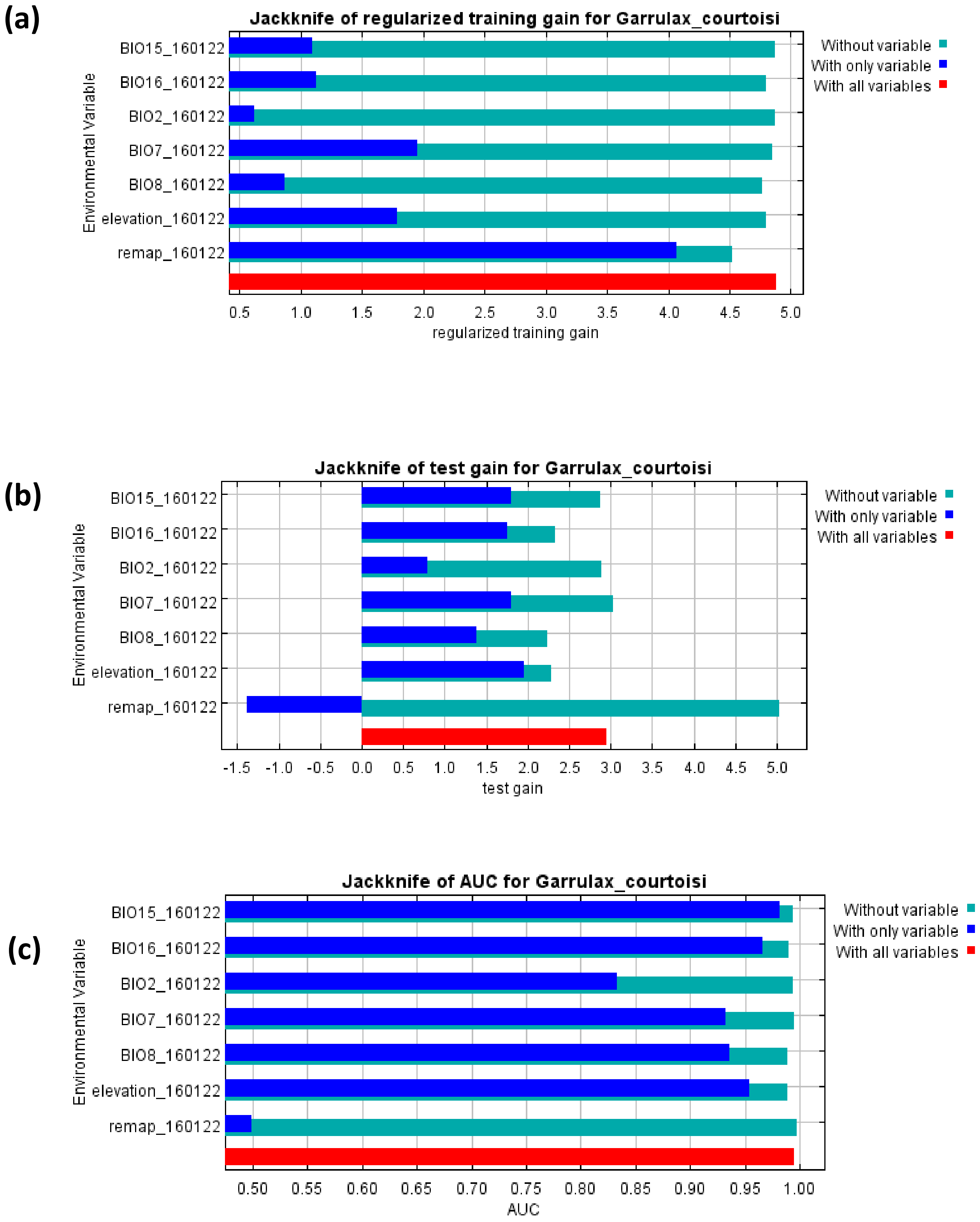


Figure S6. Jackknife tests of variable importance for final Maxent model, showing (a) training gain (b) test gain and (c) AUC on test data.

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4. Local ecological knowledge can detect breeding locations, landscape changes and threats associated with the Critically Endangered Blue-crowned Laughingthrush *Pterorhinus courtoisi* in China

Rosalind A. Gleave, Sarah K. Papworth, David Bauman, Steven J. Portugal, Weiwei Zhang, Yikang Liu, Xiaojin Cheng, Zhiming Cao & Samuel T. Turvey

4.1 Abstract

Designing conservation interventions for rare species can be hindered by a lack of relevant data. Local ecological knowledge (LEK) can provide rapid, cost-effective baseline data across large spatial and temporal scales, giving insights missed by traditional ecological approaches. The Blue-crowned Laughingthrush (BCLT) *Pterorhinus courtoisi* is a Critically Endangered passerine found only in southeastern China, with no available data explaining why its breeding range is highly restricted or why the population is so small, as it occurs in a human-occupied forest-agricultural landscape seemingly undifferentiated from surrounding environments in southern China. We conducted the first systematic, range-wide interviews on the BCLT (n=519) to collect novel information from local respondents on the species' temporal and spatial distribution, and on possible threats and landscape changes associated with its presence or absence. Recognition of BCLT was moderate, with 44.6% of respondents reporting having seen a BCLT and with sightings within the last 18 months occurring across the entire study landscape. Sightings of BCLT were higher in the breeding season; sightings during the non-breeding season were more likely to be away from breeding sites. Nine (56.25%) breeding villages were confirmed as such by LEK data, and two villages reported nesting BCLTs where no breeding had been previously recorded. Trapping BCLTs was reported across the study landscape, mostly dated within the last 10 years and linked to people from urban centres. Trapping BCLTs and lack of *fengshui* forest were associated with sites where BCLTs did not breed, while breeding sites were associated with increases in vegetable gardens, and other sites within the species' range were associated with decreases in bush/scrub. This is the first evidence of ongoing bird trapping as a threat to the BCLT, and remedial measures are urgently required across the region. We demonstrate that LEK thus here identifies potential threats, new breeding sites, and landscape changes correlated with presence or absence of local breeding sites.

Keywords: local ecological knowledge, China, laughingthrush, *Pterorhinus courtoisi*, trapping, landscape change, Asian songbird crisis

4.2 Introduction

The aim of halting biodiversity decline and extinctions must be underpinned by an understanding of species' status and threats (Williams, Balmford and Wilcove, 2020). Diagnosing the mechanism(s) responsible for species declines, low population sizes or range restrictions is critical. While range restriction is an indicator of threat (Mace *et al.*, 2008), understanding whether it is driven by natural or anthropogenic processes like habitat loss (Zhou *et al.*, 2005) or exploitation (Yang *et al.*, 2018) is pivotal. Designing interventions when threats are poorly understood risks inefficient use of money and time (Sutherland, Newton and Green, 2004), population collapse (Caughley, 1994) or other unintended consequences (Larrosa, Carrasco and Milner-Gulland, 2016). Key to addressing such threats is understanding the nature of their spatiotemporal patterns and dynamics, and their relationship with population declines (Turvey *et al.*, 2013; Zöckler *et al.*, 2016).

Identifying specific threats and population constraints can sometimes be difficult with standard ecological surveys, necessitating the identification of alternative approaches to provide conservation evidence (Turvey *et al.*, 2014). One such potential resource is Local Ecological Knowledge (LEK), an important source of data representing first-hand information obtained from people's interactions with, and observations of, their environment (Newing 2011). LEK can provide information on the current and past status of target species through information on last sightings and occurrences, as well as associated human-wildlife interactions and conservation-relevant patterns of local awareness, perceptions and attitudes (Turvey *et al.*, 2010, 2014). LEK has been used for establishing baseline information on key population parameters for threatened species and identifying anthropogenic-related threats (Turvey *et al.*, 2013; Parry and Peres, 2015; Archer *et al.*, 2020). These insights can inform interventions such as the establishment of protected areas (Archer *et al.*, 2020). LEK has been used to inform conservation efforts for several easily identifiable species of mammals (Nash, Wong and Turvey, 2016; Turvey *et al.*, 2017; Archer *et al.*, 2020; Zanvo *et al.*, 2020) and other large charismatic vertebrates or economically important taxa, such as for spatial conservation planning including future reintroductions or restocking (Chen *et al.*, 2018). LEK has also previously given insights into levels of bird ownership and trapping (Biddle *et al.*, 2021) and some bird population declines (Mallory *et al.*, 2003).

A system where LEK could prove beneficial is for threatened songbirds where no clear threat has been identified. Multiple Asian songbird species have been nearly driven to extinction in the wild by trade (Eaton *et al.*, 2015; Shepherd *et al.*, 2016; Nijman *et al.*, 2017; Heinrich *et al.*, 2021). Threats to songbirds are considered high in China, with over-hunting and wildlife trade a major threat to Chinese biodiversity (Nijman 2010). Songbird markets take place in many Chinese cities (Huo *et al.* 2009; Dai and Zhang, 2017; Cheng, 2019), and there is widespread and ongoing domestic hunting and trade of wildlife for use and sale within China (Martinez and Lewthwaite 2013; Zhou *et al.*, 2014; Kamp *et al.*, 2015). However, these threats are not fully understood, with patchy knowledge of wildlife hunting and general consumption (Liang, Cai and Yang, 2013; Cheng, 2019) and weak animal trade monitoring (Zhang, Hua and Sun, 2008).

One highly threatened Chinese songbird is the Blue-crowned Laughingthrush *Pterorhinus courtoisi* (hereafter BCLT). This species has a breeding population restricted to a small part of northeast Jiangxi Province, a subtropical region ranging from 50 to 1,600 m in elevation, and with its core breeding population in Wuyuan County (coordinates 29°01’-29°35’N, 117°22’-118°11’E) (Hong *et al.* 2006; He *et al.* 2017). It is classified as Critically Endangered by the IUCN (BirdLife International, 2018), due to its restricted, fragmented range (estimated extent of occurrence 610 km^2) and small population, estimated to be 323 individuals in 2016 (He *et al.* 2017). The extent of its past range is unknown, but a second population, sometimes treated as a distinct subspecies, *P. c. simaoensis*, was known from Yunnan Province, southwestern China (approximately 2,000 km from Jiangxi), but is now considered extinct (He *et al.* 2017).

Captive collections have existed since the 1990s, after BCLTs appeared in international trade (Long *et al.* 2004; Pasini *et al*. 2004), and the species now breeds in zoos in Europe, North America, Hong Kong and mainland China. However, almost all of these captive individuals are thought to be *P. c. simaoensis* (He 1994; Wilkinson *et al*. 2004; Wilkinson & He 2010a).

Although a single report of captive birds in Hong Kong during the 1990s was traced back to Wuyuan (Yu 2003), there is no recent evidence of trapping for trade affecting BCLTs in Jiangxi (Yu 2003; Richardson 2005; Wilkinson & He 2010b). Indeed, there have been no recent reports of BCLTs in either international or domestic trade.

BCLTs in Wuyuan are colonial and cooperative breeders, with colonies nesting near or within villages (Wilkinson *et al.* 2004). Their breeding landscape is characterised by low forested hills and agricultural riverine valleys dominated by rice, oilseed rape and tea plantations, interspersed with small villages surrounded by vegetable plots (Richardson 2005; He *et al.* 2017) and village *fengshui* forests (mature broadleaf or mixed forest stands found close to villages that have been locally protected for centuries; Coggins *et al.*, 2012). BCLT frequently nest in the latter habitat (Hong *et al.* 2003; Wilkinson *et al.* 2004) as well as bamboo, fruit trees and fir (He *et al.* 2017; Zhang et al. 2017), and forage mainly within broadleaf forest (including but not limited to *fengshui* forest), bush/scrub plots, tea plantation and vegetable plots during the breeding season (Yu 2003; Hong *et al.* 2006; Wilkinson and He 2010b; He *et al.* 2017; Zhang *et al.*, 2017; Liu *et al.*, 2020). As this landscape is broadly similar to other human-occupied landscapes across much of southern and central China, it is unclear why the BCLT is not more widespread. Building developments and road traffic are known to have affected BCLT breeding sites in Jiangxi, even causing their abandonment (He *et al.* 2017), but it is unknown whether local patterns of land use differ between areas occupied and adjacent ones unoccupied by BCLT, which could potentially be a factor restricting the species' present distribution. Moreover, it is not known where BCLTs spend their non-breeding season, although anecdotal reports suggest this may be in nearby hills and mountains, possibly as far south as Wuyishan National Nature Reserve, 120 km south of Wuyuan (Yu 2003; Cheng and Lin 2011; He *et al.*, 2017).

Recent conservation-oriented research has looked at BCLT habitat use (Shi 2017, Huang *et al.* 2018, Liu *et al.*, 2020) and responses to disturbance by tourists (Zhang *et al.*, 2017a), but the potential information-content of LEK for informing BCLT conservation has hitherto not been investigated. This type of research has never been carried out explicitly to conserve specific bird species in China, thus has the potential to collect new information for this species and help establish this approach for Chinese birds. The BCLT is a distinctive and attractive species both visually and aurally, suggesting that it must be familiar to many people living within its home range. Furthermore, it is now a species of local cultural and socio-economic importance, attracting photographers to its long-term breeding sites (Zhang *et al.*, 2017a) and featuring on local murals throughout the region (R. Gleave pers. obs.).

Here, we explore the ability of LEK to provide information on three issues pivotal to the conservation of BCLT: (1) can LEK identify new BCLT breeding sites and BCLT seasonal distributions; (2) can LEK identify reported threats and habitat changes potentially associated with BCLT presence and absence; and (3) can LEK identify priority areas for further research and conservation (e.g. sightings outside the known range, and/or areas of high potential threat). This baseline information is needed to design targeted interventions to address potential drivers of BCLT population or range restriction. By investigating the extent to which LEK can provide conservation-relevant data on key management parameters such as distribution and threats for a highly threatened passerine, our findings also provide broader lessons on using LEK to gather pertinent data on other species that have not traditionally been the focus of research using social-science methods.

4.3 Methods

4.3.1 Field survey

Community-based surveys were conducted between 4 June and 31 July 2019 in Wuyuan, Dexing and Leping counties, Jiangxi Province, and Xiuning County, Anhui Province, which encompass the total known geographic range of the BCLT (data from unpublished censuses, 2000–2017, and from citizen science website www.eBird.org; F. He 2019, personal communication), and also include nearby unsurveyed and unoccupied regions (**Figure 1**). We digitised and labelled over 900 villages in southern China using the Google Satellite plugin, QGIS version 2.18 (Las Palmas; QGIS Development Team 2021). Villages were digitised within (1) a core area comprising a 725.93 km^2 minimum convex polygon (MCP) generated in QGIS around all recorded BCLT presence locations, and (2) a 25 km buffer area around the core area (**Figure 1**).

We conducted interviews in 18 villages where BCLT are known to breed or have bred in 2000–2017 (unpublished data; F. He 2019, personal communication), and in a further series of 21 ‘control’ villages with no previously recorded evidence of BCLT breeding. Our sample of 18 active or former BCLT breeding sites included all known breeding sites except one (which we were only aware of later). We selected control villages by (1) targeting all those within 1 km of known BCLT localities reported on eBird (n=6) or in field reports (n=3; He 1994), and (2) randomly picking another 12 from within the combined core and buffer polygons. There were no significant differences between breeding and control villages within a set of basic characteristics (Mann-Whitney U Test): approximate number of buildings (W = 143, p = 0.14), distance to main road (W = 105, p = 0.91), distance to river (W = 124, p = 0.51), and elevation (W = 89, p = 0.43), taken from a Google Satellite layer within QGIS.

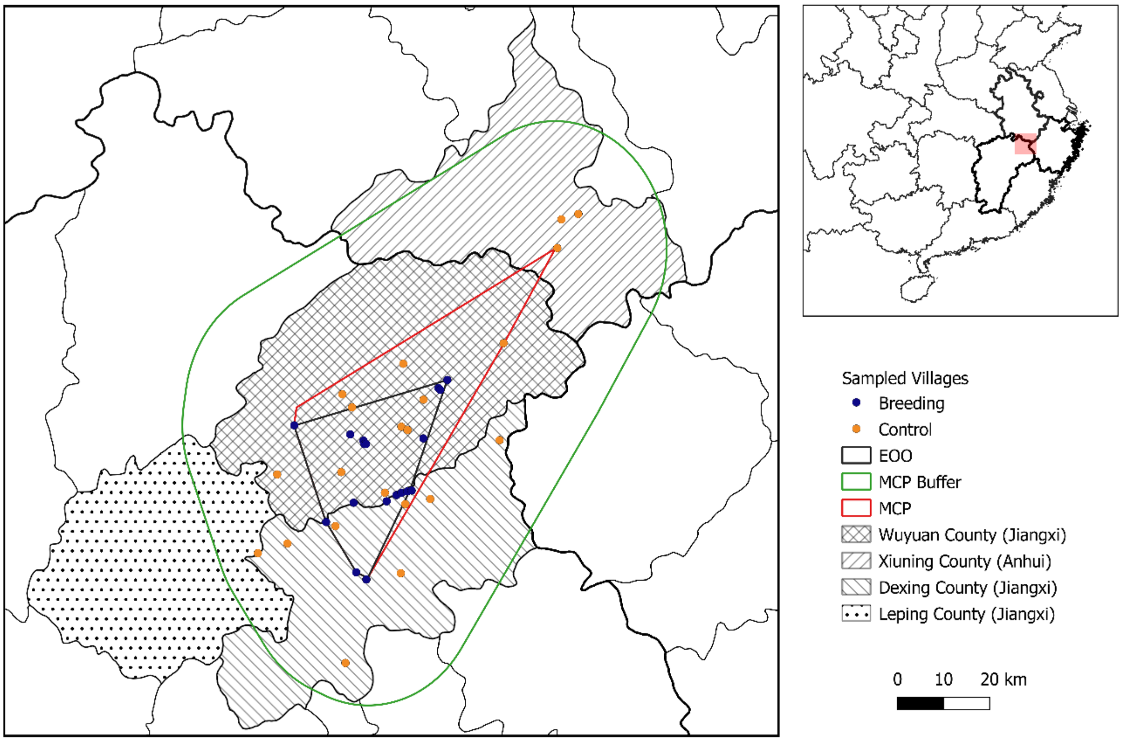

Figure 1. The distribution of sampled villages depicted as coloured circles. Shaded areas cover the counties of Wuyuan, Dexing, Leping (Jiangxi Province) and Xiuning (Anhui Province). Thick black lines demark the boundaries between provinces. The polygons show the Extent of Occurrence (EOO) drawn around known Blue-crowned Laughingthrush breeding sites, the Minimum Convex Polygon (MCP) drawn around all known Blue-crowned Laughingthrush sightings (including those from eBird), and the outer polygon shows the 25km buffer region around the MCP.

A target number of ≥10 interviews were conducted per village, based on the threshold of data saturation for interviews (Guest *et al.*, 1995). Household plans for villages were unavailable, so respondents were recruited through random encounters in villages and surrounding farmland. Village leader(s) or, if unavailable, other appropriate individuals were first located to grant permission for our research and to give information on village population size (number of individuals or families). Individuals below the age of 18 were not interviewed. Respondents were interviewed irrespective of sex or occupation.

Interviews were conducted in Mandarin or local dialect (Wuyuanhua), and recorded on paper in Mandarin, by volunteer field assistants from Jiangxi Agricultural University or local high schools. All interviewers received prior training. Each new interviewer was initially supervised by R.Gleave or another more experienced interviewer. Pilot interviews were conducted in May–June 2019 (n=40) and questions then modified to improve data collection. Our research was explained at the start of each interview, with consent given verbally beforehand and in writing afterwards. Respondents were informed that their responses were anonymous, that they could stop the interview at any time, and that they could decline to answer a question without explanation. Research was permitted by Jiangxi Wuyuan National Forest Bird Nature Reserve Management Office, and project design was approved by the Royal Holloway, University of London ethics committee (reference no. 1536-2019-02-21-16-10-PEBA015).

A standard questionnaire comprising 52 closed and open-ended questions was used in all interviews, which took 15–20 minutes to complete (see **Figure S1, Supplementary Information**). Following questions collecting basic demographic information, respondents were asked about landscape changes around their village over their lifetime. Landscape types included in the interview were: rice paddy, vegetable gardens, tea plantation, oilseed rape, fir forest, pine forest, bamboo forest, *fengshui* forest, broadleaf forest, bush/scrub, and fruit trees. Example photographs of these land use types were shown as necessary. Subsequent questions sought information on local population changes, number of houses, road, bridge and highway construction, and use of chemicals on crops.

Respondents were then asked if they recognised the BCLT (藍冠噪鹛, *languan zaomei*) and four locally common bird species (MacKinnon and Phillipps 2018): Chinese Hwamei *Garrulax canorus* (画眉, *huamei*), Masked Laughingthrush *Pterorhinus perspicillatus* (黑脸噪鹛, *heilian zaomei*), Light-vented Bulbul *Pycnonotus sinensis* (白头鹎, *baitoubei*) and Eurasian Tree

Sparrow *Passer montanus* (麻雀, *maque*). Species were always mentioned in the order listed above, with the BCLT last. Respondents were asked if they recognised each bird based on its standard Mandarin or Wuyuanhua name, then shown colour photographs of each species (**Figure S2, Supplementary Information**; all obtained through Google Images marked as 'labelled for non-commercial reuse') and asked if they recognised and/or could name them. All the species are sexually monomorphic. Finally, respondents were played an audio recording of a wild BCLT call, recorded by R.Gleave in July 2018. Most respondents were expected to recognise sparrows, which are locally abundant (Gleave, Zhang, Liu pers. obs. 2019) and were thus included as a positive control. Including a range of species was intended to allow comparisons, e.g. to assess respondents' ability to identify BCLT in relation to their knowledge of other species, and also functioned to obscure the possible importance of a single species within the interview, making it more likely that respondents might disclose sensitive knowledge or activities associated with BCLTs (Turvey *et al.*, 2015).

Respondents who recognised BCLT were asked if they had ever seen one; those who had done so were then asked about their last BCLT encounter, including time of year, location, breeding activity, and flock size based upon four simplified images of different-sized bird flocks (see **Figure S3, Supplementary Information**): 'small' = two birds, 'medium' = 10, 'large' = 18 and 'very large' = 40. All respondents were asked final questions about bird-related threats and conservation, including awareness of local bird capture and killing, and awareness of legal protection. If respondents could identify BCLT we also asked about specific captures of BCLT. If respondents had knowledge of BCLT captures, we attempted to follow up with a key informant interview, asking additional questions on trapping location and methods and the identity of trappers.

4.3.2 Analysis

4.3.2.1 *Interview data processing*

Interview data were translated from Mandarin to English by a single assistant fluent in both languages. All BCLT last-sighting dates were converted to calendar years where possible (**Table S1**, **Supplementary Information**); all dates that could not be converted due to lack of precision were excluded from analysis of last-sighting dates (n=149 retained). For the purposes of analysis, a new core area comprising a convex hull around all recorded BCLT breeding locations from 2000–2017 (F. He 2019, personal communication) was created in QGIS (area = 725.93 km^2), referred to as the Extent of Occurrence (EOO; **Figure 1**). A buffer region of 25 km^2 distance around the EOO was created, for comparison of villages between the two regions.

4.3.2.2 *Quantitative analysis*

All analyses were performed in R version 3.5.2 (R Core Team 2021). Chi-squared (or Fisher's exact) tests were used to investigate differences between: (1) breeding and control villages and between villages in the EOO and buffer region in the number of respondents who could recognise BCLT from its standard common name, a photo or audio recording; (2) these same villages, in the number of recent (2018–2019) reports of BCLT sightings or in flock sizes; (3) breeding (spring–summer) and non-breeding (autumn–winter) seasons in the number of BCLT sightings in breeding and control villages.

Five regression models were built to investigate the relationship between reported land use changes and human threats on five different metrics of BCLT presence and absence. Variables influencing whether responses came from a breeding or a control village, or within the EOO or in the buffer area, were investigated using generalised linear models (GLMs) with a binomial error structure (logit link), as response variables are binary. Respondents reported past BCLT breeding activity in two villages with no previous record of breeding, so two separate 'breeding/control' models were built, alternately assigning these villages as either 'breeding' or 'control' to compare model outputs. Variables influencing whether a respondent had ever seen a BCLT, or had seen a BCLT within the previous 18 months, were investigated using generalised linear mixed models (GLMMs), again with a binomial error structure. A Bayesian inference framework was used (Stan via R package *brms*; Bürkner 2017) to account for the unbalanced design of the data, and to capture and report model coefficient uncertainty.

Multiple Correspondence Analysis using the *factoextra* package (Kassambara and Mundt 2020) was performed on landscape change variables, aiming to reduce the number of covariates necessary in the models. However, because a low proportion of the total variance was described by the first few axes (axes 1–4: 19%), with little associated variability, covariates were not separated for the models (**Figure S4, Supplementary Information**). All

GLMM models included varying intercepts for Interviewer (to account for between-data collector variation) and Village (to account for between-site variation). For each covariate, factors were re-levelled so the reference level was either ‘No’ or ‘No change’, generating more biologically plausible baselines for interpretation. For all models, variation in respondent demographics between response types was investigated using either chi-squared tests (occupation, sex) or univariate GLMs (age) with a Gaussian error structure using the *lme4* package in R (Bates *et al.*, 2015), where each response variable was treated as a binary predictor.

4.3.2.3 *BCLT breeding responses*

For breeding/control and EOO/buffer models, all responses within entire spatial locations (villages) were allocated an identical binary output. This generated significant levels of autocorrelation (**Spatial autocorrelation in models, Supplementary Information**) and pseudo-replication. To remove this from models, we split each predictor (all categorical) into separate factor levels, with each factor level treated as a new, separate variable. Individual GLMs were then run based on these factor levels. This process was repeated for each of the *a priori* selected categorical predictor variables. Variables for inclusion in the models (increases/decreases/no change in or lack of: bamboo, *fengshui* forest, bush/scrub, tea plantation, and vegetable gardens, and building or not of new roads, awareness or not of people trapping BCLTs) were chosen *a priori* based on existing literature and basic data exploration (**Table S2, Supplementary Information**); all these variables had past evidence for impacting breeding BCLT, or potential to influence BCLT populations (Yu 2003; Hong *et al.* 2006; Wilkinson and He 2010b; He *et al.* 2017; Zhang *et al.* 2017; Liu *et al.* 2020).

The responses from each village for each factor level were summed and scaled (subtracting the variable mean, then dividing by the variable standard deviation) to improve running of the model (Zuur *et al.* 2009; McElreath 2016). Collinearity between each factor level was checked using the R package *corrplot* (Wei and Simko 2021), running pairwise correlations and a threshold of 0.70 (Wei and Simko 2021), with all correlations below this level. Factor levels where responses were not deemed useful for later inference were excluded from analysis. These were mostly ‘do not know’ responses, except for awareness of people catching BCLT (response could indicate withholding of sensitive information) and increase in *fengshui* forest (even if this habitat type increased within living memory, the trees might not yet be mature enough to typify this land type).

4.3.2.4 *BCLT sighting responses*

To lower risks of model overfitting, statistical biases from unsupervised addition of covariates, and stepwise variable selection issues (Mundry and Nunn, 2009; McElreath 2020), we compared a global model to a set of four reduced models (**Table 1**), used to find a more parsimonious model, and to examine different key combinations of habitat change and threat covariates. For BCLT sightings, our global model contained the same covariates as breeding/EOO models to enable direct comparison. The first two reduced models contain fewer habitat covariates (removing change in tea plantation and then bush/scrub, as these showed weaker importance for breeding BCLT), the third contains the two 'threat' covariates (new roads and trapping), and the fourth contains all habitat covariates. For recent BCLT sightings, our global model covariates were the same as for the model of all BCLT sightings, but excluding changes in *fengshui* forest, bush/scrub or new roads (linked by evidence to BCLT breeding sites as opposed to general distribution), and including reported types of caught birds (to examine the effect of catching songbirds, gamebirds/waterfowl and sparrows/other birds locally considered as pests). Model comparison was performed using Leave-One-Out (LOO) cross-validation: dividing the dataset into a series of 'folds', removing a single observation each time, and predicting each fold after training the model on the rest of the dataset (McElreath 2020). We used regularising priors to limit the risks of overfitting for slope coefficients (McElreath 2020).

To test and potentially control for spatial autocorrelation in the model residuals, models were run both with and without a Gaussian process regression. This technique allows the varying effects of 'village' to be treated as a continuous category by incorporating the spatial coordinates of surveyed villages, hence correcting for the fact that geographically close villages may share more similar features than expected from independent observations (e.g., topography; McElreath 2020). We present the model with the best expected out-of-sample predictive accuracy, as well as outputs from alternative candidate models with similar accuracy.

Bayesian updating of the model parameters was performed through the No-U-Turn Sampler (NUTS) in Stan, using the R package *brms* (Bürkner 2017). Models were fitted using 3,000 iterations on four chains, with 1,500 warm-ups per chain to optimise the sampler prior to sampling. Model convergence was checked using Rhat values, and posterior distributions were handled and visualised using the R package *tidybayes* (Kay 2022). All models converged and had a sufficiently high Effective Sample Size. Posterior predictive checks were performed for all models to assess how well each model retrodicted the real observations using *tidybayes* (Kay 2022). We only report covariates with a coefficient posterior 90% credible interval not encompassing zero, i.e., with a 90% mass probability either lower or higher than zero.

able 1. Global and reduced GLMMs for investigating Blue-crowned Laughingthrush sighting responses in relation to habitat change and human threat covariates. Model specification uses R notation.

	Respondent seen BCLT	**Respondent seen BCLT within last 18 months**
Global model (random intercepts)	Seen_BCLT ~ Catching_BCLT + Fengshui_forest_change + Veg_garden_change + Tea_plant_change + Bamboo_change + Bushscrub_change + Roads + (1|Village) + (1|Interviewer)	Recently_seen_BCLT ~ Catching_BCLT + Tea_plant_change + Veg_garden_change + Types_caught_birds + Bamboo_change + (1|Village) + (1|Interviewer)
Reduced model 1	Seen_BCLT ~ Catching_BCLT + Fengshui_forest_change + Veg_garden_change + (1|Village) + (1|Interviewer)	Recently_seen_BCLT ~ Bamboo_change + Tea_plant_change + Veg_garden_change + (1|Village) + (1|Interviewer)
Reduced model 2	Seen_BCLT ~ Catching_BCLT + Fengshui_forest_change + Veg_garden_change + Bamboo_change + Bushscrub_change + (1|Village) + (1|Interviewer)	Recently_seen_BCLT ~ Tea_plant_change + Types_caught_birds + (1|Village) + (1|Interviewer)
Reduced model 3	Seen_BCLT ~ Catching_BCLT + Roads + (1|Village) + (1|Interviewer)	Recently_seen_BCLT ~ Tea_plant_change + Types_caught_birds + (1|Village) + (1|Interviewer)
Reduced model 4	Seen_BCLT ~ Fengshui_forest_change + Veg_garden_change + Bamboo_change + Tea_plant_change + Bushscrub_change + (1|Village) + (1|Interviewer)	Recently_seen_BCLT ~ Catching_BCLT + Types_caught_birds + (1|Village) + (1|Interviewer)

4.4 Results

We interviewed a total of 519 respondents in 39 villages across four counties (Wuyuan = 281; Dexing = 189; Leping = 16; Xiuning = 33) with a mean of 13.3 interviews per village. Twenty-five of our villages were within the EOO, 14 within the buffer region. Not all respondents answered all questions asked (n=23). Respondent demographics are shown in **Table S3, Supplementary Information**. Based on given population estimates, 1.1% of the population at target locations were surveyed. Most respondents lived in the target survey village (95.2%, n = 494) and, of those, most had been residents their whole lives (80.1%, n = 396). The mean amount of time that people had lived in their villages was 49.9 years (SD = 19.4, n = 516).

4.4.1 Local bird species identification

Recognition of different bird species ranged from 27.8% to 82.9% by photo, and 2.1% to 86.1% by name, with sparrows the most widely recognised in both categories (**Figure 2**). Three out of the five species were better recognised by photo than name (**Figure 2**), possibly because interviewers used standardised common names rather than local names. Variations in bird species names given are shown in **Local bird names, Supplementary Information**.

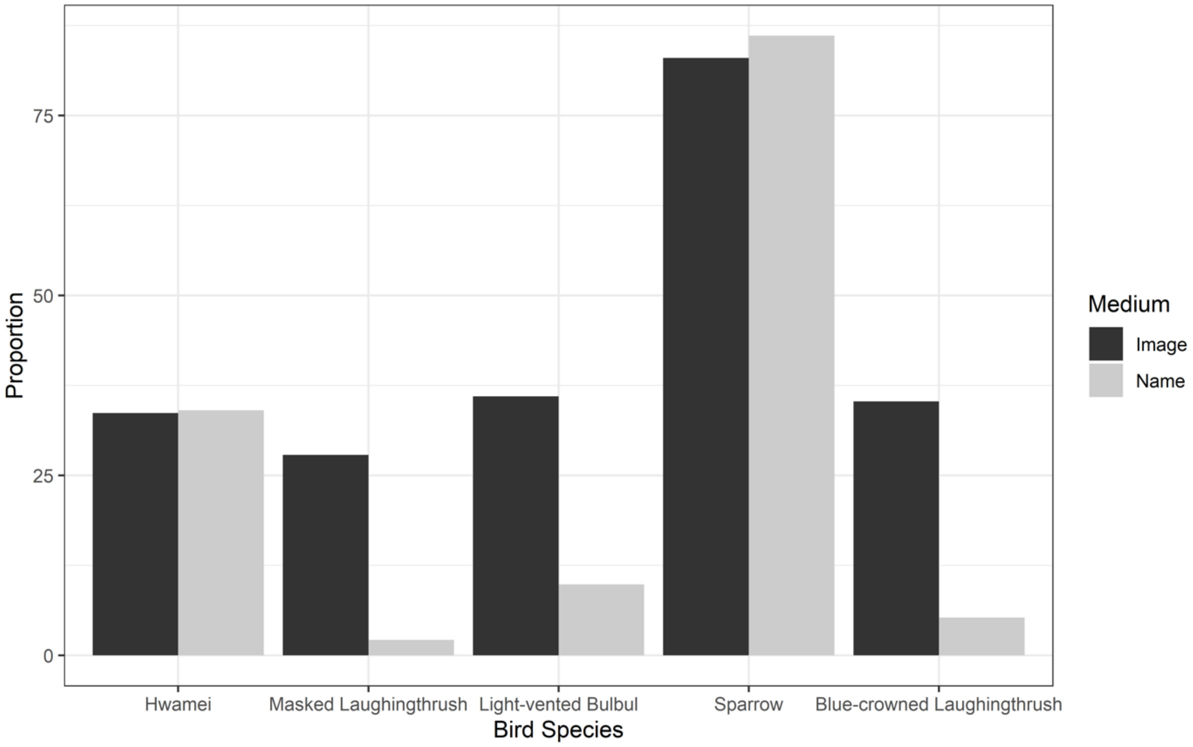

Figure 2. Proportion of respondents who recognised each of five local bird species by either photograph or standard common name.

4.4.2 BCLT recognition

In total, 44.96% (n=232/516) of respondents reported recognising BCLT from either name, photo or audio recording (**Figure S5, Supplementary Information**), with 11.63% (n=27/232) recognising the name, 78.44% (n=182/232) recognising the photo, and 60.34% (n=140/232) recognising the recording. Of these 232 respondents, 69.4% (n=161) recalled the last time they saw the species in the wild (other respondents could not recall seeing them or had only seen the species on TV). No respondents recognised BCLT from their standard name in control villages (n=0/162) or the buffer region (n=0/186), with this being statistically different in breeding villages (X^2 = 27.55, df = 1, p = >0.001) and in the EOO (X^2 = 15.86, df = 1, p = >0.001). There was significantly higher recognition of BCLT by respondents from a photo in the EOO (46.09%, n=130/282) compared to the buffer region (30.41%, n=52/171) (X^2 = 10.26., df = 1, p = 0.001), but no significant difference between breeding (43.56%, n=105/241) compared to control (36.32%, n =77/212) villages (X^2 = 3.18, df = 1, p = 0.07). There was no significant difference between respondents who recognised BCLT from the auditory recording in breeding (32.69%, n = 68/208) compared to control (39.56%, n=72/182) villages (X^2 = 2.89, df

= 1, p = 0.08), or in the EOO (34.01%, n=83/244) compared to the buffer region (39.04%, n=57/146) (X^2 = 0.79, df = 1, p = 0.37).

4.4.3 BCLT sightings

Of the 232 respondents who recognised BCLT, 45.68% (n=106) had seen one within the last 18 months, or recently (**Figure S6, Supplementary Information**). There was no significant difference in the proportions of respondents in breeding villages who had seen a BCLT recently (48.57%, n= 51) compared to those in control villages (42.63%, n = 55) (X^2 = 0.89478, df = 2, p = 0.6393), or in the EOO (50.00%, n = 73) compared to the buffer region (37.50%, n = 33) (X^2 = 3.4846, df = 2, p = 0.175). Respondents at breeding sites reported more recent mean last sighting dates (2016, n = 77) than those at control sites (2013, n = 74), and at sites in the EOO (2015, n = 98) than in the buffer region (2012, n = 53).

4.4.4 Season

Frequencies of BCLT sightings varied between seasons (X^2 = 56.32, d.f. = 3, p = <0.001), with more respondents reporting last seeing BCLTs in spring or summer (breeding season; 75.2%, n = 161) compared to autumn or winter (non-breeding season; 24.76%, n = 53). Some respondents (n = 26) gave more than one season for their last-sighting information. Seasonality of last sightings was close to being significantly different between breeding and control villages (X^2 = 7.42, d.f. = 3, p = 0.059), with a higher proportion of last sightings in breeding villages made during the breeding season (breeding villages = 75.90%, control villages = 63.70%), and a higher proportion of sightings in control villages made during the non-breeding season (breeding villages = 14.81%, control villages = 29.84%; **Figure 3**).

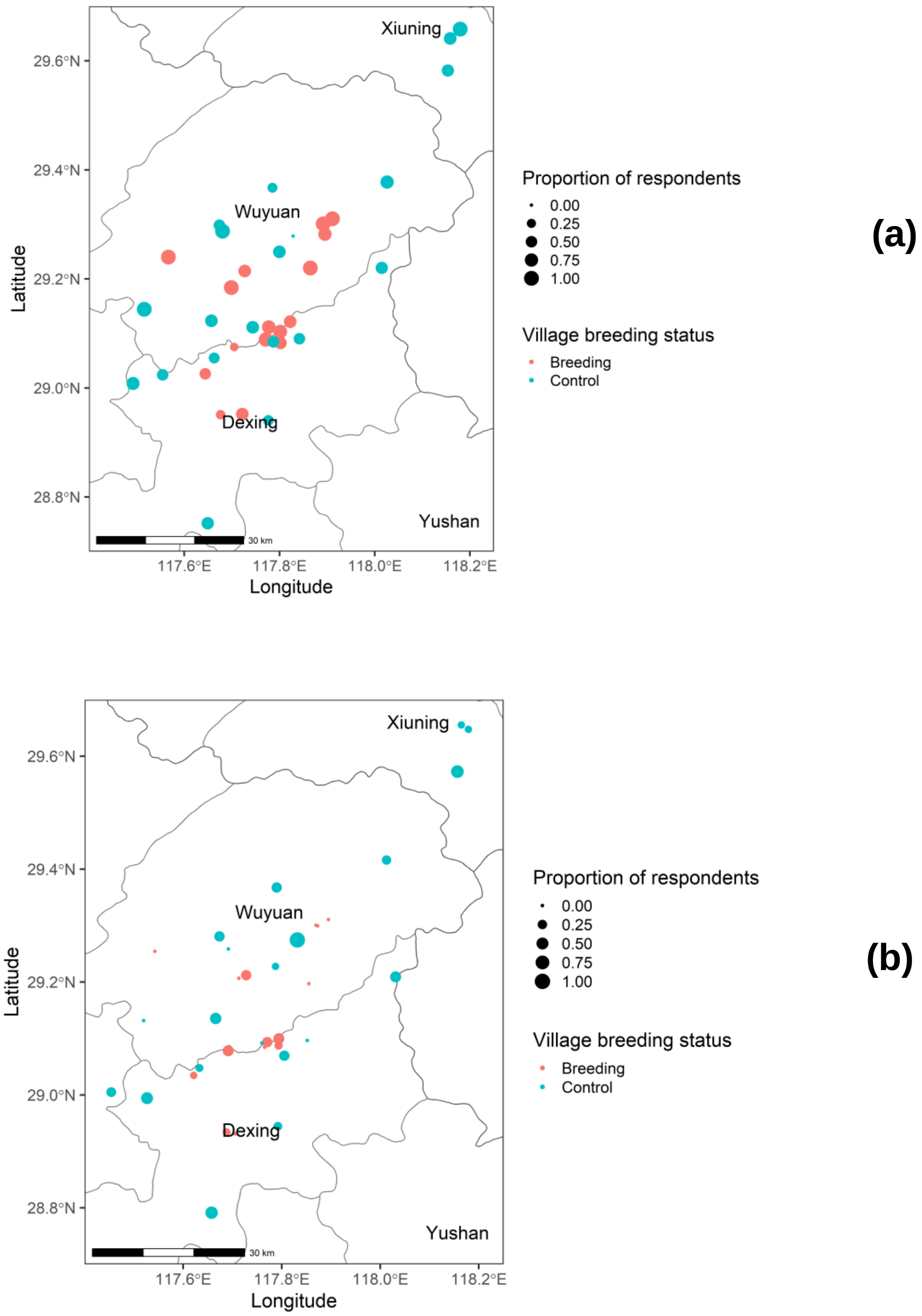

Figure 3. Spatial distribution of sampled villages, showing the proportion of respondents who recognised Blue-crowned Laughingthrush that last saw the species in (a) the breeding season (spring/summer) or (b) the non-breeding season (autumn/winter). Pink = breeding villages, blue = control villages.

4.4.5 Flock size

Of respondents who recalled the flock size of their last BCLT sighting 64.00% (n=90) stated they had seen a ‘small’ flock, 15.71% (n=22) a ‘medium’ flock, 14.28% (n=20) a ‘large’ flock, and 5.71% (n=8) a ‘very large’ flock. A higher but non-significant proportion of respondents saw a ‘small’ flock in control villages, outside the EOO, with more respondents seeing a ‘medium’, ‘large’ or ‘very large’ flock in breeding villages and within the EOO (p= 0.10). The spatial distribution of these respondents is shown in **Figure 4**.

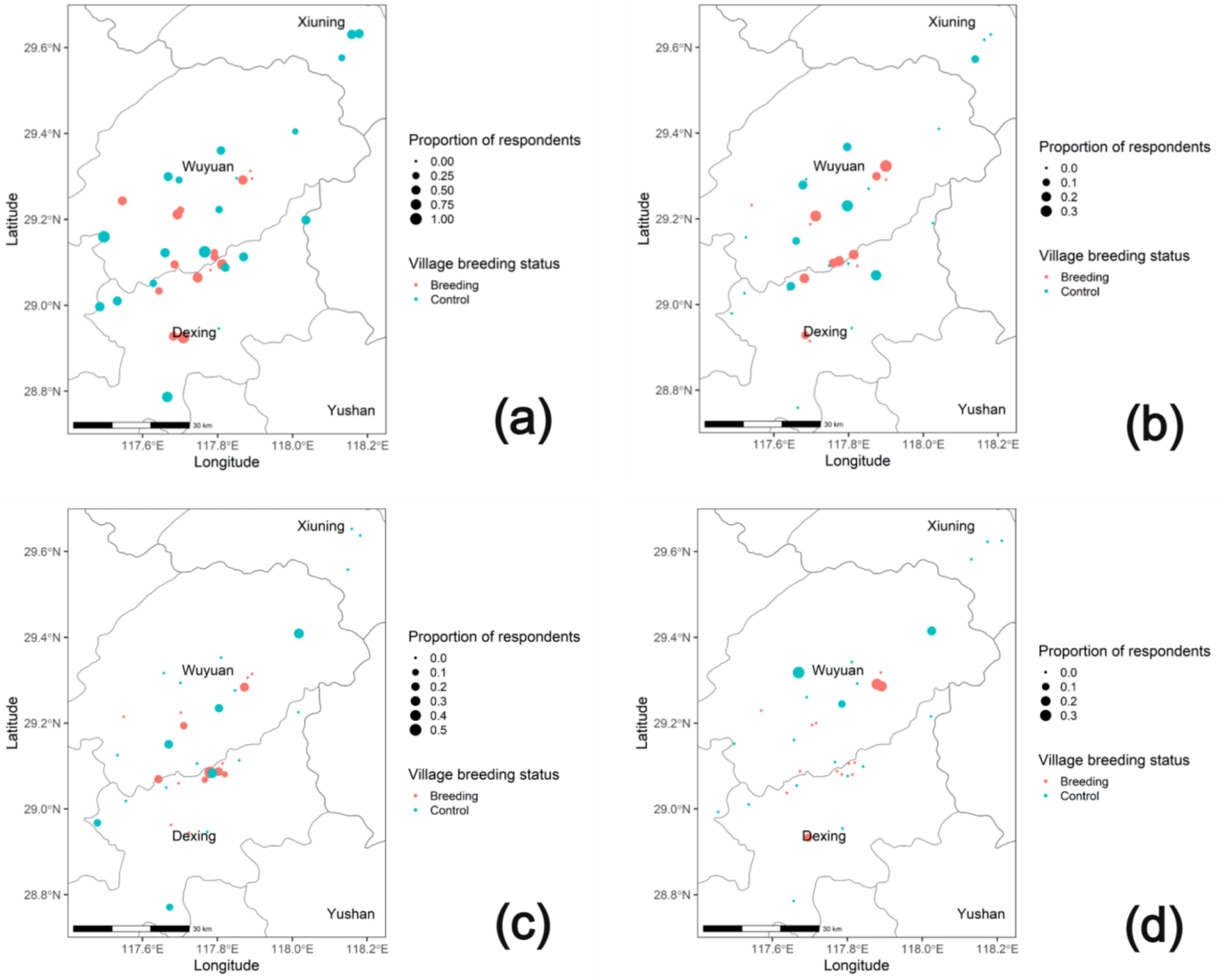

Figure 4. Spatial distribution of sampled villages, showing proportion of respondents who reported seeing different-sized flocks in breeding (pink) and control (blue) villages. (a) ‘small’ flocks, (b) ‘medium’ flocks, (c) ‘large’ flocks, (d) ‘very large’ flocks.

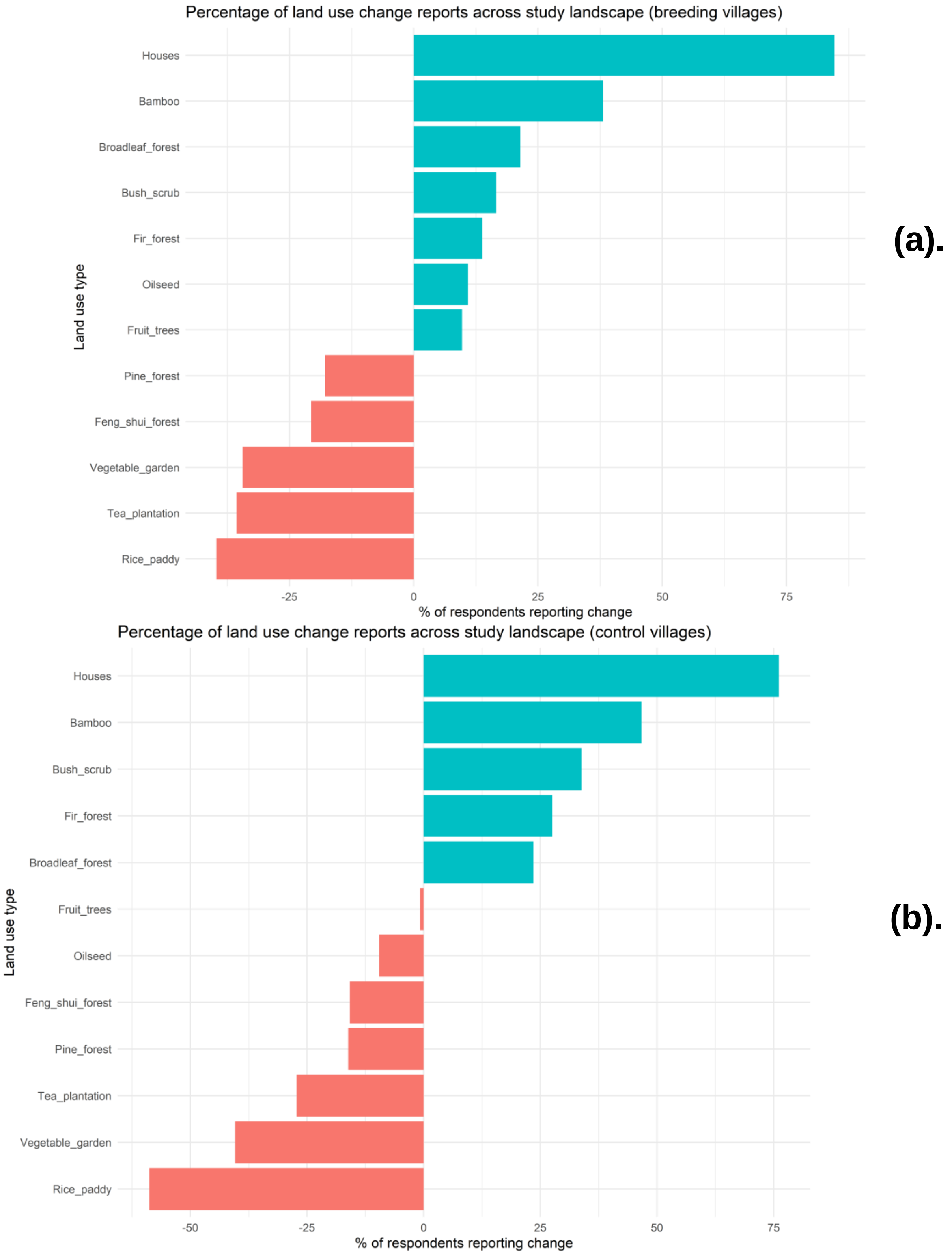

Figure 5. Percentage of respondents reporting a change in different land use types around their home villages during their lifetime in (a) breeding villages and (b) control villages. Blue bars show an overall percentage of people reporting an increase in a land type, and pink bars show an overall decrease.

4.4.6 Breeding reports

A total of 14 respondents across 11 villages had seen BCLTs nesting near their village; of these villages, nine (56.25%) were known breeding villages, and two ('village 1' and 'village 2') were previously unknown breeding sites. In village 1 (in the buffer region, near a past eBird sighting), birds were reported nesting in camphor trees within the village. In village 2 (in the EOO, also near a past eBird sighting, and close to other breeding sites), they were reported nesting in old trees in a field. Respondents reporting past or present BCLTs nesting in their village did not provide exact locations but stated that the trees used were 'high trees', 'fruit trees', 'huge trees near the village', 'old trees', 'Camphor trees' (*Cinnamomum camphora*), 'Pomelo trees' (*Citrus maxima*), 'Chinese yew trees' (*Taxus chinensis*), and 'all kinds of trees'.

4.4.7 Landscape changes and threat activity

Across the whole study landscape, respondents reported various changes (increases/decreases/lack of) in different land use types around their home villages during their lifetime (**Figure 5; Table S4, Supplementary Information**). In addition, 81.5% (n=423) reported a change in the number of houses in their village, with 99.1% reporting an increase, and 72.1% (n=374) reported new roads being built during their lifetime. Furthermore, 85.0% (n=440) reported the use of chemicals on crops around their village; of these, 51.6% (n=268) reported that the amount of chemicals used had changed over their lifetime, 56.7% (n=152) of whom reported an increase.

As many as a quarter (25.5%; n=129/506) of respondents had heard of people catching birds from the wild. Of these, 24.8% (n=32) reported birds being caught by villagers, 56.6% (n=73) by outsiders, and 8.5% (n=11) by both villagers and outsiders. Respondents reported a mean last bird catching date of 2014 (range 1995–2019). Types of bird, reasons for catching and methods of catching are given in **Table S5, Supplementary Information.** Nearly a tenth (9.3%; n=48/514) of respondents had heard of people killing wild birds. Bird-killing events were reported with a mean last date of 2007 (range 1970–2019). When asked whether people in their county kept songbirds, 6.5% (n=34) said yes. Of these, 47.1% (n=16) said people bought birds from others or received them as gifts from friends.

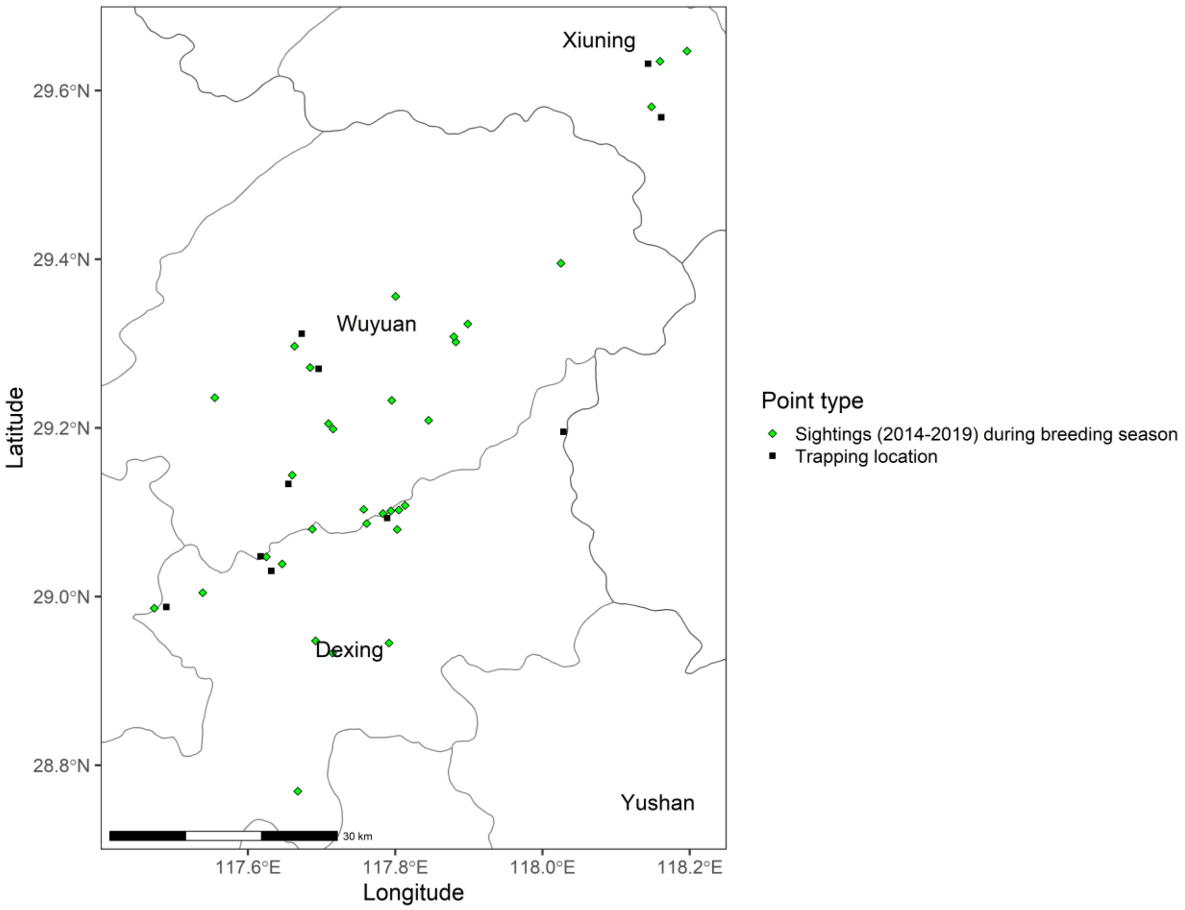

Figure 6. Locations where Blue-crowned Laughingthrushes have been reported as being caught (blue squares) and where Blue-crowned Laughingthrushes were sighted by at least one respondent during the breeding season (spring–summer) between 2014–2019 (green circles). Villages are shown in groups, with some physically close pairs of villages grouped together as one. Polygons and names indicate Chinese counties.

When asked whether they had heard of anyone catching BCLT from the wild, in 10 villages across all four counties, 3.3% (n=16/487) of respondents said yes: Wuyuan (n=6 respondents), Dexing (n=4), Leping (n=3), and Xiuning (n=3) (**Figure 6**). Five of these villages were outside the EOO, and two were in Xiuning County, Anhui Province, a region that has not been surveyed regularly for BCLT. All 16 respondents reported having seen a BCLT. Six said BCLT were caught 'to sell', six said they were caught 'for fun', 'to keep' or because 'their voice is lovely', and four said they did not know or gave no details. Respondents had heard of BCLT being caught at intervals between the spring of 2019 and 15 years earlier; seven reports dated from within the previous 10 years, with a mean reported last catching event in 2012. Five respondents did not give a date. Nine of the villages where BCLT were reported as being caught also had at least one respondent reporting a BCLT sighting both within the previous five years (2014–2019) and during the breeding season (spring–summer) (**Figure 6**).

Some respondents gave additional qualitative information on bird catching/trapping activity. At a village in Wuyuan County, two respondents stated that 'someone came here to capture the blue-crowned laughingthrush and sell for a high price' and 'someone came here specifically to capture the blue-crowned laughingthrush'. Other respondents at multiple villages in Wuyuan County generally stated, post-interview, that people came from the copper mine area near the town of Sizhou, Dexing County, in order to trap wild birds; two respondents specifically stated that 'people in the copper mine area would come here to catch birds'. In Xiuning County, one key informant interview revealed the respondent previously saw one or two people trapping BCLT and Hwamei in the forested hills near his village. By their accents, the respondent could tell they were from Huangshan City. They had come to trap birds once or twice a year for the previous several years, netting members of a flock using a caged bird as a lure. No direct evidence of BCLT trapping was observed, but reports of Hwamei trapping and keeping were corroborated by our observation of a caged Hwamei near one BCLT breeding site.

When asked whether BCLT is a protected species, 17.1% of respondents (n=89) said yes, 34.9% (n=181) said no, and 47.2% (n=245) did not know.

4.4.8 Effects of land use change and threats on BCLT sightings and breeding sites

BCLT sightings were more likely to be reported by men than by women (X^2 = 6.048, df – 1, p = 0.013). Respondents were more likely to be farmers in control villages than in breeding villages (X^2 = 5.255, df = 1, p = 0.022), and more likely to be older inside the EOO than in the buffer (p=0.05), or in control villages than in breeding villages (p=0.01).

Respondents who had seen a BCLT were more likely to report awareness of people catching BCLTs according to the optimal candidate model (**Figure 7a**). In contrast, respondents who had seen a BCLT were less likely to report having no vegetable garden, an increase in bush/scrub, and not knowing whether either *fengshui* forest or bush/scrub amounts changed over their lifetime, according to the next most plausible candidate models (**Figure S7, Supplementary Information)**. Respondents who had recently seen a BCLT were also more likely to report awareness of people catching BCLTs, according to the optimal candidate model (**Figure 7b**), and less likely to report having no tea plantation, according to the next most plausible candidate model (**Figure S8, Table S6, Supplementary Information**). In addition, within the GLMM models, the village-level and interviewer-level parameters of deviation from the average intercept did not encompass zero, indicating important between-village and between-interviewer variation, with models containing some variance that cannot be explained by the fixed effects (**Figure 7a & b**).

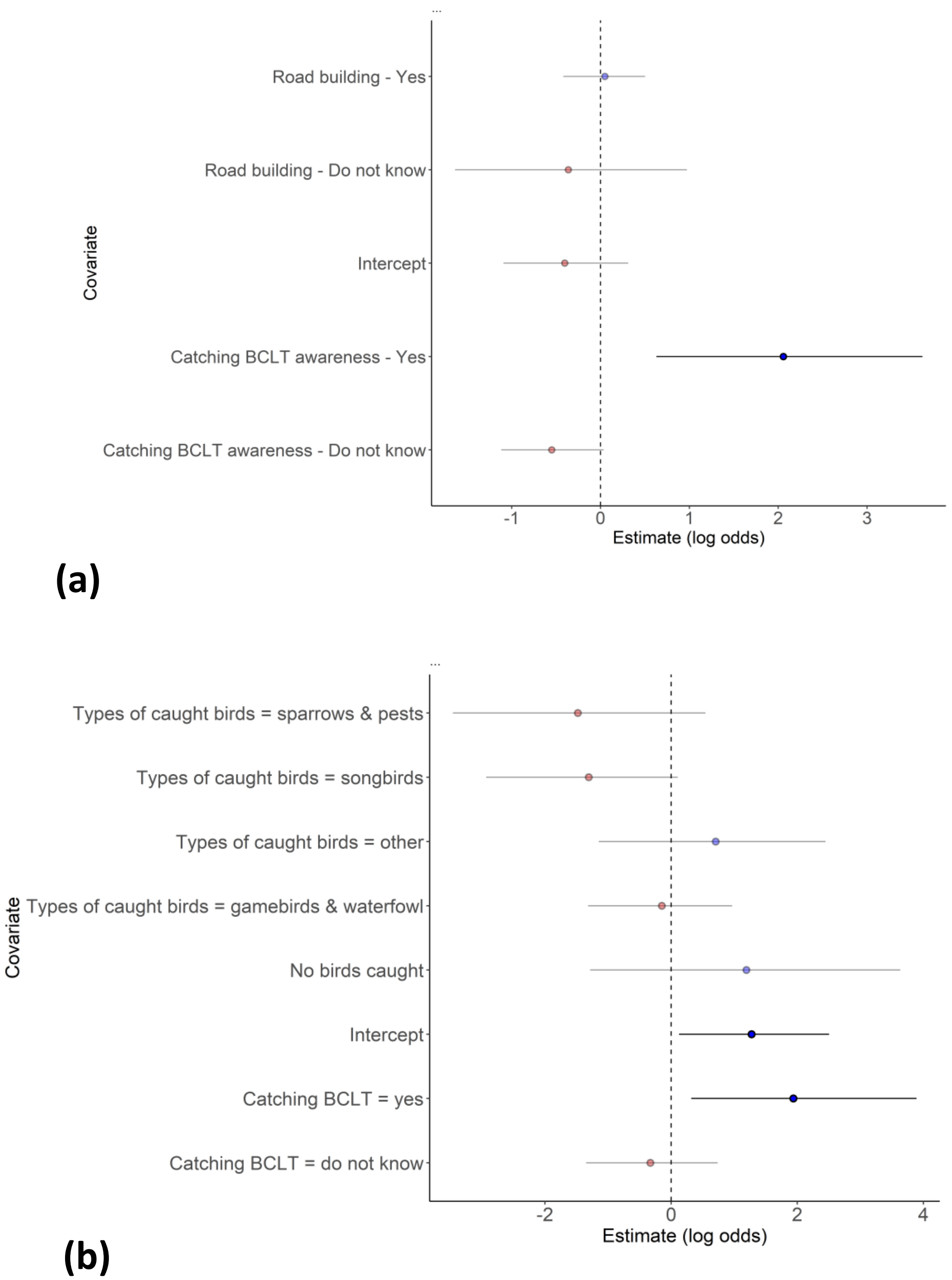

Figure 7. Interval plot showing the 90% credible intervals (CI, represented by black horizontal lines) for the posterior distribution of each factor level, in relation to **(a) whether respondents had seen a Blue-crowned Laughingthrush** or **(b) whether respondents had seen Blue-crowned Laughingthrush within the previous 18 months.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Plot displays the optimal candidate models. Variables in the model are: road building, and awareness of people catching Blue-crowned Laughingthrush.

Breeding villages were less likely to have reports of people catching BCLT than control villages (**Table 2**), and more likely to report decreases in bush/scrub and increases in vegetable gardens (**Table 2**). Control villages were more likely to have no reported *fengshui* forest. When villages with uncertain breeding status were included in the model as breeding rather than control villages, results varied only slightly (**Table S7, Supplementary Information**), with breeding villages positively associated with respondents reporting no change in tea plantation, and no significant relationship with reported changes in vegetable garden. Respondents within the EOO were more likely to report a decrease in bush/scrub, and less likely to report an increase in bamboo forest, no change in bush/scrub, or increase in road building (**Table 2**).

Table 2. Outputs from a series of univariate Bayesian GLMs for breeding vs control villages, and EOO vs buffer villages. Variables where the 90% credible interval (CI) range does not overlap with zero represent the equivalent of statistically significant.

Response	**Breeding/control**		**EOO/buffer**	
Covariate				
Bamboo forest change	**Estimate**	**90% CI range (lower/upper)**	**Estimate**	**90% CI range (lower/upper)**
More	-0.33	-1.13 – 0.42	**-1.04**	**-2.06 - -0.19**
No change	-0.21	-1.02 – 0.54	0.25	-0.57 – 1.12
Less	0.44	-0.26 – 1.25	0.08	-0.67 – 0.89
No bamboo forest	-0.45	-1.38 – 0.37	-0.47	-1.36 – 0.39
Catching BCLT				
Do not know	-0.29	-1.16 – 0.49	**-0.75**	**-1.61 – 0.00**
No	-0.38	-0.33 – 1.19	0.20	-0.60 – 1.07
Yes	**-0.89**	**-2.01 – 0.00**	-0.63	-1.59 – 0.22
Fengshui forest change				
No change	0.09	-1.08 – 0.45	-0.25	-1.03 – 0.53
Less	-0.21	-0.73 – 0.93	-0.50	-1.28 – 0.24
No fengshui forest	**-1.26**	**-2.52 - -0.19**	-0.66	-1.57 – 0.18
Bush/scrub change				
More	0.22	-0.79 – 1.20	-0.43	-1.38 – 0.43

No change	**-2.02**	**-3.79 - -0.61**	**-1.60**	**-2.82 - -0.55**
Less	**2.78**	**1.16 – 4.93**	1.28	0.19 – 2.56
No bush/scrub	0.56	-0.40 – 1.63	0.42	-0.65 – 1.68
Tea plantation change				
More	-0.36	-1.27 – 0.43	**-1.06**	**-2.14 - -0.17**
No change	0.68	-0.13 – 1.55	0.01	-0.87 – 0.88
Less	0.15	-0.72 – 1.03	-0.36	-1.25 – 0.53
No tea plantation	-0.12	-0.97 – 0.75	-0.76	-1.73 – 0.13
Roads				
Yes	0.23	-0.48 – 0.98	-0.14	-0.88 – 0.59
No	-0.65	-1.49 – 0.09	**-0.76**	**-1.61 – 0.00**
Vegetable garden change				
Less	-0.18	-0.99 – 0.55	-0.14	-0.88 – 0.61
More	**0.88**	**0.05 – 1.96**	0.13	-0.67 – 1.02
No change	-0.65	-1.57 – 0.15	-0.69	-1.51 – 0.06
No vegetable garden	0.47	-0.30 – 1.27	0.12	-0.68 – 0.96

4.5 Discussion

This study provides the first large-scale, systematically-collected LEK dataset for the Blue-crowned Laughingthrush (BCLT). With previous data on the species limited to site-scale observations, our comprehensive analysis of these new LEK data provides important insights into distribution and seasonal occurrence of the BCLT, as well as identifying direct threats and patterns of habitat change across its range associated with local BCLT presence or absence. This study also supports the usefulness of LEK in gathering rapid, wide-scale and novel data (Nash, Wong and Turvey, 2016; Archer *et al.*, 2020) and demonstrates its application in informing conservation measures for distinctive passerines.

Our LEK data are consistent with existing baseline data on the BCLT. Just under 45% of respondents across our study area recognised the species, with no recognition by name outside breeding sites or its breeding range (EOO), and higher recognition by photo within its EOO. Mean last sighting dates were more recent at breeding sites and within the EOO; this may reflect the long presence of BCLT at breeding sites during the breeding season, or more opportunistic observations of BCLT being made in the EOO during the breeding season, with flocks showing mobility close to villages immediately prior to breeding and upon fledging (F. He 2019, personal communication; R.Gleave pers. obs.). The accuracy of using LEK to identify known BCLT breeding sites was nearly 60%, and where breeding BCLTs were reported, respondents described nesting trees that were consistent with previous data on nesting sites (He and Xi 2002; Hong *et al.*, 2006; Zhang *et al.*, 2017; Huang *et al.*, 2018). Whereas small flocks were reported across the whole study landscape, more larger-sized flocks typical of breeding colonies (colony sizes typically range between 20–80 birds; He *et al.,* 2017) were seen within the EOO. This approach therefore has value for providing accurate data on BCLT presence and breeding activity, although we acknowledge that it may be more effective when combined with other techniques, such as species distribution modelling and bird surveys.

BCLT sightings were made year-round and across the entire study landscape, including outside of their known breeding range. Reported sightings of BCLT were higher overall in spring/summer (breeding season) than in autumn/winter (non-breeding season), although this may reflect the fact that our interviews took place during the summer. Similarly, more sightings during the breeding season were made at breeding sites, although these occurrences are non-independent: sightings are more likely to be recent (and during the breeding season) at active breeding sites. However, the numerous reported BCLT sightings from the non-breeding season support previous suggestions that BCLTs spend the non-breeding season in a broadly similar geographical area to the breeding season, but away from breeding sites (He *et al.*, 2017). Notably, recent (2014–2019) sightings were also reported outside of the known breeding range in Xiuning County, Anhui Province during the breeding season, highlighting the importance of conducting further surveys for the species in this region to investigate the possibility of a wider breeding distribution than currently recognised. Importantly, our respondents also identified two potentially overlooked BCLT breeding sites. One site was located within a few miles of a known long-term breeding site, so it is possible that the respondent was reporting seeing the birds nesting at this established site. However, BCLTs have also been recorded as nesting at several other adjacent villages in the same area along a river, several of which were initially overlooked by census observers, which lends this new finding plausibility. The other site was outside the known breeding range, along the same river network as many of the other riparian breeding sites and in an area with a substantial number of *fengshui* forest trees. Although these sites have not yet been independently verified, our findings thus suggest that future wider-ranging surveys could reveal yet more potential breeding locations.

Known threats to the Jiangxi population of the BCLT have previously been confined to disturbance through increased vehicle traffic (He *et al.*, 2017), photographers (Zhang *et al.*, 2017a) and construction of infrastructure (He *et al.*, 2017), with trapping only acknowledged once in the late 1990s (Yu 2003). However, our results indicate that bird trapping is relatively widespread in the study region, with trapping of BCLTs occurring across their range and multiple BCLT trapping events reported within the last 10 years. However, this evidence shows there is a relatively widespread knowledge of trapping in the region, not evidence of trapping itself. This has been previously undocumented and may be more common than previously considered, and the extent of this requires empirical investigation.

Our results show that trapping is significantly more likely to be reported in villages where BCLTs have been seen, or seen within the previous 18 months, but is significantly less likely to be reported at specific BCLT breeding sites. These findings might indicate that trappers, if they do occur, are drawn to the general region where BCLT are found, but that existing breeding sites may confer some protection; it is also possible that some BCLT breeding colonies have been eliminated through trapping, and/or that BCLT will not breed where trapping occurs. Wuyuan County has a reputation for high bird diversity and abundance which could attract trappers for other species (He *et al.*, 2014), however, trappers may also be attracted chiefly by the BCLT given its popularity with photographers (Zhang *et al.*, 2017a). Alternatively, trapping may be underreported at breeding sites. BCLT trapping is reportedly not carried out by local rural communities, but instead by people from outside of the local area; in particular, respondents from Xiuning, Wuyuan and Dexing counties reported that individuals from nearby urban centres were carrying out songbird trapping near their villages. This is consistent with the suggestion that the Huizhou region (Wuyuan and neighbouring parts of Anhui) traditionally lacked a culture of caged bird keeping, in contrast to many other parts of China (D. Liu, 2019, personal communication). Concerningly, awareness among respondents of the BCLT's protection status was low, highlighting the need for targeted conservation awareness-raising based on locally-relevant approaches (Qian *et al.*, 2021).

Although relatively few people reported awareness of BCLT trapping, it has previously been suggested that few trapping events would be needed to have a large impact on BCLT colonies (Yu 2003). In other bird species, a fine line exists between sustainable and unsustainable harvest (Valle *et al.*, 2018), and even those traded in low numbers are thought to be in slow decline (Nijman *et al.*, 2021). Awareness of people catching BCLT was significant in most models, and in optimal models for both GLMMs, lending support for the importance of this variable on different metrics of BCLT presence. Trapping could potentially restrict the breeding range of BCLTs and suppress population recovery, even if BCLT trapping was infrequent and opportunistic rather than targeted. Our key informant interviews suggested that trappers in Xiuning County were trapping both BCLT and Hwamei; the latter species is traded in large numbers throughout Southeast Asia (Shepherd *et al.*, 2020), and thus could be a main target species. However, domestic trade is also a significant issue for Asian songbirds (Zhang, Hua and Sun, 2008; Dai and Zhang, 2017; Nijman *et al.*, 2017; Wang, Leader-williams and Turvey, 2021). In parrots, trapping risk is highest where birds are most abundant in the wild, where they are easiest to catch and sell, and where demand is high (Pires and Clarke, 2012), which might explain why people who reported seeing BCLT were more likely to be aware of trapping. Further investigation into the wider distribution and prevalence of BCLT trapping, potentially using specific interview techniques such as the unmatched count technique for investigating sensitive behaviours (Hinsley *et al.*, 2019, 2021), is thus an urgent priority for future conservation research.

In addition to revealing the previously overlooked threat of trapping, our results also show evidence of overall changes to the study landscape, with respondents widely reporting increases in houses, bamboo, bush/scrub, broadleaf forest and fir tree forest, and decreases in pine forest, *fengshui* forest, tea plantation and vegetable gardens around their villages over their lifetime. It is important to acknowledge the potential for overlap in meaning between some responses; for example, ‘less’, ‘no change’ and ‘none of that land type’ might all possibly be used to mean ‘none left’ by respondents in some contexts, particularly for tea plantation and *fengshui* forest, where in many places most or all of these land types had disappeared during respondents’ lifetimes. Decreases in, rather than initial lack of, tea plantation and *fengshui* forest may therefore be more common than our data suggest. However, several reported habitat changes are correlated in our models with varying likelihood of BCLT occurrence across the landscape. These should thus be considered as a useful signal of potential drivers of population decline or factors influencing population growth and dynamics, with implications for landscape management to support BCLTs. Additionally, respondents reported the use of agricultural chemicals across the study landscape, with nearly a third reporting an increase during their lifetime**;** pesticides have been linked to losses of farmland birds such as the Javan Pied Starling *Gracupica jalla* (Van Balen and Collar, 2021).

Vegetable gardens were more likely to be perceived as increasing at breeding sites, and respondents who had seen a BCLT were less likely to report a lack of vegetable garden. This supports existing evidence that vegetable gardens are used disproportionately to other habitats except woodland by BCLTs for foraging (Liu *et al.*, 2020). There is some evidence that vegetable plots are declining across Wuyuan County, sparking concerns over potential loss of available foraging habitat (He *et al.*, 2017). Bush/scrub decreases were more likely to be reported at both breeding sites and within the EOO. This habitat typically consists of patches dominated by cogongrass (*Imperata cylindrica*) or a shrubby form of bamboo (*Pleioblastus amarus*), both of which are common on abandoned farmland and recently clear-cut woodland (R.Gleave pers. obs.). This gives nuance to recent findings from breeding sites that BCLTs disproportionately use shrub/grass plots compared to most other habitat types (except for woodland) (Liu *et al.*, 2020). Further differences in patterns of land use change associated with varying likelihood of local BCLT occurrence may be specific to breeding sites, and not the entire breeding landscape. Perceived change in *fengshui* forest showed no difference between EOO and buffer regions, but BCLT breeding sites were less likely to have a reported absence of *fengshui* forest. This potentially suggests that *fengshui* forests are more important for individual breeding sites than as a feature across the EOO, and supports previous findings that this habitat is a common feature of breeding sites, even if these trees are not always used as nesting sites (He *et al.*, 2017; Zhang *et al.*, 2017b). Finally, road building has been linked to BCLT disturbance (He *et al.*, 2017), but roads were more likely to be reported being built within the EOO compared to the buffer region. This finding might reflect the fact that Wuyuan County has seen more infrastructure development due to a recent regional increase in tourism (Zhang, Long and Zhao, 2019), and most breeding sites happen to be in Wuyuan (He *et al.*, 2017), but it raises concerns about future increases in disturbance to BCLTs. Until the 1950s, Wuyuan County was dominated by old subtropical broadleaf forests (Hong *et al.*,

2006) and village *fengshui* forest loss has been recorded at multiple breeding sites, making way for roads and buildings (Hong *et al.*, 2006). In recent years, *fengshui* forests have received greater protection across Jiangxi Province (Zheng 2003; Yan 2014), but it is unclear whether this policy is spreading to neighbouring provinces, which may be critical for BCLT dispersal beyond Jiangxi. *Fengshui* forests still face threats in the form of changing cultural values, urban sprawl and infrastructure (B. Chen *et al.*, 2018).

Although our results are based on respondents' memories and perceptions rather than direct evidence, respondent ability to recognise BCLTs was relatively high across the study landscape (at similar levels to other locally common songbirds), and our study provides possible new insights into why BCLTs only breed in a restricted area of northeast Jiangxi. Our data revealed two possible new breeding sites, and highlighted southern Anhui as an important new area to target breeding bird surveys and associated conservation efforts to counter potential trapping. These results also suggest that respondents who manage farmland have the potential to play a future role in citizen science monitoring and community-based conservation initiatives. Furthermore, trapping may be more widespread than previously suspected and should not be discounted as a past threat; instead, it should be given full consideration alongside other potential current threats to the species. Respondents showed an awareness of trappers and whether they were local people or outsiders, suggesting the potential for community-based conservation, with local people acting as an early-warning system of trapping activity carried out by external actors. Our results thus demonstrate that LEK can make an important contribution to understanding potential reasons behind species' low population size or range restriction, and can also provide new insights for future conservation action for the BCLT. We also demonstrate that LEK represents a good data source for uncommon birds, countering suggestions that it is more appropriate for large or common species (Nyhus, Sumianto and Tilson, 2003).

4.6 Conclusion

Our data suggest that BCLT in southeast China are both more widespread around our study landscape, as well as under greater threat from trapping, than previously thought (Wilkinson and He 2010b). Given the dire circumstances of widespread songbird declines across Asia due to trade (Sykes, 2017), this potential threat needs to be addressed across the BCLT's range as a matter of priority. Wider survey work is needed to better establish the distribution of BCLT sightings and the co-occurrence of trapping, as well as to investigate the possibility that BCLTs are found all year round across our study landscape. Subpopulations of breeding birds may yet be undocumented, and birds may be affected by trapping throughout the year. Equally, landscape management also has implications for BCLT conservation, with support for past observations that both *fengshui* forests and vegetable gardens are associated with breeding BCLT. Habitat loss and overexploitation of wildlife populations form a common synergy in driving species loss (Symes *et al.*, 2018), and these effects are notoriously difficult to unpick (Brook, Sodhi and Bradshaw, 2008; Ni *et al.*, 2018). Further declines of these land types should be prevented across the wider region, including outside of Jiangxi Province. Our LEK results can be used to inform this work, and show that LEK can provide important insights into correlates of BCLT presence and absence, its temporal and spatial distribution, and local people's interactions with this Critically Endangered species.

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Supplementary Information

Figure S1. English language copy of the final questionnaire used during data collection in June-July 2019.

Date:

Interview number:

Name of Interviewer:

Location: (Village name, Village group, County name, Province name)

Opening Statement: "We are local scientists from Jiangxi Agricultural University, conducting ecological/environmental research. We are conducting a study on the birds and landscape of this region and would like to ask you some questions for our studies. We have a questionnaire that takes about 15 minutes to complete. Information that you tell us will be completely confidential, we will not write down your name, and you will not be identified – we just want to try to learn more about the local environment from you."

Section 1

1). Are you prepared to participate in this survey and answer the following questions?

YES / NO

2). Are you:

Male / Female?

3). How old are you?

---

4). Do you live in this village?

YES / NO

5). (If **NO** to **Q4**) which village do you live in?

____

6). How many years have you lived in your home village?

____

a). If you have not always lived in your home village, where did you live before?

____

7). What is your occupation?

____

8). How many people live in your household?

____

<u>Section 2</u>

9). Has the landscape around this village changed over your lifetime?

YES / NO / DON'T KNOW

a). If YES, please briefly describe what has changed

____

____

10). Does this village have its own fengshui forest / fengshui tree?

YES / NO / DON'T KNOW

a). If YES, where is it/they?

____

For Questions 11-20 show respondent images of habitat type if they are unsure what is meant.

11). During your lifetime, has the amount of **rice paddy** changed in and around this village? By this I mean, all the land that is used by your village and not shared with any neighbouring villages.

YES/NO/DON'T KNOW / THERE ARE NO RICE PADDIES

a). If **YES**, is there **MORE** or **LESS** ride paddy now?

____

b). If **YES**, by how much has amount of rice paddy changed?

____

c). If **YES**, when did this happen?

____

d). If **YES**, where did this happen?

____

e). If **YES**, do you know why this happened?

____

12). During your lifetime, has the amount of **vegetable gardens** changed in and around this village?

YES / NO / DON'T KNOW / THERE ARE NO VEGETABLE GARDENS

a). If **YES**, is there **MORE** or **LESS** vegetable garden now?

____

b). If **YES**, by how much has amount of vegetable garden changed?

____

c). If **YES**, when did this happen?

____

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

13). During your lifetime, has the amount of **tea plantation** changed in and around this village?

YES / NO / DON'T KNOW / THERE ARE NO TEA PLANTATIONS

a). If **YES**, is there **MORE** or **LESS** tea plantation now?

b). If **YES**, by how much has amount of tea plantation changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

14). During your lifetime, has the amount of **oilseed rape field** changed in and around this village?

YES / NO / DON'T KNOW / THERE IS NO OILSEED RAPE FIELD

a). If **YES**, is there **MORE** or **LESS** oilseed rape field now?

b). If **YES**, by how much has amount of oilseed rape field changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

15). During your lifetime, has the amount of **fir tree forest** changed in and around this village?

YES / NO / DON'T KNOW / THERE IS NO FIR TREE FOREST

a). If **YES**, is there **MORE** or **LESS** fir tree forest now?

b). If **YES**, by how much has amount of fir tree forest changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

16). During your lifetime, has the amount of **pine tree forest** changed in and around this village?

YES / NO / DON'T KNOW / THERE IS NO PINE TREE FOREST

a). If **YES**, is there **MORE** or **LESS** pine tree forest now?

b). If **YES**, by how much has amount of pine tree forest changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

17). During your lifetime, has the amount of **bamboo forest** changed in and around this village?

YES / NO / DON'T KNOW / THERE IS NO BAMBOO FOREST

a). If **YES**, is there **MORE** or **LESS** bamboo forest now?

b). If **YES**, by how much has amount of bamboo forest changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

18). During your lifetime, has the amount of **feng shui forest** changed in and around this village?

YES / NO / DON'T KNOW / THERE IS NO FENG SHUI FOREST

a). If **YES**, is there **MORE** or **LESS** feng shui forest now?

b). If **YES**, by how much has amount of feng shui forest changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

19). During your lifetime, has the amount of **broadleaved forest** changed in and around this village?
YES / NO / DON'T KNOW / THERE IS NO BROADLEAVED FOREST

a). If **YES**, is there **MORE** or **LESS** broadleaved forest now?

b). If **YES**, by how much has amount of broadleaved forest changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

20). During your lifetime, has the amount of **bush/scrub** changed in and around this village?

YES / NO / DON'T KNOW / THERE IS NO BUSH/SCRUB

a). If **YES**, is there **MORE** or **LESS** bush/scrub now?

b). If **YES**, by how much has amount of bush/scrub changed?

c). If **YES**, when did this happen?

d). If **YES**, where did this happen?

e). If **YES**, do you know why this happened?

21). During your lifetime, have the number of **fruit trees** changed in this village?

YES / NO /DON'T KNOW / THERE ARE NO FRUIT TREES

a). If **YES**, are there **MORE** or **LESS** fruit trees inside the village?

b). If **YES**, how much has this changed?

c). If **YES**, when did this happen?

d). If **YES**, why did this happen?

____

22). Has the **number of people** in this village changed in your lifetime?

YES / NO / DON'T KNOW

a). If **YES**, are there **MORE** or **FEWER** people now?

____

b). If **YES**, by how much has the number of people changed?

____

c). If **YES**, when did this happen?

____

c). If **YES**, do you know why this happened?

____

23). Has the **number of houses** in this village changed in your lifetime?

YES / NO / DON'T KNOW

a). If **YES**, are there **MORE** or **FEWER** houses?

____

b). If **YES**, by how much has the number of people changed?

____

c). If **YES**, when did this happen?

____

d). If **YES**, do you know why this happened?

____

24). Have any **roads been constructed** in or near this village in your lifetime?

YES / NO / DON'T KNOW

a). If **YES**, when did this happen?

____

b). If **YES**, where did this happen?

c). If **YES**, do you know why this happened?

25). Have any **bridges been constructed** in or near this village in your lifetime?

YES / NO / DON'T KNOW

a). If **YES**, when did this happen?

b). If **YES**, where did this happen?

c). If **YES**, do you know why this happened?

26). Have any **highways been constructed** near this village in your lifetime?

YES / NO / DON'T KNOW

a). If **YES**, when did this happen?

b). If **YES**, where did this happen?

c). If **YES**, do you know why this happened?

27). Do people in this village use chemicals on their crops?

YES / NO / DON'T KNOW

a). If **YES**, what types of chemicals are used?

b). If **YES**, which crops are they used on?

c). If **YES**, why are they used?

d). If **YES**, how often are they used?

28). (If **YES** to **Q27**) Has the use of chemicals on crops around this village changed in your lifetime?

YES / NO /DON'T KNOW

a). If **YES**, are there **MORE** or **FEWER** chemicals?

b). If **YES**, how much has this changed?

c). If **YES**, when did this happen?

d). If **YES**, why did this happen?

29). Have there been any other changes to the landscape around here during your lifetime?

Section 3

30). Have you ever seen a Hwamei / Hua mei?

YES / NO / DON'T KNOW

30). Have you ever seen a Masked Laughingthrush / Heilian zaomei?

YES / NO / DON'T KNOW

31). Have you ever seen a Light-vented Bulbul / Baitou bei?

YES / NO / DON'T KNOW

32). Have you ever seen a Sparrow / Ma que?

YES / NO / DON'T KNOW

33). Have you ever seen a Blue-crowned Laughingthrush / Languan zaomei?

YES / NO / DON'T KNOW

34). ***(Show interviewee a series of photographs – includes Blue-crowned Laughingthrush, Sparrow, Masked Laughingthrush, Light-vented Bulbul, Hwamei)***

a). Do you recognise this bird? *(Hwamei)*

YES / NO / DON'T KNOW

i) If **YES**, what is it called?

____

b). Do you recognise this bird? *(Light-vented Bulbul)*

YES / NO / DON'T KNOW

i) If **YES**, what is it called?

____

c). Do you recognise this bird? YES / NO / DON'T KNOW *(Sparrow)*

i) If **YES**, what is it called?

____

d). Do you recognise this bird? YES / NO / DON'T KNOW *(Masked Laughingthrush)*

i) If **YES**, what is it called?

____

e). Do you recognise this bird? YES / NO / DON'T KNOW *(Blue-crowned Laughingthrush)*

i) If **YES**, what is it called?

____

35). *(Play recording of Blue-crowned Laughingthrush flock)* Do you know which bird this is?

YES / NO / DON’T KNOW

a). If **YES**, what is it called?

If respondent recognises Blue-crowned Laughingthrush by name, image or sound then ask them Questions 36-46. If not, go straight to Question 47.

36). When was the last time you saw a Blue-crowned Laughingthrush?

37). How often have you ever seen a Blue-crowned Laughingthrush?

38). (If **YES** to **Q37**) Do you remember what time of year **(spring, summer, autumn, winter)** you last saw a Blue-crowned Laughingthrush?

a). Where was the last place you saw a Blue-crowned Laughingthrush? (describe nearest village)

b). What type of land did you see it on *(select one from each list)*

i). FIELD / FOREST / FENG SHUI FOREST

ii). VILLAGE / RIVER

iii). HILLSIDE / VALLEY

c). How many birds did you see?

d). Did the group of birds look like….? **(*Show 4 pictures of different-sized flocks and ask interviewee to pick one)***

SMALL / MEDIUM / LARGE / VERY LARGE / DON'T KNOW

39). Were the Blue-crowned Laughingthrushes nesting?

YES / NO / DON'T KNOW

a). If **YES**, which tree(s) did they nest in?

b). If **YES**, have you seen them nest before?

40). When was the first time you saw a Blue-crowned Laughingthrush?

41). How many Blue-crowned Laughingthrush do you think there are around this village?

42). Do you know any stories, myths, legends, traditions or customs about the Blue-crowned Laughingthrush?

YES / NO / DON'T KNOW

43). Do you think that the numbers of wild Blue-crowned Laughingthrush have changed in your lifetime?

YES / NO / DON'T KNOW

a). if **YES**, are there:

MORE / LESS

b). If **LESS**, approx. **by how much** have they decreased?

c). If **LESS**, approx. **when** did they decrease?

d). If **LESS**, why do you think they decreased? (what caused it)

44). Have Blue-crowned Laughingthrushes disappeared from any specific areas/places?

YES / NO / DON'T KNOW

a). If **YES**, where have they disappeared from?

45). (If **YES** to **Q44**) In places where Blue-crowned Laughingthrushes used to be found but aren't anymore, do you know what happened to make the birds disappear?

YES /NO / DON'T KNOW

a). If **YES**, what made the birds disappear?

b). If **YES**, when did this happen?

46). What do you think are the main threats to the Blue-crowned Laughingthrush?

Section 4

47). Have you ever heard of anyone catching birds from the wild?

YES / NO / DON'T KNOW

a). If **YES**, what types of birds are caught?

b). If **YES**, why are they caught?

c). If **YES**, how are they caught? **NETS / TRAPS / OTHER**

d). If **YES**, when is the last time you heard of this happening?

e). If **YES,** is this done by local people or people coming from outside the village?

f). If **YES**, how often does this happen?

g). If **YES**, what happens to the birds once they are caught?

48). Have you ever heard of anyone killing wild birds?

YES / NO / DON'T KNOW

a). If **YES**, what types of birds are killed?

b). If **YES**, why are they killed?

c). If **YES**, how are they killed? **GUNS / POISON / STONES / OTHER**

d). If **YES**, when is the last time you heard of this happening?

49). Do people keep songbirds in cages in this county?

YES / NO / DON'T KNOW

a). If **YES**, approximately how many people?

b). If **YES**, what types of bird are kept?

c). If **YES**, where do they get the birds from?

d). If **YES**, do you keep any songbirds in cages?

50). How many people have you heard of catching birds from the wild?

51). Have you ever heard of anyone catching a Blue-crowned Laughingthrush from the wild?

YES / NO / DON'T KNOW

a). If **YES**, why was it caught?

b). If **YES,** how was it caught?

c). If **YES**, when was the most recent time this happened?

d). If **YES**, how often have you heard of this happening?

52). Do you know if the Blue-crowned Laughingthrush is a protected species?

YES / NO / DON'T KNOW

a). If **YES**, what is its protection status??

Figure S2. Bird species images used in the questionnaire.

Masked Laughingthrush *Pterorhinus perspicillatus*

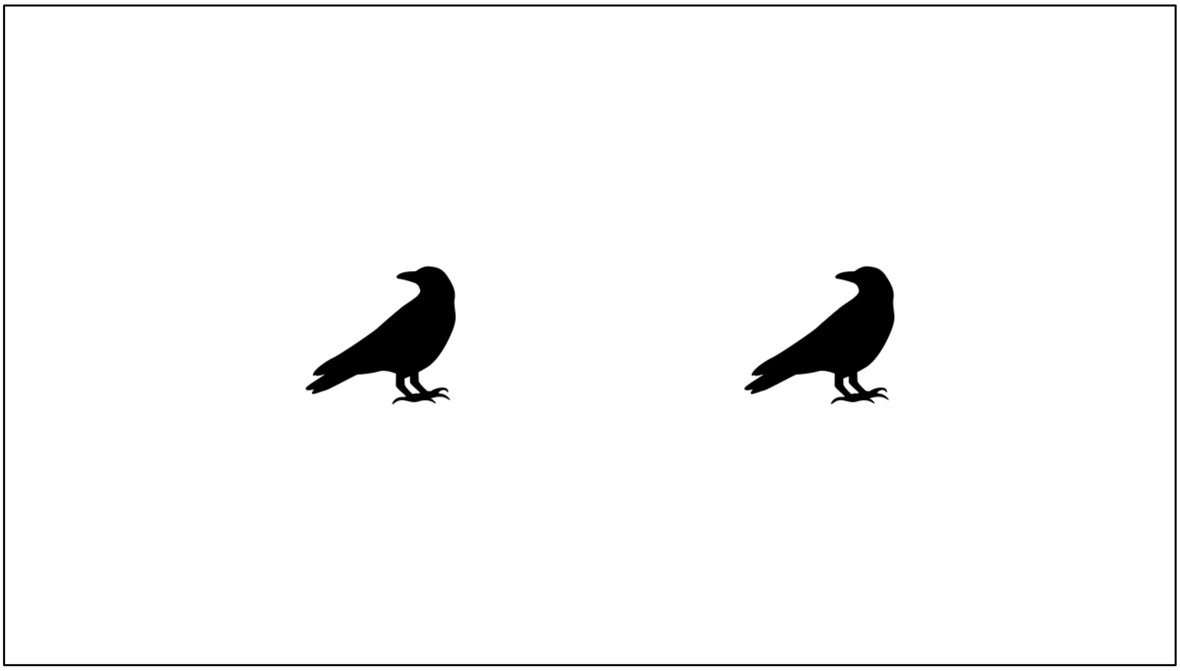
Eurasian Tree Sparrow *Passer montanus*

Blue-crowned Laughingthrush *Pterorhinus courtoisi*

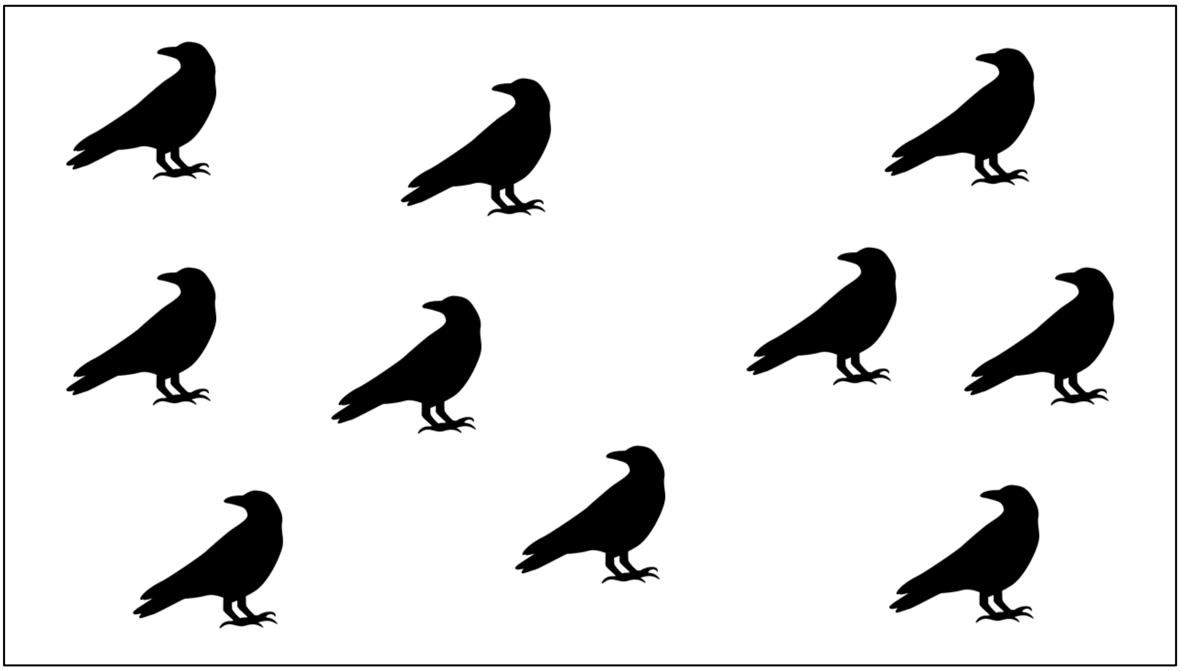
Chinese Hwamei *Garrulax canorus*

Light-vented Bulbul *Pycnonotus sinensis*

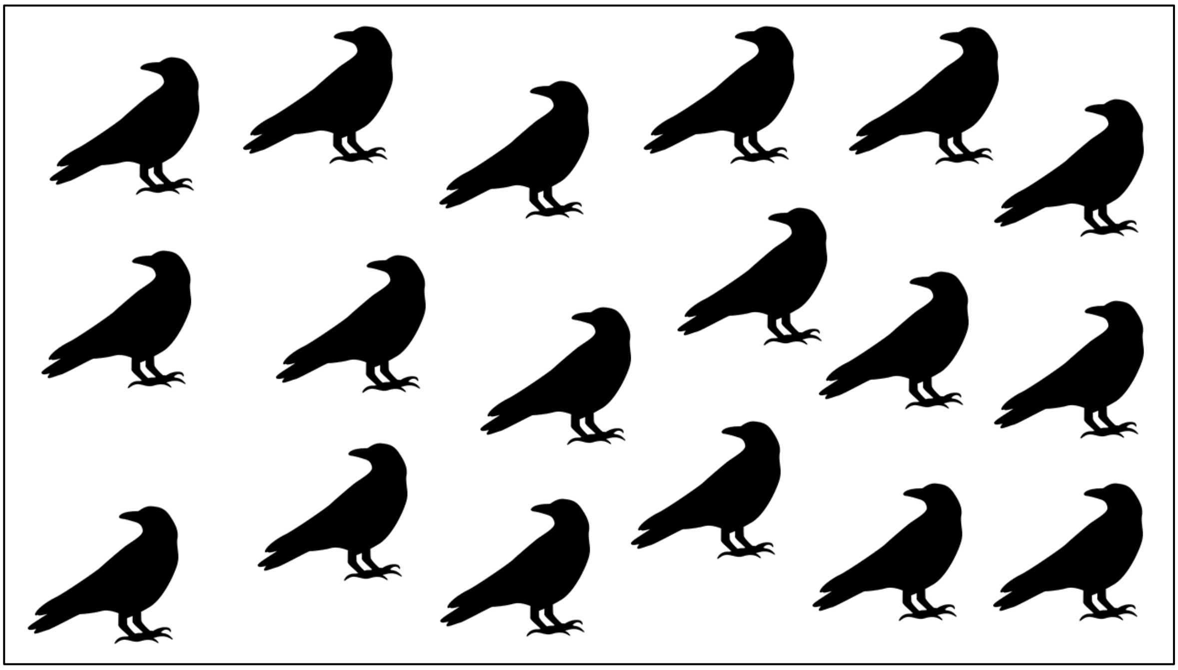
Figure S3. Flock sizes used in questionnaire.



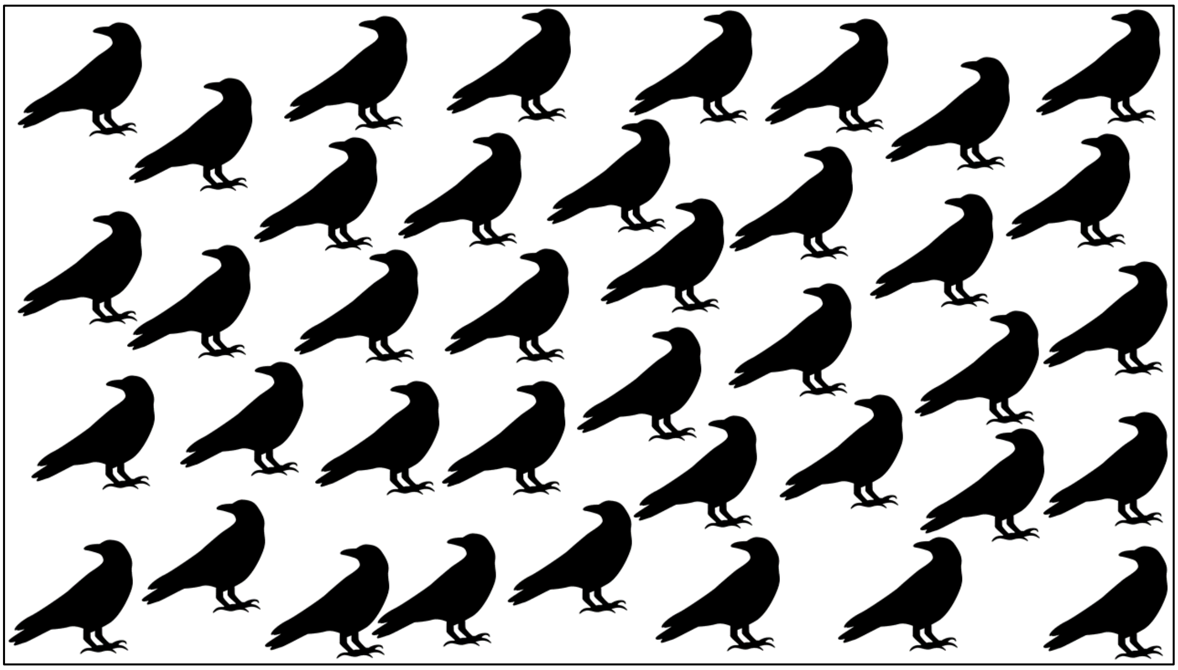
‘Small’ flock



‘Medium’ flock



‘Large’ flock



‘Very large’ flock

Table S1. Questionnaire data processing protocol, listing examples of main response types and how these are processed/standardised.

Reporting format	Example	Method of conversion to direct calendar year
Direct calendar year	1984	Already in correct format for analysis
Time elapsed/number of years ago	“20 years ago”	Number of years before 2019
Specified multi-year range	“Five or six years ago 五六年前” ／ “Wu liu nian qian”	Equal probability of being randomly assigned to any calendar year within given range
End date only (1)	“Before 2000”	Equal probability of being randomly assigned to any calendar year in the reported decadal interval (e.g. between 1991 and 1999 for this example)
End date only (2)	“Over 10 years ago”	Equal probability of being randomly assigned to any calendar year in the reported decadal interval (e.g., between 10 and 19 years ago for the given example)
Start date only (1)	“Since 2015 2015年后”／ “2015 nian hou”	Taken conservatively as earliest year after the one given by respondent (e.g. 2016 in this example)
Start date only (2)	“Recent 2 decades”	Equal probability of being randomly assigned to any calendar year in the reported decadal interval (e.g., between 10 and 20 years ago for the given example)
With reference to national, local or personal events	“Since the reform and opening-up (1978)” “Since the great cultural revolution” “When the highway was built”	Equal probability of being randomly assigned to any calendar year in the reported decadal interval, when date of reference event can be determined (with given example, within the 10 years after 1978 (1978 – 1988) Refer to the date that respondent gave as the local event; otherwise, discard.
Vague, general	“years ago”, “recent years”, “many years ago” , “when the interviewee was young”, “When the interviewee was a child”, “childhood” “a few years ago” ‘several years ago ji nian qian’ Qian ji nian 前几年	Treat ‘recent years’ as equal probability of being randomly assigned calendar year within last decade. ‘When the interviewee was a child’, calculate the first 18 years of their life. ‘A few years ago’ or ‘several years ago’ – too vague, discard.
Incremental change	“year by year 逐年”／ Every year”	Put down as last year (2018)
	“All the time”	Discard

NA = 267

Don’t know = 54

Where respondents reported seeing a Blue-crowned Laughingthrush within the last 18 months, some answered ‘Do not know’ or the reported last-sighting date could not be converted to a calendar year. These responses were excluded from analysis (n=87).

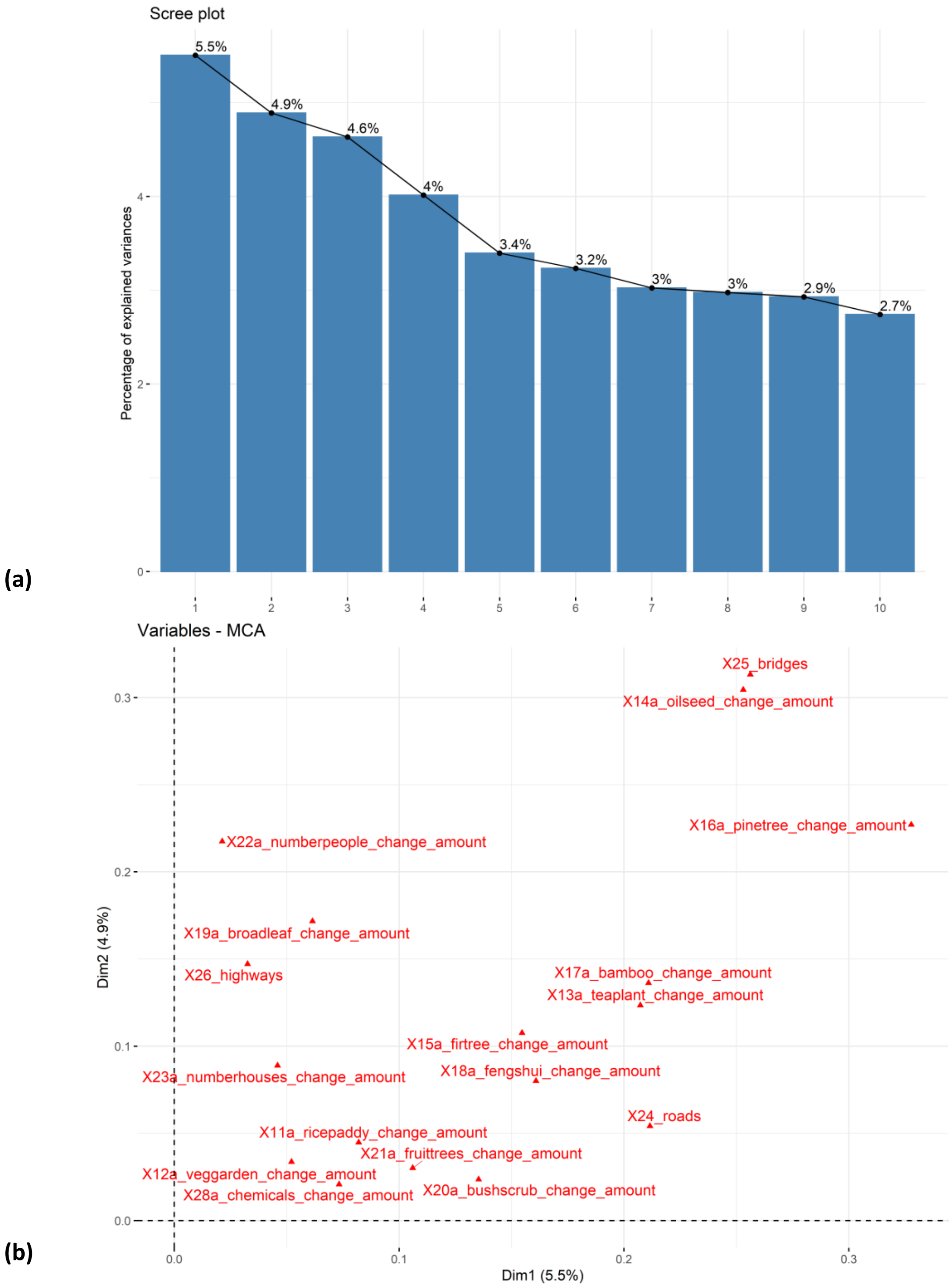


Figure S4. Multiple Correspondence Analysis (MCA) (a) scree plot showing the percentage variance explained by each MCA dimension and (b) the correlation between each variable and MCA principal dimensions 1 and 2.

Spatial autocorrelation in models

All models were initially run as frequentist binomial GLMMs. Models showed significant spatial dependency within residuals, likely resulting from the tendency for breeding villages to be clustered relatively close together, and from comparing spatially discreet landscapes in an irregular formation (e.g. comparing respondents inside and outside of the EOO). Autocorrelation within models was initially tested using the *check_autocorrelation* function from the *performance* package (Lüdecke et al. 2020) and spatial autocorrelation was tested using *moran.test* on the model residuals from the package *spdep* (Bivand, Pebesma, & Gómez-Rubio, 2013; Bivand & Wong, 2018).

However, the frequentist GLMMs ultimately could not be run. For the response type (binomial) with categorical predictor variables and high levels of spatial autocorrelation at multiple scales, the most appropriate approach would have been to fit each model with optimised Moran's Eigenvector Maps (MEMs; Dray et al. 2006; (Bauman, Drouet, Dray, & Vleminckx, 2018; Bauman, Drouet, Fortin, & Dray, 2018). However, too many MEMs were needed (35+) in order to remove spatial autocorrelation, each of which added an extra predictor variable to the dataset, thus requiring more degrees of freedom than the data possessed and/or making the model unstable. This remained the case even when noise was added to the spatial coordinates through the *jitter* function in R. A distance-based autocovariate approach was also tried (Dormann et al., 2007) however this failed to adequately remove spatial autocorrelation. So, a Bayesian approach was used instead as this addresses spatial autocorrelation through fundamental differences in the way Bayesian and frequentist statistics are calculated, especially using MCMC (McElreath 2016).

Table S2. All variables considered for inclusion in final models. Black ticks show variables *a priori* included in final full models.

Predictor Type	**Variable Predictor**						**Data format**	**Description of dependent variable and hypothesised relationship**	**Variable type**	**Examples from literature/reason for inclusion**
		Breeding status (Unsure villages = Non-breeding)	**Breeding status (Unsure villages = Breeding)**	**Within EOO or outside of EOO**	**Recently seen BCLT (last 18 months)**	**Seen BCLT**				
Land use	Rice paddy change						Categorical (nominal - More, Less, No change, None of land type)	Change in amount of rice paddy in or around the respondent's village, over their lifetime.	Fixed	
	Tea plantation change	✓	✓	✓	✓	✓	Categorical (nominal - More, Less, No change, None of land type)	Change in amount of tea plantation or around the respondent's village, over their lifetime.	Fixed	Significant chi-squared result Zhang et al. (2017)
	Oilseed rape change						Categorical (nominal - More, Less, No change, None of land type)	Change in amount of oilseed rape in or around the respondent's village, over their lifetime.	Fixed	Significant chi-squared result
	Vegetable garden change	✓	✓	✓	✓	✓	Categorical (nominal -More, Less, No change, None of land type)	Change in amount of vegetable garden in or around the respondent's village, over their lifetime.	Fixed	Zhang et al. (2017)
	Fir tree forest change						Categorical (nominal – More, Less, No change, None of land type)	Change in amount of fir tree forest in or around the respondent's village, over their lifetime.	Fixed	He & Xi (2002)
	Pine tree forest change						Categorical (nominal - More, Less, No change, None of land type)	Change in amount of pine tree forest in or around the respondent's village, over their lifetime.	Fixed	He & Xi (2002)
	Fengshui forest change	✓	✓	✓	✓	✓	Categorical (nominal - More, Less, No change, None of land type)	Change in amount of fengshui forest in or around the respondent's village, over their lifetime. BCLTs have	Fixed	Yu 2003, Hong et al. 2006, Zhang et al. (2017)

								been recorded as nesting in fengshui trees.		
	Broadleaf forest change						Categorical (nominal - More, Less, No change, None of land type)	Change in amount of broadleaf forest in or around the respondent’s village, over their lifetime.	Fixed	Zhang et al. (2017)
	Bamboo forest change	✓	✓	✓	✓	✓	Categorical (nominal - More, Less, No change, None of land type)	Change in amount of bamboo forest in or around the respondent’s village, over their lifetime.	Fixed	Significant chi-squared result Zhang et al. (2017), Liu et al. (2020)
	Bush/scrub change	✓	✓	✓	✓	✓	Categorical (nominal - More, Less, No change, None of land type)	Change in amount of bush/scrub in or around the respondent’s village, over their lifetime.	Fixed	Significant chi-squared result Liu et al. (2020)
	Fruit trees change						Categorical (nominal - More, Less, No change, None of land type)	Change in amount of fruit trees in or around the respondent’s village, over their lifetime. BCLTs have been recorded as nesting in fruit trees.	Fixed	Richardson 2005, Zhang et al. (2017), He et al. (2017)
	Number of people change						Categorical (nominal - More, Less, No change)	Change in number of people living in respondent’s village, over their lifetime.	Fixed	Human disturbance mentioned as important factor at breeding sites by Zhang et al. (2017), He at al. (2017
	Number of houses change						Categorical (nominal - More, Less, No change)	Change in number of houses in respondent’s village, over their lifetime.	Fixed	Zhang et al. (2017), He at al. (2017
	Use of chemicals change						Categorical (nominal - More, Less, No change)	Change in use of chemicals on land in and around respondent’s village, over their lifetime.	Fixed	

	Roads	✓	✓	✓	✓	✓	Categorical (binary – Yes/No)	Whether or not new roads were built in or around respondent’s village, over their lifetime.	Fixed	Significant chi-squared result Zhang et al. (2017), He at al. (2017
	Bridges						Categorical (binary – Yes/No)	Whether or not new bridges were built in or around respondent’s village, over their lifetime.	Fixed	Zhang et al. (2017), He at al. (2017
	Highways						Categorical (binary – Yes/No)	Whether or not new highways were built in or near respondent’s village, over their lifetime.	Fixed	Zhang et al. (2017), He at al. (2017
Threat	Catching birds – Yes/No						Categorical (nominal)	Whether or not the respondent has ever heard of anyone catching birds from the wild. Areas or villages with higher number of respondents reporting bird catching may affect where BCLTs choose to breed, as BCLTs could be at greater risk of capture.	Fixed effect	
	Catching birds – Types				✓		Categorical (nominal)	If the respondent has heard of people catching wild birds, what types of birds are caught. Areas or villages reporting more/higher proportions of songbirds caught may have fewer, declining or no BCLT, and so may differ between where BCLTs are and are not found.	Fixed effect	
	Catching birds – Reason						Categorical (nominal)	If the respondent has heard of people catching wild birds, why birds are caught. Birds caught for sale may be intended for the caged bird trade, which is thought to have led to the extirpation of	Fixed effect	

								BCLTs in Yunnan province. Areas or villages reporting more birds being caught for sale may have fewer, declining or no BCLT, and so may differ between where BCLTs are and are not found.		
	Catching birds – Who						Categorical (nominal)	If the respondent has heard of people catching wild birds, who catches the birds (villagers or outsiders). If birds are being caught by outsiders, this may indicate this is for the commercial bird trade.	Fixed effect	
	Killing birds - Yes/No						Categorical (nominal)	Whether or not the respondent has ever heard of anyone killing wild birds. BCLTs may be affected by bird killing activity.	Fixed effect	
	Killing birds - Types						Categorical (nominal)	If the respondent has heard of people killing wild birds, what types of birds are killed.	Fixed effect	
	Keep songbirds – Yes/No						Categorical (nominal)	If the respondent reports that people keep songbirds in cages in their county.	Fixed effect	
	Keep songbirds – Where from						Categorical (nominal)	If the respondent reports that people in their county keep caged songbirds, where they get them from (catch from the wild, or buy from others). If more people buy from others, this may indicate a functioning local bird trade, and could affect where BCLTs breed (they may avoid or be negatively affected in areas where there is an active songbird trade).	Fixed effect	

	Catching BCLTs – Yes/No	✓	✓	✓	✓	✓	Categorical (nominal)	If the respondent has heard of anyone catching a BCLT from the wild. Areas where this happens may deter BCLT from breeding there, and so may differ between areas where they are and are not found.	Fixed effect	
External	Estimated village population size						Continuous (numeric)	The number of people living in the respondent’s village. Population size could influence land use practices and patterns, which could in term affect the likelihood of BCLTs choosing a village as a breeding territory.	Fixed	
	Village				✓	✓	Categorical (nominal)	The village in which the interview was carried out. Villages are included as a random effect to account for non-independence in the data.	Random effect	
	Interviewer				✓	✓	Categorical (nominal)	This will be included in models to account for bias.	Random effect	

Table S3. Demographic characteristics of interview respondents.

Demographic characteristics	**Variable**	**Number of respondents**
Sex	Male	272 (52.4%)
	Female	247 (47.6%)
Age	Age range + (mean)	18-93 (55.8) years
Occupation	Farmer	296 (57.0%)
	Housewife	33 (6.3%)
	Unemployed	34 (6.5%)
	Retired	20 (3.8%)
	Professional	22 (4.2%)
	Shop worker	20 (3.8%)
	Businessperson	17 (3.3%)
	Official	14 (2.7%)
	Manual worker	13 (2.5%)
	Clerical worker	9 (1.7%)
	Student	9 (1.7%)
	Miscellaneous worker	32 (6.1%)

Local bird names

Names for sparrow were given by many respondents as ‘*Ma Que* **麻雀**’ (common name), or ‘*Tou Liang* 偷梁, a local name meaning ‘grain thief’ (Terry Townshend pers. comm. 2020). Of the 182 respondents who recognised the BCLT from a photo, 26.4% (n=48) were able to give an ‘appropriate’ name for the species, including ‘*Lan Guan Zao Mei*’, ‘*Huang Hou Zao Mei* **黄喉噪**鹛’, ‘*Huang Zhu Niao* **黄竹**鸟’, ‘*Huang Li Niao* **黄**鹂鸟’, ‘*Huang Niao* **黄**鸟’, ‘*Huang Mei Niao* **黄**眉 鸟’,‘ *Bao Chun Niao/Spring-announcing bird* 报春鸟’ and ‘*Huang Niao Mei* **黄**鸟眉’. Many of these names are variants of ‘yellow bird’, which may refer to its colouring or its former species name of ‘Yellow-throated Laughingthrush/**黄喉噪**鹛’. The remainder of respondents either did not know the name, or called it a Hwamei, woodpecker, or ‘*Zhua Yu Niao*抓鱼鸟’ (‘catching fish bird’, suggesting confusion with kingfishers, which may have similar colouring). The species was re-named ‘Blue-crowned Laughingthrush/蓝冠**噪**鹛’ in 2006 and it is therefore not unexpected that many local people still use its old name. Although ‘*Hua mei* **画眉**’ strictly refers to *Garrulax canorus*, in local dialects and popular culture the term may also be used as a general term for various birds, including Laughingthrushes (Terry Townshend, personal communication 2020). Thus, local people may not be confusing BCLTs with other species and may simply be using a more general term such as ‘thrush’.

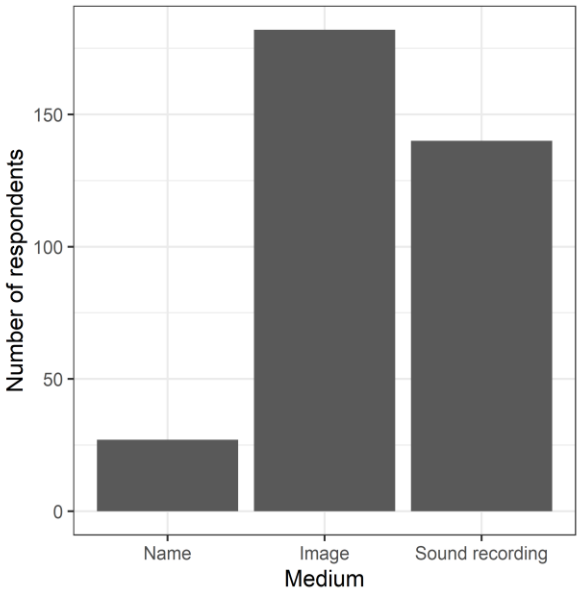


Figure S5. Number of respondents who recognised the Blue-crowned Laughingthrush by either its name, an image or a sound recording of the birds calling.

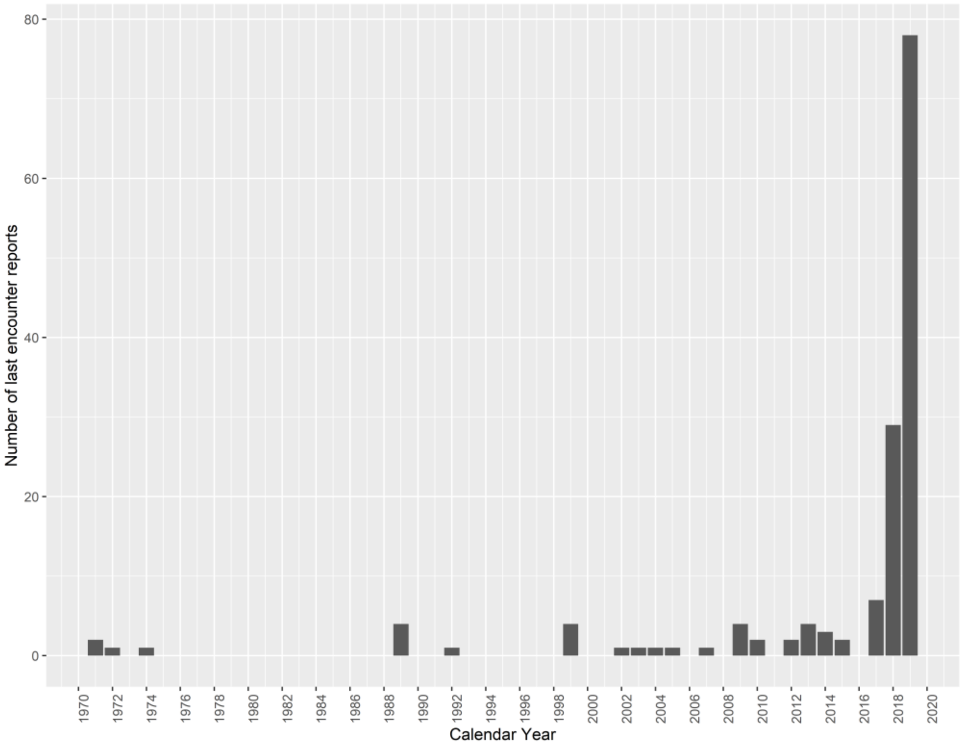


Figure S6. Proportion of respondents reporting the year they last saw a Blue-crowned Laughingthrush.

Table S4. Changes in land types around respondent home villages: overall percentage of respondent reporting (a) an increase or decrease, and (b) no change/absence of land types.

(a)

Land type	Overall Percentage	Number of respondents
Houses	80.0%	419
Bamboo	48.2%	250
Bush/scrub	39.1%	203
Broadleaf forest	23.1%	145
Fir forest	20.4%	181
Fruit trees	4.2%	74
Oilseed	0.2%	127
Pine forest	-16.7%	144
Fengshui forest	-17.5%	103
Tea plantation	-39.1%	203
Vegetable garden	-43.5%	226
Rice paddy	-58.6%	304

(b)

Land type	No change (%)	Absence of land type (%)
Houses	16.57	NA
Bamboo	31.41	7.89
Bush/scrub	27.17	7.71
Broadleaf forest	35.84	14.06
Fir forest	31.02	9.05
Fruit trees	25.05	47.01
Oilseed	31.60	14.06
Pine forest	24.85	29.67
Fengshui forest	51.06	19.46
Tea plantation	11.17	38.92
Vegetable garden	42.39	1.73
Rice paddy	23.51	1.73

Table S5. General types of birds, reasons for catching or killing, and methods for catching and killing birds.

Caught birds			Killed birds		
Types	Reasons	Methods	Types	Reasons	Methods
Gamebirds & waterfowl Songbirds Sparrows & pests	Eat Sell Protect crops Entertainment	Cage Hand Net Slingshot Trap Sound recording Whistle	Gamebirds & waterfowl Sparrows	Eat Entertainment Protect crops	Guns Poison Slingshot Net Stick Stones Suffocated

Table S6. Leave-One-Out Cross Validation differences between Expected Log Pointwise Predictive Density (ELPD) scores and Standard Error scores of the 'Seen BCLT' and 'Recently seen BCLT' GLMMs. Moment matching was performed on the LOO cross validation for values with a pareto k value of >0.7, which indicates outlier observations which have a disproportionate effect on the model and make estimating out-of-sample accuracy difficult. '_gp' denotes a Gaussian process model. Optimal models highlighted in bold.

	Seen BCLT		**Recently seen BCLT**	
Model name	**ELPD diff.**	**SE diff.**	**ELPD diff.**	**SE diff.**
brms_fit_1	-8.9	7.5	-16.2	6.1
brms_fit_2	-1.0	5.1	-3.2	5.2
brms_fit_2_gp	NA	NA	-2.5	5.4
brms_fit_3	-2.7	6.8	-7.8	4.8
brms_fit_3_gp	NA	NA	-6.4	5.0
brms_fit_4	**0.0**	**0.0**	-1.4	3.7
brms_fit_4_gp	NA	NA	-0.4	4.0
brms_fit_5	-6.0	7.9	**0.0**	**0.0**
brms_fit_5_gp	NA	NA	0.0	1.1

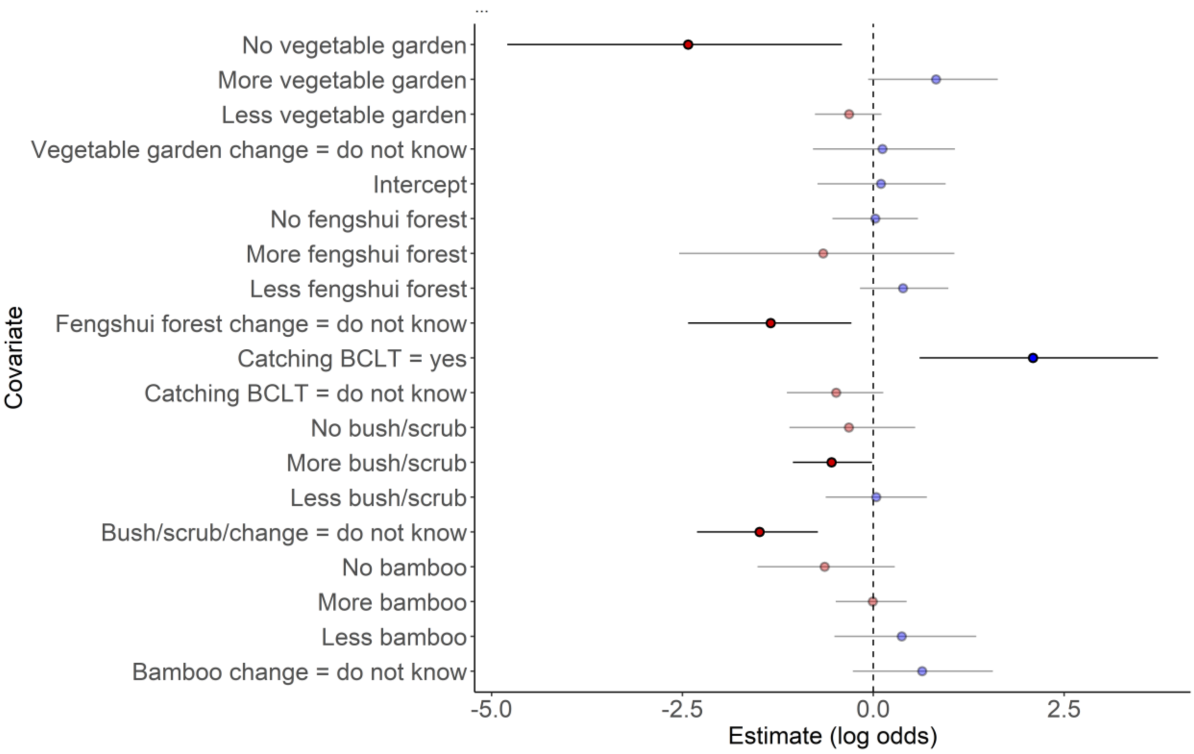


Figure S7. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each factor level, in relation to **whether respondents had seen a Blue-crowned Laughingthrush**. Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. **Plot displays the third most optimal candidate model (within -2.7 ELPD).** Variables in the model are: vegetable garden change, *fengshu*i forest change, awareness of people catching Blue-crowned Laughingthrush, bush/scrub change, and bamboo forest change.

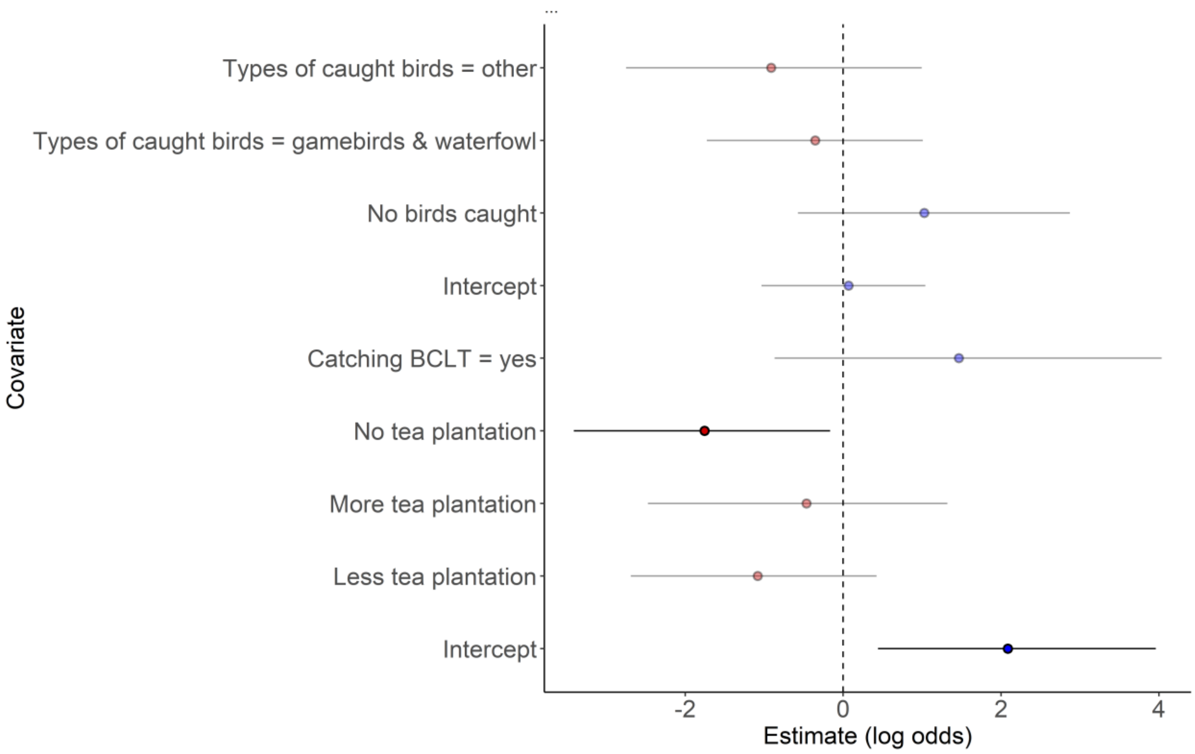


Figure S8. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each factor level, in relation to **whether respondents had recently seen a Blue-crowned Laughingthrush**. Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. **Plot displays the second most optimal candidate model (within -0.4 ELPD).** Variables in the model are: types of birds caught, change in tea plantation.

Table S7. Outputs for breeding model variations, and the EOO models.

Response	**Breeding/control (unsure villages = control)**		**Breeding/control (unsure villages = breeding)**		**EOO/buffer**	
Covariate						
Bamboo forest change	**Estimate**	**90% CI range (lower/upper)**	**Estimate**	**90% CI range (lower/upper)**	**Estimate**	**90% CI range (lower/upper)**
More	-0.33	-1.13 – 0.42	-0.36	-1.12 – 0.35	**-1.04**	**-2.06 - -0.19**
No change	-0.21	-1.02 – 0.54	-0.27	-1.04 – 0.49	0.25	-0.57 – 1.12
Less	0.44	-0.26 – 1.25	0.22	-0.47 – 0.97	0.08	-0.67 – 0.89
No bamboo forest	-0.45	-1.38 – 0.37	-0.15	-0.92 – 0.60	-0.47	-1.36 – 0.39
Catching BCLT						
Do not know	-0.29	-1.16 – 0.49	-0.41	-1.25 – 0.39	**-0.75**	**-1.61 – 0.00**
No	-0.38	-0.33 – 1.19	-0.42	-0.35 – 1.29	0.20	-0.60 – 1.07
Yes	**-0.89**	**-2.01 – 0.00**	**-1.09**	**-2.32 - -0.12**	-0.63	-1.59 – 0.22
***Fengshui* forest change**						
No change	0.09	-1.08 – 0.45	0.28	-0.53 – 1.14	-0.25	-1.03 – 0.53
Less	-0.21	-0.73 – 0.93	-0.46	-1.29 – 0.30	-0.50	-1.28 – 0.24
No *fengshui* forest	**-1.26**	**-2.52 - -0.19**	**-1.28**	**-2.45 - -0.29**	-0.66	-1.57 – 0.18
Bush/scrub change						
More	0.22	-0.79 – 1.20	-0.06	-0.93 – 0.77	-0.43	-1.38 – 0.43
No change	**-2.02**	**-3.79 - -0.61**	**-1.12**	**-2.27 - -0.16**	**-1.60**	**-2.82 - -0.55**
Less	**2.78**	**1.16 – 4.93**	**1.54**	**0.48 – 2.84**	1.28	0.19 – 2.56
No bush/scrub	0.56	-0.40 – 1.63	0.10	-0.73 – 0.97	0.42	-0.65 – 1.68
Tea plantation change						
More	-0.36	-1.27 – 0.43	-0.48	-1.40 – 0.34	**-1.06**	**-2.14 - -0.17**
No change	0.68	-0.13 – 1.55	**0.84**	**0.05 – 1.79**	0.01	-0.87 – 0.88
Less	0.15	-0.72 – 1.03	-0.10	-0.97 – 0.77	-0.36	-1.25 – 0.53
No tea plantation	-0.12	-0.97 – 0.75	-0.16	-1.05 – 0.68	-0.76	-1.73 – 0.13
Roads						
Yes	0.23	-0.48 – 0.98	0.09	-0.67 – 0.68	-0.14	-0.88 – 0.59
No	-0.65	-1.49 – 0.09	-0.51	-1.31 – 0.18	**-0.76**	**-1.61 – 0.00**
Vegetable garden change						

Less	-0.18	-0.99 – 0.55	-0.45	-1.30 – 0.29	-0.14	-0.88 – 0.61
More	**0.88**	**0.05 – 1.96**	1.07	-1.30 – 0.29	0.13	-0.67 – 1.02
No change	-0.65	-1.57 – 0.15	-0.67	-1.59 – 0.17	-0.69	-1.51 – 0.06
No vegetable garden	0.47	-0.30 – 1.27	0.73	-0.05 – 1.64	0.12	-0.68 – 0.96

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5. Seeing the wood for the trees: using resource selection functions at multiple spatial scales to inform conservation of the Critically Endangered Blue-crowned Laughingthrush *Pterorhinus courtoisi*

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5.1 Abstract

The Blue-crowned Laughingthrush (BCLT; *Pterorhinus courtoisi*) is a Critically Endangered cooperative breeding bird found in subtropical southeastern China. Breeding sites are associated with mature broadleaved forests, villages, and rivers, and are situated within agricultural mosaic landscapes, but it is unclear why the species is not more widely distributed across similar landscapes in southern China. Breeding habitat use has previously been investigated only at a few breeding and control (non-breeding) sites, focussed on comparing patches of broadleaved forest within the existing breeding range. We quantified the BCLT's habitat preferences by comparing fine-scale vegetation measures and topographical and remote sensing data at 39 villages within and beyond its known breeding range, applying resource selection functions at both the nest and breeding site scales (range: 100m^2 – 0.346km^2). Overall, we find little evidence of habitat differences between breeding and control sites across the study landscape. However, nesting sites were significantly more likely to contain broadleaved trees of larger diameter at breast height (DBH), stands of bamboo, conifer or mixed forest, and to be situated on areas of lower slope incline, and sites outside of the breeding range were at significantly higher elevation. Our results generally support, but further nuance, previous studies of BCLT habitat preference, and suggest that the species shows strongest habitat preference at the nest site scale.

Key words: Resource selection function, habitat selection, laughingthrush, *Pterorhinus courtoisi*, China

5.2 Introduction

Reliable information on species' ecological requirements forms a core component of conservation (Luck, 2002; Hayward *et al.*, 2006), allowing conservation managers to effectively address any major factors driving species decline or restricting recovery (Sutherland *et al.*, 2004). One key ecological requirement is species' habitat use or preference, knowledge of which is essential for effective conservation planning (Caughley, 1994). Information on this ecological parameter can inform habitat management plans (Oppel *et al.*, 2004), protected area design (Roberts *et al.*, 2010; Beatty *et al.*, 2014) and species reintroductions (Van Schmidt *et al.*, 2014). Determining which habitats are used disproportionately compared to those that are available also provides fundamental conservation-relevant information on the degree to which habitat availability restricts species' ranges (Behnke, Pejchar and Crampton, 2016). This is key to revealing the importance of habitat loss versus other factors as determinants of the current status of threatened species (Mellanby *et al.*, 2008).

Resource Selection Functions (RSFs) are an important tool in elucidating species' habitat requirements, defined as probabilities of use for resource units of different types (Manly *et al.*, 2002). RSFs have been applied to a broad range of ecological questions, including drivers of species' geographic ranges (Aldridge *et al.*, 2008; Brambilla *et al.*, 2009) and spatial predator-prey interactions (Courbin *et al.*, 2013). Within this framework, 'habitat preference' is defined as the likelihood of a habitat or resource being selected if offered on an equal basis to others (Johnson, 1980). Habitat preference operates at multiple hierarchical biologically-relevant scales, which can be assessed separately (Manly *et al.*, 2002; Meyer and Thuiller, 2006). These scales, all of which may be investigated using RSFs, encompass the species' geographic range (landscape, 1st order), the breeding site of an individual or group (home range, 2nd order), and specific parts of home ranges such as nesting or foraging sites (3rd order; Johnson, 1980). Many studies now investigate habitat selection at multiple scales to inform conservation management (Oppel *et al.*, 2004b; Walker, Cahill and Marsden, 2005; Donald *et al.*, 2012; Sawyer and Brashares, 2013) as habitat selection may be scale-dependent (Johnson, 1980; Gustine *et al.*, 2010; Sawyer and Brashares, 2013), which has a bearing on planning for habitat restoration, land-use policy, translocations and other applications (Currie *et al.*, 2003;

Colyn *et al.*, 2020). However, there is still a lack of studies applying RSFs at multiple scales to extremely rare species with limited datasets.

The Blue-crowned Laughingthrush (BCLT; *Pterorhinus courtoisi*) is a Critically Endangered bird species only found breeding in two counties (Wuyuan, Dexing) in north-east Jiangxi Province, China. The species' IUCN Red List classification is based on its restricted, fragmented breeding range and small population size (BirdLife International 2018). As it is unknown where BCLTs go during the non-breeding season (He and Xi 2002; Hong *et al.* 2003; Yu 2003; Wilkinson *et al.* 2004), all habitat analyses are necessarily based upon their breeding distribution. This is still critical to conserving the BCLT, as breeding habitat can be a limiting factor to distribution and population size (Colyn *et al.*, 2020; Segal *et al.*, 2021). BCLTs breed in colonies (Wilkinson *et al.* 2004, Zhang *et al.,* 2017) often in association with large, old trees, very close to or within areas of human settlement, at low elevation, and near rivers (Hong *et al.* 2003; Richardson 2005). However, this generalisation is complicated by the fact that most villages in Wuyuan occur near rivers (Huang *et al*. 2018), not all breeding sites have occurred near rivers, and BCLT are also known to breed in bamboo, fir, or fruit trees (Richardson 2005; Zhang *et al.*, 2017). The exact habitat requirements of this species remain unclear, as there are many villages in both north-east Jiangxi and surrounding regions with the same general characteristics as breeding sites, but which lack recorded BCLT breeding activity. There are many descriptive studies of BCLT habitat use (He and Xi 2002; Hong *et al.* 2003; Richardson 2005; Hong *et al.* 2006; Liao *et al.* 2007; He *et al.* 2017) but comparatively few systematic studies (Zhang *et al.* 2017; Huang *et al.* 2018; Liu *et al.*, 2020), and there remains no conclusive evidence for why BCLTs are found only within such a restricted area; addressing this question will shed important light on how to effectively conserve the species. Wuyuan County, the centre of the BCLT's known breeding range, is rapidly changing due to tourism and development (Zhang, Long and Zhao, 2019), and gathering evidence on the BCLT's habitat preferences is thus also important for ensuring future developments do not compromise the species' chance of persistence within this human-occupied landscape.

BCLT habitat selection has been examined during the breeding season by comparing forest breeding site patches with control patches of the same forest type, revealing a preference for breeding sites in broadleaf forests, at low elevation and near villages and sources of water, and for nesting sites in tall broadleaf trees, with higher herb coverage under nesting trees

(Huang *et al.*, 2018). However, this study used a limited sample of breeding sites (nine breeding sites, and four control sites per breeding site). Furthermore, it only compared characteristics of forest patches rather than the land around different villages, potentially overlooking important breeding site cues such as associated foraging habitat. Huang et al. (2018) found that BCLT nested more in Chinese sweetgum *Liquidambar*, Hackberry *Celtis* and Chinese ash *Pterocarya* trees among their surveyed sites; these findings contrast with Zhang *et al.* (2017), who only found this pattern at a single breeding site, with camphor *Cinnamomum* trees preferentially used for nesting at other sites. Subsequently, Liu *et al.* (2020) tracked BCLT habitat use within breeding sites, and found a disproportionate use of woodland, followed by shrubland and vegetable plots. No study to date has compared a large sample of sites, including those outside of Wuyuan or the BCLT breeding range, which would allow more robust statistical inferences regarding the species' habitat preference.

We build on this existing body of information and provide a more conclusive baseline on BCLT breeding habitat requirements by comparing data from all known breeding sites against a series of control sites across a much greater geographical area than previous studies, both within and outside of the known BCLT breeding range. We apply RSFs at the 2nd and 3rd orders of habitat preference (Johnson, 1980), specifically in terms of nesting habitat. We use ecological surveys and analysis of satellite imagery to: (1) contrast landscape characteristics within the BCLT breeding range (their 'Extent of Occurrence' or EOO, **Figure 1**) and within a surrounding buffer region, (2) characterise BCLT breeding site preference in comparison to random control sites, (3) characterise nest site selection in comparison to control habitat features, and (4) compare proportions of land cover types between breeding and control sites. We assess the implications of our findings for ongoing conservation of the BCLT, through an improved understanding of whether the species exhibits local-scale habitat selection, or whether its restricted range may instead or also be determined by environmental characteristics at the wider landscape scale or by other factors such as human exploitation.

5.3 Methods

5.3.1 Study area

Habitat surveys were conducted between 4th June and 31st July 2019 in Wuyuan (29°14’53”N, 117°51’43”’E), Dexing (28°55’50”N, 117°35’41”E) and Leping (28°58’41”N, 117°09’07”E) counties (Jiangxi Province) and Xiuning County (Anhui Province) (29°47’02”N, 118°11’38”E). This region consists of a subtropical human-modified mosaic landscape containing some remaining evergreen broadleaf forest (Hong *et al.*, 2006). These landscapes feature many traditional village ‘*fengshui* forests’ (stands or larger patches of mature broadleaved trees). *Fengshui* forests have high cultural and spiritual importance and have been locally protected for centuries (Coggins, 2003). Land surrounding villages also contains plantation stands of bamboo, fir, and pine trees (He 1994; Richardson 2005) as well as mature broadleaf trees, mixed forest stands and other remnant forest patches (He *et al.*, 2014). Dominant crop types are rice, tea, vegetable plots and oilseed rape (Richardson 2005; Hong *et al.* 2006; He *et al.* 2017), with a decline of vegetable fields observed in recent years (He *et al.*, 2017). The wider landscape is characterized by forested hills, agricultural valleys, river networks and small villages, similar to surrounding landscapes in southern China (Ellis, 2004). In Wuyuan County, the core of the BCLT’s breeding range, many of the *fengshui* forest sites have been protected by the County Government since 1993 (Huang *et al.*, 2018).

To select survey sites, we digitised human settlements using the Google Satellite plugin in QGIS v.3.16.5 (Hannover; QGIS Development Team 2021). Human settlements were chosen as the main spatial unit for BCLT breeding sites, as all known breeding sites to date have been either inside or directly adjacent to villages or small towns (He *et al.*, 2017). Settlements were digitised within two main areas: a core area comprising the minimum convex polygon (MCP) of all recorded BCLT sighting or breeding locations, and a buffer area of 25km around the MCP (**Figure 1**). Over 900 settlements were digitised in total, with names taken from Google Earth. Settlement names were verified in the field. In addition to the MCP, to specify the known BCLT breeding range, a core area comprising a convex hull around all recorded BCLT breeding locations from 2000-2017 (F. He, 2019, personal communication; W. Zhang, 2019, personal communication) was created using QGIS, with area 725.93km^2. This will hereafter be referred to as the EOO, or Extent of Occurrence (**Figure 1**). A buffer region comprising a 25km distance around the EOO was created, for the purpose of comparing villages within the two regions.

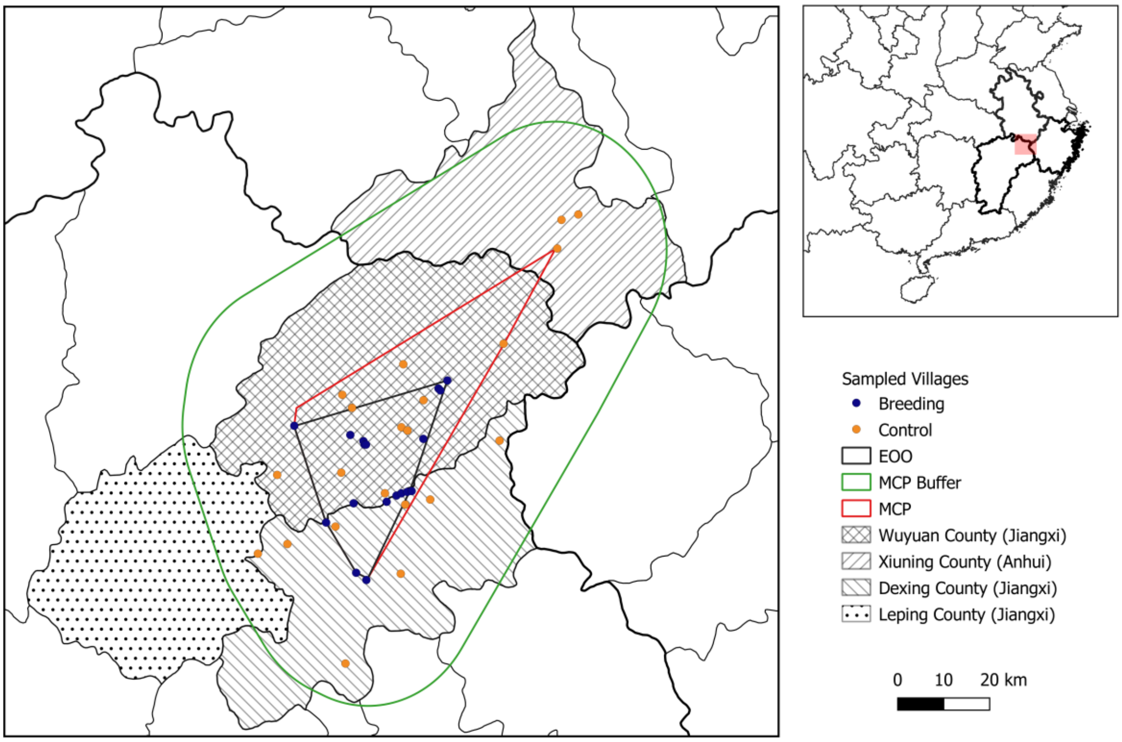

Figure 1. Map showing the distribution of sampled villages, depicted as coloured circles. Shaded areas cover the counties of Wuyuan, Dexing, Leping (Jiangxi Province) and Xiuning (Anhui Province). Thick black lines demark the boundaries between provinces. The polygons show the Extent of Occurrence (EOO) drawn around known Blue-crowned Laughingthrush breeding sites, the Minimum Convex Polygon (MCP) drawn around all known Blue-crowned Laughingthrush sightings (including those from eBird), and the outer polygon shows the 25km buffer region around the MCP.

To select villages to be surveyed, the locations of all villages known to be either active or former BCLT breeding sites (n=18) were compiled using unpublished data as per **Chapter 3** (F. He, 2019, personal communication; W. Zhang, 2019, personal communication). All but one of these breeding villages were surveyed (one site was discovered after fieldwork was completed). To select control sites, non-breeding villages close to past sightings of BCLTs, as reported by eBird.org (n=6) or mentioned in an unpublished field report (n=3; He 1994), were included. To generate further potential ‘control’ villages, which represent sites where BCLTs were not thought to have nested within living memory, a subset of settlements (n=12) was randomly chosen from within the core and buffer polygons combined. This gave a total of 21 control sites. Control sites were further checked to have not had past breeding BCLT through interviews with local community members, carried out as part of **Chapter 4**. There were no significant differences between control and breeding villages within a key set of characteristics (Mann-Whitney U Test): approximate number of buildings (W = 143, p = 0.14), distance to main road (W = 105, p = 0.91), distance to river (W = 124, p = 0.51), and elevation (W = 89, p = 0.43). Approximate number of buildings was estimated by eye from Google Earth imagery, and distance to main road was measured within QGIS. These characteristics were chosen for their potential association with BCLT presence (elevation, distance to river) or disturbance (number of buildings, distance to main road). Habitat characteristics at breeding sites were investigated at the level of individual villages and the land around them. 'Nest sites' are defined here as habitat 'characteristics in the immediate vicinity of the nest' (Jones, 2001).

The central point of each breeding site survey area was created using QGIS, using a known past nesting point, or the centre of the village if precise nest sites within it were not known. A circular buffer zone was created around each point (radius = 332m, area = 350,000m^2), representing an estimate of the furthest distance that BCLT will travel from their breeding sites to forage (B. Mo, 2018, personal communication). The mean area of a BCLT home range has been estimated as 100,000m^2 (Shi *et al.,* 2017; Liu *et al.*, 2020), so our sampling areas covered three times the average BCLT home range.

For the 2nd and 3rd order RSFs, 15 points were surveyed per village. To create these, 20 points were randomly generated at least 10m apart within the circular buffer zone, then all points located in any rivers or bodies of water were removed (n=23), to prevent a potential bias towards riparian trees. If more than 15 points were still available, we found points that were closest together and selected one of the pair (n=93), chosen either at random before entering the field, or whichever was found to be more accessible in the field. Points within inaccessible terrain were replaced with either the closest point, or by getting as close as possible to the existing point (n=61).

5.3.2 Data collection protocol

To collect data for the 2nd and 3rd order RSFs, surveys were conducted between 08:00 and 16:00h by a team of two or three people. Strict safety rules were followed, including not surveying unsafe steep slopes, waist-height or higher thorny vegetation, or flood water. Heavy flooding during the field season restricted access to 61 points. Navigation was performed using a Garmin eTrex10 GPS, a screenshot of the survey points displayed on a phone, and a compass. At each point, the closest tree over 2m in height was chosen. If the point was approximately equidistant between trees, the tree visually estimated to be closest, or the most accessible tree (if one tree was not) was chosen. At each breeding site, if known, one or two former or current nesting trees (F. He, 2019, personal communication) were substituted for the closest equivalent points. Once a tree was selected, a 100m^2 (10m x 10m) quadrat was measured with the selected tree at the centre of the quadrat. Tree diameter at breast height (DBH), height and species were recorded, as well as the quadrat ID (point ID), number of trees over 2m high, percentage of land cover types within quadrat, herb density and height, and disturbance level (see **Data Collection Protocol, Supplementary Information** for details). Data on elevation, slope and aspect were generated post-fieldwork using QGIS (see **Data Collection Protocol, Supplementary Information**). Research was permitted by Jiangxi Wuyuan National Forest Bird Nature Reserve Management Office.

To generate land cover type percentages for the 2nd order RSF for entire villages, atmospherically corrected Sentinel-2 imagery Level-2A Surface Reflectance imagery (10m x 10m resolution), overlapping with all village locations (representing the least cloudy images available between the dates 1st February 2019 – 31st August 2019), was used within Google Earth Engine (Gorelick *et al*., 2017). Prior to image analysis, cloud masks were applied using a function that detected probabilities of pixel being cloud, cloud shadow and snow. Supervised imagery classification (Wegmann *et al.*, 2016) was conducted using the random forest algorithm (Breiman 2001). This is a machine learning algorithm, building multiple decision trees and merging them to achieve a more stable and accurate prediction. The eight land cover types classified were: broadleaf forest, vegetable plots, other forest, tea plantation, rice paddy, bush/scrub, settlement/road and water. Training points were taken from high resolution Google Earth imagery. Accuracy assessment was performed using validation points, taken from a combination of ground-truthed GPS data (n=637) collected in April-May 2019 and Google Earth imagery of (a) villages visited during habitat surveys, and (b) other areas that the lead author passed through during fieldwork in Wuyuan, Dexing, Leping and Xiuning counties. A confusion matrix was generated, and the overall accuracy, producer's accuracy and user's accuracy was calculated for each land cover type.

5.3.3. Data analysis

5.3.3.1 *Analysis overview*

Resource selection models were developed for five spatial analyses, at the scale of the BCLT breeding site (2nd order selection) and the BCLT nest site (3rd order selection): (a) comparing habitat characteristics within breeding sites to those within control sites; (b) comparing habitat characteristics at breeding or control sites within the EOO to those within the buffer region; (c) comparing habitat characteristics at known nest sites to random control sites within the study area; (d) comparing proportions of land cover types between breeding and control villages; and (e) comparing proportions of land cover types at breeding or control sites within the EOO to those within the buffer region.

All analyses were performed in R version 4.0.2 (R Core Team, 2021). Data exploration was carried out on all variables using Principal Component Analysis (PCA) and simple box plots, with the aim of reducing the number of explanatory variables necessary in the models (see **Figures S1 & S2, Supplementary Information**). An initial PCA of all land type percentages captured c.10% of the data variance per dimension, so some land types were merged in order to produce stronger patterns: 'Mixed forest', 'Bamboo forest' and 'Conifer forest' were all merged into 'Other forest', '*Fengshui* forest' was merged into 'Broadleaf forest', and 'Oilseed rape' was merged into 'Rice paddy'. The subsequent PCA captured only marginally higher variance in the first dimension (c.16%), and tests of contribution and quality of representation for each variable revealed that only 'Other forest' and 'Village/Town' were strongly represented on the first two dimensions, indicating that these variables should be used alone. Correlation among continuous variables was tested using the *corrplot* package in R (Wei and Simko 2021, **Figure S3, Supplementary Information**). No variables had a correlation coefficient of >0.7, so were not excluded from the model on that basis (Green 1979).

5.3.3.2 *EOO, breeding and nest site selection from quadrat data*

Regression models were built to investigate 2nd order habitat selection by characterising differences between sites within the EOO (n=25) and in the buffer region (n=14), and between breeding sites (n=18) and control sites (n=21), and to investigate 3rd order habitat selection by characterising differences between known nesting quadrats (n=23) and control quadrats (n=562). For all models, responses were converted to either a '1' for 'breeding', 'inside the

EOO' and 'nesting', or '0' for 'control' and 'buffer region'. Models were analysed as a 'case-control' sampling design (Keating and Cherry, 2004), and thus outputs are interpreted as odds ratios rather than probabilities. As two of the surveyed villages had possible but unverified past BCLT breeding activity, these were modelled alternately classed as both 'breeding' and 'control' villages, to contrast the results. As landscape changes are likely to have occurred since the BCLT was rediscovered in 2000, models were also fitted with just the breeding villages recorded from 2019 (n=9), with all other villages classed as control sites. For nesting sites, a random slope was fitted to see if the magnitude of effect of total broadleaf DBH on nest site choice differs among villages. All models were fitted using the *brms* package (Bürkner 2017) with a Bernouilli distribution and logit link, and included a varying intercept for village (to account for between-site variation). All predictor variables were standardised prior to analysis (Harrison *et al.*, 2018, McElreath 2020). Modelled variables are listed in **Table 1**. A full list of potential predictor variables is given in **Table S1, Supplementary Information**.

Table 1. Response variables (*) and covariates used in resource selection models for the Blue-crowned Laughingthrush**.**

Variable	**Description**	**Justification**
Breeding site*	Village verified as former or current BCLT breeding site between 2000-2017.	
Nesting site*	Tree verified as former or current tree used by breeding BCLT (can include single or multiple nests) between 2000-2017. Years of use unknown.	
Elevation	Elevation in metres at the recorded way point	Past studies indicate BCLT breeding sites at elevation <100m (Huang *et al.*, 2018)
Slope	Percentage slope	Observation that breeding sites were often in flat areas (R.Gleave, pers. obs.)
Total broadleaf DBH	Combined DBH of broadleaf trees (of over 20cm DBH) within a quadrat	Past studies showed BCLT prefer nesting in large broadleaf trees (Zhang *et al.*, 2017)
Village/Town percent	Percentage of 'village or town' land type within quadrat. 'Village or town' defined as a building, or area of concrete or gravel.	Nesting trees often close to human habitation (Hong *et al.*, 2003)

Other Forest percent	Percentage of 'Other Forest' land type within quadrat. 'Other Forest' defined as conifer forest, bamboo forest or mixed forest/trees.	Nesting trees shown to sometimes be in bamboo or fir trees (Hong *et al.*, 2006; Zhang *et al.*, 2017)
Broadleaf Forest percent	Percentage of 'Broadleaf Forest' land type within quadrat. 'Broadleaf Forest' defined as broadleaf forest or *fengshui* forest/trees.	Nesting trees shown to sometimes be in broadleaf or *fengshui* trees (Zhang *et al.*, 2017, Huang *et al.*, 2018)
Total *Cinnamomum*	The total number of *Cinnamomum* sp. trees (of over 2m tall) within the quadrat	BCLT showed preference for nesting in *Cinnamomum* trees at most sites (Zhang *et al.*, 2017)
Village	Random effect term, identity of each breeding or control site village	

To control for pseudo-replication of the use of 15 sampling points per village, 'village' was included as a random intercept term within models. To balance the risk of model overfitting with that of statistical biases related to unsupervised addition of explanatory variables in a regression model (e.g. multicollinearity) while avoiding stepwise variable selection issues (Mundry and Nunn, 2009, McElreath 2020), a full model (**Table 2**) was compared to a set of four sub-models. For the EOO/breeding site selection, these sub-models contrast the effects of variables hypothesised to be most influential on breeding site selection: elevation, slope and total broadleaf DBH. Nesting site selection models also contain an extra variable, total *Cinnamomum* trees, as these are thought to be the most selected tree type by breeding BCLT, so thought to affect 3rd order habitat selection. Full reasons for the choice of sub-models are given in **Reasons for sub-model selection, Supplementary Information.** The full model contained a carefully selected set of explanatory variables, while the sub-models were used to look for a more parsimonious model. Model comparison was performed using Leave-One-Out cross validation (LOOCV) (Zuur 2009; McElreath 2020).

Table 2. All full model and candidate sub-model resource selection functions for the Blue-crowned Laughingthrush. Model specification uses R notation.

Model name	Breeding site and EOO selection	Nesting site selection
Full model (random intercept and slope)	NA	Nesting ~ Elevation + Slope + Total *Cinnamomum* + Other Forest % + Broadleaf Forest % + Village/Town % + Total broadleaf DBH + (1 + Total broadleaf DBH|village)
Full model (random intercept)	Breeding/EOO ~ Elevation + Slope + Other Forest % + Broadleaf Forest % + Village/Town % + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope + Total *Cinnamomum* + Other Forest % + Broadleaf Forest % + Village/Town % + Total broadleaf DBH + (1|village)
Sub-model 1	Breeding/EOO ~ Slope + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope * Total broadleaf DBH + Total *Cinnamomum* + (1|village)
Sub-model 2	Breeding/EOO ~ Elevation + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope + Total broadleaf DBH * Total *Cinnamomum* + (1|village)
Sub-model 3	Breeding/EOO ~ Elevation + Slope + Other Forest % + Village/Town % + (1|village)	Nesting ~ Elevation + Slope + Total broadleaf DBH + (1|village)
Sub-model 4	Breeding/EOO ~ Elevation + Slope + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope + Total *Cinnamomum* + (1|village)

For all analyses, weakly-informative priors were used, bounding the priors to plausible values. Posterior predictive checks were performed for all models to assess how well the model retrodicted the real observations. To do so, response variable outcomes were generated from the fitted model and compared to the real observations. We only report the covariates with coefficient posterior 90% credible intervals that did not encompass zero, that is, with a 90% mass probability either lower or higher than zero (hereafter, ‘significant’).

Bayesian updating of the model parameters was performed through the No-U-Turn Sampler (NUTS) in Stan. The models were fitted using 2,000 iterations on four chains, with 1,000 warmups per chain to optimise the sampler prior to sampling. Model convergence was checked using Rhat values, and posterior distributions were handled and visualised using R package ‘*tidybayes*’ (Kay 2022). All models converged and had a sufficiently high Effective Sample Size (ESS).

To test and if necessary, control for spatial autocorrelation in the model residuals, all models were run using a Gaussian process regression, as well as without Gaussian processes. This technique allows the varying effects of individual quadrat locations to be treated as a continuous category through their spatial coordinates, hence if necessary correcting for the fact that geographically close points may share more similar features than expected from independent observations (e.g. topography; McElreath 2020). These models were then compared using LOO cross-validation. We present the model with the best expected out-of-sample predictive accuracy, as well as outputs from alternative candidate models with the next-best accuracy (especially those with Expected Log Pointwise Predictive Density (ELPD) and Standard Error difference of <1.0; see **Table S2, Supplementary Information**).

5.3.3.3 *Breeding site selection from remote sensing data*

For the 2nd order habitat selection analysis, breeding and control villages were compared by gathering data on proportion of land cover types around villages by creating circular shapefiles (332m radius) from our classified Sentinel-2 imagery, centred around either known nesting points or village centre-points in QGIS. Using R, pixel values (0-7) were extracted from within each shapefile using the *raster* package. The raw values of each land cover class were converted to a percentage within the shapefile area, resulting in a dataset of one datapoint per village (n=40), each with eight variables containing land cover percentages.

Four regression analyses were conducted to investigate the relationship between proportions of eight land types around villages, and whether these occur within (a) breeding or control villages (three versions of the regression, as described in **section 5.3.3.2**), and (b) villages within the EOO versus within the buffer region. As before, all responses were converted to either a ‘1’ or ‘0’. The ‘breeding’ and ‘control’ response models were also fitted to the variations on these data as described above. Variables included in the models were selected *a priori*, based on past observations of BCLT breeding habitat use and preference: the percentages of broadleaf forest, vegetable plot and bush/scrub within a 332m radius of each village (He *et al.*, 2017; Huang *et al.*, 2018; Liu *et al.*, 2020). All models were fitted as earlier, using 1,000 iterations on four chains, with 500 warmups per chain, to optimise the sampler prior to sampling. Model convergence and outputs were checked as in the previous section.

5.4 Results

5.4.1 Overview

A total of 585 habitat quadrats were surveyed during fieldwork, at 39 villages, and a total of 5,414 trees of 223 species were surveyed within these quadrats. Bamboo *Phyllostachys heterocycla* and Chinese fir *Cunninghamia lanceolata* were the most abundant tree species overall and occurred in over 30% of quadrats (**Table 3**). There were also 179 fruit trees of various species. There was a mean of 1.95 tree species per quadrat (range: 1-7 species). The sampled quadrats for 3rd order analysis (containing nests) contained a total of 423 trees. The highest tree densities were seen when the quadrat contained part of a bamboo stand.

5.4.2 EOO and breeding site selection - 2nd order analysis (quadrat data)

Elevation was significantly lower within the EOO than in the buffer region (Odds Ratio **=** 1.54; EOO mean = 76.86m, buffer region mean = 115.75m, difference between means = 38.89m) (**Figure 2**), but slope and total broadleaf DBH did not influence the odds that a potential home range was within the EOO, according to the second-best fitting model (see **Tables S3 & S4, Supplementary Information** for full model outputs). There was little difference in measures of fit between the optimal and all candidate models (maximum ELPD difference: -0.3, SE difference: 0.1).

For breeding site selection, no predictors (elevation, slope, total broadleaf DBH, or percentage of quadrat that was village or road, broadleaf forest or other forest) influenced the odds of a potential home range being a breeding site (**Figure 3**). There were minimal differences between the LOOCV scores of all candidate models. These patterns were consistent for all variations of the breeding site models (where two ‘unsure’ villages were assigned either breeding or nonbreeding, or breeding site locations from just 2019 were included) (see **Figures. S4 & S5, Supplementary Information**). In addition, the village-level parameters of deviation from the average intercept did not encompass zero, indicating important between-village variation, and that the models contain some variance that cannot be explained by the fixed effects (**Figures 2 & 3**).

Table 3. The most commonly occurring tree species found within 585 survey quadrats within villages formerly or currently containing breeding Blue-crowned Laughingthrush colonies, and control villages.

Commonest species			**Most abundant species (all quadrats, n=585)**		**Most abundant species (nesting quadrats, n=22)**		**Other key statistics**	
Species	**Percentage of quadrats**	N	**Species**	**N**	**Species**	**N**		
Bamboo *Phyllostachys heterocycla*	32	189	Bamboo *Phyllostachys heterocycla*	(n=3,008)	Bamboo *Phyllostachys heterocycla*	(n=321)	Mean height of each tree in the centre of the quadrat	7.65m (range 2.00 – 36.80m
Chinese Fir *Cunninghamia lanceolata*	31	182	Chinese Fir *Cunninghamia lanceolata*	(n=708)	Chinese Fir *Cunninghamia lanceolata*	(n=28)	Mean no. trees per quadrat	9.25 (range 1-253 trees)
Chinese Windmill Palm *Trachycarpus fortunei*	13	79	Sweet Osmanthus *Osmanthus* sp.	(n=204)	Camphor *Cinnamomum camphora*	(n=10)	Number trees with a DBH of 20cm or over	347, mean of 40.75cm DBH (range 20 – 196cm)
Sweet Osmanthus *Osmanthus fragrans*	12	74	Sweetgum *Liquidambar* sp.	(n=164)	Sweet Osmanthus *Osmanthus fragrans*	(n=5)	Mean elevation at all quadrats	90.8m
Chinese Chestnut *Castanea mollissima*	10	58	Chinese Windmill Palm *Trachycarpus fortunei*	(n=116)	Bald Cypress *Taxodium distichum*	(n=5)	Mean slope at all quadrats	11.5
Chinkapin *Castanopsis* sp.	8	51	Chinkapin *Castanopsis* sp.	(n=110)	Sweetgum *Liquidambar formosana*	(n=4)	Mean elevation at nesting quadrats	76.5m
Camphor *Cinnamomum* sp.	8	49	Camphor *Cinnamomum* sp.	(n=68)	-	-	Mean slope at nesting quadrats	6.4
Sweetgum *Liquidambar* sp.	8	49	Pine *Pinus massoniana*	(n=57)	-	-	-	-

-	-	-	Wingnut *Pterocarya* sp.	(n=49)	-	-	-	-

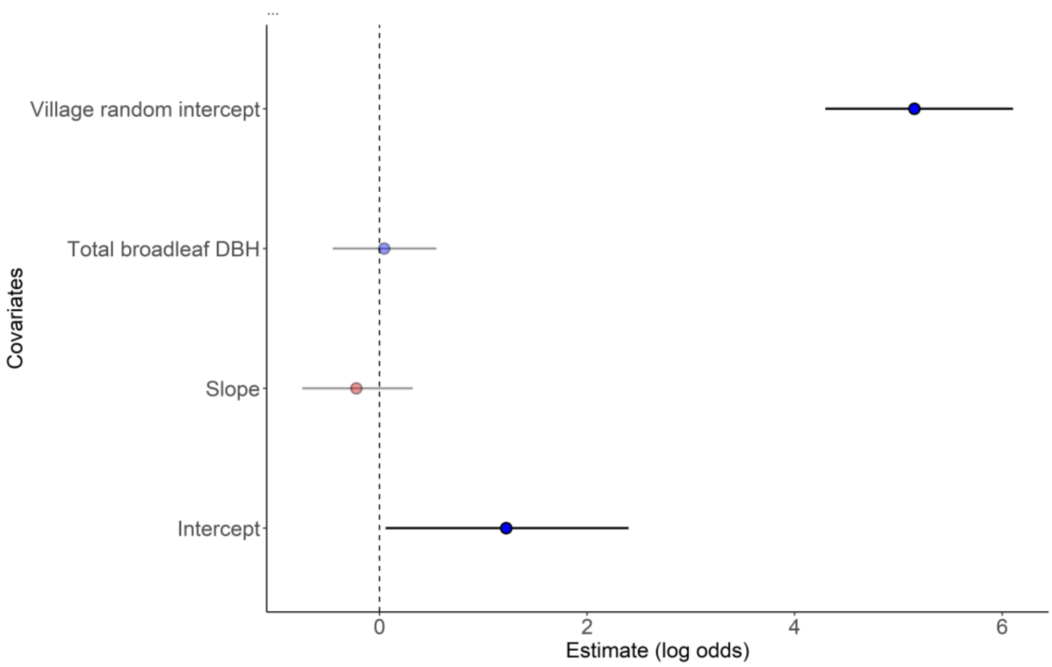

Figure 2. Interval plot showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a village was in the EOO.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship with villages in the EOO if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the second most optimal candidate model (*submodel 1*).

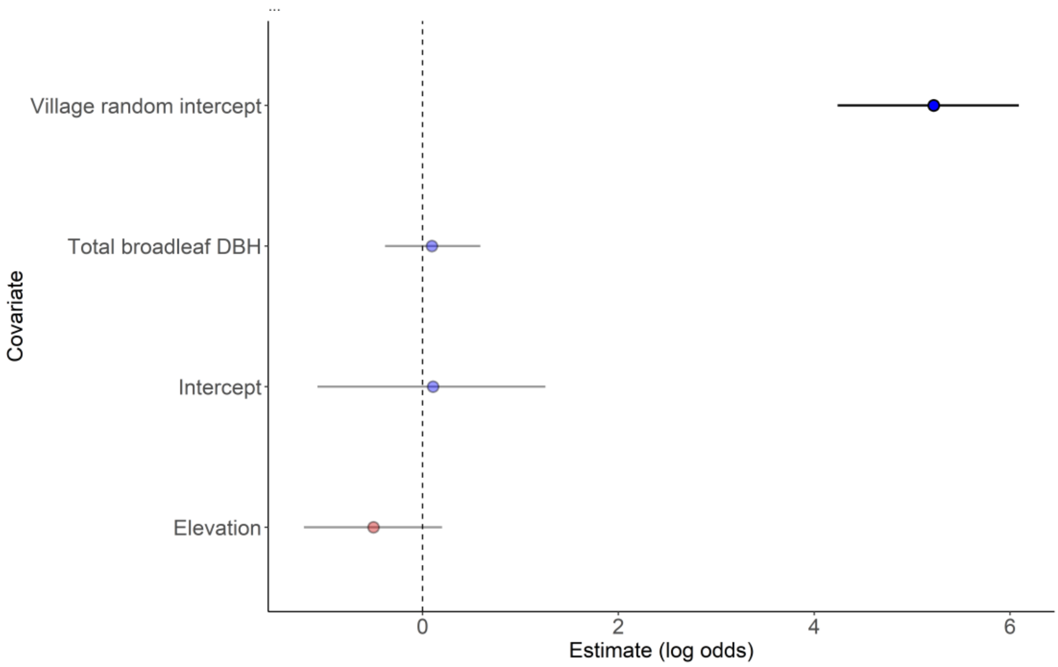

Figure 3. Interval plot showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a village was a breeding site.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to breeding sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the optimal candidate model (*submodel 2*).

5.4.3 Nest site selection – 3rd order analysis (quadrat data)

Nesting sites were significantly positively related to the size (total DBH) of broadleaf trees (Odds Ratio = 1.16) and percentage of 'other' (bamboo, fir or pine) forest within the quadrat (Odds Ratio = 1.25), according to the optimal model (**Figure 4**). There was a significant negative relationship between nesting sites and slope (Odds Ratio = 1.32). There was no significant relationship detected between nesting sites and elevation, the number of *Cinnamomum* trees, or the percentage of broadleaf forest or village and town in the quadrat.

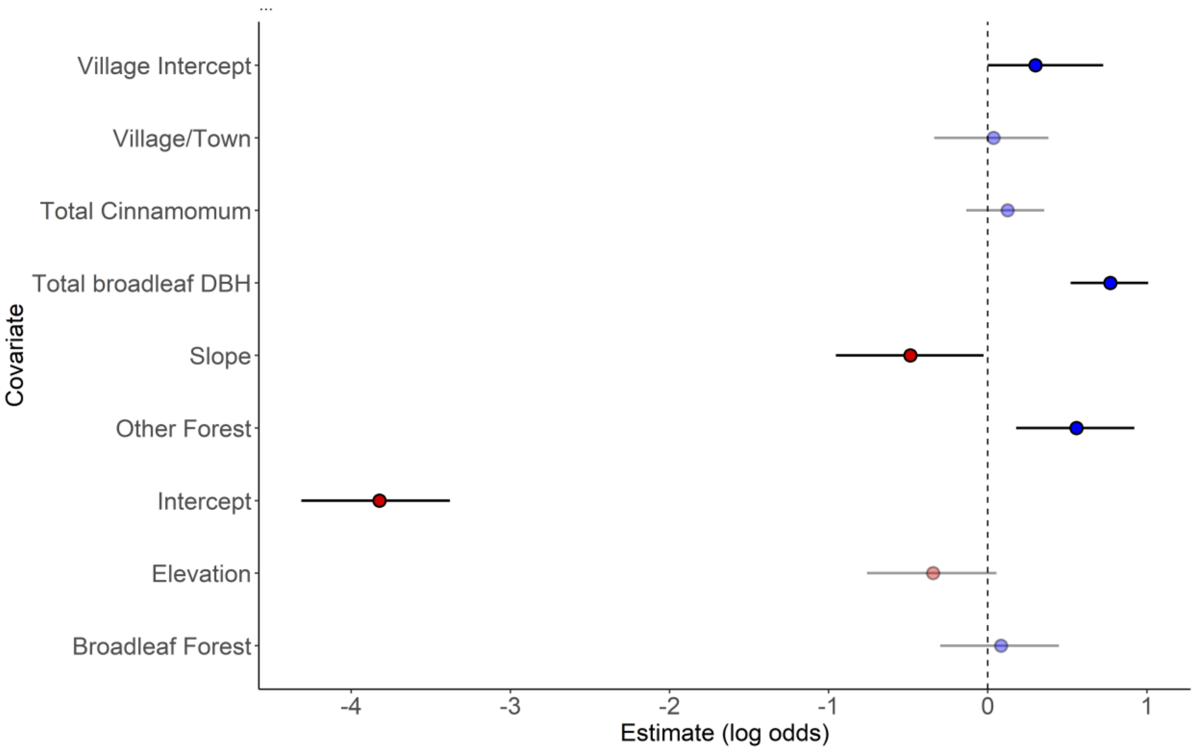

Figure 4. Interval plot showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a survey quadrat was ever a nesting site.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to nesting sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the optimal candidate model (*global model, random intercept only*).

5.4.4 Breeding site selection (remote sensing data)

From the remote sensing images, the mean percentage of land types taken from a 332m diameter circular area around villages were: broadleaf forest 9%, vegetable plot 13%, other forest 23%, tea 15%, rice paddy 26%, bush/scrub 23%, settlement/road 36%, and water 27%.

Land cover classification distinguished land cover across the three remote sensing images with moderate overall accuracy (mean: 67.82%), with 64.64% and 60.51% accuracy in distinguishing types of broadleaf and 'other' forested pixels, respectively; and similar accuracy for distinguishing agriculture (vegetable plot, rice paddy, tea) and bush/scrub pixels (60.51–66.92%; **Table S5, Supplementary Information**). Land cover classification had the highest accuracy for settlement/road and water (**Table S5, Supplementary Information**). We found no evidence of a difference in the proportions of eight different land types between breeding and control villages, or between villages inside the EOO and the buffer region (**Figure 5**). Wide 90% credible intervals show high levels of uncertainty in both models.

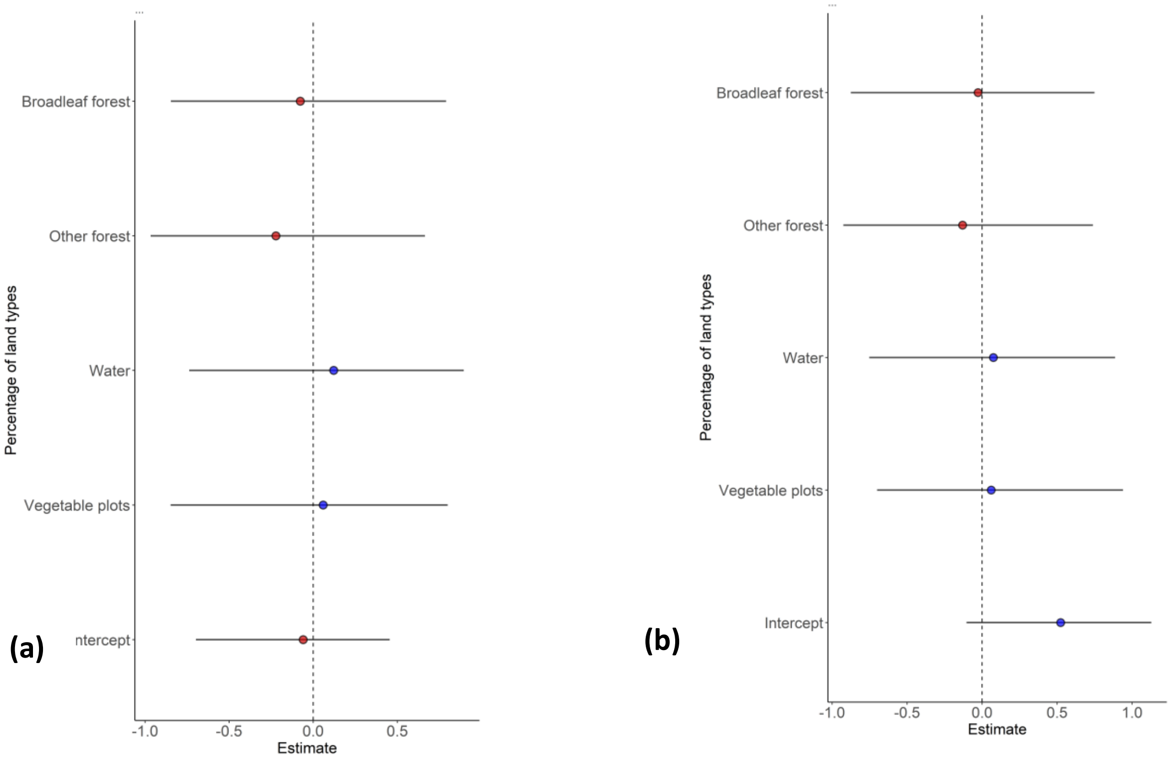

Figure 5. Interval plots showing the 90% credible intervals (CI, represented by black lines) for the posterior distribution of each predictor, in relation to **whether a village was a) a breeding site or b) within the EOO** based on remote sensing land cover data**.** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to a breeding or EOO site if the CI is to the right of plot, and negative if they are to the left of the plot.

5.5 Discussion

Our results show that habitat selection studies of threatened species, at more than one scale, can provide insights relevant to conservation planning and landscape policy. This study developed Resource Selection Functions (RSFs) to identify habitat factors important to the distribution of Blue-crowned Laughingthrush (BCLT) at multiple spatial scales, comparing the largest number of breeding sites and broadest geographic range for the species to date.

No habitat selection in terms of topography (elevation, slope), tree characteristics (species, DBH) or land cover proportions was detected at the 2nd order (breeding site) selection level, between a total of 39 breeding and control sites. Differences were, however, detected between sites inside and outside of the BCLT's Extent of Occurrence (EOO), with villages inside the EOO at a significantly lower elevation than villages outside of the EOO. This result is consistent with previous smaller-scale studies of BCLT breeding habitat (Hong *et al.*, 2006; Huang *et al.*, 2018), where breeding sites were found at lower elevation than control sites. However, the overall difference in elevation was small, with a difference of only 38.89m between mean elevations inside and outside the EOO. Many breeding sites were located within the river basin of the Le'An river, which may contribute to the similarity in elevation among breeding sites, rather than reflecting a specific biological requirement. This could be interpreted as indicating that sites at lower elevations, or in lowland areas, are more suitable as BCLT habitat at the breeding site scale, but otherwise BCLT may be thought of as a broadly generalist species at this spatial scale within the context of our study landscape.

Although elevation was lower within the EOO, this may not necessarily be a direct causal factor determining BCLT range. Elevation affects species distributions through influencing factors such as temperature and precipitation and by generating habitat gradients (Franklin 2009; Jankowski *et al.*, 2013), which may not occur within the relatively gentle elevation increases observed across the study landscape (14.59-1566.58m, mean = 261.54m). Furthermore, BCLT have been reported as foraging in hills at 900m outside of the EOO during the breeding season (Cheng and Lin 2011), at higher elevations than within the EOO. This suggests that BCLT are unlikely to have their range strongly limited by habitat, at least at the 2nd order spatial scale.

No difference in land cover proportions (from remote sensing imagery) was found in breeding and control villages, or villages within or outside of the EOO, at the 2nd order scale. Although past work has identified vegetable gardens and broadleaved forest as potentially important foraging habitat for BCLT (He *et al.*, 2017; Liu *et al.*, 2020), we do not find evidence that these land cover types differ significantly between villages with and without breeding BCLTs. However, our results do not contradict past findings that these habitats are important to the BCLT; they may simply be reflecting that these land cover types are relatively common across our study landscape (mean of 9% broadleaf forest and 13% vegetable gardens around study villages), and that they are not limiting factors regulating BCLT distribution. Sites with larger amounts of these habitats within the study landscape may, therefore, not influence breeding site selection at the 2nd order scale. In contrast, other bird species' home ranges do sometimes contain higher proportions of certain habitats than expected by chance (Lee *et al.*, 2005; Van Schmidt *et al.*, 2014). These findings, in combination with our breeding-site quadrat data, suggest that BCLT habitat selection may be weaker at the breeding site scale.

Conversely, in contrast to the lack of signal in our 2nd order analyses, analysis of BCLT nesting site preference, the 3rd order selection level, showed that nesting quadrats had a significantly higher total broadleaf DBH compared to control quadrats. This result is again consistent with past findings that BCLT prefer nesting in broadleaf trees with higher DBH, or in taller trees, which correlates with higher DBH (Zhang *et al.*, 2017; Huang *et al.*, 2018); this preference has not been reported in other Chinese laughingthrush species (Wang *et al.*, 2011; Li *et al.*, 2017; Liu, Qin and Shang, 2021). Nesting sites also had a significantly higher proportion of bamboo, fir or mixed forest stands within the quadrats. This may be linked to these habitats being plantation forests, which are typically quite dense, thus providing good cover for birds. Selection of large broadleaf trees or dense bamboo, fir or mixed forest stands as nest sites may be related to nest protection, as nest sites generally minimize detection or predation risk (Martin and Roper 1988; Oppel *et al.*, 2004a). Some other laughingthrushes, such as Masked Laughingthrush (*Garrulax perspicillatus*), also nest in similar habitat, showing preferences for *Osmanthus*, bamboo and camphor (Li *et al.*, 2017). Bamboo is a member of the grass family and therefore structurally different to other trees, and pure stands of young bamboo are generally more dense than other tree types. However other young plantation forests (e.g. Chinese fir, Chinese Sweetgum) can reach similar densities (R. Gleave pers. obs). Nesting sites were also on significantly less steep land; this preference for gentler slopes could be linked to lower elevation within the EOO. Conversely, we found no significant preference for other habitat characteristics on nest site selection, such as the total number of camphor Cinnamomum trees, which contrasts somewhat with past findings that BCLT prefer to nest in specific tree species (Liao *et al.,* 2007; Zhang *et al*., 2017; Huang *et al*., 2018). Large broadleaf trees near villages are often only found across the BCLT's range within *fengshui* forests (Coggins *et al.*, 2012); however, we also found no evidence of preference for nesting in quadrats with higher proportions of broadleaf or *fengshui* forest, which also contrasts with past evidence (Huang *et al*., 2018). This departure from previous studies could be due to our dataset containing a greater number and therefore greater variety of breeding/nesting sites; Huang *et al.* (2018) only compared breeding sites in forests with other forests of the same type, whereas some nesting sites in our dataset were not found within forest patches.

Overall, our results indicate that across our study landscape, there is mainly evidence for habitat selection by BCLTs at the nesting site (3rd order) scale. The importance of the 3rd order scale may be linked to the BCLT's life history traits (Jedlikowski *et al.*, 2016); as the species breeds colonially, and has been recorded engaging in nest defence, nest site selection may be more important than foraging opportunities in surrounding areas of land. Liu *et al.* (2020) similarly concluded that the area of suitable available habitat is not a limiting factor in BCLT population increase, as high food availability and relatively weak long-distance movement ability mean that only a small area is needed to meet their reproductive needs. Given the species' tiny population and small number of breeding sites, we echo previous recommendations to protect broadleaf trees within or beside villages, as well as other existing stands of forest and bamboo (Liu *et al.*, 2020), considering the available evidence for their ecological importance for BCLTs. The breeding habitat requirements of the BCLT differ from its closest relative, the Yellow-throated Laughingthrush (*Pterorhinus galbanus*), which nests in shrubs, bushes and tall grasses rather than trees (Baker 1932; Hong *et al.* 2004), as do some other laughingthrush species in China such as the Plain Laughingthrush (*Pterorhinus davidi concolor*) and Elliot's Laughingthrush (*Trochalopteron elliotii*) (Liu, Qin and Shang, 2021). The positive relationship between the BCLT's EOO and low elevation could mean their range is restricted by elevation; as BCLT showed a preference for gentler slopes at the 3rd order scale, preferences over slope at the smaller scale could be influencing the wider patterns in elevation at a larger scale. As for other Chinese species (Li, Pan and Oxnard, 2002; Zhu *et al.*, 2013; Turvey, Crees and Di Fonzo, 2015), lower elevations have historically been more accessible to people, and seen greater habitat conversion and human population growth, potentially meaning that the BCLT remains particularly vulnerable to ongoing human disturbance. Alternatively, the BCLT's range may not 'naturally' be restricted to low elevations: a species' breeding habitat, including its elevation range, is not always in its ecologically optimal location and may be located "*in the habitat least favourable to the agent of decline*" (Caughley, 1994; Channell and Lomolino, 2000). In which case, the present day range may represent a lack of other anthropogenic drivers of decline such as trapping or loss of habitat. Moreover, the BCLT may not be restricted by its breeding habitat, if it is mainly threatened during its non-breeding season, as other bird species are threatened by human activities within their wintering range (Martinez and Lewthwaite 2013). Our findings suggest that the BCLT's current restricted breeding range may be regulated, in part, by landscapes at lower elevation (or lowlands), and in the availability of large broadleaf trees or stands of mixed forest, bamboo or fir trees on gentle slopes. However, other factors or cues could also be playing a role in determining the distribution of BCLT breeding colonies.

Both extrinsic and intrinsic factors may be involved with determining BCLT nesting site choice. In terms of extrinsic factors, human disturbance has been posited as a threat to BCLT breeding success (He *et al.*, 2017; Zhang *et al.*, 2017), and nests or entire past breeding sites have been anecdotally reported as being abandoned due to disturbance (He *et al.*, 2017); for instance, following removal of bamboo stands containing BCLT nesting sites, presence of aggressive dogs, building developments, and loud markets with firecrackers (F. He, 2019, personal communication; L. Gardner, 2020, personal communication). This observed behaviour is consistent with studies showing that colonially breeding birds tend to be more vulnerable to disturbance (Buckley and Buckley 1976), with cooperative-breeding birds often showing more flighty behaviour in response to human approach than non-cooperative breeders (Blumstein, 2006). Other direct human impacts, such as persecution for the bird trade, could also feasibly shape the restricted distribution of the BCLT within a wider landscape containing potentially suitable habitat (Yang *et al.*, 2018). In terms of intrinsic factors, several BCLT breeding sites (n=8) have been or were used for multiple continuous years (He *et al.*, 2017), suggesting some level of site fidelity. Breeding site fidelity is well-documented amongst many bird species

(Harvey, Greenwood and Perrins, 1979; Hoover, 2003; Brown, Roche and Brown, 2017) and may also contribute to the specific observed distribution of BCLT versus wider habitat availability.

An important potential limitation of this study is the placement of the central point of each ‘home range’. Breeding villages were centred on a known nesting site, which may either be at the edge of, adjacent to, or in the centre of a village. Control sites were instead always centred at the central point of a village, which could result in the inclusion of more built-up land within data analysis for these sites than in breeding sites. Future analyses could thus randomise central point placement within a set boundary for control sites. However, village sizes varied considerably, with some extremely small control site villages where the central point placement would make little difference to the area surveyed; and there was no between-site bias detected in models, with control sites showing no significant difference in settlement/road proportion to breeding sites. Control villages were selected from a mixture of sources, including near eBird locations, from old reports, and selected at random from within the two polygons. Those selected from eBird or old reports may be more suitable for BCLT and differ slightly to control villages in general. However, some of these were from non-breeding season sightings so may not represent more favourable potential breeding habitat. In addition, nesting trees included in this analysis represent a subset of all nesting trees, and their selection was based on expert knowledge collected from across multiple nesting seasons, rather than upon our own survey of nest sites within a single year. We acknowledge that this approach may bias the selection of nesting sites to those that are more memorable (such as larger or more distinctive trees), and future studies could map all nesting trees across all breeding sites within a breeding season to overcome this potential bias. However, this selection of trees is probably mostly representative: BCLT sometimes nest in the same tree in multiple years (F. He, 2019, personal communication), and we directly observed some nesting behaviour during fieldwork. Furthermore, our expert deliberately mentioned specific nesting trees which countered the conventional wisdom on the BCLT for preferring *fengshui* forest.

Future work could further address the 1st order scale habitat selection of the BCLT: we surveyed and compared villages within the EOO and a 25km surrounding buffer region at the 2nd and 3rd order scales, but it is possible that the landscape may change further outside this area, potentially revealing greater disparities in habitat and revealing clearer insights into

BCLT range limits. For example, elevation remains similar to the immediate BCLT landscape across much of southern China, but increases steeply in the far west (Feng *et al.*, 2007). This knowledge gap can be overcome by performing analyses on BCLT occurrence at the landscape scale with tools such as species distribution modelling, which is addressed in Chapters 3 and 6.

Our findings have implications for other species. Our results support the need for non-crop vegetation, such as broadleaf trees or stands of bamboo, mixed forest or fir trees, within the agricultural landscape of north-east Jiangxi Province and surrounding regions to support BCLT and other bird populations. Many species across China occur within human-occupied agricultural mosaic landscapes (Wang and Young, 2003), but there is evidence that bird diversity is positively influenced by the amount of non-crop vegetation and habitat heterogeneity within these mixed habitats (Li *et al.*, 2020). Our results also highlight the importance of integrating conservation-relevant data across multiple scales. Had we only investigated the 2nd order (breeding site) scale, we would have overlooked the important relationship of BCLT nesting sites with large broadleaf trees and plantation trees. Since these are of clear importance for the species, we recommend scaling up legal protection of *fengshui* forests across southern China, as these will likely form habitat refugia for many species beyond the BCLT (Coggins, 2003; Hong *et al*., 2003; Liao *et al.*, 2007).

Like other species, habitat selection of the BCLT differs according to distinct spatial scales. We found no clear driver of breeding site selection at the 2nd order scale, in contrast to some other Critically Endangered species (Sawyer and Brashares, 2013). Instead, a strong relationship was found between nesting sites (3rd order scale) and large broadleaf trees, plantation forest stands and gentle slopes. Our findings for the 3rd order scale broadly match, but also nuance, other studies on BCLT nesting habitat (Zhang *et al.*, 2017, Huang *et al.*, 2018). Our results show that habitat surveys to develop RSFs at different scales can be a useful, rapid tool in elucidating potential range restriction drivers for rare species with few breeding sites. We also provide evidence for the importance of protecting large broadleaf trees near villages, such as *fengshui* forests, which should be applied across southern China and not just within the regions currently utilised by the BCLT. This approach would help to ensure that suitable available habitat remains for a future potentially expanding breeding BCLT population, as well as for many other bird species.

5.6 References

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Supplementary Information

Data Collection Protocol

A quadrat of 100m^2 was chosen through pilot studies, as this area was sufficiently large to capture a detailed information on land immediately around trees, but also sufficiently small to allow 15 survey points to be measured in one day. This size also prevented significant overspill of surveys into inaccessible land, such as private property. Tree DBH was calculated using method described by City of Portland, Oregon (https://www.portlandoregon.gov/trees/article/424017). Tree species were identified using a combination of professional or local knowledge, local Chinese tree ID guides, and a phone app (Xing Se). If tree species were not identifiable in the field, photos were taken of the tree for later identification. These were compared with images from an identification book (Liu 2015), Kew Science Plants of the World Online, and efloras.org Floras of China (accessed 13th – 21st April 2020), using descriptions of range, plant physical characteristics and illustrations. If no positive identification was made then 'Broadleaf sp.' is given (n=22). All non-broadleaf trees were identified. Tree height was measured using the Theodolite 7.0 app (Hunter Research & Technology LLC, 2019). If tree height could not be measured, we visually estimated height and gave this to the nearest half metre. Photographs were taken of each quadrat. Percentage land use type assessed by eye to the nearest 5%. Land types are listed in **Table S1**. Herb height and herb density were assigned categories by eye.

QGIS Collection of Elevation, Slope, Aspect

GPS estimates were unreliable in pilot surveys (possibly due to slow responses to elevation change). These were generated in QGIS from a USGS DEM layer (30m x 30m resolution), using the Point Sampling Tool plugin. Slope data were extracted by processing a DEM layer with lat/long coordinates in decimal degrees using the QGIS GDAL slope tool. A ratio of vertical units to horizontal units was set to 111120 and slope outputs were expressed as percentages rather than degrees.

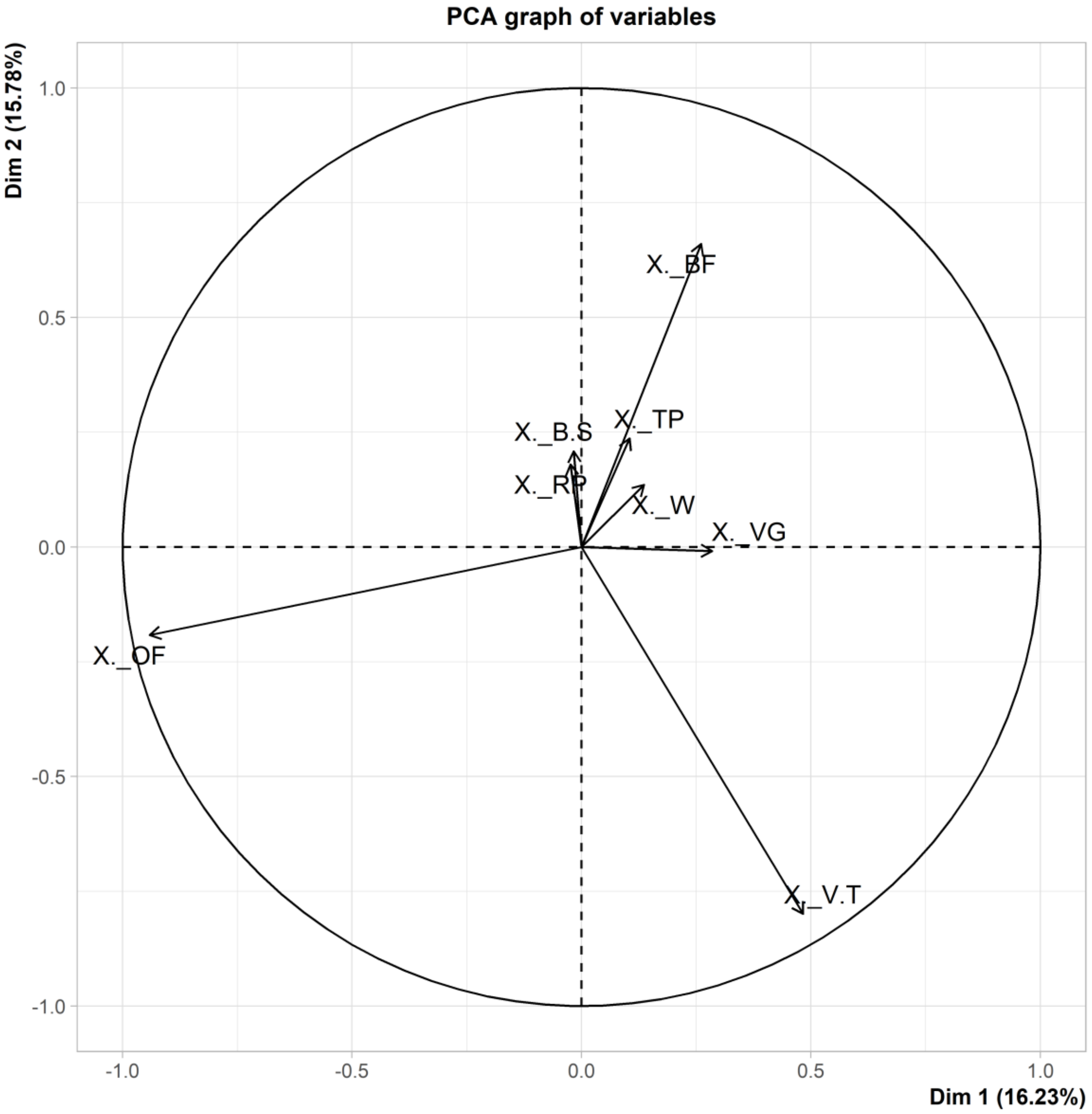


Figure S1. Principal Component Analysis plot of Dimensions 1 and 2 of land cover type percentages.

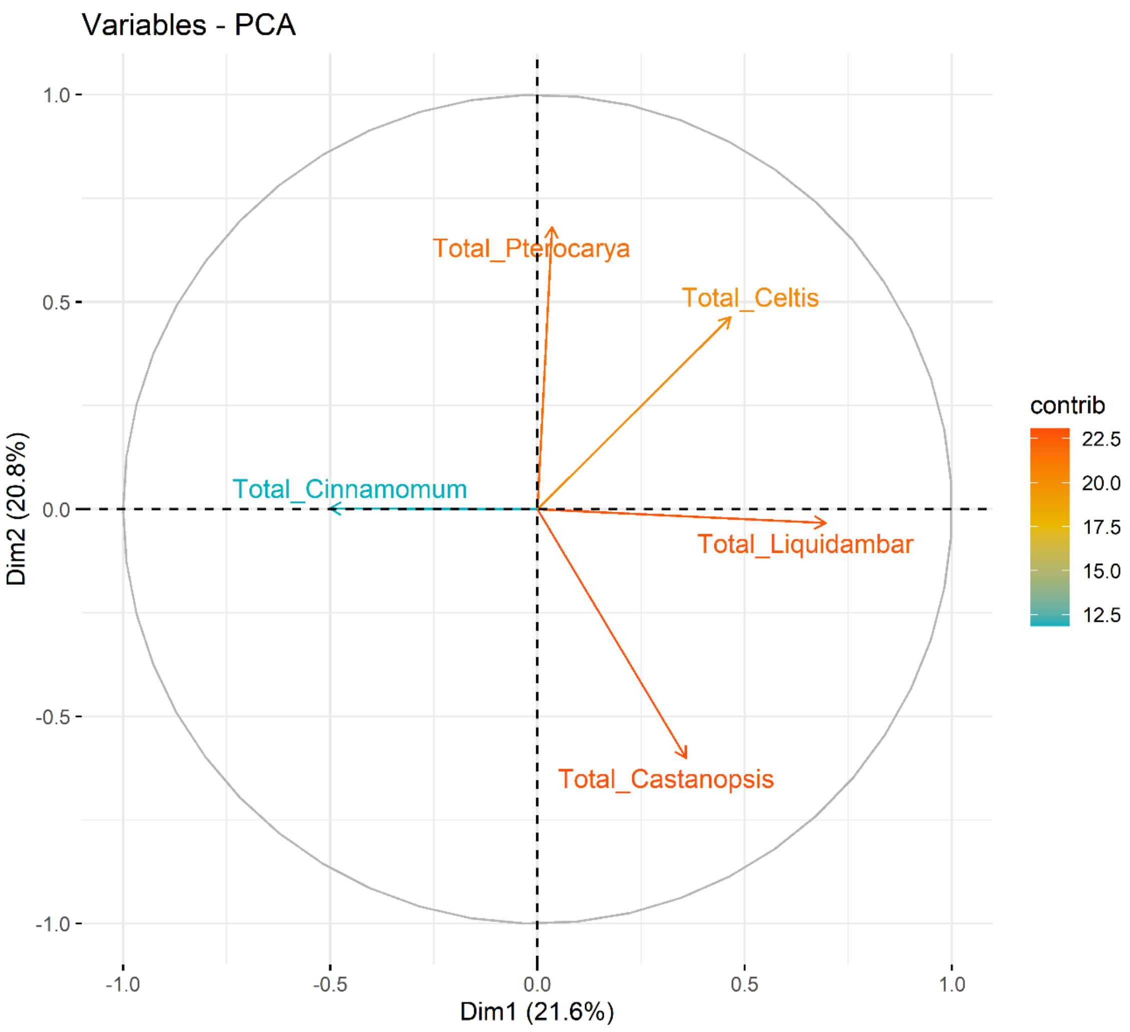
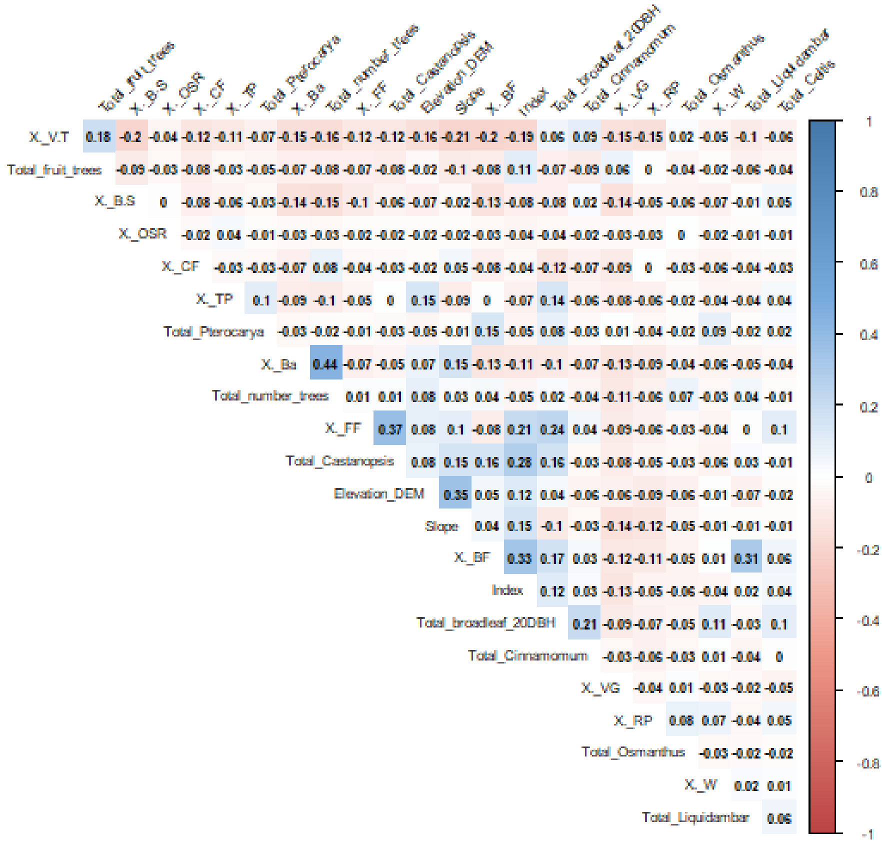


Figure S2. Principal Component Analysis plot showing total contribution of tree species percentages to Dimensions 1 and 2.



	Total_fruit_trees	X_B.S	X_OSR	X_CF	X_TP	Total_Pterocarya	X_Ba	Total_number_trees	X_FF	Total_Castanopsis	Elevation_DEM	Slope	X_BF	Index	Total_broadleaf_20DBH	Total_Cinnamomum	X_VG	X_RP	Total_Osmanthus	X_W	Total_Liquidambar	Total_Celtis
X_V.T	0.18	-0.2	-0.04	-0.12	-0.11	-0.07	-0.15	-0.16	-0.12	-0.12	-0.16	-0.21	-0.2	-0.19	0.06	0.09	-0.15	-0.15	0.02	-0.05	-0.1	-0.06
Total_fruit_trees		-0.09	-0.03	-0.08	-0.03	-0.05	-0.07	-0.08	-0.07	-0.08	-0.02	-0.1	-0.08	0.11	-0.07	-0.09	0.06	0	-0.04	-0.02	-0.06	-0.04
X_B.S			0	-0.08	-0.06	-0.03	-0.14	-0.15	-0.1	-0.06	-0.07	-0.02	-0.13	-0.08	-0.08	0.02	-0.14	-0.05	-0.06	-0.07	-0.01	0.05
X_OSR				-0.02	0.04	-0.01	-0.03	-0.03	-0.02	-0.02	-0.02	-0.02	-0.03	-0.04	-0.04	-0.02	-0.03	-0.03	0	-0.02	-0.01	-0.01
X_CF					-0.03	-0.03	-0.07	0.08	-0.04	-0.03	-0.02	0.05	-0.08	-0.04	-0.12	-0.07	-0.09	0	-0.03	-0.06	-0.04	-0.03
X_TP						0.1	-0.09	-0.1	-0.05	0	0.15	-0.09	0	-0.07	0.14	-0.06	-0.08	-0.06	-0.02	-0.04	-0.04	0.04
Total_Pterocarya							-0.03	-0.02	-0.01	-0.03	-0.05	-0.01	0.15	-0.05	0.08	-0.03	0.01	-0.04	-0.02	0.09	-0.02	0.02
X_Ba								0.44	-0.07	-0.05	0.07	0.15	-0.13	-0.11	-0.1	-0.07	-0.13	-0.09	-0.04	-0.06	-0.05	-0.04
Total_number_trees									0.01	0.01	0.08	0.03	0.04	-0.05	0.02	-0.04	-0.11	-0.06	0.07	-0.03	0.04	-0.01
X_FF										0.37	0.08	0.1	-0.08	0.21	0.24	0.04	-0.09	-0.06	-0.03	-0.04	0	0.1
Total_Castanopsis											0.08	0.15	0.16	0.28	0.16	-0.03	-0.08	-0.05	-0.03	-0.06	0.03	-0.01
Elevation_DEM												0.35	0.05	0.12	0.04	-0.06	-0.06	-0.09	-0.06	-0.01	-0.07	-0.02
Slope													0.04	0.15	-0.1	-0.03	-0.14	-0.12	-0.05	-0.01	-0.01	-0.01
X_BF														0.33	0.17	0.03	-0.12	-0.11	-0.05	0.01	0.31	0.06
Index															0.12	0.03	-0.13	-0.05	-0.06	-0.04	0.02	0.04
Total_broadleaf_20DBH																0.21	-0.09	-0.07	-0.05	0.11	-0.03	0.1
Total_Cinnamomum																	-0.03	-0.06	-0.03	0.01	-0.04	0
X_VG																		-0.04	0.01	-0.03	-0.02	-0.05
X_RP																			0.08	0.07	-0.04	0.05
Total_Osmanthus																				-0.03	-0.02	-0.02
X_W																					0.02	0.01
Total_Liquidambar																						0.06

Figure S3. Correlation plot of all candidate numerical covariates for inclusion in generalised linear mixed models.

Table S1. The full set of potential predictor variables, with descriptions and reasons given for their inclusion. A subset of these will be included in the final analyses. An ‘x’ symbol is given for predictor variables which are being considered for each response variable, based on the outcomes of exploratory analyses.

Predictor Type	**Variable Predictor**	**Response variables comparing habitat preferences between:**				**Data format**	**Description of dependent variable and hypothesised relationship**	**Variable type**	**Examples from literature**
		Breeding status	**Breeding status (2019 only)**	**Within EOO or outside of EOO**	**Nesting quadrat**				
Topography	Elevation (m)	**X**	**X**	**X**	**X**	Continuous (numeric)	Elevation in meters at the recorded way point. BCLTs shown to breed at low altitude (<100m)	Fixed effect	Wilkinson et al. (2010), He & Xi (2002), Huang et al. (2018)
	Slope (°)	**X**	**X**	**X**	**X**	Continuous (numeric)	Percentage (%) slope at specific habitat survey point. Shown in ecological census literature	Fixed effect	Sutherland (2006)
	Aspect (°)					Continuous (numeric)		Fixed effect	Sutherland (2006)
Land type proportions	Percentage of broadleaf forest within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to choose broadleaf forest as nesting and foraging sites	Fixed effect	He & Xi (2002), Liu et al. (2020)
	Percentage of conifer (fir or pine) forest within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to choose fir trees as nesting sites	Fixed effect	He & Xi (2002), Hong et a. (2006)
	Percentage of bamboo forest within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to choose bamboo forest as nesting sites	Fixed effect	Hong et al. (2006), He at al. (2017)
	Percentage of mixed forest within 10m^2 quadrat					Proportion (numeric)		Fixed effect	
	Percentage of fengshui forest within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to choose fengshui forest as nesting sites	Fixed effect	Hong et al. (2006), Zhang et al. (2017)
	Percentage of bush/scrub within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to use shrub and grassland for foraging	Fixed effect	Hong et al. (2006), Liu et al. (2020)

	Percentage of water within 10m^2 quadrat					Proportion (numeric)		Fixed effect	Huang et al. (2018)
	Percentage of rice paddy within 10m^2 quadrat					Proportion (numeric)		Fixed effect	
	Percentage of tea plantation within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to forage in tea plantation	Fixed effect	Hong et al. (2006)
	Percentage of vegetable garden within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to forage in vegetable plots	Fixed effect	Hong et al. (2006), Liu et al. (2020)
	Percentage of oilseed rape within 10m^2 quadrat					Proportion (numeric)	BCLTs shown to forage in oilseed rape	Fixed effect	Liu et al. (2020)
	Percentage of village or town within 10m^2 quadrat	**X**	**X**	**X**	**X**	Proportion (numeric)	BCLTs shown to choose breeding sites close to villages	Fixed effect	Huang et al. (2018)
	Percentage of 'other' land type within 10m^2 quadrat					Proportion (numeric)		Fixed effect	
Tree variables	Shannon Index	**X**	**X**	**X**	**X**	Continuous (integer)	Total number of tree species (over 2m high) recorded within the quadrat. Species richness may affect the types or abundance of food available to breeding BCLTs.	Fixed effect	
	Total number of non-broadleaf trees over 20cm DBH					Continuous (integer)	Total number of trees (over 2m high) within the quadrat with a Diameter at Breast Height of over 20cm. BCLTs have been shown to show preference for trees with a large DBH for nesting.	Fixed effect	Zhang et al. (2017), Huang et al. (2018)
	Total DBH of broadleaf trees over 20cm	**X**	**X**	**X**	**X**	Continuous (integer)	Total number of broadleaf trees (over 2m high) within the quadrat with a Diameter at Breast Height of over 20cm.	Fixed effect	Zhang et al. (2017), Huang et al. (2018)
	Total number of fruit trees					Continuous (integer)	Total number of cultivated fruit trees (over 2m high) within the quadrat. BCLTs	Fixed effect	Zhang et al. (2017), He et al. (2017)

							have been shown to use fruit trees for nesting, therefore presence of or higher abundance of fruit trees may influence BCLTs choosing a village as a nesting site.		
	Total number *Osmanthus sp.* trees					Continuous (integer)	Total number of *Osmanthus sp.* trees (over 2m high) within the quadrat. BCLTs have been shown to use *Osmanthus* trees for nesting, therefore presence of or higher abundance of *Osmanthus* trees may influence BCLTs choosing a village as a nesting site.	Fixed effect	Zhang et al. (2017)
	Total number of *Cinnamomum sp.* trees				**X**	Continuous (integer)	Total number of Cinnamomum sp. trees (over 2m high) within the quadrat. BCLTs have been shown to disproportionately choose *Cinnamomum* trees for nesting, therefore presence of or higher abundance of *Cinnamomum* trees may influence BCLTs choosing a village as a nesting site.	Fixed effect	Hong et al. (2006), Zhang et al. (2017)
	Total number of *Celtis sp.* trees					Continuous (integer)	Total number of *Celtis sp*. trees (over 2m high) within the quadrat. BCLTs have been shown to disproportionately choose *Celtis* trees for nesting, therefore presence of or higher abundance of *Celtis* trees may influence BCLTs choosing a village as a nesting site.	Fixed effect	Zhang et al. (2017), Huang et al. (2018)
	Total number of *Pterocarya sp.* trees					Continuous (integer)	Total number of *Pterocarya sp.* trees (over 2m high) within the quadrat. BCLTs have been shown to disproportionately	Fixed effect	Zhang et al. (2017), Huang et al. (2018)

							choose *Pterocarya* trees for nesting, therefore presence of or higher abundance of *Pterocarya* trees may influence BCLTs choosing a village as a nesting site.		
	Total number of *Liquidambar sp*. trees					Continuous (integer)	Total number of *Liquidambar* sp. trees (over 2m high) within the quadrat. BCLTs have been shown to disproportionately choose *Liquidambar* trees for nesting, therefore presence of or higher abundance of *Liquidambar* trees may influence BCLTs choosing a village as a nesting site.	Fixed effect	Hong et al. (2006), Zhang et al. (2017), Huang et al. (2018)
	Total number of *Castanopsis sp.* trees					Continuous (integer)	Total number of *Castanopsis sp.* trees (over 2m high) within the quadrat. BCLTs have been shown to disproportionately choose *Castanopsis* trees for nesting, therefore presence of or higher abundance of *Castanopsis* trees may influence BCLTs choosing a village as a nesting site.	Fixed effect	Hong et al. (2006)
	Total number of trees					Continuous (integer)	Total number of trees (over 2m high) within the quadrat. This is an approximate measure of tree density. BCLTs have been shown to choose nest sites in dense vegetation, and so tree density may influence their selection of breeding site.	Fixed effect	Hong et al. (2006), He et al. (2017)
	Herb height					Factor (nominal)	Description of herb height within quadrat. Herbs = both forbs and grasses. None, low, medium and tall.	Fixed effect	Huang et al. (2018)

	Herb density					Factor (nominal)	Description of herb density within quadrat. Herbs = both forbs and grasses. None, sparse, dense.	Fixed effect	Huang et al. (2018)
	Forest floor disturbance					Factor (ordinal)	Score describing the degree of human habitat disturbance to ‘forest floor’ type, from 0 = concrete/brick/tarmac through to 4 = fully ‘natural’ or undisturbed vegetation (leaf litter, forbs, ferns and small trees)	Fixed effect	Huang et al. (2018)
Random effects	Way Point Number	X	X	X	X	Continuous (integer)	Unique way point number per quadrat. Potentially include as random effect, to account for autocorrelation within villages.	Random effect	
	Village	X	X	X	X	Factor (nominal)	Village in which quadrat was measured. 15 quadrats are measured per village, thus there is non-independence between quadrats measured at the same village.	Random effect	

Reasons for sub-model selection

EOO/breeding site models the same for comparison (i.e. do patterns of selection observed at breeding site scale also play out across breeding range scale? Do characteristics of breeding sites exist across breeding landscape or are they unique to breeding sites?).

Sub-models contrasting effects of variables hypothesised to be most influential on breeding site selection: elevation, slope and total broadleaf DBH. Sites with generally lower elevation, lower slope and higher broadleaf DBH hypothesised to be more likely to be breeding sites, so examining the effects of these variables in various combinations.

Nesting site models also contain extra variable, total *Cinnamomum* trees, as these are thought to be the most selected tree type for breeding by BCLT across most sites, so thought to affect 3rd order habitat selection.

Sub-models are again contrasting effects of variables hypothesised to have greatest influence on selection at this scale: elevation, slope, total DBH of broadleaf trees and total number of *Cinnamomum* trees. Sub-model 1 contains an interaction term between slope and the total DBH of broadleaf trees in the quadrat, to see if areas with less slope and larger trees are more likely to be chosen as nesting sites, and sub-model 2 contains an interaction between the total number of Cinnamomum trees and the total DBH of broadleaf trees in the quadrat, to see if the presence of these two variables are more likely to lead to nesting site selection.

Table S2. Leave-One-Out Cross Validation outputs for GLMMs. Shows the difference in Expected Log Pointwise Predictive Density (ELPD) and difference in Standard Error between candidate sub-models and full models.

	Breeding 1 (unsure = breeding)		Breeding 2* (unsure = control)		Breeding (2019 data)**		EOO***		Nesting****	
	ELPD Difference	SE Difference	ELPD Difference	SE Difference	ELPD Difference	SE Difference	ELPD Difference	SE Difference	ELPD Difference	SE Difference
brms_fit_ris	NA	NA	NA	NA	NA	NA	NA	NA	-1.9	0.8
brms_fit_ri	-0.2	0.1	-0.1	0.1	-0.3	0.1	-0.3	0.1	**0.0**	**0.0**
brms_fit_sub1	-0.1	0.1	0.0	0.1	**0.0**	**0.0**	**0.0**	**0.0**	-2.8	2.6
brms_fit_sub2	**0.0**	**0.0**	**0.0**	**0.0**	0.0	0.1	-0.2	0.1	-2.3	2.6
brms_fit_sub3	-0.1	0.1	-0.1	0.1	-0.1	0.1	-0.3	0.1	-1.6	2.6
brms_fit_sub4	-0.1	0.1	0.0	0.1	-0.1	0.0	-0.3	0.1	-18.1	6.7

*Breeding 2 model posterior predictive checks – R squared very high, 0.99, plots showed optimal model predicts well.

**Breeding 2019 model posterior predictive checks – R squared very high, 0.99, plots showed optimal model predicts well.

***EOO model posterior predictive checks – R squared very high, 0.99, plots showed optimal model predicts well.

****Nesting model posterior predictive checks – R squared low, 0.2, plots showed optimal model doesn't predict as well as breeding models.

Table S3. Generalised linear mixed model estimates and credible interval range (full models).

Selection scale:	**EOO/buffer**		**Breeding site/control**		**Nesting site/control**	
Covariate						
	Estimate (log odds)	**90% CI range (lower/upper)**	**Estimate (log odds)**	**90% CI range (lower/upper)**	**Estimate (log odds)**	**90% CI range (lower/upper)**
Intercept	**1.29**	**0.11 – 2.43**	-0.35	-1.55 – 0.84	**-3.84**	**-4.34 - -3.40**
Elevation	**-0.91**	**-1.62 - - 0.19**	-0.58	-1.28 – 0.12	-0.35	-0.77 – 0.05
Slope	-0.12	-0.67 – 0.42	-0.21	-0.78 – 0.35	**-0.49**	**-0.99 - -0.05**
Total broadleaf DBH	0.04	-0.45 – 0.56	0.08	-0.41 – 0.60	**0.77**	**0.53 – 1.02**
Other Forest %	0.02	-0.51 – 0.54	0.04	-0.50 – 0.54	**0.56**	**0.18 – 0.93**
Broadleaf Forest %	-0.01	-0.50 – 0.50	-0.00	-0.54 – 0.51	0.08	-0.30 – 0.45
Village/Town %	0.01	-0.51 – 0.53	0.03	-0.47 – 0.54	0.03	-0.34 – 0.38
Total Cinnamomum	-	-	-	-	0.12	-0.14 – 0.35
Village (random intercept)	**4.96**	**4.07 – 5.93**	**5.27**	**4.37 – 6.26**	**0.35**	**0.03 – 0.87**

Table S4. Generalised linear mixed model estimates and credible interval range (optimal models).

Selection scale:	**EOO/buffer**		**Breeding site/control**		**Nesting site/control**	
Covariate						
	Estimate (log odds)	**90% CI range (lower/upper)**	**Estimate (log odds)**	**90% CI range (lower/upper)**	**Estimate (log odds)**	**90% CI range (lower/upper)**
Intercept	**1.22**	**0.06 – 2.40**	-0.33	-1.46 – 0.80	**-3.84**	**-4.34 - -3.40**
Elevation	**-0.93**	**-1.75 - -0.07**	-0.60	-1.29 – 0.09	-0.35	-0.77 – 0.05
Slope	-	-	-	-	**-0.49**	**-0.99 - -0.05**
Total broadleaf DBH	0.05	-0.52 – 0.65	0.09	-0.37 – 0.58	**0.77**	**0.53 – 1.02**
Other Forest %	-	-	-	-	**0.56**	**0.18 – 0.93**
Broadleaf Forest %	-	-	-	-	0.08	-0.30 – 0.45
Village/Town %	-	-	-	-	0.03	-0.34 – 0.38
Total Cinnamomum	-	-	-	-	0.12	-0.14 – 0.35
Village (random intercept)					**0.35**	**0.03 – 0.87**

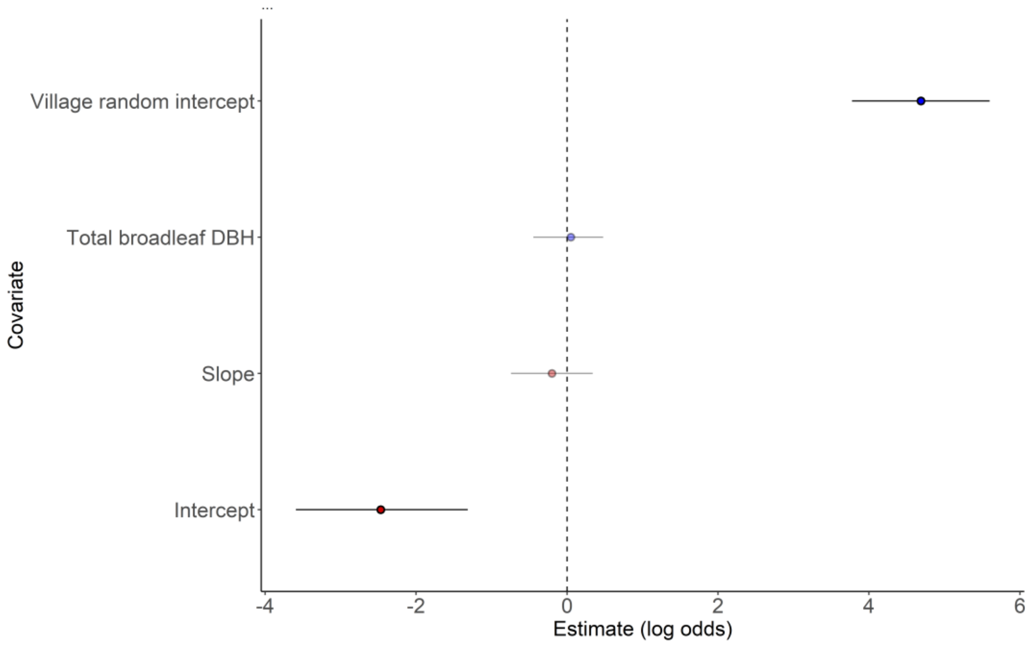


Figure S4. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each predictor, in relation to **whether a village was ever a breeding site (2nd order analysis; 2019 breeding sites only).** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to Blue-crowned Laughingthrush breeding sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays *submodel 1*.

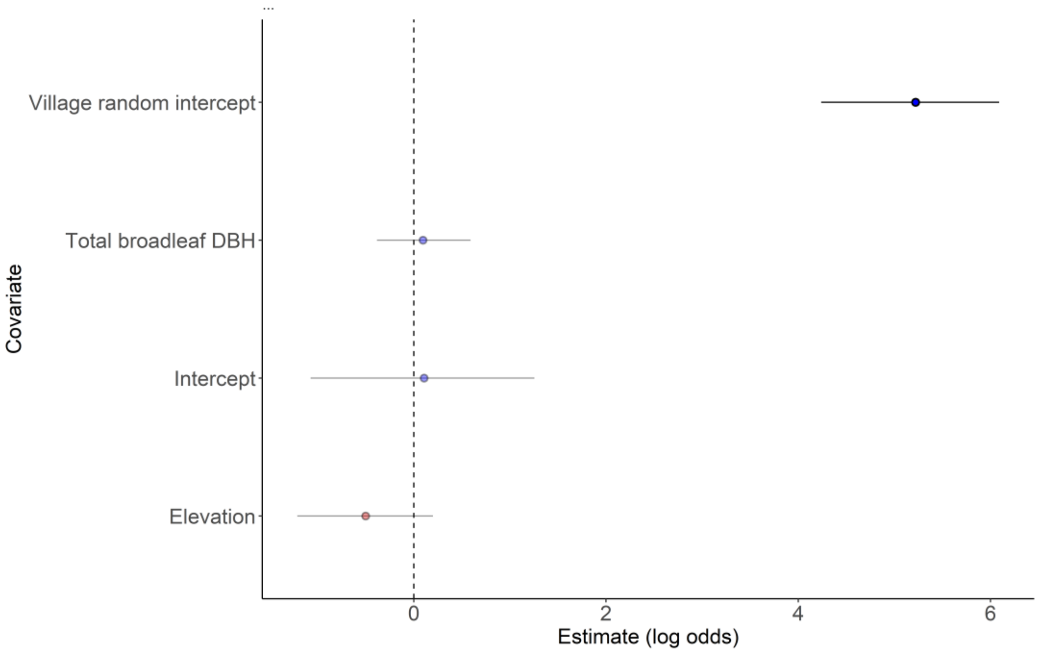


Figure S5. Interval plot showing the 90% credible intervals (CI), represented by the black lines, for the posterior distribution of each predictor, in relation to **whether a village was ever a breeding site (where the two villages where past breeding is unsure, are classed as breeding).** Coloured circles within each line represent the estimate. Predictor levels are considered significant if the CI does not encompass zero on the x axis. Predictors are considered to have a positive relationship to Blue-crowned Laughingthrush breeding sites if the CI is to the right of plot, and negative if they are to the left of the plot. Plot displays the optimal candidate model.

Table S5. Mean user's, producer's and balanced accuracy (%) of random forest supervised classification of eight land cover types.

	Broadleaf Forest	**Vegetable Garden**	**Other Forest**	**Tea**	**Rice Paddy**	**Bush / Scrub**	**Settlement / Road**	**Water**
User's accuracy	64.99	68.59	60.64	68.16	55.81	63.42	81.42	93.23
Producer's accuracy	64.29	56.54	60.38	65.69	66.44	58.15	90.42	95.32
Balanced accuracy	64.64	62.56	60.51	66.92	61.12	60.78	85.92	94.27

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6. Determinants of environmental range restriction in the Critically Endangered Blue-crowned Laughingthrush *Pterorhinus courtoisi* at the landscape scale

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6.1 Abstract

Species occurrence at the landscape scale is dependent on many environmental factors, and understanding those of primary importance in determining occurrence is critical to conservation planning. Species distribution models offer a means of understanding these factors, but provide more accurate answers when given more ecologically relevant and finer-scale habitat data, and when rigorously validated. The Blue-crowned Laughingthrush *Pterorhinus courtoisi* (BCLT) is a Critically Endangered, colonially breeding songbird. It is only known from a restricted area in an agricultural mosaic human-occupied landscape of Jiangxi Province, southeast China, with no obvious differences in landscape between the area within its range and surrounding regions. Here, we compare the outputs from 14 models: seven species distribution model algorithms (Random Forest, Generalised Linear Model, Boosted Regression Tree, Generalised Additive Model, Flexible Discriminant Analysis, Multiple Adaptive Regression Splines, and Maxent), two pseudo-absence methods and k-fold cross validation, to show that BCLT range is largely predicted by precipitation during the wettest month, and land cover. BCLT occurred in areas which are wetter at low elevation than surrounding areas, and with higher coverage of tea plantations. This distribution may be linked to the occurrence of non-crop vegetation or mature trees within tea fields in the study area. Such information should inform land management practices in the wider region. Pseudo-absence methods (convex hull and presence point based) gave varied outputs, with the finer scale method showing greater importance for land cover, highlighting the utility of comparing pseudo-absence methods. We also identify regions of potentially suitable habitat outside the known BCLT range that could be surveyed to look for unknown populations in

Anhui, Jiangxi and Zhejiang provinces. Our results provide the first evidence that the BCLT may be limited by both climate and land cover at the landscape scale.

Key words: species distribution modelling, China, bioclimate, land cover, *Pterorhinus courtoisi*

6.2 Introduction

Understanding the factors determining whether species have a restricted range can be challenging (Warren *et al.*, 2001; Angel *et al.*, 2006; Bladon *et al.*, 2018) because species occurrence can depend on a multitude of factors, such as biotic and abiotic environmental characteristics, climate, and anthropogenic influences (Donald *et al.*, 2012; Karunarathna *et al.*, 2017). Habitat availability is a key determinant of species recovery, affecting species at multiple spatial scales (Oppel *et al.*, 2004; Zhang *et al.*, 2010; Sawyer and Brashares, 2013). Understanding species distribution at the landscape scale (e.g. a species geographic range) is of particular importance as this enables the study of variables and ecological processes that act at coarser scales, such as climate (Elith and Leathwick, 2009; Gutiérrez, Snell and Bugmann, 2016), which may affect species differently to processes at finer scales (e.g. a home range or nest site). For example, habitat preference may be explained by topographical features for birds at the nest site scale, but climate and disturbance at the home range and landscape scale (López-López *et al.*, 2006); alternatively, species' ranges may be better explained by fine-scale climate variables at local scales (Gillingham *et al.*, 2012). It is important to know determinants of species' landscape-scale occurrence to guide spatial prioritisation for restoration (Adams *et al.*, 2016), species protection (Yang *et al.*, 2018) or land-use policy (Bladon *et al.*, 2018). Species Distribution Models (SDMs) are extrapolations of species distribution data in time and space, typically based on statistical models fitting associations between geographic species occurrences and sets of environmental predictors (Araujo & Guisan 2006). When fitted well, SDMs can give insight into environmental tolerances and preferences for species (Franklin 2009), and can be used for conservation planning and identifying suitable habitat for threatened species (Elith and Leathwick, 2009). However, due to fundamental underlying differences in model construction, different SDM algorithms can produce very different outputs which can affect inferences; it is therefore best practice to compare outputs from multiple model algorithms (Franklin 2009; Bladon *et al.*, 2018).

However, it is not just differences in model output that are a source of variation, but also the quality of the input information.

In particular, data for SDMs on threatened species often have very small sample sizes, which can constrain model performance depending on the SDM type used (Franklin 2009). Moreover, threatened species may lack appropriate absence data, supplying a further barrier to generating SDMs using some approaches. However, there is a paucity of studies comparing multiple SDMs using datasets with small numbers of occurrences and a broad range of land cover types, to allow us to determine the effectiveness or limitations of this approach to guide conservation planning. Most studies on threatened species utilise either a single SDM algorithm (Gillingham *et al.*, 2012; Adams *et al.*, 2016; Biddle *et al.*, 2021), and/or simple land cover data (Yang *et al.*, 2018; Biddle *et al.*, 2021). Furthermore, where no true absence data are available, many studies do not contrast the effects of alternate pseudoabsence generation methods on model outputs (Yang *et al.*, 2018; Miranda *et al.*, 2019). Studies combining these approaches would deliver more robust inferences on species distributions, which is paramount for understanding threatened species' environmental preferences or requirements.

The Blue-crowned Laughingthrush (BCLT) (*Pterorhinus courtoisi*) is a species of passerine with a highly restricted range (Extent of Occurrence) of 610 km^2, and is only known to breed in a small part of north-east Jiangxi Province, China (BirdLife International 2018). BCLT research to date has focussed on conducting censuses and understanding habitat requirements at individual breeding sites (He *et al.*, 2017; Zhang *et al.*, 2017; Huang *et al*., 2018; Liu *et al.*, 2020); indeed, no study has attempted to understand habitat characteristics regulating their range at a broader spatial scale. BCLTs are colonial and cooperative breeders, with colonies nesting both near and within villages occurring within a mixed mosaic agricultural landscape (Wilkinson *et al.*, 2004). As this habitat mosaic is at least superficially similar to surrounding human-occupied landscapes in southern China, it is unclear why the BCLT is not more widespread, as with other sympatric Laughingthrush species (MacKinnon and Phillips 2000). Human modification over past centuries has converted much of south China's original climax vegetation to cultivated land, plantation forest, or scrub (Elvin 2004; Coggins *et al.*, 2012; Su *et al.*, 2020). Moreover, it is likely that habitat change will show different patterns of forest or agricultural habitat composition and extent across different parts of southern China.

Additionally, areas of different climatic (precipitation, temperature) conditions may generate strong regional variation in biodiversity (Brown *et al.*, 2016). Small-scale studies at the local scale within Wuyuan County suggest that vegetable plots are declining, and these have been suggested to represent key BCLT foraging habitat (He *et al.*, 2017; Liu *et al.*, 2020). However, it is unknown if land types important to BCLT at a local scale show importance at larger spatial scales, or if previously unknown factors are equally important for BCLT distribution and subsequent conservation planning.

In this study, we explore why the known BCLT population is restricted to its current range in northern Jiangxi, by investigating whether this limited distribution is related to bioclimatic factors, topography, and the availability of certain land cover types, particularly different forest or agricultural land types, at the landscape scale. Many species distribution studies use limited sets of habitat/land cover types, for example where multiple forest or agriculture types are grouped into a single metric (Rose, Halstead and Fisher, 2020; Peng *et al.*, 2021). However, specific sub-types of habitat can affect species' ranges (Rocha *et al.*, 2018), and using simplistic or restricted land cover types can miss important patterns and nuance that might affect habitat suitability for a given species. For example, Bo *et al.* (2009) found Sichuan Partridges (*Arborophila rufipectus*) significantly preferred primary and older secondary broadleaf forest over degraded forests or scrub, which would be overlooked by a single forest metric. Creation of more complex metrics can be facilitated using high-resolution remote sensing data such as Landsat 8, Sentinel-2 and QuickBird, allowing classification of many specific habitat types (Laba *et al.*, 2008; Brinkhoff, Vardanega and Robson, 2020; Reuleaux *et al.*, 2020).

We conducted a comparison of seven SDMs: Random Forest (RF), Generalised Linear Model (GLM), Boosted Regression Tree (BRT), Generalised Additive Model (GAM), Flexible Discriminant Analysis (FDA), Multiple Adaptive Regression Splines (MARS), and Maximum Entropy (Maxent); enabled by the generation of pseudo-absence data. Models were based upon environmental variables including a novel land classification map that incorporated eight land cover types, derived from ground-truthed field data. Our aims were to (a) use SDM comparison to establish whether any environmental factors can be identified as limiting BCLT range at the landscape scale, and (b) indicate more precise locations for surveying subpopulations of breeding BCLT outside of their known breeding range. Our results also help more widely to refine methods used in determining the environmental factors associated with range restriction, for threatened species occurring in landscapes with complex habitats and where presence data are limited. This is done by contrasting both multiple SDM algorithms and pseudoabsence methods, and including a fine-scale, biologically relevant land cover map for our study species.

6.3 Methods

6.3.1 Study area

The core study area comprises locations where BCLT have occurred, in Wuyuan (29°14’53”N, 117°51’43”’E) and Dexing (28°55’50”N, 117°35’41”E) counties, Jiangxi Province, and Xiuning County (29°47’02”N, 118°11’38”E), Anhui Province. The core study area is located within the Changjiang Plain evergreen forest region (WWF Global 200 Ecoregion; Olsen *et al.*, 2001) with elevation ranging from 50 to 1,600m (Hong *et al.*, 2006; He *et al.*, 2017). Mean annual precipitation is 1330.3mm, with a mean temperature of 17.7°C (Liu *et al.*, 2020). The core of the BCLT range, Wuyuan County in northern Jiangxi Province, contains 48.0% subtropical broadleaf forest, most of which is secondary (He 1994; Hong *et al.*, 2006). The landscape is human-occupied and modified; Wuyuan County, for example has an area of 2,947.51km^2 (Shi 2017) and a population of 360,000 (He *et al.*, 2014). The area of the study extent is 65,097km^2 (**Figure 1**). This region was selected because it is significantly larger than the BCLT’s known range and should incorporate a range of climatic variables, but is small enough to be biologically relevant for a species with a small range. The BCLT’s breeding landscape is characterised by low, forested hills, and agricultural riverine valleys dominated by rice, oilseed rape and tea plantations. These are interspersed with small villages surrounded by vegetable plots (Richardson 2005; He *et al.*, 2017) and mature broadleaf or mixed forest stands known as *fengshui* forests (Coggins *et al.*, 2012), with BCLT frequently recorded to be nesting in the latter habitat type (Hong *et al*., 2003; Wilkinson *et al.*, 2004).

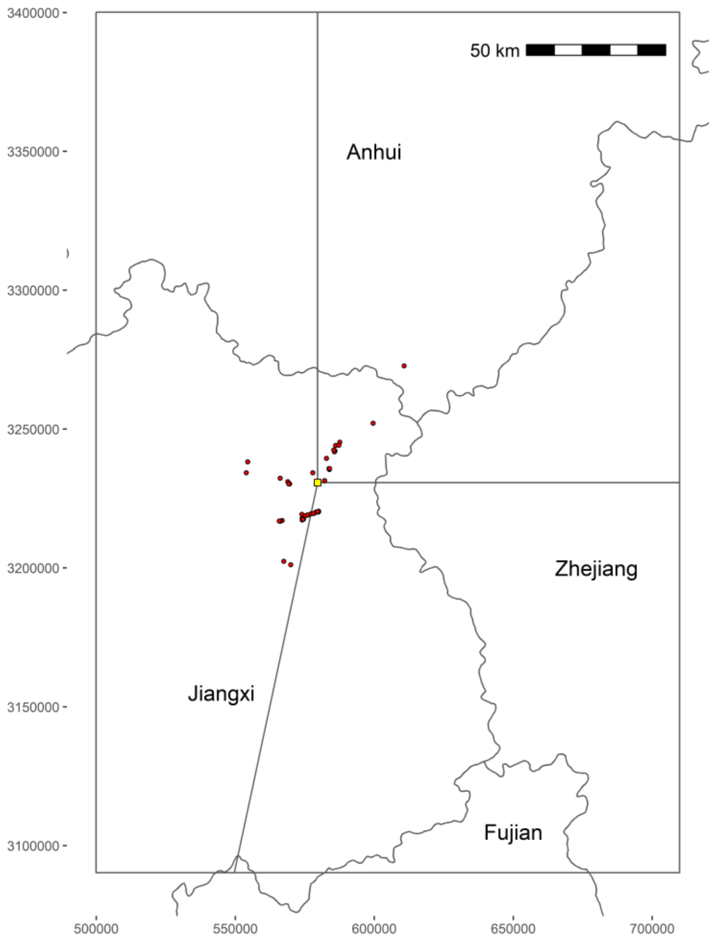


Figure 1. Range map for the Blue-crowned Laughingthrush, showing coordinates of all presence locations used for fitting species distribution models. Extent extends from 499910,709850 to 3090200,3400080 UTM (117.20, 118.50 to 28.50,29.80 lat/long). The rectangular box demarcates the area from which pseudo-absence locations were drawn for modelling, and for which current simulations were projected. The lines radiating from the Blue-crowned Laughingthrushes' range centre show the three segments of the map used for leave-one-out cross-validation of models. Provincial and county borders are plotted using the 'GADM' dataset available via the *raster* package in R (Hijmans and van Etten 2012). Not all presence points are visible as separate.

6.3.2 Image classification

6.3.2.1 *Ground-truthed data protocol*

Ground-truthed habitat data were collected in April-May 2019, when BCLT typically select breeding sites (Yu 2003; Zhang *et al.*, 2017), with any seasonal land cover types present during this period considered as potentially having an impact on BCLT presence. Fourteen land cover classes were used, based on forest and agricultural land types mentioned as being utilized by BCLT during the breeding season (He and Xi 2002; Richardson 2005; Hong *et al.*, 2006; Liao *et* *al.*, 2007, He *et al.*, 2017; Zhang *et al.*, 2017; Huang *et al*., 2018; Liu *et al*., 2020) Using QGIS, stretches of road were digitised as lines, and sample points were generated at random within a spatially constrained 100m buffer of the roads (Wohlfart *et al.,* 2016). Points were visited on foot using a GPS device and information recorded during field surveys is given in **Figure S1, Supplementary Information**. Points were assigned to one of 14 land cover classes (**Table S1, Supplementary Information**) until a minimum of 50 points per class was reached (except for orchards, where too few points were encountered, and the class was dropped) (Wegmann *et al.*, 2016). Of the 645 points sampled, following removal of incorrect points (n=8), a total of 637 survey points were suitable for inclusion in the classification procedure (**Field survey data cleaning protocol, Supplementary Information)**. The 14 land cover classes were merged into eight for ease of classifying at the 10 x 10m pixel scale (**Table S1, Supplementary Information**). The final eight land cover types classified were: broadleaf forest, vegetable plots, other forest, tea plantation, rice paddy, bush/scrub, settlement/road, and water.

6.3.2.2 *Classification procedure*

Atmospherically corrected Sentinel-2 Level-2A Surface Reflectance imagery (10 x 10m pixel resolution) were analysed within Google Earth Engine (Gorelick *et al.*, 2017), using the most cloud-free images available between the dates 1st February 2019 – 31st August 2019 that overlapped with both the known BCLT breeding range and surrounding landscapes in China. Prior to image analysis, cloud masks were applied using a function detecting probabilities of pixels being cloud, cloud shadow and snow. Supervised imagery classification (Wegmann *et al.*, 2016) was conducted using the random forest algorithm (Breiman, 2001). This machine learning algorithm builds multiple decision trees and merges these together to achieve a more stable and accurate prediction. Training points were taken from high-resolution Google Earth imagery from 2021, and checked against Sentinel-2 imagery from 2019 to ascertain if any land cover types had changed (e.g. from farmland to human settlement). Accuracy assessment was performed using validation points (n = 9,342, across eight Sentinel-2 tiles), taken from a combination of the ground-truthed GPS data and Google Earth imagery of a) villages visited during habitat surveys and b) other areas collected in the same manner as the training data. A confusion (validation) matrix was generated, and the producer's accuracy, user's accuracy and balanced accuracy for each land cover class were calculated, as well as the overall accuracy.

6.3.3 Presence and absence dataset

Our presence dataset for the BCLT were obtained from three different sources: a) official census datasets (n=21), b) opportunistic field observations (n=6), and c) eBird locations (n=41). The first census dataset was collected in 2000-2017 by Prof. Fenqi He of the Chinese Academy of Sciences, and the second was collected in 2012-2017 by Dr Weiwei Zhang of Jiangxi Agricultural University and her MSc students; all of these data are georeferenced to the scale of the nearest village as a minimum. Both census datasets are from Wuyuan and Dexing counties, northern Jiangxi Province. Model performance of SDMs is known to quickly decrease for sample sizes below 20 (Stockwell and Peterson, 2002), and thus boosting available presence data is necessary to improve accuracy. As a result, opportunistic field observations were obtained from the 2018 and 2019 BCLT breeding seasons and georeferenced BCLT location records given by eBird.org were collated alongside the official census data. The eBird.org observations were predominantly from within Wuyuan County, with a single sighting made in southern Anhui Province; all were made from 2008-2018, and all during the BCLT breeding season (April to June). All eBird sightings were included, as the BCLT is a highly distinctive species that is difficult to confuse with other local bird species. After removing duplicates using QGIS from identical 10 x 10m pixels we had 66 georeferenced BCLT records with sufficiently accurate metadata for inclusion in SDMs and were all from within the last 13 years.

As no reliable absence data were available for the BCLT, pseudo-absence points were generated via two methods: a) random points at least 10km outside a buffer region around a convex hull fitted around presences (‘convex hull method’); and b) random points at least 10km outside a buffer around each individual presence datum (‘presence point method’) (**Figure S2; Supplementary Information**). These pseudo-absence points were taken from within the study extent (**Figure 1**). A total of 5,000 pseudo-absence points were generated for each method. Both methods were used to compare to one another, as potential biases exist for either method; as the presence point method gives more precise divisions between presence and pseudo-absence landscapes, this allowed a finer-scale understanding of environmental predictors of BCLT occurrence within the study area (**Figure S2b; Supplementary Information)**.

6.3.4 Environmental dataset

Administrative provincial and county boundaries were downloaded from WorldMap (available at http://worldmap.harvard.edu/chinamap/; Guan *et al.*, 2012). Bioclimate variables were obtained from the Worldclim global climate database (http://www.worldclim.org/) (Hijmans *et al.*, 2005). To avoid model overfitting, multicollinearity was checked between the 19 Worldclim variables (Parra, Graham and Freile, 2004) as follows. Raster layers were clipped to the study extent in QGIS, and 2,000 random points were generated in a shapefile of the same extent. Values were extracted from each raster layer using the 'Point Sampling Tool' plugin, which were then saved to CSV format. These data were checked for collinearity within the *corrplot* package in R (Wei and Simko 2017). Variables were excluded that had a coefficient of correlation >0.7 (Green 1979) but did not have relevance to the BCLT breeding season. As including higher numbers of predictors can lead to misleading correlations, it is better practice to identify a small number of predictors which are likely to have relevance to the study species (Pearce-Higgins and Green 2014). Four bioclimate variables were selected that were not strongly intercorrelated (**Figure S3 and S4, Supplementary Information**), with most of these selected variables chosen to represent bioclimatic conditions during the BCLT breeding season (Yu 2003; Zhang *et al.*, 2017; Liu *et al.*, 2020).

Elevation data were extracted from NASA Shuttle Radar Topography Mission (SRTM) Digital Elevation imagery at a resolution of 1 arc-second (approximately 30m) using Google Earth Engine (Gorelick *et al.*, 2017). Imagery was clipped to the appropriate spatial extent. Normalised Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) data were generated from Sentinel-2 imagery Level-2A Surface Reflectance imagery, also using Google Earth Engine. All images used had a cloudy pixel percentage of <5.00% (0.06-4.93%) and dated from between 1st February 2019 and 31st August 2019, aiming to represent the BCLT breeding season. Prior to image analysis, cloud masks were applied using a function detecting probabilities of pixels being cloud, cloud shadow or snow, and NVDI was then calculated from the data. The Google Earth Engine code for this function is available under **Supplementary Information**. Additional pre-processing was avoided due to the likelihood of introducing unnecessary biases to the data (Young *et al.*, 2017). A total of eight environmental variables were selected for modelling: elevation, land cover, NDVI, EVI, isothermality (BIO3), mean temperature of the wettest quarter (BIO8), mean temperature of the driest quarter (BIO9) and precipitation of the wettest month (BIO13) (**Table S2, Supplementary Information**).

6.3.5 Species Distribution Modelling

Environmental rasters were re-projected to UTM zone 50 and extended to the same geographic extent (the study extent, **Figure 1**), using NA values to fill in any gaps, in R version 4.1.2 (R Core Team 2021). All eight environmental rasters were extended to the same resolution (10 x 10m), using the NDVI raster as the reference layer to reduce computation/processing time. All datasets were then re-extended to ensure they were not influenced by sampling, and were written as GTiff files.

The geographical distribution of the BCLT was related to the eight environmental variables by fitting SDMs to the presence and pseudoabsence data using the *biomod2* package (Thuiller *et al.*, 2009) in R version 4.1.2 (R Core Team 2021). Seven model algorithms were used: RF, GLM, BRT, GAM, FDA, MARS, and Maxent. The ability of each model to predict the BCLT's range was assessed using a k-fold partitioning cross-validation method, with radial partitions (k=3) to avoid spatial autocorrelation, fitting each model three times and leaving data out from one segment each time. Partitions were generated from the centre of the BCLT's range, based on the mean of the x and y coordinates of all recorded BCLT locations (**Figure 1**). Three partitions were chosen to ensure that occurrences were still high enough per segment (minimum n=20) to ensure robust model testing, as shown in **Figure 1**. Occurrences were balanced per segment such that each contained close to identical numbers of occurrences (n=20/23/23). Pseudo-absences (NAs) were converted to true absences (0s) for k-fold analyses, as *biomod2* is unable to code pseudo-absences into evaluation data. Model performance was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (Fielding & Bell 1997). Further details are provided in **Methods used to model geographical distribution in relation to environmental predictor variables, Supplementary Information**.

To assess variable importance, the two best-fitting model algorithms were selected for each pseudo-absence method, determined by k-fold cross-validation AUC scores greater than 0.7. These models were re-fitted using k-fold cross validation, with each variable of interest dropped in turn and with new AUC scores calculated for each model. The ΔAUC was calculated for each variable, by subtracting the k-fold AUC for each model with the variables of interest progressively removed, from the maximal k-fold model with all variables included (Bladon *et al.*, 2018). To visualise variable importance, ΔAUC values were plotted against one another for the two best performing model algorithms, for each pseudo-absence method. To map predicted BCLT occurrence, simulated distributions for the BCLT under each algorithm were compared with their known breeding season range map, using all available data.

6.4 Results

6.4.1 Image classification

Land cover classification distinguished types across the eight Sentinel-2 images with moderate overall accuracy (overall mean: 69.82%), with 72.34% and 64.84% accuracy in distinguishing types of broadleaf and 'other' forested pixels, respectively; and similar accuracy for distinguishing bush/scrub and agriculture (vegetable plot, rice paddy, tea) pixels (57.72–66.88%; **Table S3, Supplementary Information**). Land cover classification had the highest accuracy for settlement/road and water (84.54% and 95.54%, respectively) (**Table S3, Supplementary Information).**

6.4.2 Species Distribution Modelling

The FDA algorithm performed best for both pseudo-absence sampling methods according to the AUC scores from k-fold cross-validation (convex hull based sampling = 0.821, presence point based sampling = 0.852; **Table 1**). The second-best performing algorithms were Maxent (AUC = 0.798, presence point method) and GLM (AUC = 0.797, convex hull method) (**Table 1**). As expected, AUC scores were much higher when all available data were used to fit each model than when data were partitioned for the k-fold analysis (**Table 1**). Overall, differences between pseudo-absence methods were much smaller when all available data were used (AUC = 0.001 - -0.002), and larger during k-fold analyses (AUC = -0.109 – 0.138) (**Table 1**). There were also only slight differences between the upper and lower CIs of AUC values for full data models fitted with either pseudo-absence selection method (**Figure S5, Supplementary Information**).

Table 1. Blue-crowned Laughingthrush SDM AUC scores for all variables, with all presence/pseudo-absence data included and also using segmented k-fold models. The two best model algorithms for each pseudo-absence method, as identified by k-fold analysis, are highlighted in bold.

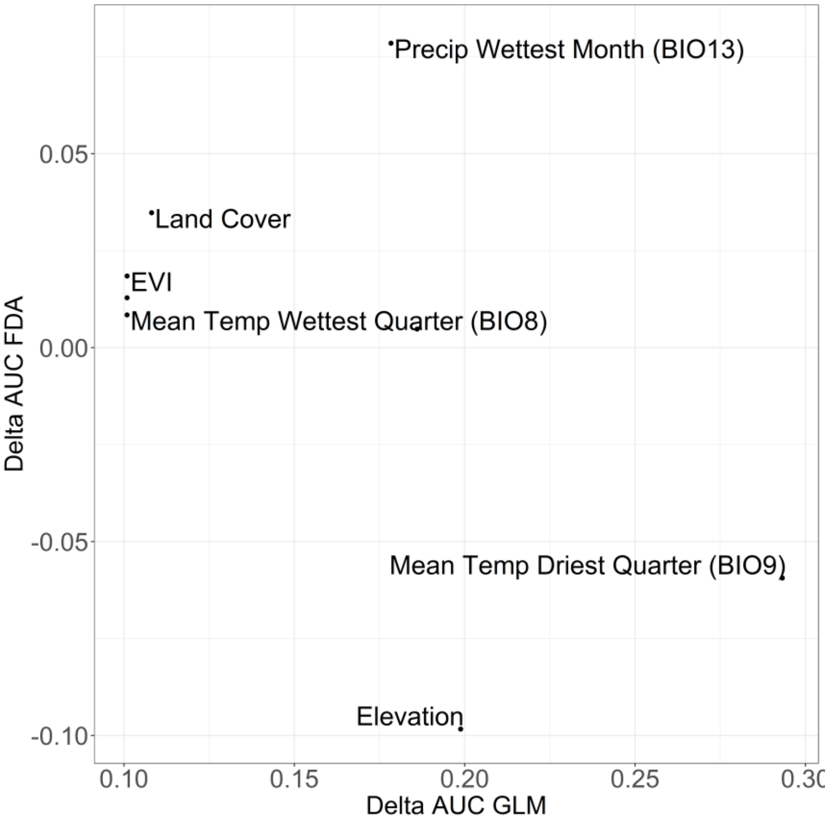
Model	All predictors convex hull-based pseudo-absence method (all data)	All predictors convex hull method (k-fold)	All predictors presence-point based pseudo-absence method (all data)	All predictors presence point method (k-fold)
RF	1.000	0.658	1.000	0.639
GLM	0.983	**0.797**	0.982	0.659
GBM	0.997	0.675	0.997	0.633
GAM	0.999	0.681	0.999	0.790
FDA	0.966	**0.821**	0.966	**0.852**
MARS	0.986	0.757	0.988	0.750
Maxent	0.976	0.796	0.974	**0.798**

Models containing precipitation of the wettest month (BIO13) and land cover gave the highest ΔAUC scores, using both convex hull and presence point based pseudo-absence methods, according to best-performing k-fold cross-validated algorithm (FDA; **Figure 2**). For the next best-ranking model algorithms, the most important variables were mean temperature of the driest quarter (BIO9) and elevation, using the convex hull pseudoabsence method (GLM; **Figure 2a**); however, the most important variables were land cover and precipitation of the wettest month (BIO8) using the presence point pseudoabsence method (Maxent; **Figure 2b**). Based on the FDA and GLM algorithms, the least important variables in the convex hull models were mean temperature of the wettest quarter (BIO8) and NDVI, and the least important variables (lowest ΔAUC) in the presence point models were NDVI, EVI, BIO3, BIO13 and BIO9 (**Figure 2**).

Modelled probability of BCLT occurrence against rainfall during the wettest month (BIO13) in the FDA and GLM models, using the convex hull method, shows a relatively narrow occurrence range of 275-310mm. This range has a sharp peak of occurrence at 300mm and decline above 310mm (**Figure 3a**), tending to be wetter than surrounding regions. Modelled probability of BCLT occurrence against land cover in the FDA model, using both the convex hull and presence point methods, shows a small peak in predicted occurrence for tea plantation (**Figure 3**). The GLM algorithm indicated a decrease in predicted occurrence over water (**Figure 3a**). All algorithms predicted equal probabilities of occurrence across all other land cover types. Although a less important variable in the models, elevation showed the highest predicted occurrence between 0-300m for both pseudo-absence methods using model algorithms MARS and Maxent, although there was no drop in predicted occurrence for higher elevations with the FDA models (**Figure 3**).

In the best models (Maxent, GLM), areas of high habitat suitability occur in Wuyuan, Dexing and Fuliang counties (Jiangxi Province); also, Kaihua and Changshan counties (Zhejiang Province), and Xiuning and Qimen counties (Anhui Province) showed high suitability according to MARS (**Figure 4**). Model projections are unavailable for the FDA models. The BRT model algorithm, though it performed less well, also predicts similar regions to Maxent, GLM and MARS to be suitable. Conversely, other model algorithms (RF and GAM) predict very little suitable habitat, without overlapping (and therefore not predicting) the known BCLT range. However, generally, there was a relatively small area of high predicted occurrences across the suite of model algorithms, compared to the size of the study area.

(a)



(b)

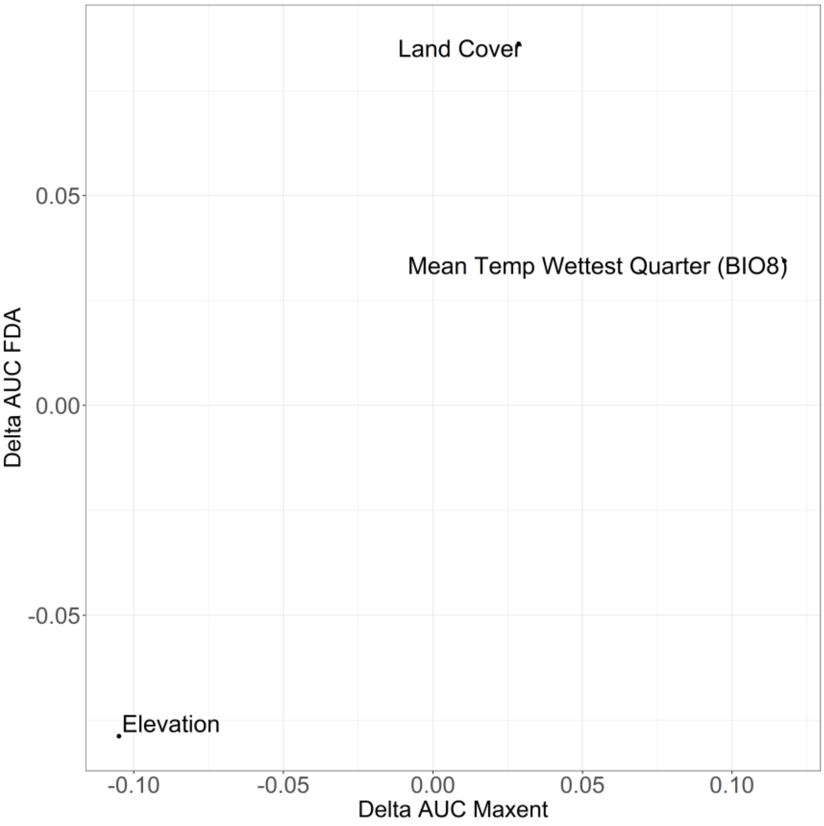


Figure 2. Delta AUC scores for each variable from the two best-fitting model algorithms based on k-fold analysis AUC scores, for (a) convex hull method models, and (b) presence point method models. Each point represents one of the bioclimatic predictor variables used in the models.

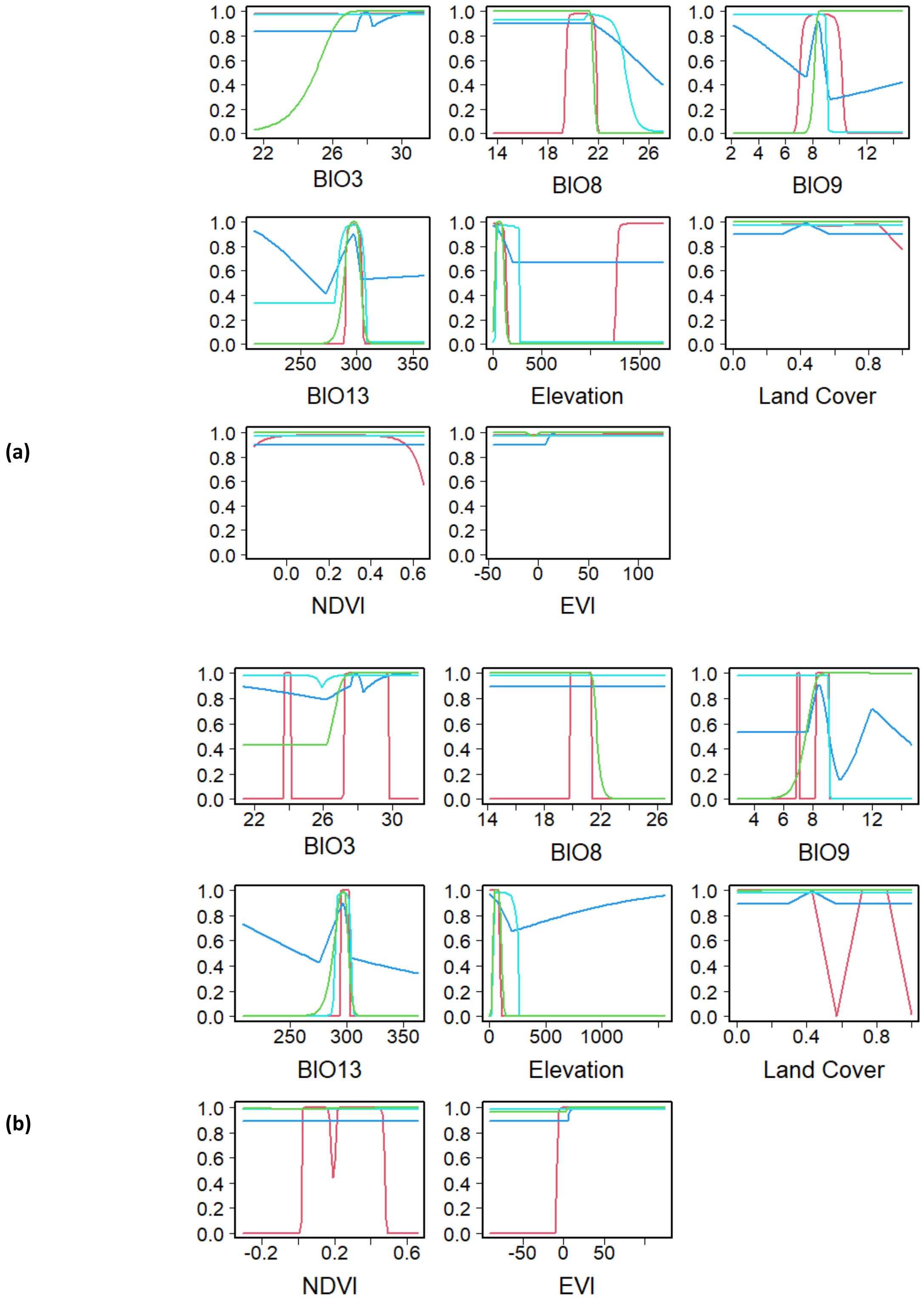
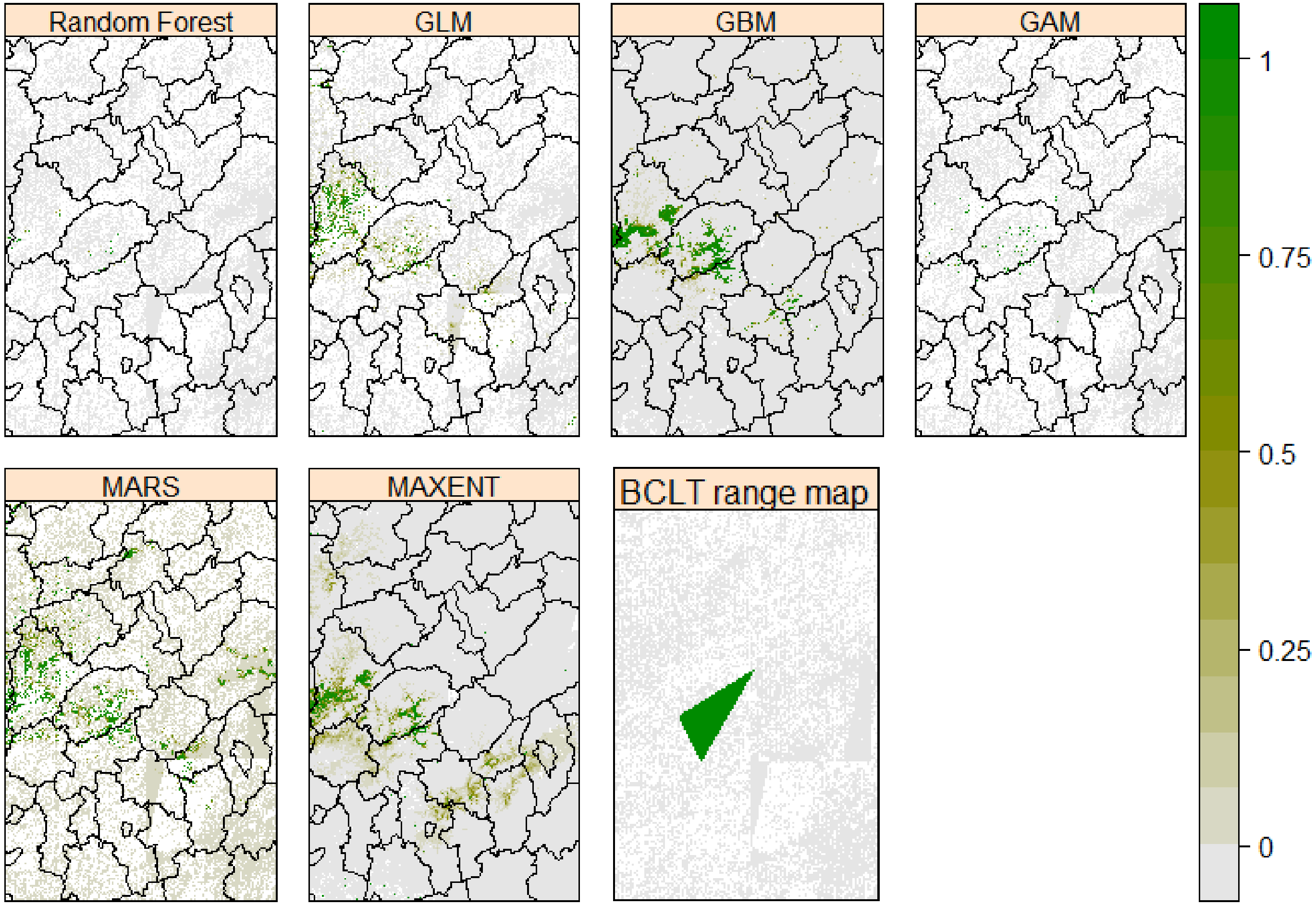


Figure 3. Response curves of Blue-crowned Laughingthrush occurrence records to each variable, using (a) the convex hull method, and (b) presence point method. FDA = blue, GLM = red, Maxent = green, MARS = turquoise. Land cover values correspond as follows: **broadleaf forest = 0.00, vegetable garden = 0.14, other forest = 0.28, tea plantation = 0.42, rice paddy = 0.57, bush/scrub = 0.71, settlement/road = 0.85, water = 1.00**. Values are decimals due to the raster conversion process.

(a)


Random Forest
GLM
GBM
GAM
MARS
MAXENT
BCLT range map
1
0.75
0.5
0.25
0

(b)

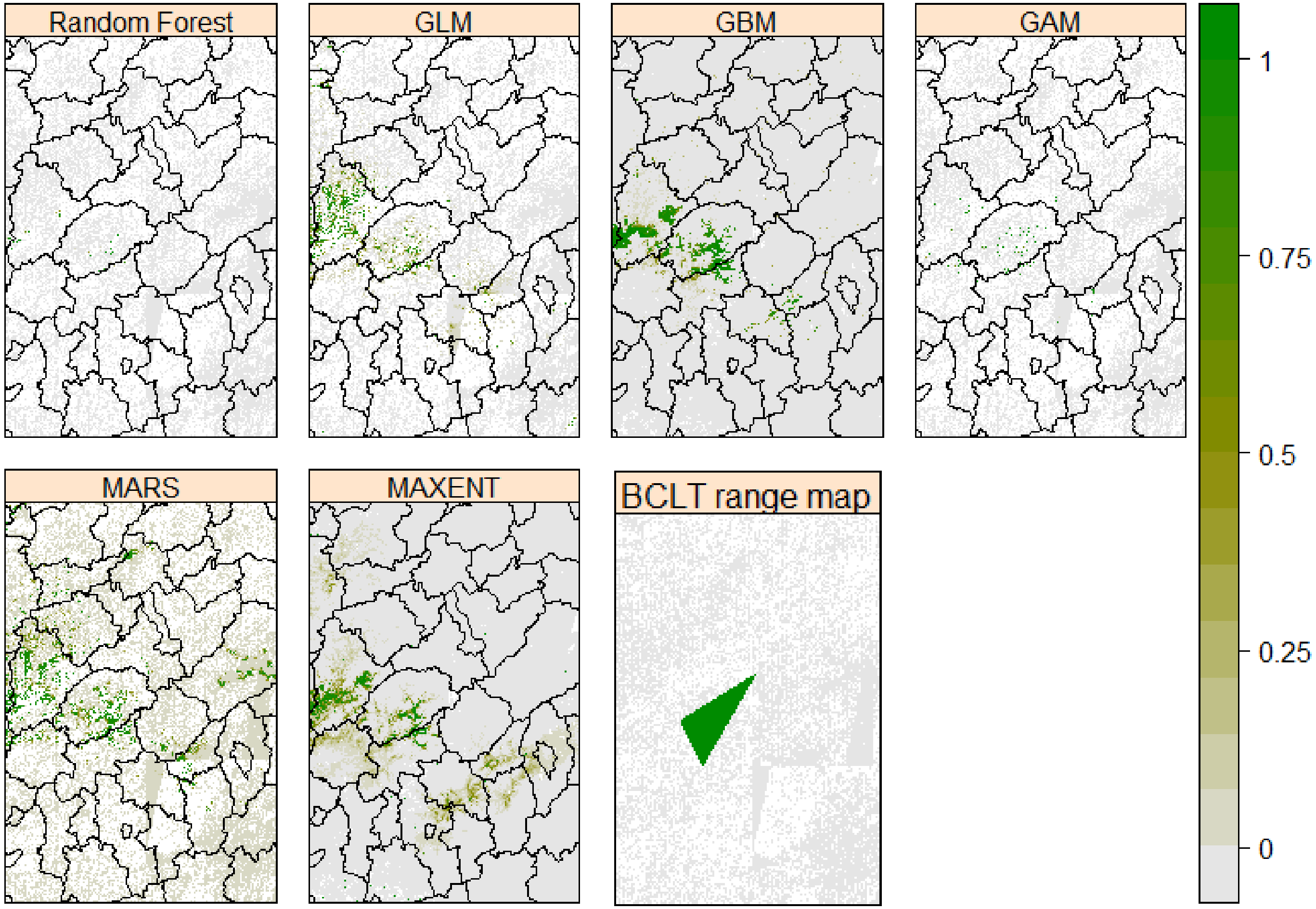


Figure 4. Projections for all model algorithms using (a) the convex hull based method and (b) presence point based method. Projections are unavailable for the FDA models

6.5 Discussion

In studying species distributions, many studies use single model algorithms, or land cover maps with single forest or agriculture type metrics, which may misrepresent species' study landscapes. Equally, studies reliant on pseudoabsence data typically generate such data through a single method (Warren *et al.*, 2021). Our findings support the use of combining multiple SDM algorithms, different pseudo-absence generation methods, and land cover maps with sufficiently high complexity for the study species (Reuleaux *et al.*, 2020), with these maps produced with the study species' habitat associations in mind. In our study, comparing seven model algorithms and using eight land cover types, the restricted global range of the Blue-crowned Laughingthrush is described predominantly by precipitation of the wettest month, land cover and mean temperature of the wettest quarter. We also show that where true absences are missing, contrasting different methods of generating pseudoabsences can show alternate patterns in models. For example, land cover is considered of higher importance when using a higher-resolution pseudo-absence approach, giving greater significance to the BCLT's higher predicted probability of occurrence where there is more tea plantation.

BCLT are predicted to occur in areas that are generally wetter (during the wettest month) than surrounding areas; and in areas that tend to be cooler (during the wettest quarter) than surrounding areas. The wettest month in Jiangxi is typically June (Climate-Data.org), the peak of the BCLT breeding season (April-August) (Zhang *et al.*, 2017), suggesting the BCLT is affected by precipitation and temperature during the breeding season. This may suggest that the BCLT's breeding range is at least partially restricted by climate, both by rainfall and temperature during the breeding season, which could be linked to food availability (Brambilla *et al.*, 2018), nest sites, incubation and provisioning (Schöll and Hille, 2020; van de Ven *et al.*, 2020).

BCLT are also predicted to occur in areas with greater tea plantation land cover than surrounding regions, within our study area. This may be because tea plantations often have large trees and other vegetation dispersed around and within them, notably at several BCLT breeding sites (**Chapter 3**; **Figure S6, Supplementary Information**). Moreover, tea plantations containing mature trees are also present more generally in the surrounding landscape, particularly in Wuyuan County (R. Gleave, pers. obs**.**), suggesting their importance to BCLT conservation. However, this was not supported by the BCLT's relationship to forest land cover types: there was no higher prediction of occurrence in areas with more broadleaf forest. This may be because *fengshui* forest and other broadleaf forests were combined into a single landcover metric, which therefore does not distinguish areas of large, mature trees over younger secondary growth. This shows some similarities with the BCLT's closest relative: Yellow-throated Laughingthrushes (*Pterorhinus galbanus*) occupy habitats with tall grassland, scrub and secondary mixed forest (Collar and Robson 2007), thus also tolerate more open habitats than closed-canopy forest. These results also highlight the potential importance of including granular or fine-scale land cover data within SDMs, derived from both ground-truthed data and high-resolution imagery. This is particularly the case in highly human-modified landscapes with a complex range of distinct natural and anthropogenic land cover types (Frolking *et al.*, 1999). Notably, land cover was the most important variable in the presence-based pseudo-absence method models, possibly reflecting the finer scale differences in occurrence across the study landscape this method was able to identify.

These results are based upon the outputs of seven model algorithms, two methods for generating pseudo-absences, and k-fold cross validation. They are, therefore, substantially more robust than the single SDM output from **Chapter 3**, which used a single model algorithm, presence-only data, a less complex land cover map, and lacked k-fold cross-validation. As expected, model performance varied, with four model algorithms scoring an AUC of over 7.0, and three below 7.0. Projections also displayed inter-model variability (Figure 4), potentially generating ambiguity over potential locations for BCLT searches. Ensemble forecasting could present a future approach to generating a more consistent signal from across model algorithms. The use of pseudoabsence data enabled the comparison of seven model algorithms; using only presence data would restrict how many model types we could use (Elith and Leathwick, 2009; Araújo *et al.*, 2019). In this previous model, precipitation during the wettest month was also identified as an important predictor of BCLT distribution, but this model identified elevation as the most important predictor. Elevation is considered a key factor in determining BCLT range (Hong *et al.*, 2003; Wilkinson *et al.*, 2004; **Chapter 5**), which is not supported by its lack of importance in our analysis. However, a relationship with elevation may only exist at smaller spatial scales, as habitat selection can be highly scale dependent (Sawyer and Brashares, 2013; Fattebert *et al.*, 2018). Similarly, we also expected a stronger relationship between BCLT predicted occurrence and vegetable gardens, which were perceived to be increasing at BCLT breeding sites (**Chapter 4**), and are used disproportionately to other habitats except woodland by breeding BCLT (Liu *et al.*, 2020). However, this may be because vegetable gardens are only important at smaller spatial scales, or because they were harder to distinguish from other land cover types than tea (**Table S3, Supplementary Information**).

This study looks only at the landscape scale: this is one key piece of a wider puzzle. At the landscape scale, we can detect the influence of factors acting at coarser scales, such as climate, which may be less detectable at finer scales (Elith and Leathwick, 2009; Ewers *et al.*, 2011). Hence, our predictors were variables displaying patterns at coarser landscape scales, such as patterns in NDVI, bioclimate and land cover, as opposed to tree species and sizes, or understorey vegetation, which would be expected to vary and influence distribution at finer scales (Mellanby *et al.*, 2008). Our approach highlighted unexpected bioclimatic and habitat associations at this scale, with both climate and land cover (specifically tea) influencing BCLT occurrence. These are driven by different processes: in China, land cover is chiefly driven by anthropogenic factors, while regional climate is less so. However, our results have potential implications for future synergistic effects of human-induced climate and land cover changes.

Our findings have important implications for future BCLT searches and wider conservation. One of four best-fitting model algorithms, MARS (>0.7 AUC for both pseudoabsence methods), predicted high likelihood of BCLT occurrence in Wuyuan, Dexing and Fuliang counties (Jiangxi Province), Kaihua and Changshan counties (Zhejiang Province), and Xiuning and Qimen counties (Anhui Province). This is important because BCLT are not known to occur in many of these areas, with occurrence records only obtained to date from Wuyuan, Dexing and Xiuning counties. We suggest that data on precipitation during the wettest month and relative amounts of tea plantation, along with habitat data at smaller spatial scales (**Chapter 5**), could be used in targeting specific regions to search for isolated populations which may continue to survive outside the species' known distribution. However, we recognise that BCLT range could also be limited by direct human impacts such as overexploitation, which could not be included within our environmental models (Yang *et al.*, 2018). Future work for the BCLT could build upon this study by conducting structured surveys of potential BCLT habitat based on the above model predictions, and including true absences from these new data. It could also widen the study area, especially to the west and south where further areas of predicted suitability may yet occur. Other future studies could examine correlations between climate data such as rainfall and ambient temperature patterns to BCLT population monitoring and/or breeding success.

We recommend gaining a better understanding of why tea plantations are important to BCLT at the landscape scale, given these are human-modified, and not strictly 'natural', landscape features. This may be due to the practice of having mature trees in and around this habitat type in this region of China, and if so, this could inform future land management practice in the wider region. In support of this theory, woodland and shrubs were the most utilised habitat types at BCLT breeding sites (Liu *et al.*, 2020), BCLT preferred breeding in tall trees surrounded by high herb coverage (Huang *et al.,* 2018) and the importance of non-crop vegetation for bird diversity has been demonstrated in other parts of southern China (Li *et al.*, 2020). Additionally, in Fujian Province, a bird survey found 82 bird species occurring in tea plantations, many of which typically forage in forests, with higher diversity in plantations interspersed with semi-natural habitats and forest fragments (Imboma *et al.*, 2020). Similarly, forest windbreaks were shown to maintain bird diversity in a tea dominated landscape in India (Sreekar *et al.*, 2013). As tea (*Camellia sinensis*) was originally a forest species, occurring where forests used to be, and is subject to mild disturbance regimes with tea shrubs remaining in place for long time periods (Imboma *et al.*, 2020), it may possibly act as an understorey plant where sufficient natural vegetation is in close proximity. Furthermore, isolated mature trees are argued to be important keystone structures across open, human-modified landscapes (Manning et al. 2006) and have been shown to support more biodiversity than open areas without scattered trees (Prevedello et al. 2017).

This study, although conducted with as much rigour as possible, still has some limitations that must be considered. Despite our overall robust methods, especially regarding validation and approaches for reducing spatial autocorrelation, our model outputs are ultimately dependent on the limited data that are available for the BCLT. SDMs are built on the assumption that sample data cover the species' full ecological range (Sánchez-Fernández, Lobo and Hernández-Manrique, 2011), and our outputs would therefore be biased if the BCLT does not occupy its full realised niche. Predicted BCLT range and its explanatory variables may also depend on the data available within a given time frame, as when past or historical records are also available for species distribution modelling, these may predict very different ecological niches should the species have previously occupied a wider area (Chatterjee, Tse and Turvey, 2012; Turvey *et al.*, 2020). For example, the ranges of many threatened species, such as Chinese pangolin (*Manis pentadactyla*), have changed over time, with more recent distributions confined to mountainous areas in response to human activity (Yang *et al.*, 2018). Other threatened species do not occupy representative areas of their full historical range, instead occupying marginal or peripheral habitat as 'refugee' species (Channell and Lomollno, 2000; Cromsigt, Kerley and Kowalczyk, 2012), including others in China (Turvey, Crees and Di Fonzo, 2015; Kerley *et al.*, 2020). If historical records were available for the BCLT, their predicted distribution and the importance of different predictors could drastically change (Nüchel *et al.*, 2018). Alternatively, LEK interviews could be conducted in regions of high predicted occurrence to validate model findings (Chen *et al.*, 2018).

Despite our efforts to collect BCLT occurrence data from a range of different sources, our dataset contained <70 presence locations, and no reliable true absences were available. However, this is the case for many threatened species (Turvey *et al.*, 2020; Biddle *et al.*, 2021; Bladon *et al.*, 2021), and high accuracy has been observed for models built on sample sizes as low as 25 records (Hernandez *et al.*, 2006), as well as for species with spatially restricted ranges (Elith *et al.*, 2006). Furthermore, although our use of radial segments aimed to minimise spatial autocorrelation by separating training from test data, an approach that will reduce spatial autocorrelation compared to cross-validation based on random sampling (Pearce-Higgins and Green, 2014), most available BCLT location records are close to the centre of their current range and so some remained close together. In addition, pseudo-absences were converted to true absences for k-fold cross-validation, which could affect model outputs. However, we are reasonably confident that BCLT are unlikely to breed outside of their current known breeding range, because surveys for breeding BCLT actively seeking new colonies have taken place annually since 2000, and have covered parts of Anhui and Zhejiang provinces in the past (F. He, 2019, personal communication).

Our data suggest that the BCLT is likely in-part restricted by a combination of precipitation and temperature during its breeding season, and by the presence or absence of tea plantation, which may be related to non-crop habitat features found within this agricultural land type. Research to explore whether these habitat features are important for future landscape management to benefit the BCLT is recommended. Surveys are now required to see if breeding or other populations persist in areas predicted as highly suitable by our best performing models. Our study shows that incorporating high-resolution, fine-scale habitat maps in agricultural mosaics can reveal new habitat associations for threatened species, and that when lacking true absence data for SDMs, contrasting pseudoabsence methods can emphasise different relationships between a species and its environment, giving greater insight into future conservation management.

6.6 References

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Supplementary Information

Figure S1. Example field survey sheet used to collect ground-truthed data for remote sensing image classification.

Field Survey – May 2019

Date:

Location: Wuyuan – Qiukouzhen route

Object measures						
Land cover type	1	2	3	4	5	6
	7	8	9	10	11	12
	13	14				
Homogeneity	Dense	Sparse	Open	None		

Conditions					
Clouds	High	Medium	Low	None	
Rain	High	Medium	Low	None	
Accessibility	Easy	Difficult	None		
Temperature (◦C)					

Comments

Land cover key:

1 – Conifer tree forest

2 – Broadleaf forest

3 – Bamboo forest

4 – Mixed forest

5 – Mature broadleaf forest/tree

6 – Bush / scrub

7 – Rice paddy

8 – Tea plantation

9 – Vegetable plot

10 – Oilseed rape

11 – Village or town

12 – Road

13 – Orchard

14 – Water

Table S1. Land cover categories, their definitions, and quantities of data points per category from a field survey in May 2019. Data collected are intended to classify remote sensing imagery.

Land cover number	Land cover type	Definition	Number data points collected (pre-cleaning)	Number data points collected (post-cleaning)	New land cover number	New land cover type
1	Conifer forest	>80% conifer trees (either fir, pine or both)	52	52	2	Other forest
2	Broadleaf forest	>80% broadleaf trees	51	50	0	Broadleaf forest
3	Bamboo forest	>80% *Phyllostachys heterocycla* bamboo	51	51	2	Other forest
4	Mixed forest	Mix of broadleaf/conifer, broadleaf/bamboo or conifer/bamboo	47	47	2	Other forest
5	Mature broadleaf forest/tree	Single tree or tree stand composed of over 50% broadleaf trees with DBH of approx. >30cm	50	48	0	Broadleaf forest
6	Bush/scrub	Wild habitat with few/no trees, typically characterised by dense stands of elephant grass and/or *Pleioblastus amarus.* Lack of canopy	50	66	5	Bush/scrub
7	Rice paddy	-	50	54	4	Rice paddy
8	Tea plantation	-	50	49	3	Tea plantation
9	Vegetable plot	-	50	49	1	Vegetable plot
10	Oilseed rape	Oilseed rape either in flower or during harvest	53	49	4	Rice paddy
11	Human settlement	Any area of human settlement, characterised by the use of concrete on the ground	44	42	6	Settlement/road
12	Road	Either minor concrete road or tarmac highway	22	32	6	Settlement/road
13	Orchard	Orchard of any tree species, such as *Camellia japonica*	4	6	NA	NA
14	Water	Rivers, streams, lakes, ponds	52	42	7	Water
-	NA or indeterminate	Indeterminate class	19	NA	NA	NA

Field survey data cleaning protocol

In addition to the pre-cleaning classes given in **Table S1**, seven points were classed as 'NA' and 12 were indeterminate (one of two) classes. Less than 50 points of class four were initially collected, and seven points of indeterminate class 4/6 were also collected. All data then underwent checking and cleaning within QGIS, checking point accuracy against a Google Satellite map layer. Inaccurate points were deleted (n=8) or the type re-classified where it was easy and clear to do so (e.g. the point was classed as village but was actually falling on a water pixel).

Less than 50 points of classes 11 and 12 were initially collected as planned to merge the two classes. These were first merged to 12 classes (converted orchards to bush/scrub, and merged settlement with road). Then, points of indeterminate class (n=12) were converted to a single class, including points of either mixed forest or bush/scrub (4/6), which were converted to bush/scrub, and two other indeterminate points which were converted to class six.

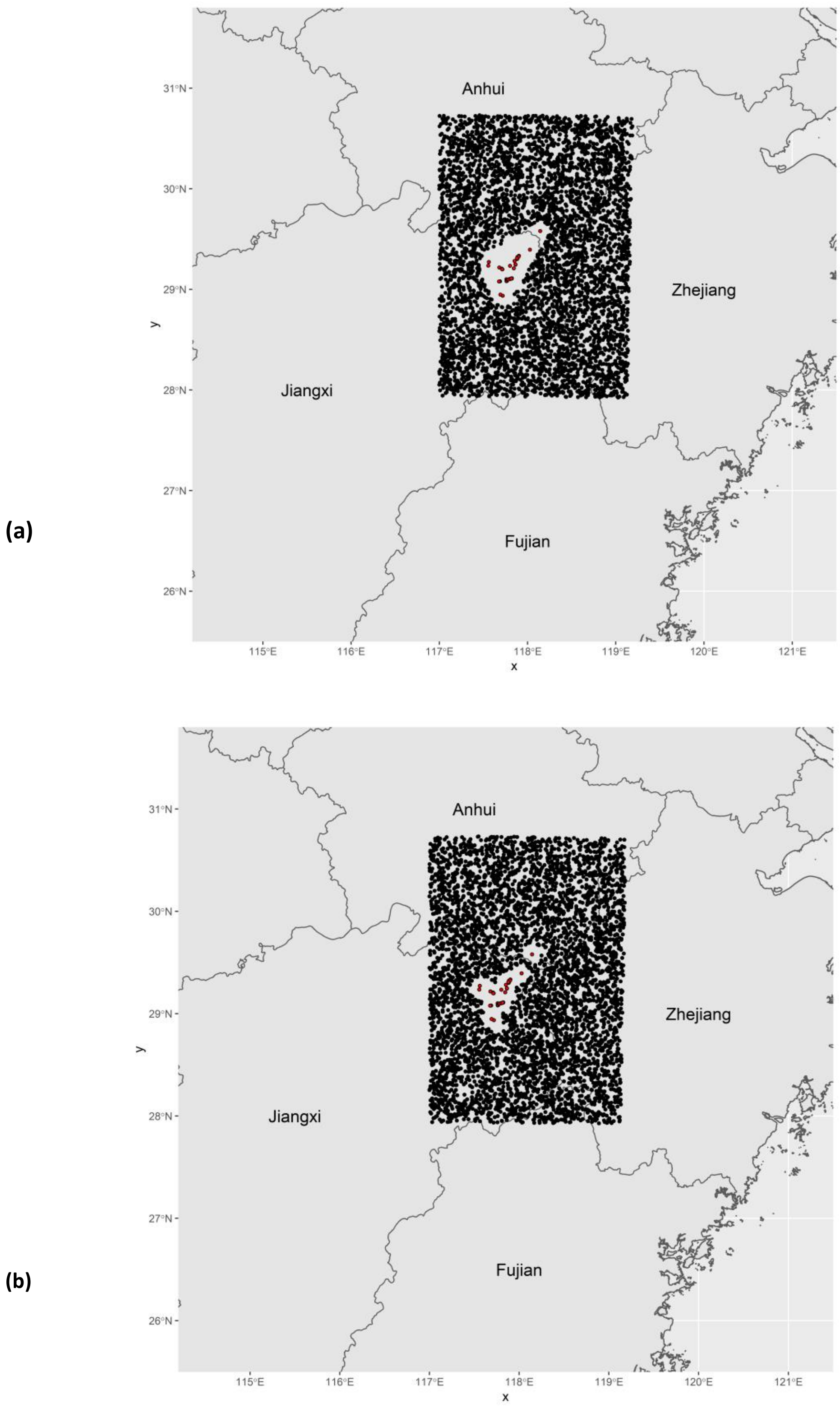
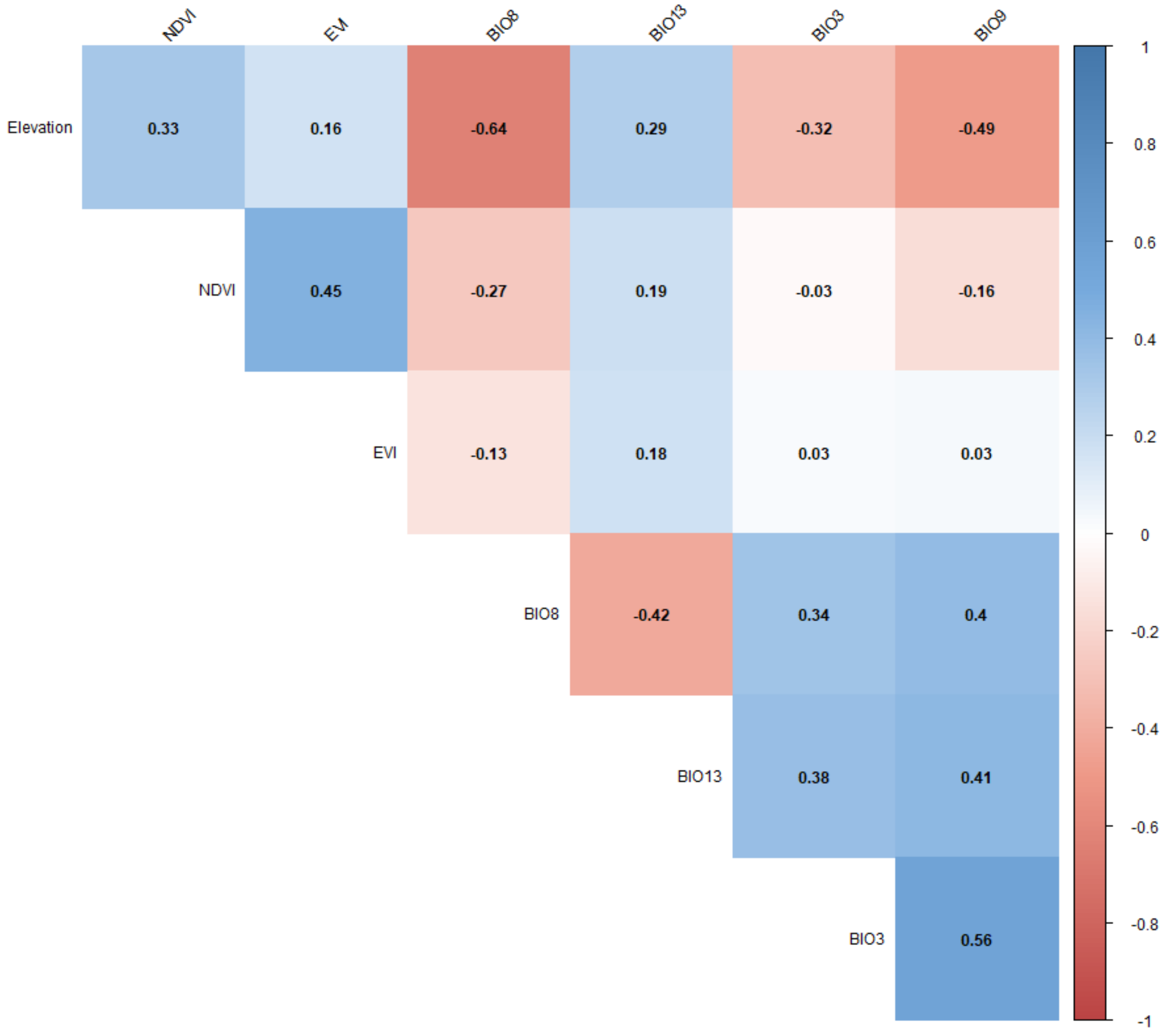
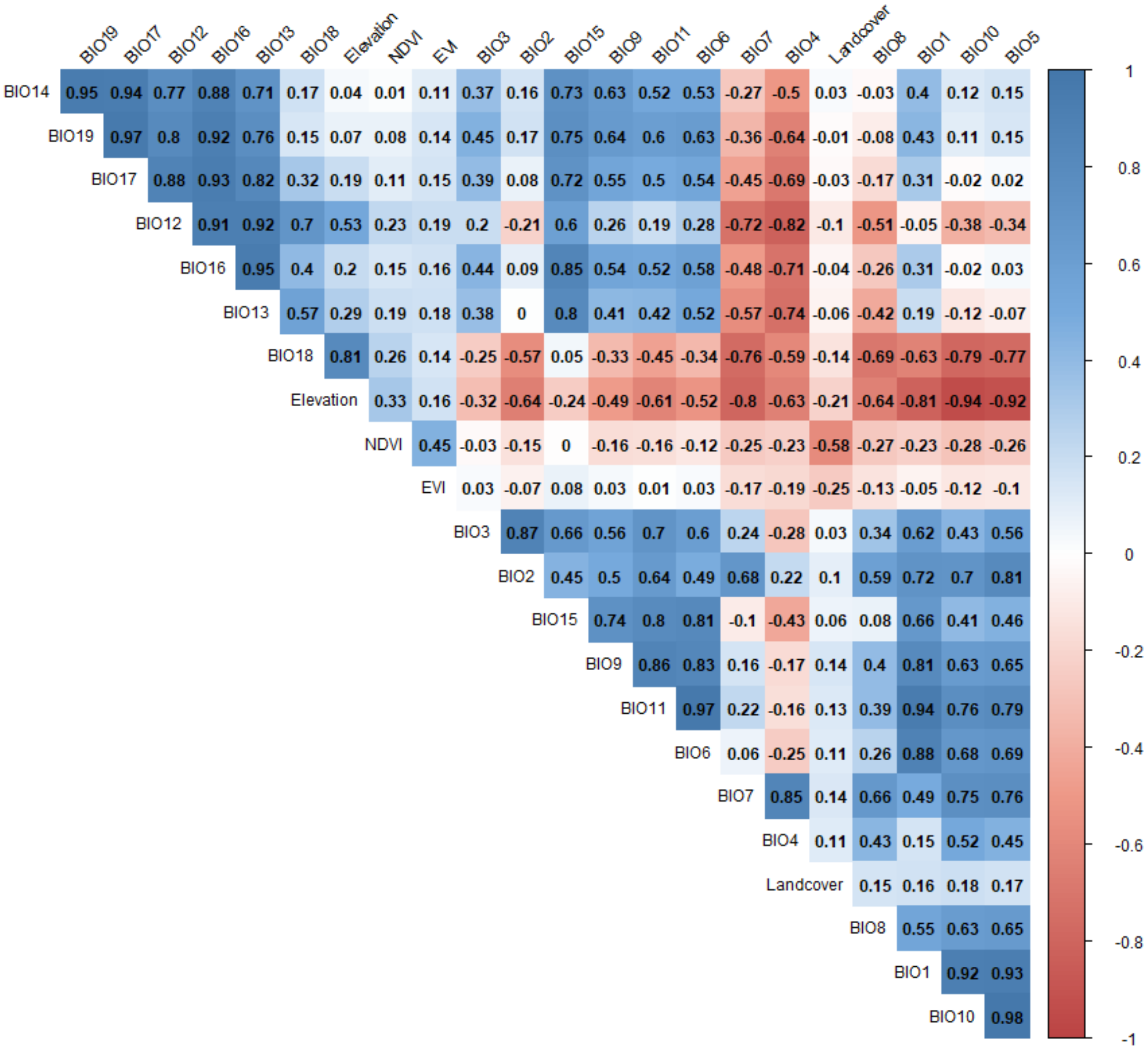


Figure S2. Methods of generating pseudo-absence points (two types of buffer): (a) convex hull based and (b) presence point based.



	NDVI	EVI	BIO8	BIO13	BIO3	BIO9
Elevation	0.33	0.16	-0.64	0.29	-0.32	-0.49
NDVI		0.45	-0.27	0.19	-0.03	-0.16
EVI			-0.13	0.18	0.03	0.03
BIO8				-0.42	0.34	0.4
BIO13					0.38	0.41
BIO3						0.56

Figure S3. Correlation plot of the final numerical environmental variables chosen for inclusion in the species distribution model. Land cover is excluded as it is categorical.



	BIO19	BIO17	BIO12	BIO16	BIO13	BIO18	Elevation	NDVI	EVI	BIO3	BIO2	BIO15	BIO9	BIO11	BIO6	BIO7	BIO4	Landcover	BIO8	BIO1	BIO10	BIO5
BIO14	0.95	0.94	0.77	0.88	0.71	0.17	0.04	0.01	0.11	0.37	0.16	0.73	0.63	0.52	0.53	-0.27	-0.5	0.03	-0.03	0.4	0.12	0.15
BIO19		0.97	0.8	0.92	0.76	0.15	0.07	0.08	0.14	0.45	0.17	0.75	0.64	0.6	0.63	-0.36	-0.64	-0.01	-0.08	0.43	0.11	0.15
BIO17			0.88	0.93	0.82	0.32	0.19	0.11	0.15	0.39	0.08	0.72	0.55	0.5	0.54	-0.45	-0.69	-0.03	-0.17	0.31	-0.02	0.02
BIO12				0.91	0.92	0.7	0.53	0.23	0.19	0.2	-0.21	0.6	0.26	0.19	0.28	-0.72	-0.82	-0.1	-0.51	-0.05	-0.38	-0.34
BIO16					0.95	0.4	0.2	0.15	0.16	0.44	0.09	0.85	0.54	0.52	0.58	-0.48	-0.71	-0.04	-0.26	0.31	-0.02	0.03
BIO13						0.57	0.29	0.19	0.18	0.38	0	0.8	0.41	0.42	0.52	-0.57	-0.74	-0.06	-0.42	0.19	-0.12	-0.07
BIO18							0.81	0.26	0.14	-0.25	-0.57	0.05	-0.33	-0.45	-0.34	-0.76	-0.59	-0.14	-0.69	-0.63	-0.79	-0.77
Elevation								0.33	0.16	-0.32	-0.64	-0.24	-0.49	-0.61	-0.52	-0.8	-0.63	-0.21	-0.64	-0.81	-0.94	-0.92
NDVI									0.45	-0.03	-0.15	0	-0.16	-0.16	-0.12	-0.25	-0.23	-0.58	-0.27	-0.23	-0.28	-0.26
EVI										0.03	-0.07	0.08	0.03	0.01	0.03	-0.17	-0.19	-0.25	-0.13	-0.05	-0.12	-0.1
BIO3											0.87	0.66	0.56	0.7	0.6	0.24	-0.28	0.03	0.34	0.62	0.43	0.56
BIO2												0.45	0.5	0.64	0.49	0.68	0.22	0.1	0.59	0.72	0.7	0.81
BIO15													0.74	0.8	0.81	-0.1	-0.43	0.06	0.08	0.66	0.41	0.46
BIO9														0.86	0.83	0.16	-0.17	0.14	0.4	0.81	0.63	0.65
BIO11															0.97	0.22	-0.16	0.13	0.39	0.94	0.76	0.79
BIO6																0.06	-0.25	0.11	0.26	0.88	0.68	0.69
BIO7																	0.85	0.14	0.66	0.49	0.75	0.76
BIO4																		0.11	0.43	0.15	0.52	0.45
Landcover																			0.15	0.16	0.18	0.17
BIO8																				0.55	0.63	0.65
BIO1																					0.92	0.93
BIO10																						0.98

Figure S4. Correlation plot of all environmental variables considered for inclusion in the species distribution models.

Link to Google Earth Engine code:

https://code.earthengine.google.com/28d94edb30cdb7451c3550cee111a2d2

Table S2. Environmental predictor variables included in the species distribution model.

Environmental variable	**Variable meaning**	**Variable source**	**Reason for inclusion**
Elevation	Elevation in metres	Google Earth Engine (via USGS SRTM)	Low elevation has been linked to BCLT breeding sites (Hong *et al.* 2004, Wilkinson *et al.* 2004)
Land cover	Classification of Sentinel-2 imagery into eight land cover types: broadleaf forest, vegetable plot, other forest, tea plantation, rice paddy, bush/scrub, settlement/road, water	Google Earth Engine (via Sentinel-2)	Different habitat have been linked to BCLT foraging (Richardson 2005; Hong *et al.* 2006; Liao *et al.* 2007; He *et al.* 2017; Liu *et al.* 2020)
NDVI	Normalised Difference Vegetation Index: quantifies vegetation greenness	Google Earth Engine (via Sentinel-2)	NDVI may indicate different types of vegetation associated with BCLT occurrence
EVI	Enhanced Vegetation Index: as NDVI, but corrects for some atmospheric conditions, and is more sensitive in areas with dense vegetation	Google Earth Engine (via Sentinel-2)	Study region is subtropical with dense vegetation, so may be particularly suitable for identifying areas associated with BCLT occurrence
BIO3	**Isothermality** quantifies how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations	WordClim.org	Variable is not intercorrelated with others and may affect BCLT distribution
BIO8	Mean temperature wettest quarter (°C)	WordClim.org	Wettest quarter is during BCLT breeding season (Yu 2003; Zhang *et al.* 2017)
BIO9	Mean temperature driest quarter (°C)	WordClim.org	Variable is not intercorrelated with others and may affect BCLT distribution
BIO13	Precipitation of wettest month (mm)	WordClim.org	Wettest month is during BCLT breeding season (Yu 2003; Zhang *et al.*, 2017)

Methods used to model geographical distribution in relation to environmental predictor variables

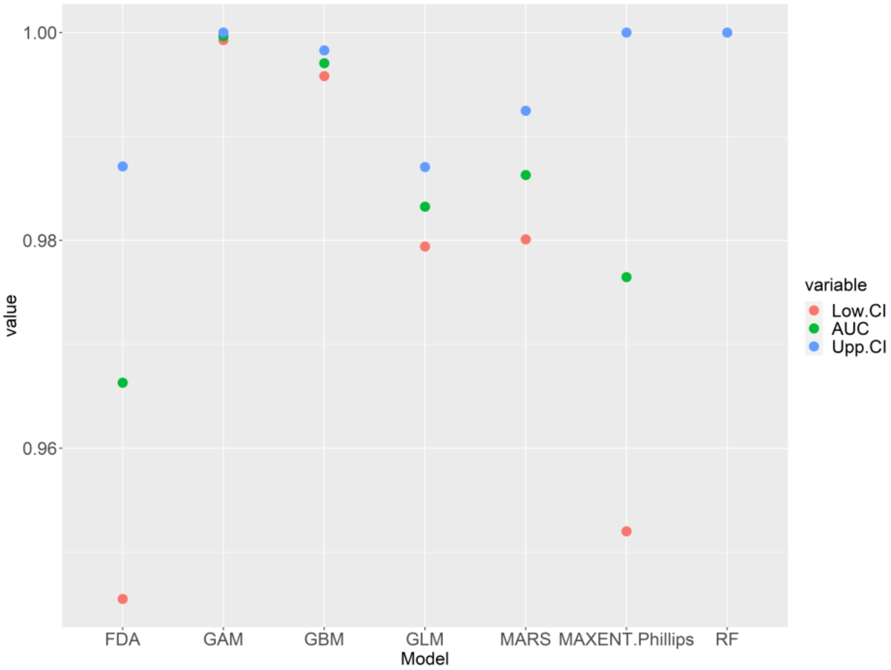
Creating robust evaluations of SDM prediction are best assessed through independent data (Fielding and Bell 1997). As we had only one set of presence data for the BCLT, we used *k*-fold partitioning as a cross-validation procedure, where data are divided into *k* subsets. Typical methods partition at random, however this overlooks the potential for spatial autocorrelation between points, which inflate model performance estimates (Pearce-Higgins and Green 2014).

We assessed model performance by linking observed presence/absence at each sampled point with its predicted probability of occurrence, calculated with the model version missing the specific data segment containing the observed point. These outputs were used to calculate the AUC of the ROC plot (Hanley and McNeil 1982). AUC was used as it provides a measure of prediction accuracy that is independent of a single threshold, as this would require continuous probabilities to be converted to a binary presence/absence score, and threshold-dependent measures are sensitive to species prevalence (Franklin 2009). Kappa and True Skill Statistic (TSS) are alternative model evaluation measures; however these are both threshold-dependent measures and are sensitive to species prevalence within a sample (McPherson *et al.*, 2004; Allouche *et al.*, 2006). AUC values of 0.7-0.9 are considered moderate model performance, and >0.9 are considered high (Manel *et al.*, 2001). Each modelling technique's ability to predict the BCLT range was assessed through comparison of their AUC scores.

Table S3. Mean user's, producer's and balanced accuracy (%) of random forest supervised classification of eight land cover types.

	Broadleaf Forest	Vegetable Garden	Other Forest	Tea	Rice Paddy	Bush / Scrub	Settlement / Road	Water
User's accuracy	70.29	67.28	65.92	73.36	58.50	58.63	84.40	95.57
Producer's accuracy	74.40	66.48	63.77	69.57	60.55	56.80	84.68	95.52
Balanced accuracy	72.34	66.88	64.84	71.46	59.52	57.72	84.54	95.54

(a)



(b)

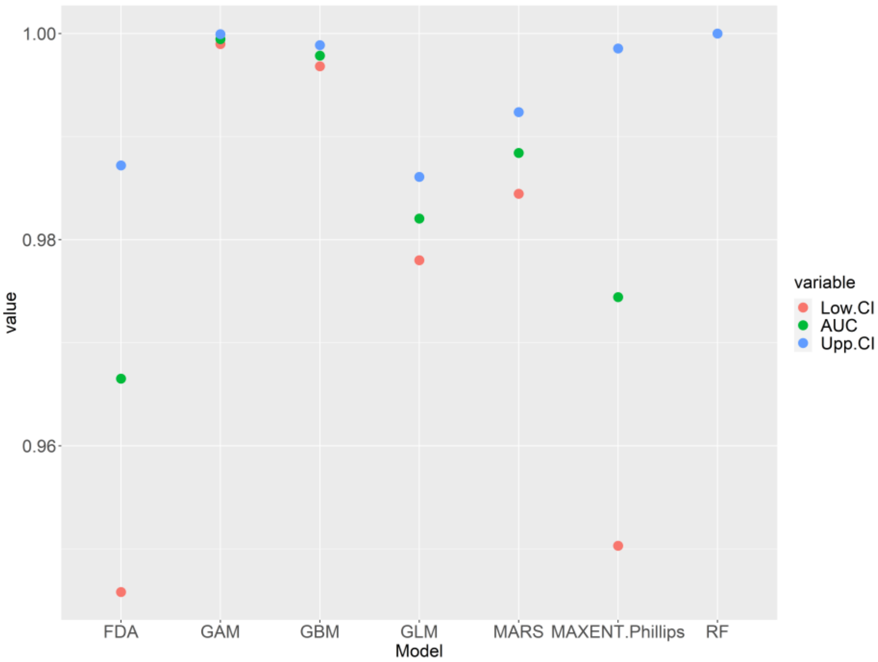


Figure S5. AUC estimates with 95% CIs, from models using all data. (a) convex hull-based method and (b) presence point based method.

Figure S6. Tea plantations surrounded by mature trees and other non-crop vegetation at Blue-crowned Laughingthrush breeding sites and other sites in Wuyuan and Xiuning counties.

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7. Discussion

Globally, restricted ranges are an important indicator of threat to species, and it is crucial to understand why species have small geographic ranges before relevant conservation actions can be designed and applied (Williams, Balmford and Wilcove, 2020). For threatened species, however, data may be limited, hampering efforts to understand the reasons behind a restricted range (Chen *et al.*, 2018; Biddle *et al.*, 2021; Segal *et al.*, 2021). This thesis adds to the understanding of diverse drivers behind species' restricted ranges, and further develops techniques to disentangle the complexities of these drivers in the face of limited existing data and few presence locations. It brings together varied approaches, in the form of habitat surveys, social surveys and remote sensing data to tackle the pressing question of: why is the Blue-crowned Laughingthrush restricted to a small region of China? And, can we identify additional areas for further conservation research and action? Gaining a better understanding of this single species will have ramifications for other species in their local region, threatened species across China, and will add to the evidence base of approaches for other global threatened species (Turvey *et al.*, 2013; Archer *et al.*, 2020). Additionally, and unexpectedly, this study demonstrated the importance of bringing sources of data together; this shed greater light on how and why a species is range restricted, as well as its true population size. This important step (**Chapter 3**) benefited all subsequent chapters in terms of the number of confirmed breeding sites (**Chapters 4** and **5**) and availability of locality data for SDMs (**Chapters 3** and **6**).

7.1 Red List Status

A given species' Red List status depends upon information on its population and range size, population trend, and threats (IUCN, 2012). Since 2007, the Blue-crowned Laughingthrush has been listed as Critically Endangered on the IUCN Red List (Birdlife International 2018a). However, the findings from my research have brought together diverse sources of information on the Blue-crowned Laughingthrush for the first time, giving us the opportunity to review this threat status. In **Chapter 3**, bringing together independent census datasets showed the Blue-crowned Laughingthrushes' population was larger than previously believed, and analysis of the population incorporating all breeding sites showed a recent increasing population trend. However, I also demonstrated the recent threat of trapping affecting the Jiangxi Blue-crowned Laughingthrush population, and possibly loss of habitat (**Chapter 4**). This has conflicting implications for its probable Red List status, with the Jiangxi population both larger and under greater threat than previously assumed. The Blue-crowned Laughingthrushes' Red List status as Critically Endangered is based on criterion C2a(i,ii) and justified by its 'very small, fragmented known range and an extremely small known population which is likely to be declining owing to a number of threats' (BirdLife International 2018a). However, the assessment also states that 'further survey effort may reveal additional sub-populations, in which case it may warrant downlisting' (BirdLife International 2018a)**.** As more sub-populations or breeding sites have been discovered, this could potentially meet this requirement. Similar situations have occurred for other threatened species, for example the Ludwig's Bustard (*Neotis ludwigii*) in southern Africa, where no decline over two decades was detected however mortality due to powerline collisions was high (Shaw *et al.*, 2016, 2018). This species ultimately retained its Endangered status (criterion A4cd) justified by the expansion of the existing threat and lack of successful mitigation measures (BirdLife International 2018b). My findings have implications for other threatened and Red Listed species, by showing the importance of integrating and reassessing existing data sources to better understand population dynamics. My research also further demonstrates the use of LEK as a data source to better understand threats (Turvey *et al.*, 2014) which may have a bearing on Red List assessments. Such threat assessments are sensitive to spatial and temporal scales of decline, which can give contrasting information to help understand species status.

7.2 The importance of comparing spatial and temporal information

Biotic and abiotic factors can influence the distribution and range size of any species, but as these influences and their magnitude can vary over spatial and temporal scales, it is vital to study these separately and make comparisons. For example, habitat selection can be a multi-scale process with some scales showing higher importance than others (Jedlikowski *et al.*, 2016). To this end, I strove to use consistent measures (such as land cover classes, elevation) between scales (**Chapters 4, 5, 6**), except where these needed simplifying for technical reasons (**Chapter 6**). **Chapters 3, 5** and **6** all looked at habitat and environmental influences at a static snapshot in time, finding differences in habitat associations between the landscape, breeding site and nesting site scales. This work is only one of four studies looking systematically at Blue-crowned Laughingthrush habitat use (Zhang *et al.*, 2017; Huang *et al.*, 2018; Liu *et al.*, 2020)**,** contrasts both breeding and nesting sites, and is the only to look at landscape scale effects.

However, **Chapter 4** differs by looking back in time over the last 50 or so years, at perceived changes to local landscapes, enabled by the collection of LEK data. Typically, studies using LEK aim to better understand where a species is, and how that is affected by human demographic characteristics (Pan *et al.*, 2016; Zanvo *et al.*, 2020). However, this study differs by using established, previously known breeding sites and related this to local perceptions of Blue-crowned Laughingthrush awareness, landscape change and threats. Moreover, this study is the first LEK dataset for the Blue-crowned Laughingthrush, giving us information on its range outside of the breeding season, potential new breeding sites, recent threats, and changes to the landscape associated with sites where they do and do not breed. Strikingly, two new potential breeding sites were revealed by local people, who reported past Blue-crowned Laughingthrush nesting behaviour in large trees at their villages. Moreover, both breeding sites were near locations reported by eBird, however neither have yet been investigated further. In addition, LEK showed regions (such as Xiuning County, Anhui Province) where Blue-crowned Laughingthrushes had been seen during the breeding season and within the last five years, but where very recent bird trapping activity had also been reported, suggesting an area with high potential for conservation interventions. Overall, my findings give further evidence for the importance of investigating across spatial and temporal scales for range restriction. However, these findings need combining to assess how they contribute to the restricted range of the Blue-crowned Laughingthrush.

7.3 Range restriction in the Blue-crowned Laughingthrush

Evidence at the landscape scale indicates the Blue-crowned Laughingthrush range is shaped by temperature, precipitation during their breeding season (at the wettest part of the year), and land cover, which is consistent between our two SDM approaches (**Chapter 3** and **Chapter 6**). However, the other most important variables from these separate approaches also contrast between the importance of elevation (**Chapter 3** and **5**) and of tea plantation (**Chapter 6**). **Chapter 3** used a more typical approach for modelling distributions of threatened species by using presence only data, a single model algorithm, and simple habitat metrics, validated with a randomised split in presence data. **Chapter 6**, however, used a more sophisticated approach, with contrasting methods of generating pseudo-absences, multiple SDM algorithms, more complex habitat metrics, and k-fold cross validation based on spatial segments to counteract spatial autocorrelation.

The SDM from **Chapter 3** and suite of SDMs from **Chapter 6** gave contrasting outputs. First, **Chapter 3** found low elevation to be associated with Blue-crowned Laughingthrush occurrence, whereas **Chapter 6** found no relationship. Perhaps most strikingly, **Chapter 3** gave land cover as an important variable; however, with only four land cover types, the model was unable to give a land type with higher prediction of occurrence for the Blue-crowned Laughingthrush, but also the highest gain when used in isolation, and a negative gain base on test data only. This suggested that land cover played an important role in BCLT occurrence, but the land types used were not sufficiently fine scale to reveal how. **Chapter 6** then used eight land cover types, which showed the high importance of tea plantation, which was simply part of the 'agriculture' land cover type in **Chapter 3**. This new land cover map plus the rigour of comparing multiple SDM outputs, and using segments to cross-validate the models, enabled the production of a more informative map showing likelihood of occurrence which can be used to target areas to search for Blue-crowned Laughingthrush in a more specific manner.

At the breeding site scale, Blue-crowned Laughingthrush range is only influenced by elevation, with breeding sites more likely to occur within landscapes at low elevation (**Chapter 5**). However, when using data on past landscape changes based on local people's perceptions of their village landscapes, *fengshui* forest and vegetable gardens were significantly associated with breeding Blue-crowned Laughingthrushes (**Chapter 4**). Blue-crowned Laughingthrush were shown to be selective of habitat at the nest site scale in terms of large broadleaf trees, stands of bamboo, fir or mixed forest, and on gentle slopes (**Chapter 5**).

In summary, all our combined available evidence suggests a wide climate envelope (**Chapter 3** and **6**) but also an influence of tea plantations at the landscape scale (**Chapter 6**). We found good overall habitat availability at potential breeding sites within the study landscape (**Chapter 5**), but some specific habitat selection which could restrict choice at the nesting site scale (**Chapter 5**). However, Blue-crowned Laughingthrush are also trapped/exploited, though to an unknown degree (**Chapter 4)**; while this evidence of trapping does not directly support restriction of range, it does suggest it may be an overlooked factor.

However, while this evidence gives some support for why the Blue-crowned Laughingthrush persists within a small range, it does not necessarily occupy its optimal niche (Channell and Lomollno, 2000; Cromsigt, Kerley and Kowalczyk, 2012). Indeed, Caughley (1994) proposed that a precautionary hypothesis for declining species is 'not in the habitat most favourable to it, but in the habitat least favourable to the agent of decline'. In the case of the Blue-crowned Laughingthrush, assuming the current population has declined from a more abundant and widespread one in the past, its current range may be where the least habitat was destroyed and where trapping pressure may have been lower, either due to inaccessibility of the region or local cultural attitudes towards trapping. In support of this, Yu (2003) described Wuyuan and its surrounding areas as 'one of the best areas for birds in the South China region', which helps to explain why Blue-crowned Laughingthrush have persisted here. as In contrast, the Chinese Hwamei (*Garrulax canorus*), a related Laughingthrush species, has a wide geographic range across China despite ongoing trapping pressure (Dai and Zhang, 2017; Shepherd *et al.*, 2020). This could be due to broader habitat or climatic requirements (BirdLife International 2018c). Certainly, other species across mainland China show evidence of occupying a suboptimal niche, such as the Giant Panda (*Ailuropoda melanoleuca*) (Kerley *et al.*, 2020) as well as the Chinese Pangolin (*Manis pentadactyla*), where SDM outputs on elevation changed as its range was pushed by human activity into mountainous regions: therefore, not necessarily occupying a 'naturally' optimal elevation range (Yang *et al.*, 2018). While I do not have direct evidence of this, it must be acknowledged alongside all other data. These range contractions of Chinese species had a key feature in common: they were accompanied by large-scale changes to the rural landscape over time.

7.4 Changes in rural landscapes and wildlife exploitation in south China: then and now

In this study, I found a link between breeding Blue-crowned Laughingthrush, *fengshui* forests and vegetable gardens (**Chapter 4**), which was further supported in **Chapter 5,** showing large broadleaf trees as important to nesting Blue-crowned Laughingthrush, which may be less available beyond the study landscape. Agricultural landscapes may be different further away from the study region, for example they may have less non-crop vegetation, in landscapes like tea plantation (**Chapter 6**). However, we were unable to research this during the current study. Rural landscape change and wildlife exploitation in China has been in flux both past and present (Elvin 2004; Coggins 2017; Miller 2020). Anthropogenic processes have occurred over millennia but intensified in the last few hundred years: deforestation and massive population expansion across southern China (Marks 1998), and in the 20th century, loss of *fengshui* forest (Coggins *et al.*, 2012). These changes have led to many species now having diminished geographic ranges, by pushing the availability of suitable habitat up mountain slopes and or into less productive or less accessible land (Kerley *et al.*, 2020). This has impacted species including the Chinese Giant Salamander (*Andrias davidianus*) (Chen *et al.*, 2018), Gibbons (Chatterjee, Tse and Turvey, 2012), Elephants (*Elephas maximus*) (Elvin 2004) and Chinese Pangolin (Coggins 2003;Yang *et al.*, 2018). If we could determine whether it has suffered a contracted range, the Blue-crowned Laughingthrush may fit in this pattern affecting other species; however, unlike these species, we are missing historical data for past Blue-crowned Laughingthrush range. If the Blue-crowned Laughingthrush's range had followed a similar pattern to other range-restricted Chinese species, it may have experienced range contraction during the 19th century with further declines and fragmentation throughout the 20th century (Turvey, Crees and Di Fonzo, 2015; Yang *et al.*, 2018).

In terms of exploitation, we found ongoing and recent evidence of people trapping Blue-crowned Laughingthrush and other birds within the study region (**Chapter 4**); the last evidence of trapping affecting the Jiangxi Blue-crowned Laughingthrush population is from the late 1990s/early 2000s (Yu 2003). This has implications for other threatened species, especially in Southeast Asia (Turvey *et al.*, 2015; Sykes, 2017). Where threats are not fully understood, LEK interviewing is a useful tool in establishing them, particularly in human-occupied landscapes (Turvey *et al.*, 2014). Trapping is a key threat to songbirds across Southeast Asia, but is poorly understood in China (Fiennes *et al.*, 2021), where the activity is not well monitored across the country and therefore its true impacts are not known.

Moreover, past changes to the Chinese landscape have impacted wildlife, but this transition and change is ongoing, for example, the transition from traditional to modern agriculture practices (Liu, Duan and Yu, 2013). In Wuyuan County, rapeseed is grown as an ornamental crop to encourage tourism, which is partly symptomatic of management of landscapes for tourist revenue as much as for food, to cater for an expanding middle class (Fu *et al.*, 2016)**.**

In my study, respondents across our study landscape reported decreases in vegetable gardens and tea plantations (**Chapter 4**). **Chapter 4, 5** and **6** also potentially point to the importance of non-crop vegetation within the agricultural landscape (Imboma *et al.*, 2020; Li *et al.*, 2020). Similarly, respondents reported increasing urbanisation, with increasing numbers of houses in villages and towns (**Chapter 4**), which has been reported across China (Zhang and Song, 2003). Climate change may also pose a future issue for Blue-crowned Laughingthrush, if this exacerbates current annual flooding patterns in their breeding range (Lyu *et al.*, 2018)**.**

7.5 Limitations and future research questions

While this research helped to add evidence and clarify uncertainties related to the Blue-crowned Laughingthrush, it also generated additional questions. While we found evidence of the Blue-crowned Laughingthrush right across the study landscape, this cannot answer a missing link in our understanding of this species: how large was its range in the past? How large was this in 1500 or 1750 CE, for example (Akçakaya *et al.*, 2018)? This is not available from museum records, given the only wild specimen (of the Jiangxi population) is from 1919, and gives no information beyond the county name (Menegaux 1923). However, if available, Chinese language historical records such as gazeteer records or similar sources of information should be explored, and wider LEK interviews may give insight into their past range up to approximately 50 years ago. Similarly, LEK interviews could also be used to validate the outputs of our existing SDMs, as was demonstrated by Chen *et al.* (2018). Further research could also employ more direct, invasive methods to understand both past range and present non-breeding range of Blue-crowned Laughingthrushes. For example, by testing Blue-crowned Laughingthrushes' genetics for past population bottlenecks (Brekke *et al.*, 2011) or tagging birds with satellite transmitters to reveal their non-breeding range (Lei *et al.*, 2019).

Does the agricultural landscape in south China change further outside of our study landscape? We were constrained from widening the geographic extent of our study area for habitat surveys and interviews by the COVID-19 pandemic, but beyond these bounds we may have observed stronger changes and patterns in the landscape. For example, does the landscape beyond the study area have a higher population density, more pollution, less non-crop or forest vegetation in the landscape? And if so, is this related to or impacting on the current range of the species? This can not only help us understand the range of the Blue-crowned

Laughingthrush, but is also likely to help other species across China, and could inform landscape management policies in other human-occupied agricultural areas (Liu, Duan and Yu, 2013).

To what extent are Blue-crowned Laughingthrush affected by trapping, how much is it affecting their population size, or breeding or wintering range? The species may be trapped more intensively outside of its known range, which could affect where it can breed, thus hindering any range expansion. Or, trapping may take place outside of the breeding season and constrain the number of individual birds returning to breed each year. Who is carrying out trapping, what are the key trade routes, and are there any hotspots targeted by trappers? Trapping appeared to be carried out by people from nearby urban trade centres, but we need to find out how frequently this happens, how many people carry this out, and where birds are taken once trapped. Recent work suggests trapped birds may be taken to southern trade routes via Gaungdong Province (Zhang *et al.*, 2008). These questions are linked to the need for a better understanding of the Asian songbird crisis in China: to date, there has much been focus on international trade, and Indonesia, but little focus on the domestic Chinese trade (Fiennes *et al.*, 2021).

And finally, a question that is continually echoed: where do Blue-crowned Laughingthrush go during the non-breeding season (He and Xi 2002; Yu 2003; Hong *et al.*, 2003; Wilkinson *et al.*, 2004; Zhang *et al.*, 2017)? Our findings from **Chapter 4** hints at flocks remaining in the local region, supporting findings by He *et al.* (2017), but Cheng and Lin (2011) suggest Blue-crowned Laughingthrush may wander as far as Wuyi mountain (although, that was during breeding season, which also flags additional questions: namely, could the Blue-crowned Laughingthrush breed much further south than we currently expect?). However, Blue-crowned Laughingthrush may be more vulnerable to trapping outside of the breeding season, so this is important to establish.

7.6 Recommendations for the Blue-crowned Laughingthrush

Based on the outputs of this thesis, the following recommendation can be made for the Blue-crowned Laughingthrush population in Jiangxi Province to support the expansion of its population. These may be of use to members of the Blue-crowned Laughingthrush Global

Species Management Plan, researchers, government bodies, non-governmental organizations and funders to benefit this specific species, but these recommendations may also have utility for numerous other threatened species across China and the wider world.

- Annual monitoring should be standardised to follow a specific protocol, collecting data on sampling effort, detection bias, date of survey, true absences, and georeferencing information. Additionally, all Blue-crowned Laughingthrush presences should be recorded, not just breeding sites, as populations present but not breeding could also be vulnerable to threats such as trapping, so it is vital to collate a wider map of general occurrence. Monitoring should attempt to census a core area, as previously, but also actively look for new populations through sampling a wider area on an annual basis, to a pre-agreed and repeatable framework including all absences, survey dates and the identity of observers, sampling effort and estimates of detectability (Sutherland, Newton and Green, 2004). The SDM suitability maps generated in **Chapters 3** and **6**, and habitat selection outputs from **Chapter 5**, can be used to guide areas to survey.
- Review the Blue-crowned Laughingthrush Red List status in view of the new population data, but also considering the new threat data. This would be particularly recommended following implementation of a new monitoring protocol.
- Explore whether interventions can be developed that curb trapping of Blue-crowned Laughingthrush. For example, the involvement of local communities to monitor trapping activity, especially trapping that's conducted by non-local people, and notify local authorities.
- Broader landscape management to encourage retention of or increase in stands of natural vegetation, particularly mature broadleaf trees, in agricultural mosaic landscapes. This should be emphasised in areas with gentle slope, at low elevation and in areas with tea plantation and/or vegetable gardens, and in regions both within and outside of the current Blue-crowned Laughingthrush breeding range.
- Increased collaboration between all global actors involved in conservation of the Blue-crowned Laughingthrush, including local government, researchers and captive breeding facilities, to share data and responsibilities, give mutual support and a find a common vision in achieving a sustained future for the Blue-crowned Laughingthrush. This should extend beyond Wuyuan County and join up with surrounding counties and

provinces where suitable habitat for the Blue-crowned Laughingthrush may or could exist. This could be achieved for example by holding a meeting between the Wuyuan County local government, plus local governments for surrounding regions (including in Anhui and Zhejiang provinces), and all key Blue-crowned Laughingthrush researchers and stakeholders to devise a common plan for the species across the wider region.

7.7 Recommendations for other threatened and range restricted species

Overall, this study has strong implications for rare species with limited available data. The following key lessons and recommendations are made for similar, threatened species with restricted ranges:

- Bring together all existing data sources, including all population surveys. Citizen science is still an untapped resource in many areas and could be exploited more in regions with growing bird or nature watching communities.
- Work with all local and international stakeholders and researchers: my own research benefitted enormously from having input from all local actors involved in Blue-crowned Laughingthrush conservation, many of whom did not typically work together.
- This research adds to evidence for LEK approaches for other birds in China and elsewhere. Local people displayed a good recognition of bird species, and their responses enabled the diagnosis of important threats, potential new breeding sites and helped find new places to search.
- Studying environmental factors at different spatial scales is highly important, as reinforced by this study. This is possible even for threatened species with few occupied breeding sites.
- The difference in the two SDM study outputs has wider implications for modelling species distributions of other threatened species using simpler approaches (Papeş and Gaubert, 2007; Turvey *et al.*, 2020), as it supports, where relevant, using more complex land cover maps, and comparing SDM outputs from a range of model algorithms, in better understanding the ranges of threatened species.

7.8 Conclusions

This thesis highlights the power of employing diverse approaches in understanding the restricted ranges of threatened species, and in laying foundations for future action. I show the importance of integrating and interrogating sources of existing information, of obtaining local ecological knowledge, studying environmental associations at multiple spatial scales, and using rigorous comparisons of species distribution models. These have uncovered opportunities to improve monitoring practices, regions with potentially suitable habitat to search for Blue-crowned Laughingthrushes, previously overlooked threats and potential breeding sites, and diverse relationships with habitat across scales. For the Blue-crowned Laughingthrush Global Species Management Plan, this research will lay foundations for the next steps in international cooperation to secure the future of the Blue-crowned Laughingthrush. More widely, this study provides evidence of techniques and approaches which can be applied to threatened species across China and globally. The Blue-crowned Laughingthrush has the potential to become a future symbol of conservation success, both in China and beyond; if so, its lessons learned will impact species worldwide.

7.9 References

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