

# Using large spatial scale camera trap data and hierarchical occupancy models to evaluate species richness and occupancy of rare and elusive wildlife communities in southwest China

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## Abstract

**Aim:** Owing to the broad use of camera traps, integration and standardization among camera trap studies has become key to maximizing their utility for local and global biodiversity conservation. Our goal was to introduce the use of a hierarchical modelling framework in the context of coordinated biodiversity monitoring to compare species richness and occupancy by integrating camera trap data from multiple study areas.

**Location:** Southwest China.

**Methods:** We used hierarchical occupancy models to integrate camera trap data for elusive mammal and pheasant communities from three study areas representing different habitat types: alpine and subalpine zones, dry-hot valleys and subtropical montane forests. We evaluate the responses of species occurrence to human influence and habitat parameters based on a Bayesian approach.

**Results:** We captured photographs of 23 mammal and 7 pheasant species over 10,095 trap nights. The model revealed that the alpine and subalpine zones supported the highest species richness of the target communities among the three habitat types. Surprisingly, dry-hot valleys supported similar levels of species richness to subtropical montane forest. Species richness showed a similar bell-shaped relationship with elevation, with the richness curve peaking at intermediate elevations at about 3500 m above sea level (asl). Posterior distributions for community-level hyper-parameters indicated the consistent and negative effects of human disturbance on species occupancy. The community model also revealed a strong quadratic relationship between elevation and occupancy, with the highest occupancy occurring at about 3700 m asl.

**Main conclusion:** Using hierarchical occupancy models for integrating camera trap data from multiple study areas, we show that alpine/subalpine zone and dry-hot valleys have the highest richness and should be given more priority for conservation of biodiversity in southwest China. We recommend broader application of the hierarchical occupancy modelling approach to camera trap data to obtain more comprehensive insights relevant to regional biodiversity conservation.

## KEYWORDS

alpine and subalpine zones, Bayesian modelling, dry-hot valleys, medium and large-sized mammals, multi-species modelling, pheasant, southwest China, species richness

## 1 | INTRODUCTION

Human activities and anthropogenic climate change are major pressures on wild species (Parmesan & Yohe, 2003) as highlighted by accelerated extinction probabilities in mammals and evidence of widespread population declines of wild terrestrial species (Koivula et al., 2017). In the face of these pressures and the resulting change in populations and communities, research on species distribution patterns, assessing biodiversity and elucidating the relationship between wildlife and their environment have become key focuses in ecology and conservation (Brncic, Amarasekaran, McKenna, Mundry, & Kühl, 2015; Kéry, 2010; McMahon et al., 2011). Information on species distribution and biodiversity patterns is necessary foundations for designing adaptive management plans and appropriate conservation measures, including for prioritizing of key areas across scales (Wilson, McBride, Bode, & Possingham, 2006), for evaluating the adequacy of current protected area networks (Bruner, Gullison, Rice, & Da Fonseca, 2001) and for assessing the effectiveness of conservation interventions (Tranquilli et al., 2012). Recently, the increasingly urgent need to address major environmental changes and prioritize conservation actions has led to calls for coordinated regional and global monitoring networks (Ma, Shen, Grumbine, & Corlett, 2017; Rich et al., 2017; Steenweg et al., 2017; Xiao et al., 2017).

Camera traps offer a low cost, efficient and easily replicable tool for surveys of ground-dwelling terrestrial mammals and pheasants (Ahumada, Hurtado, & Lizcano, 2013; Gálvez, Guillera-Arroita, Morgan, & Davies, 2016). The broad use of camera traps offers novel data sets for use in local and global biodiversity conservation, but integration and standardization among camera trap studies will be key in using these data effectively (Rich et al., 2017). The rise of occupancy modelling as an approach to account for incomplete or biased detection has led to its application in camera trapping surveys as an alternative to more difficult direct measures of abundance (Burton et al., 2015). Although occupancy is usually a poor surrogate for abundance (Gaston, 1999), camera trapping based presence-absence data provides a foundation for modelling of probability of occurrence of a species, while accounting explicitly for imperfect detection (i.e., the probability of detecting a species given it is present at the site) (Ahumada et al., 2013; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003; MacKenzie et al., 2002). Using a hierarchical occupancy modelling framework, camera trapping data can be integrated across study areas and study sessions (Rich, Miller, Robinson, McNutt, & Kelly, 2016; Rich et al., 2017; Tobler, Hartley, Carrillo-Percestequi, & Powell, 2015).

The fauna in southwest China are poorly studied, diverse, and subject to multiple anthropogenic threats. For example, wildlife

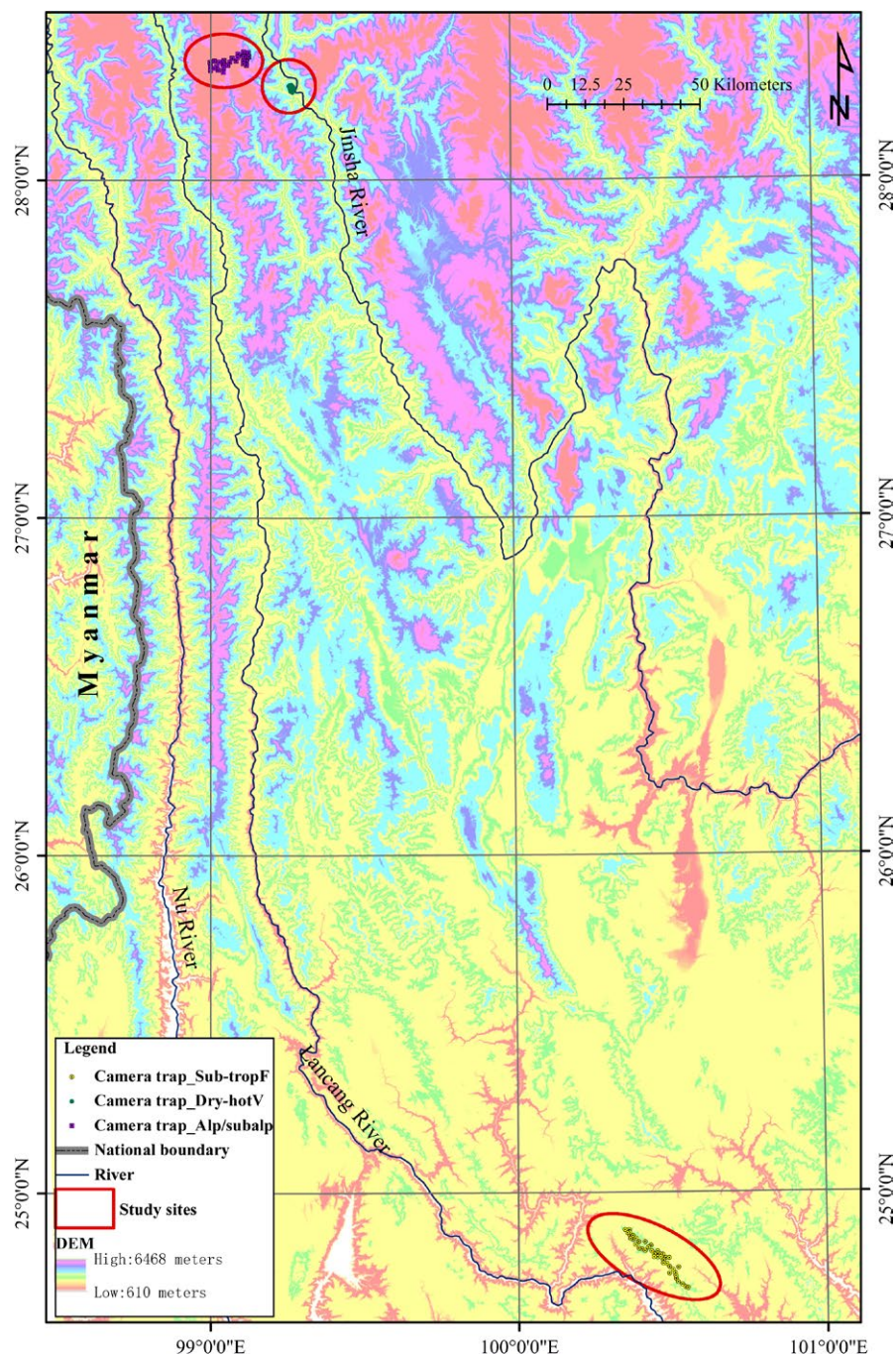
species in southwest China are threatened by livestock grazing (Haynes, Fang, & Waller, 2013), mining (Ye, Liu, Li, Wang, & Zeng, 2015), hunting (Li & Jiang, 2014) and human-wildlife conflict (Li, Buzzard, Chen, & Jiang, 2013). Broad-scale studies on wildlife communities in southwest are scarce, and very little is known about the impacts of human disturbance on species richness and occupancy.

In this study, we assessed the species richness and occupancy of medium- and large-bodied mammal and pheasant communities across a mountainous landscape in and around a World Heritage Site in southwest China. We used the Bayesian hierarchical multispecies occupancy model approach developed by Tobler et al. (2015), which allowed us to obtain estimates for species richness and occupancy based on combining camera trapping data from three monitoring areas representing different habitat types: alpine and subalpine zones, dry-hot valleys and subtropical montane forests. Our goal was to introduce the use of this hierarchical modelling framework in the context of coordinated biodiversity monitoring in China to compare species richness and occupancy by integrating camera trap data from multiple study areas. Our objectives, adapted from Rich et al. (2016), were to evaluate patterns in species richness and occupancy and to assess the effects of human disturbance and habitat variables on species occurrences using a Bayesian approach, and finally to examine the conservation value of three habitat types in southwest China. Our research was motivated by the recent call for a coordinated biodiversity monitoring network throughout China (Ma et al., 2017; Xiao et al., 2017) and was an effort to provide a case study of integration of camera trapping data across monitoring networks at a landscape scale in this context. Thus, we sought not only to inform the conservation of regionally important habitat types and wildlife communities, but also to popularize an approach to integrating camera trapping data from multiple monitoring networks to inform effective conservation planning for wildlife populations regionally and globally.

## 2 | METHODS

### 2.1 | Study areas

The mountain areas in southwest China are recognized as a biodiversity hotspot (Mittermeier et al., 2004) and include the Three Parallel Rivers UNESCO World Heritage Site. The river valleys in southwest China, such as Jinsha (Yangtze), Nu (Salween), Lancang (Mekong) and Hong (Red) River valleys, support distinctive dry-hot and dry-warm ecosystems, while the higher slopes of the Hengduan Mountain Range grade from temperate to subalpine to alpine to permanent frost on the tops of the highest peaks. Our study was carried out in the northern part of Baima Snow Mountain Reserve (c. 730 km<sup>2</sup>,



**FIGURE 1** Map of area for camera trap study in southwest China. Camera traps were located in 3 habitat types: alpine and subalpine zones at Baima Snow Mountain Nature Reserve between October 2013 and February 2014 (3513–4859 m), dry-hot valleys at Baima Snow Mountain Nature Reserve between October 2013 and February 2014 (2150–3580 m) and subtropical montane forests at Wuliang Mountain Nature Reserve between October 2014 and February 2015 (2046–2755 m)

28°19'N, 99°03'E) and in the Nanjian Wuliang Mountain Reserve (c. 75 km<sup>2</sup>, 24°45'N, 100°25'E) in Yunnan Province of southwest China (Figure 1). The Baima Snow Mountain Reserve is located in the Three Parallel Rivers World Heritage Site between the Jinsha River and Lancang River with a large elevation range (1950–5429 m above sea level (asl)) that encompasses various habitat types and climates, such as dry-hot valleys, alpine and subalpine zones (Li, 2003). Dry-hot valleys are a natural landscape in southwest China between

about 2000 and 3500 m asl and are characterized by low rainfall and fragile environments which support “semi-savanna vegetation” features characterized largely by xerophytic grasses and shrubs with scattered trees (Tang, Xie, & Hui, 2004; Zhao & Gong, 2015). Dry-hot valleys traditionally have been considered to be tree-less, barren lands of low conservation value (Gong & Tang, 2016). The alpine and subalpine zones in the region are found along mountain ranges from about 3500 to 5000 m asl, and the vegetation is characterized by



**TABLE 1** Details of camera trap surveys carried out in three habitat types in southwest China

Habitat	Elevation range (m)	Stations	Range of camera days	Total camera days
Alpine/subalpine	3513–4859	30	77–111	3395
Dry-hot valley	2105–3508	22	104–127	2203
Subtropical montane	2046–2755	42	91–127	4497

striking altitudinal zonation and diverse vegetation types (Li, 2003), and are essentially islands of montane habitats. Variation in aspect and slope results in rapid changes in habitat types with only modest changes in elevation. The main vegetation types consist of broadleaf deciduous forests, dark conifer forests, mixed broadleaf deciduous–dark conifer forests, dwarf shrub lands, alpine meadows and alpine scree (Li, 2003).

Nanjian Wuliang Mountain Reserve is located in central Yunnan, and the dominant habitat type is subtropical forest. The reserve supports primary and secondary monsoon evergreen broadleaf forests, semi-humid evergreen broadleaf forests, and mid-mountain humid evergreen broadleaf forests at an elevation range between 1700 and 2700 m asl, above which dwarf forest dominated by giant rhododendron and bamboo forest predominate (Yu, Cao, Qian, & Gu, 2004). Subtropical montane forests are considered to be a high conservation priority in southwest China (Zhu, 2016).

## 2.2 | Data collection

We conducted camera trap surveys in Baima Snow Mountain between October 2013 and February 2014, and in Nanjian Wuliang Mountain between October 2014 and February 2015, with a total of 94 camera stations and 10,095 camera trapping days (Figure 1; Table 1). We split each of the surveys into 2 sessions (October–15 December 2013, 16 December 2013–February 2014, October–15 December 2014, 16 December 2014–February 2015) and treated them as independent surveys. We assumed that the species pool remained constant (i.e., the community was closed) during each survey period.

Our target species were medium to large sized mammals and pheasants, most of which had very low density in the field. To increase the probability of photographic capture of wildlife, we placed camera traps (Ltl Acorn® 6210 mc) in areas believed to be used by our focal species based on reports of knowledgeable local guides and evidence from track and sign (Li, Buzzard, & Jiang, 2014). We placed the camera traps approximately 1 m off the ground, and the delay period between photographs was set at 3 s. We selected camera trapping stations based on habitat heterogeneity and accessibility. A minimum of 500 m separated each camera trapping station (See Supporting Information Appendix S1). This distance may be less than the home range diameter of some of the large mammals species we studied, thus violating one of the assumptions of the models below. For these species, the occupancy estimate can be thought of as an estimate of local site use probability rather than true occupancy. We took elevation range into consideration when setting camera traps in the three habitat types. We made sure that our trapping stations

covered the maximum elevation range in each study area. Sampling effort at a trapping station was calculated as the number of days for which a camera was set or until the last photo was taken if the camera stopped functioning before collection. For each station, we pooled every 6 days of camera trapping occurrence data into a single sampling occasion to reduce heterogeneity and avoid overdispersion (Tobler et al., 2015).

## 2.3 | Site covariates

We characterized each camera trapping station by habitat type, elevation and canopy cover and disturbance. Canopy cover was estimated for each plot based on visual observations in a 10 × 10 m plot centred on each trap station. To ensure consistency, all of the estimation was conducted by one observer. We defined human disturbance around a trapping station as the presence of camera trap images of livestock or humans. All of the same type of disturbance occurring at a station on the same date was combined as one independent disturbance event. Human disturbance indices of a trapping site were calculated as trapping rate of the total disturbance events per 100 camera trapping days during the study period. Pairwise correlations between habitat covariates were tested using Pearson's correlation, and all correlations were low ( $|r| < 0.3$ , Supporting Information Appendix S2).

## 2.4 | The model

Occupancy models provide an estimate of occupancy  $\Psi$ , which is the probability that a species occupied a site during the survey, calculated while taking into account that the probability of detection of the species at a site it occupies may be less than one (MacKenzie et al., 2002). The models incorporate variables assumed to impact the occupancy and detection probability (Reilly, Tobler, Sonderegger, & Beier, 2017). We used a multi-species variant of the Royle-Nichols (RN) occupancy model (Reilly et al., 2017; Royle & Nichols, 2003; Tobler et al., 2015) to analyse how habitat types (alpine and subalpine zone, dry-hot valley and subtropical montane forest), human disturbance and environmental covariates (elevation, cover) affected species, assemblage and community-level occupancy. Camera trap detection data often show high heterogeneity, and the RN model should outperform a standard occupancy model under such circumstances (Tobler et al., 2015). We used the model only to handle data overdispersion and did not base any inference on the estimated abundances (Reilly et al., 2017; Tobler et al., 2015).

Following Tobler et al. (2015) closely, we first defined  $w_{ij}$  as a latent binary variable for which  $w_{ij} = 1$  if species  $i$  is present at habitat

type  $l$ . We assumed  $w_{il}$  is a Bernoulli random variable as  $w_{il} \sim \text{Bernoulli}(\Omega_i)$ , where  $\Omega_i$  is a rate between 0 and 1. Here  $\Omega_i$  can be thought of as the occupancy probability at the level of habitat type, allowing species to be completely absent from certain habitat types. We then defined  $z_{ij}$  as a binary variable indicating the occurrence state of species  $i$  at station  $j$  and assumed to be the outcome of a Bernoulli process, denoted by  $z_{ij} \sim \text{Bernoulli}(w_{il} \times \Psi_{ij})$ , where  $\Psi_{ij}$  is the probability that station  $j$  is used by species  $i$ . For those species that are present, the multi-species RN model models the abundance of species  $i$  ( $a_{ij}$ ) at trapping station  $j$  as a random Poisson variable with  $a_{ij} \sim \text{Poisson}(\lambda_{ij})$ , where  $\lambda_{ij}$  is the expected abundance of species  $i$  around station  $j$ . Incidentally, the probability that site  $j$  is occupied by species  $i$  ( $\Psi_{ij}$ ) can be calculated as follows:

$$\Psi_{ij} = \Pr(a_{ij} > 0) = 1 - \exp(-\lambda_{ij})$$

We assumed occupancy to vary with environmental covariates (ENV: canopy cover, disturbance, elevation) and habitat types (categorical variable). We included both linear and quadratic terms for cover and elevation so that species associations with these habitat characteristics could have maxima at any intermediate level. As quadratic cover was found to have no significant effects on any species or assemblages, it was later dropped from the final analysis. We assumed the influence of disturbance on occupancy was confounded by elevation and included interaction effects between elevation and disturbance in the model. Therefore, the expected target abundances ( $\lambda_{ij}$ ) for species  $i$  at station  $j$  is specified:

$$\log(\lambda_{ij}) = \beta_0 + \sum_{x=1}^{n=5} \beta_x \text{ENV}_x + \beta_6 i_{\text{habitat}_j}$$

where  $x$  is index of the 5 environmental covariates, that is canopy cover, disturbance, elevation, quadratic elevation and interaction between elevation and disturbance. For categorical variable habitat type, the alpine/subalpine habitat serves as the baseline and in the model becomes represented by the intercept parameter.

We expected the per individual detection probability to vary with habitat types and survey sessions:

$$\text{logit}(r_{ij}) = \alpha_0 + \alpha_1 i_{\text{session}_j} + \alpha_2 i_{\text{habitat}_j}$$

We standardized all covariates so that the means of the covariates were zero (Zipkin, DeWan, & Andrew Royle, 2009). Following Reilly et al. (2017), we used a hierarchical method to improve parameter estimates for infrequently detected species, modelling all species-level parameters as random variables drawn from a normal distribution described by a mean of 0 and the respective community variance ( $\sigma^2$ ) hyper-parameters (e.g.,  $\beta_1 \sim \text{Normal}(0, \sigma_1^2)$ ).

The unique group-level responses to environmental covariates are often missed when species are all grouped together because these distinct responses are “averaged out” (Pacifi, Zipkin, Collazo, Irizarry, & DeWan, 2014). Under a multispecies hierarchical framework, ecologists often classify species into groups to examine the relative impact of ecological covariates at both species and assemblage levels (Cove, Spinola, Jackson, Sáenz, & Chassot,

2013; Rich et al., 2016; Wells et al., 2012). Thus, we divided species into four assemblages based on species-specific ecological traits: pheasants, medium sized mammals (1–10 kg), large sized mammals (>10 kg) and primates. We separated the recorded primates from medium or large sized mammals to account for possible variation in detection and occupancy between semi-arboreal and terrestrial species. We assumed species assemblage may influence a species response to environmental covariates. Following Rich et al. (2016), we assessed community-level hyper-parameters by a community model which pooled all species together in a “community” (Supporting Information Appendix S3), and we derived all species richness estimates based on the community model. We then ran another grouped model by incorporating species assemblage as a species-specific detection and occupancy covariate (Supporting Information Appendix S4). In our grouped model, we assumed species-level parameters to be governed by both an assemblage-level and community-level hyper-parameter, and modelled the assemblage-level and species-level parameters for the respective variable.

We carried out the modelling using a Bayesian approach in JAGS (Just Another Gibbs Sampler) version 3.4.0 (Plummer, 2003) via the package R2Jags (Su & Yajima, 2015) to interface with software R. We used independent, vague priors (e.g., normal prior distributions with mean zero and variance 1000 for community-level occupancy and detection covariates) and random initial values (See Supporting Information Appendix S3 and S4). We made inference from 3,000 samples of the posterior distribution obtained from three chains of 40,000 Markov Chain Monte Carlo (MCMC) after a burn-in of 100,000 and thinned by 40. We assessed convergence by visually inspecting the chains and by ensuring the Gelman-Rubin statistic for each parameter was close to 1. We assessed the adequacy of the model using the Bayesian  $p$ -value based on Pearson's  $\chi^2$  discrepancy. The Bayesian  $p$ -value is defined as the probability:  $\Pr(\chi_{\text{obs}}^2 > \chi_{\text{sims}}^2)$ . A fitting model has a Bayesian  $p$ -value close to 0.5, and extreme values (e.g., less than 0.05 or greater than 0.95) indicate that the model is inadequate. The complete model specification and the assessment of model fit results are presented in Supporting Information Appendix S3 (the community model) and S4 (the grouped model).

Occupancy models using data augmentation allow for estimation of the number of species in the community that were unobserved during the sampling period (Kéry & Royle, 2008, 2009; Zipkin, Andrew Royle, Dawson, & Bates, 2010). However, this requires the information of the total number of species that can possibly occur at a site from a timely regional a prior species list (Cove et al., 2013; Tobler, Carrillo-Percastegui, Leite Pitman, Mares, & Powell, 2008; Wells et al., 2012). As we have no well-documented a prior species list in our poorly studied region, we had to limit our species list to species that were recorded at least once in our study. We thus could not address absolute species richness, but focused on comparing the relative species richness of focal communities in different monitoring areas (habitat types) in southwest China. To estimate species richness at habitat  $l$ , we summed the number of estimated species (i.e., instances where  $w_{il} = 1$ ) in the habitat-level occurrence matrix.

We estimated station-level species richness using another station-level occurrence matrix  $z_{ij}$  ( $z_{ij} = 1$  for present and 0 absent) in the same way, and inferred station-level associations of richness with elevation, canopy cover and human disturbance by a generalized additive model (GAM) using the function “gam” in mgcv package. We also introduced a log-linear regression of the variance in the all species richness on habitat covariates (cover, disturbance and elevation, Supporting Information Appendix S5) to assess the effects of each explanatory variable on all richness and its variation (Kéry, 2010).

### 3 | RESULTS

#### 3.1 | Species richness and community-level summaries

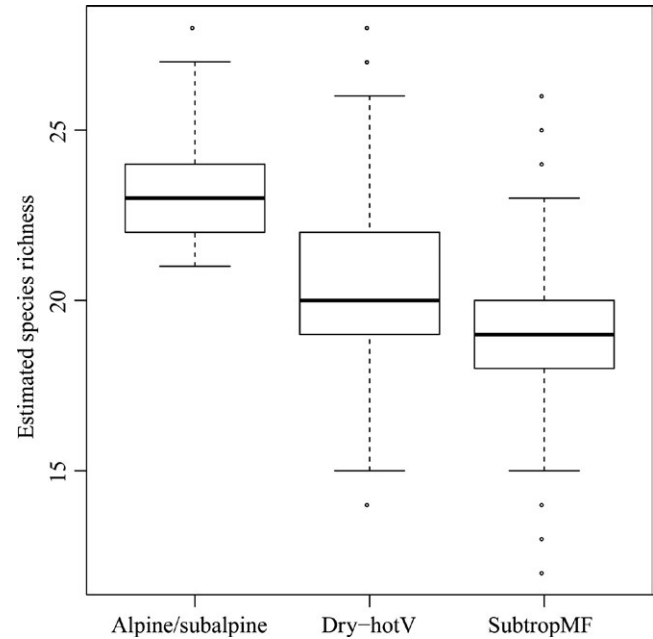
A total of 23 medium and large-sized terrestrial mammals and seven pheasant species were observed during sampling: 21 species in alpine and subalpine zones, 14 species in dry-hot valley and 11 in subtropical montane forests (Supporting Information Appendix S6). The majority of the detected species (57%, 17 of 30) were rare species in the region and were listed as protected species by Chinese Wildlife Conservation Law. Six species were categorized by IUCN (2017) as globally threatened (Vulnerable or Endangered), and five species as Near Threatened (Supporting Information Appendix S6).

The model estimated 23 species in alpine and subalpine zones (95% Bayesian Credible Interval (BCI): 21–26), 20 species in dry-hot valley (95% BCI: 17–24) and 19 species (95% BCI: 15–23) in subtropical montane forests (Figure 2). Disturbance appeared to have a negative impact on species richness (Figure 3) and had the highest apparent, although non-significant, contribution to the variance in the species richness among the three habitat covariates (mean = 0.24, 95% BCI: −0.02–0.50; Table S5.1). Elevation showed an approximate bell-shaped relationship with all species richness, with the species richness curve peaking at intermediate elevations at about 3500 m asl and showed a nearly symmetrical pattern (Figure 3).

Posterior distributions for community-level hyper-parameters indicated the consistent and negative effects of human disturbance on species occupancy (Table 2). The mean estimates for the community occupancy response to cover was positive, but the 95% BCI overlapped zero (95% BCI: −0.19 to 0.40), which is a manifestation of the variability in the community (Table 2). The community model revealed a strong quadratic relationship between elevation and occupancy, with the predicted all-species probability of occupancy increasing with elevation until reaching about 3700 m asl, then decreasing at higher elevations (Table 2; Supporting Information Appendix S7).

#### 3.2 | Assemblage-level and species-specific summaries

Disturbance appeared to have negative effects on species richness for all assemblages (Supporting Information Appendix S8).

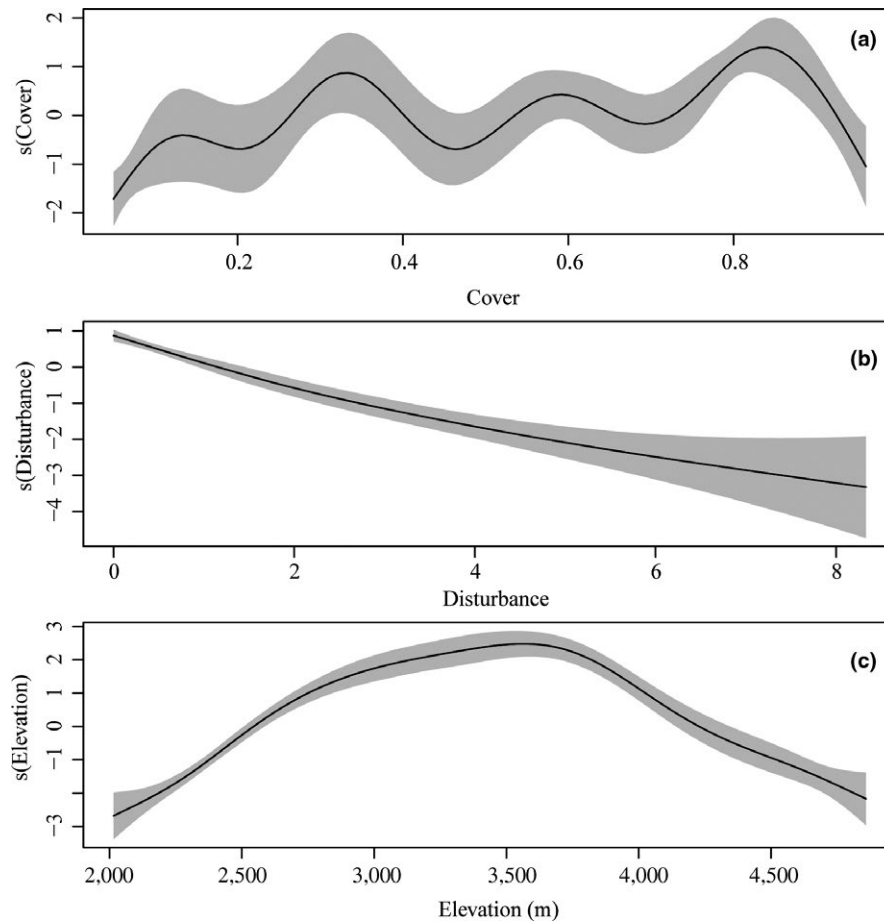


**FIGURE 2** Estimated habitat-type level species richness in alpine and subalpine zones (Alpine/subalpine), dry-hot valleys (Dry-hotV) and sub-tropical montane forests (SubtropMF) in southwest China. Box and whiskers-plot showing median, lower and upper quartiles, minimum and maximum values and outliers

The main effects of disturbance on occupancy showed strong negative relationships for all of the assemblages except for pheasants (Table 3). Elevation showed a nonlinear relationship with occupancy for all assemblages (Table 3; Supporting Information Appendix S7), with the predicted probability of occupancy peaking at about 3800 m asl for large-sized mammals, about 3900 m asl for medium-sized mammals and pheasants and about 4000 m asl for primates (Supporting Information Appendix S7). The interaction effects between elevation and disturbance were negatively related to occupancy of medium-sized mammals (95% BCI: −0.65 to −0.51; Table 3).

Considering species-specific results, the total numbers of detections per species were highly variable, ranging from 1 for Himalayan marmot *Marmota himalayana* to 93 for Chinese serow *Capricornis milneedwardsii* for the 6-day pooled data (Figure 4; Supporting Information Appendix S6). The mean probability of occurrence across all species and camera stations was  $0.24 \pm 0.17$  (mean  $\pm$  SD, 95% BCI: 0.06–0.72), but this was highly heterogeneous among species, and varied from 0.82 for Chinese serow to 0.03 for Tibetan snowcock *Crossoptilon crossoptilon*. The detection probability for many species was lower than 0.1 (Figure 4).

Of the 30 species photographed, four species (Chinese serow, tufted deer *Elaphodus cephalophus*, alpine musk deer *Moschus chrysogaster* and red muntjac *Muntiacus muntjak*) were significantly affected by disturbance. While the effects of disturbance on occupancy were not significant for other species considered individually, the mean effects of disturbance for all species except for Lady Amherst's pheasant *Chrysolophus amherstiae* were negative (Figure 5, Supporting Information Appendix S9). The mean effects of canopy cover for 22 of



**FIGURE 3** Partial GAM plots relating station-level species richness to cover (a), disturbance (b) and elevation (c). The x-axis is the range of the environmental variable, and the y-axis is the additive contribution of the variable to the nonparametric GAM smoothing function. The shaded areas represent 95% credible intervals

Community-level hyper-parameter		Mean	Standard deviation	95% BCI	
$\mu\beta 1$	Cover	0.10	0.16	-0.19	0.40
$\mu\beta 2$	Disturbance	-0.31	0.11	-0.54	-0.11
$\mu\beta 3$	Elevation (linear term)	0.93	0.27	0.47	1.53
$\mu\beta 4$	Elevation (squared term)	-0.77	0.21	-1.24	-0.38
$\mu\beta 5$	Elevation*Disturbance	-0.05	0.10	-0.24	0.13
$\mu\beta 6$	Habitat	0.08	11.29	-18.93	18.67
$\mu\alpha 1$	Habitat	0.08	11.29	-18.93	18.67
$\mu\alpha 2$	Session	-0.03	11.31	-18.73	19.04

**TABLE 2** Community-level summaries of the hyper-parameters for the detection ( $\mu\alpha 1$  and 2) and occupancy ( $\mu\beta 1$  to 6) covariates in southwest China. Posterior mean, standard deviation and 95% Bayesian credible intervals

30 species were positive, while for bhara *Pseudois nayaur*, it was negatively associated with canopy cover (Figure 5; Supporting Information Appendix S9). In dry-hot valleys there was strong evidence for higher occupancy relative to alpine/subalpine habitat for Chinese goral *Naemorhedus griseus* (intercept = -1.22, mean effects = 3.09, 95% BCI: 0.44–6.07) and bhara (intercept = -2.11, mean effects = 2.38, 95% BCI: 0.29–4.56) (Supporting Information Appendix S10). Subtropical montane forests showed strong evidence for higher occupancy (relative to alpine/subalpine habitat) of red muntjac *Muntiacus muntjak*

(intercept = -0.99, mean effect = 2.85, 95% BCI: 0.29–5.50) and wild boar *Sus scrofa* (intercept = -1.42, mean effect = 2.42, 95% BCI: 0.45–4.48) (Supporting Information Appendix S10).

## 4 | DISCUSSION

Our study sought to clarify the impacts of human disturbance and environmental variables on the occurrence of poorly studied, elusive

**TABLE 3** Assemblage-level summaries of the hyper-parameters for the occupancy covariates in southwest China. Posterior mean and 95% Bayesian credible intervals

Assemblage	Cover			Disturbance			Elevation			Squared elevation			Elevation-disturbance interaction		
	Mean	95% BCI		Mean	95% BCI		Mean	95% BCI		Mean	95% BCI		Mean	95% BCI	
Large	0.20	-0.13	0.56	-0.48	-0.75	-0.22	0.71	0.24	1.24	-0.88	-1.46	-0.39	-0.03	-0.32	0.25
Medium	0.31	-0.16	0.00	-0.10	-0.54	-0.39	1.23	0.71	0.88	-0.90	-1.53	-1.30	-0.20	-0.65	-0.51
Pheasant	0.03	-0.29	0.37	-0.27	-0.54	0.02	0.85	0.40	1.37	-0.89	-1.48	-0.34	-0.07	-0.33	0.18
Primate	0.14	-0.19	0.49	-0.35	-0.66	-0.05	0.79	0.32	1.34	-0.91	-1.50	-0.41	0.03	-0.28	0.33

communities of wildlife in southwest China using a large spatial scale camera trap data set. Under standard sampling strategies, camera trapping data sets from different study areas or study periods can be integrated into a hierarchical modelling framework by using a mixed modelling approach with random effects to accommodate multi-level influences on species occurrence (Tobler et al., 2015). In our study, both the community model and the grouped model fit the data well with a favourable fit. This highlights the robust and effective nature of hierarchical RN models for occurrence data modelling (Tobler et al., 2015) for data from long-term camera trap monitoring programmes.

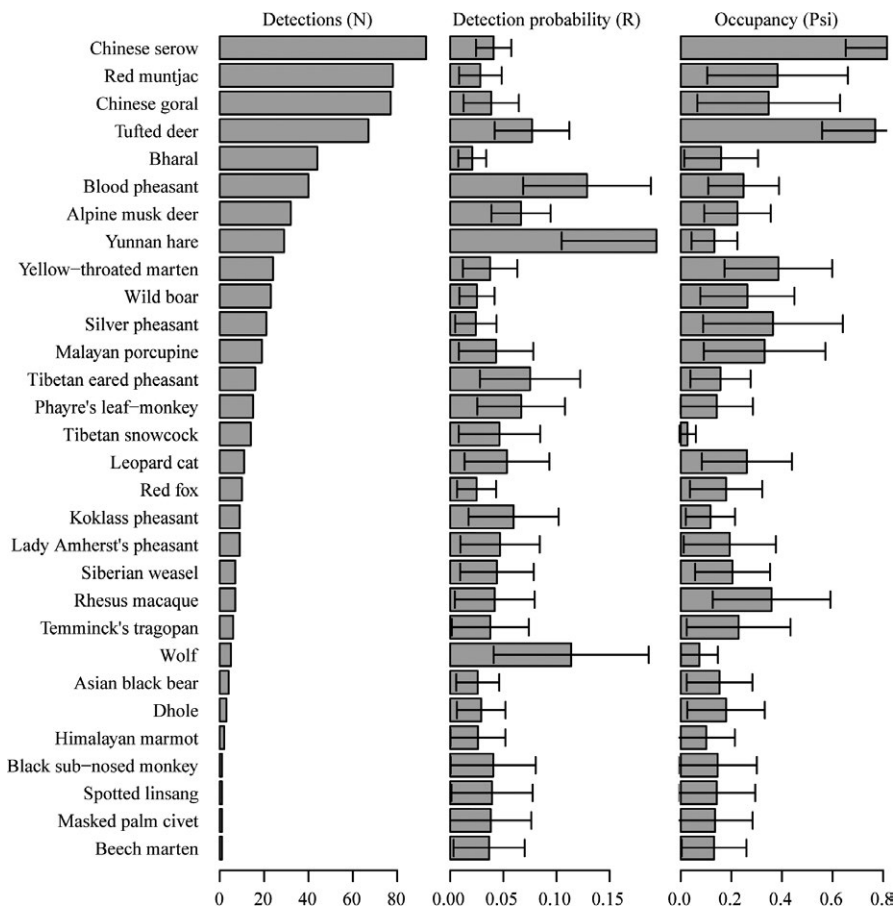
#### 4.1 | Overall patterns in species richness

The spatial ecology of a species is shaped by environmental features such as land cover, terrain, elevation, access to water, food availability and disturbance regime (Reilly et al., 2017; Rich et al., 2016). For example, in temperate forests, low- to mid-elevation regions of mountainous landscapes have been found to be highest in biodiversity (Thom et al., 2017), and variability in elevation was the most powerful variable in predicting species richness of mammals and resident birds in China (Xu et al., 2015). However, the influence of environmental conditions on species distribution varies greatly among species (Reilly et al., 2017; Schuette, Wagner, Wagner, & Creel, 2013; Vanthomme, Kolowski, Korte, & Alonso, 2013). In our study, all species richness showed a mid-elevation peak (Table 2; Figure 3). Such a pattern is frequently documented in small mammals (Hu et al., 2017; McCain, 2004) and birds (Acharya, Sanders, Vijayan, & Chettri, 2011; Price et al., 2014) and is explained by many theories such as climate, productivity, habitat heterogeneity and mass effects (Acharya et al., 2011). Possible explanations for this pattern in southwest China might be related to lower food availability above 4000 m and closer proximity to residential sites at lower elevation. Overall, relative species richness was negatively related to human disturbance (Table 2; Figure 3). Many previous studies have also identified the influence of human disturbance on species diversity and distributions (Reilly et al., 2017; Schuette et al., 2013; Vanthomme et al., 2013).

Wildlife biodiversity is positively associated with habitat heterogeneity (Kerr & Packer, 1997; Rahbek & Graves, 2001; Veech & Crist, 2007). We included one additional level of random effects for habitat type in the hierarchical RN model. This further allowed us simultaneously to account for both camera station and habitat type (study-area) level influences on species occurrence. We cannot demonstrate that differences in occurrence patterns were not caused by the different years of sampling at each study area, and strong inference is not possible with only a single study area of each habitat type. However, we suspect that much of the apparent effects of study area that we observed were due to habitat differences among the three study areas, and not because of temporal effects across all study areas.

Our study suggests that the alpine and subalpine zones supported the highest species richness of observed wildlife communities





**FIGURE 4** Species specific detection and occupancy estimates. Distribution of the total number of detections for 6-day pooled data (N), per individual detection probabilities (R) and mean occupancy (Psi) across three habitat types in southwest China

among the three habitat types (Figure 2). Although the vegetation structures in alpine and subalpine zones are simple, intense vertical relief results in dramatic variations in vegetation types, thus generating diverse habitats and harbouring more species. Additionally, alpine and subalpine zones appear to be associated with low levels of parasitism and disease (Martin, 2001). The relative value of alpine and subalpine areas as wildlife habitat has increased in the face of habitat loss and fragmentation at lower elevations caused by extensive human activities. Areas with higher elevation are not only essential for specialized alpine and subalpine resident species, but are also important for migrating terrestrial wildlife during warm seasons (Martin, 2001). They may become increasingly important as the impacts of anthropogenic climate disruption become more severe. However, comprehensive studies on the fauna in these critical ecosystems are limited, and long-term wildlife monitoring programmes are essential in these areas to understand the ecological effects of anthropogenic disturbance and climate disruption on alpine and subalpine habitats and their faunal communities.

Our research unexpectedly revealed the possible importance of dry-hot valleys in maintaining biodiversity in southwest China. Dry-hot valleys conserve similar levels of species richness to subtropical montane forests (Figure 2) and may be particularly important for some specific species such as Chinese goral and bharal (Supporting Information Appendix S9). However, the high relative diversity of dry-hot valleys should not be over-emphasized. Our study focused

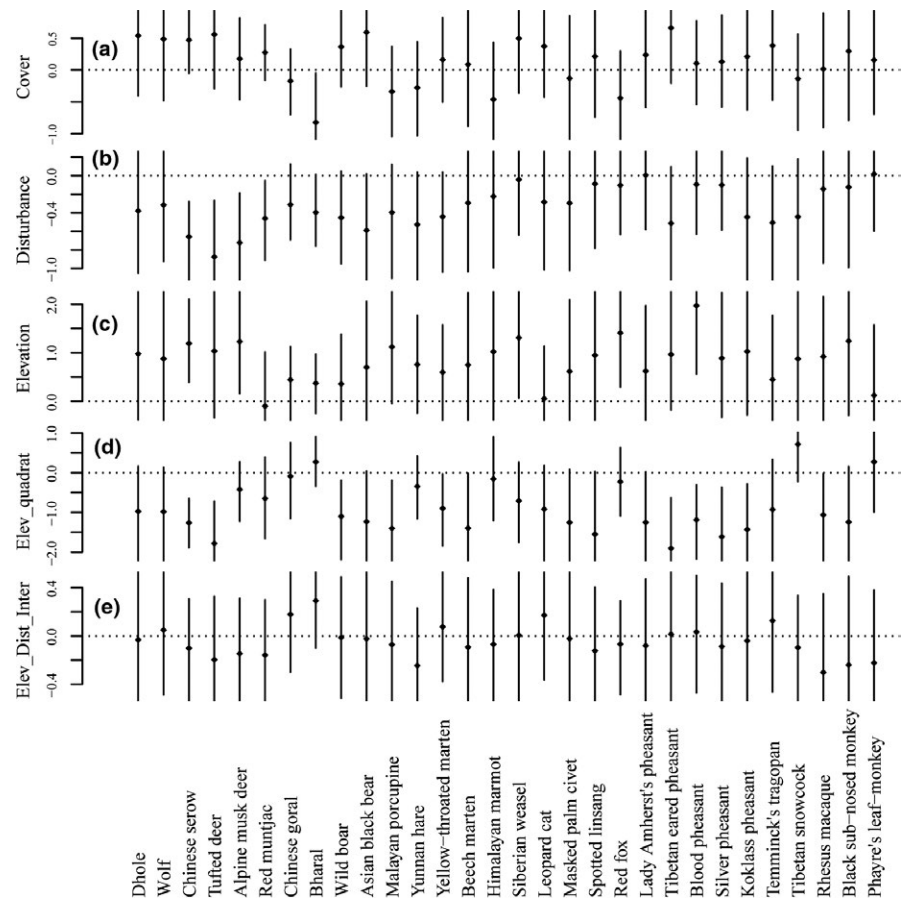
on terrestrial and semi-terrestrial species. Generally, the use of camera trapping surveys is limited to those species that regularly visit the ground, and exclusively arboreal species, which may be more prevalent in moist forest habits, are missed from camera trapping surveys even when present.

## 4.2 | Effects of human disturbance

The distribution of species and biodiversity is often shaped by human disturbance such that species richness decreases with increasing human presence (Herrera, 2017). Habitat loss, degradation and fragmentation by land-use change and infrastructure development, along with overharvesting, have become some of the greatest threats to biodiversity (Rich et al., 2016). Even livestock grazing or tourism can influence occurrence and viability of some species. These threats are predicted to affect some species more than others (Crooks, 2002).

While all four assemblages in our study displayed sensitivity to human disturbance, it appears that large mammals and primates may be more sensitive when compared with pheasants and mid-sized mammals (Table 3). This could be explained by differences in their abilities to avoid or flee from human disturbance and hunting. In a conservation context, it is useful to consider species one at a time, as summaries of community-level distribution patterns may not be meaningful (Zipkin et al., 2009). At species-specific level, only four

**FIGURE 5** Influence of habitat variables on species specific occupancy. Standardized beta coefficients and 95% Bayesian credible intervals, for the influence of cover (a), disturbance (b), elevation (c), quadratic elevation (d) and interaction effects between disturbance and elevation (e) on species use of the area around camera stations in southwest China based on the RN model



species had strong negative association with human disturbance, but the mean effects of human disturbance for all species except Lady Amherst's pheasant were negative (Figure 5, Supporting Information Appendix S9), indicating high vulnerabilities of the target species to human disturbance. Although most species occurrence patterns showed a tendency for a positive association with canopy cover, some species, significantly bharal, showed an opposite response to this covariate (Figure 5, Supporting Information Appendix S9). In a hierarchical framework, estimates for rarely observed species will be naturally drawn to community means, and thus uncertainty of species-specific responses to covariates for rare species with limited occurrence data should be anticipated.

### 4.3 | Conservation implications

Our results highlight the importance of alpine and subalpine zones for conservation of medium and large mammal and pheasant fauna in southwest China. We note that, although a lesser conservation priority, dry-hot valleys support similar levels of species richness to subtropical montane forest. Our study is the first to assess diversity and occupancy of mammalian and pheasant fauna across the three habitat types in southwest China, and the findings that species richness and occupancy were maintained even in the low cover and fragile dry-hot valleys strengthen the arguments for an increased conservation focus in such areas. Although

dry-hot valleys in southwest China support high level of species richness for the target communities, environmental degradation and deterioration in the habitats is widespread and well-known (Tang et al., 2004). Additionally, large hydropower developments are projected to continue to increase in the upper reaches of the large rivers of southwest China (National Energy Administration (NEA), 2016), and this may become a major threat to the ecosystems of dry-hot valleys. Long-term monitoring programmes will be essential to comprehensively understand the pressure of human-induced disturbance on community and species distributions and dynamics.

Recently, a rapidly growing number of camera trapping studies around the world have produced data on many species, including rare species for which it is logistically not feasible to obtain occurrence data by traditional techniques. We encourage greater integration and standardization among camera trap monitoring networks worldwide (Rich et al., 2017) to obtain more comprehensive insight relevant to local and global biodiversity conservation. Our study provides another example of the utility of hierarchical occupancy models for integrating analysis of camera trap data from multiple study areas. We recommend broader application of the hierarchical Bayesian modelling approach to camera trap data, to capitalize on the valuable information available across entire communities and to inform effective conservation planning for wildlife populations regionally and globally.

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## DATA ACCESSIBILITY

The data supporting the results are provided in the Supporting Information.

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## BIOSKETCHES

**Xueyou Li** is particularly interested in how human pressure and environmental factors affect wildlife populations. He uses long-term data on occurrence and ecological models to evaluate diversity and distribution patterns.

**William Bleisch** is interested in protected area management and the sustainable engagement of local communities in conservation, and the use of camera trapping to monitor progress in conservation.

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Author contributions: X.L. and X.J. conceived the ideas; X.L. and X.J. collected the data; X.L. analysed the data; X.L. and W.V.B. drafted the manuscript; and all authors contributed substantially to revisions.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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