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# Topography and soil type are critical to understanding how bird and herpetofaunal communities persist in forest fragments of tropical China

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## ABSTRACT

Habitat fragmentation in heterogeneous landscapes is a non-random process, with farmers selecting lands with flat topography and fertile soils. To understand the persistence of biodiversity in forest fragments in such landscapes, it is necessary to distinguish between factors associated with fragmentation (e.g., area and distance to edge) and characteristics of where fragments are located (e.g., topography and soil conditions). Location factors have been previously demonstrated to be important in explaining the persistence of trees in fragments in the environmentally diverse region of Xishuangbanna, China (Liu and Slik, Biological Conservation, 2014). However, it is unknown how location factors influence more mobile, short-lived organisms. We sampled 42 of the previous study's plots for birds and herpetofauna across two years. A multi-model inference approach indicated that topography was the most important predictor of amphibian diversity, with valleys having more than three times the species in other locations. Topography interacted with fragment size for bird species, and particularly forest interior (FI) species: diversity in valley plots climbed strongly with fragment area, but the relationship between area and diversity was less strong in other locations. Soil type (limestone or not) most strongly influenced the score of plots on the first axis of a NMDS ordination of FI birds. These results suggest that managers should consider the location of fragments in the landscape in prioritizing forest fragments for protection. For Xishuangbanna, all valley fragments are important to protect amphibians; amalgamating them into large fragments > 1000 ha will make them most useful for bird conservation.

## 1. Introduction

Tropical forests host at least two-thirds of the earth's terrestrial biodiversity and provide significant human benefits at local, regional and global scales through the provision of economic goods and ecosystem services (Gardner et al., 2009); therefore, the threat posed by anthropogenic disturbance to tropical forests is a global one. Among many problems, deforestation, driven by agricultural expansion, logging and urbanization, is considered as the primary threat to biodiversity, and habitat loss is also accompanied by fragmentation and degradation (Fahrig, 2003; Haddad et al., 2015). Much research has focused on fragmentation, and specifically how fragment area, shape and isolation affect plant and animal survival (Ewers and Didham, 2006; Fahrig, 2003; Matthews et al., 2014) and how fragmentation affects ecological and evolutionary processes, as reviewed by Haddad et al. (2015). The major conclusion from this research is that large fragments and corridors between fragments should be priorities for conservation. At the same time, protection of even very small fragments can retain some elements of biodiversity (Arroyo-Rodríguez et al., 2009; Chang et al., 2013).

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In conserving fragments in heterogeneous landscapes, however, there are other considerations beyond the size, shape and isolation of the fragments (Liu and Slik, 2014). In a topographically complex area, there is a need to understand how the location of the fragments (hereafter referred to as 'location factors') – their topography (e.g., valley vs. ridge) and soil (e.g., limestone vs. other kind of bedrock) – might influence the biodiversity they can retain. This is because agriculture is a biased process with farmers selecting flat topography, fertile soils, and sunny aspects (Liu and Slik, 2014), and agricultural expansion will consequently produce greater threats to biodiversity in these preferred areas (Warren-Thomas et al., 2015). Recently Liu and Slik (2014) showed that location factors were more important than 'fragmentation factors' (area, distance to edge) in predicting persistence of trees in forest fragments in tropical regions of southwest China. But trees are long-lived species with stationary adults, and fragmentation was recent (mostly within 40 years; Li et al., 2008). Hence, many of the individuals sampled may have simply persisted from an earlier time before fragmentation. A remaining question is whether location factors also influence short-lived mobile organisms, such as birds or herpetofauna, the latter of which is known to be understudied in fragmentation research (Deikumah et al., 2014).

The importance of location factors may vary among animal taxa, depending on the organisms' degree of mobility, and the strength and breadth of their habitat preferences. For example, amphibians are reliant on certain microhabitats and their associated abiotic conditions, often related to the availability of water (Baldwin et al., 2006; Beebee, 1996). Moreover, amphibians in particular may have difficulty moving through matrix land-types outside of forests (Behm et al., 2013). These characteristics suggest that amphibians may be particularly influenced by location factors. Reptiles may share many of the same problems of amphibians, but not be as extreme in their preferences, as they are more resistant to desiccation (Bell and Donnelly, 2006); reptiles have also been shown to be dependent on structural complexity and vegetation type at the site level (Bruton et al., 2016). Birds are much more mobile and have been a major taxa of focus in the study of fragmentation (Bregman et al., 2014; Vargas et al., 2011). Nevertheless, birds may have strong habitat preferences at some life stages, such as nesting (Walsberg, 1985), and some groups of species, such as understory insectivores, have particularly rigid habitat requirements (Powell et al., 2015). In general, assessment of habitat requirements of species, and subsequent prioritization of land for protection, requires inspection of multiple taxa, especially when these are of high conservation concern, such as amphibians (Beebee and Griffiths, 2005), and forest specialist birds (Bregman et al., 2014).

Southeast Asia is especially threatened by anthropogenic change and has been recognized as a priority region for conservation (Wilcove et al., 2013). Conversion of forest to agricultural crops, such as oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*) and tea (*Camellia sinensis*), is a key driver that leads to biodiversity loss in the region (Warren-Thomas et al., 2015; Wilcove et al., 2013). For example, in Xishuangbanna Prefecture, in Yunnan Province, China, 50% of forest cover has been converted primarily to rubber monocultures between 1976 and 2003 (Li et al., 2008; Xu et al., 2014). Xishuangbanna is located on the northern border of Southeast Asia, and is considered part of the Indo-Burma biodiversity hotspot, designated as one of the 25 biodiversity hotspots in the world (Myers et al., 2000). Unfortunately, forest conversion to agricultural land in Xishuangbanna is still continuing (Xu et al., 2014). Xishuangbanna is also a highly heterogeneous environment, with an undulating terrain (517–2415 m asl; Yi et al., 2014), and patchily distributed limestone soils (Clements et al., 2006; Tang et al., 2011), and hence a suitable area to look for the effects of location factors (Liu and Slik, 2014).

Here we compared the influence of fragmentation and location factors for multiple animal taxa in Xishuangbanna. We hypothesized that (a) that herpetofaunal species would be the taxa most influenced by location factors, due to their strong microhabitat preferences. We also hypothesized that (b) birds would be influenced by a mix of fragmentation and location factors, as topography and soil type influence structural and floristic differences of forest stands in different fragments (Bohlman et al., 2008), that then shape bird communities (MacArthur and MacArthur, 1961; Reidy et al., 2014). We further hypothesized (c) that fragmentation factors would be especially important for specific groups of birds, particularly those known to be very sensitive ('forest interior species') or tolerant ('open area species') of human disturbance, and thus influenced by fragmentation factors such as area and distance to the edge (Matthews et al., 2014).

## 2. Methods

### 2.1. Study area

The study was conducted within a 15 km radius circle centered on Xishuangbanna Tropical Botanical Garden (XTBG, 21° 55′N, 101° 15′E), a research institute of the Chinese Academy of Sciences, located in the Menglun township of Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China (Fig. 1). Xishuangbanna is bordered by Laos from the south and Myanmar from the southwest and lies within tropical Southeast Asia, with some characteristics of the subtropics (Cao et al., 2006). The climate is mainly governed by two seasons: dry, from November to April, and wet, from May to October. The annual temperature varies from 15.1 °C to 21.7 °C; annual precipitation varies from 1193 mm to 2491 mm (Cao et al., 2006). There are a few large nature reserves, and the rest of the landscape is a mosaic of forest patches, varying in their sizes and shapes, scattered among rubber monocultures. Rubber represents the majority of the matrix, with developed areas and banana plantations being minor components near the town of Menglun. Rubber itself contains a low percentage (37%) of extant bird species in the region, with only generalists being abundant in it (Sreekar et al., 2016). In this landscape, Liu and Slik (2014) established a priori 50 vegetation sampling plots that captured a wide range of environmental conditions (topographical positions, soil types) and fragment sizes (see Fig. 1, Table S1). As there were multiple plots in the larger fragments, fragment identity was included as a random variable in the analysis (see below).

### 2.2. Animal surveys

We placed a bird point count station in 42 vegetation plots from Liu and Slik's (2014) study that are found within 18 forest patches ('fragments', size ranging 1.71 ha to 13,837.27 ha), and at elevations ranging from 541 to 1477 m asl. Of the original 50 plots, two plots were deforested before the sampling for this project. In addition, we removed from the analysis two plots that had < 0.79 ha of forested area (the area of a circle of 50 m radius, the size of the point count for birds), and four plots that were too small linearly to place a 200 m long transect (for herpetofauna) inside them.

A variable radius (with all birds seen or heard designated to 10 m radius intervals within 50 m) point count method was applied to survey birds (Bibby et al., 2000). All the plots were visited five times (dry season: March–May 2014, November–December 2014 and March–May 2015; wet season: July–August 2014 and August–September 2015) by the same observer (SKD). Point counts of 15 min in length were conducted between 0700 h to 1030 h, when most of the birds are highly active, and all birds visually or aurally detected were recorded. The order of plot visitation routines was varied to ensure that each plot was sampled both early (close to 0700 h) and late (close to 1030 h) to avoid time-of-day effects. Rain, high wind and thick fog were avoided during the data collection. Camouflage clothes were worn and SKD spent 2 min motionless prior to the point count in order to minimize bias related to his disturbance.

We established one 200 × 5 m transect at each of the same 42 plots to sample herpetofauna. The transects were placed on the access paths of the vegetation plots so that the minimum distance between the starting point of transect and the forest edge was 25 m for the small (< 100 ha) forest fragments (n = 12) and > 100– m for the other fragments, and the center of the transect was at the center of the bird point count station.

We conducted visual and auditory encounter surveys, which are the most effective sampling methods for herpetofauna (Doan, 2003). Two observers (SKD and one local assistant) walked down the midline of the transect for 1 h, gently disturbing the forest ground and shrub layer with a stick and searching visually for amphibians, lizards, geckos and

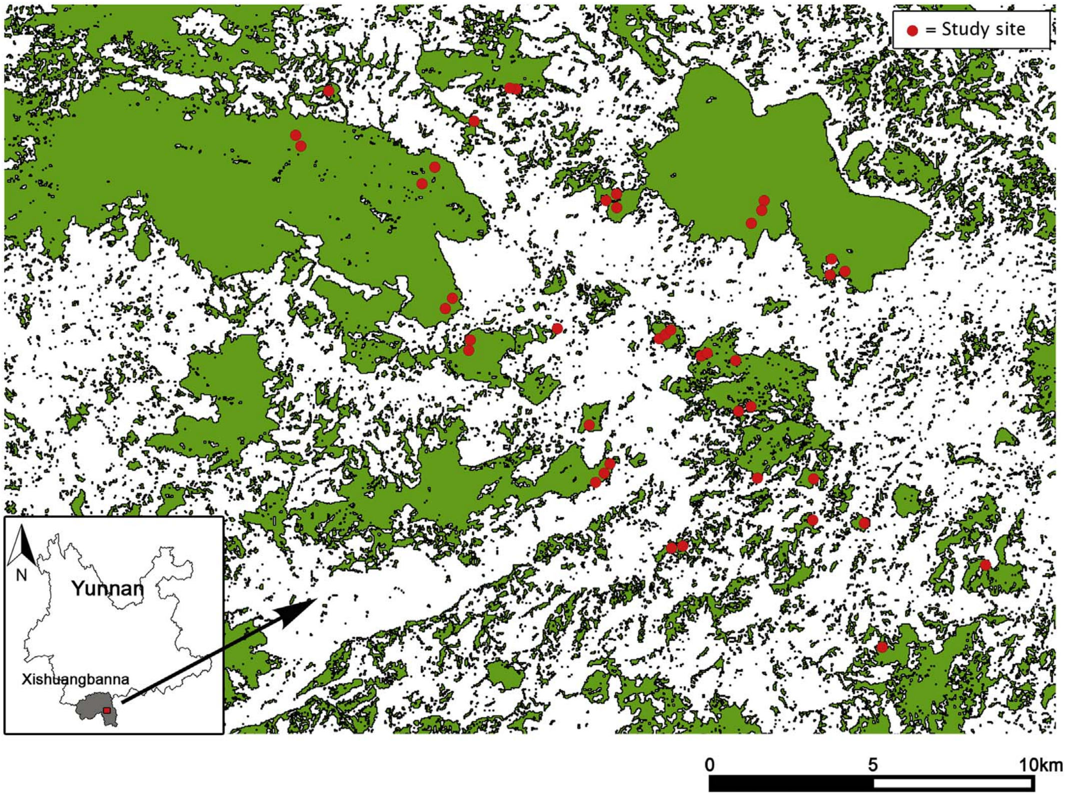

**Fig. 1.** Map showing the location of study area, natural forest (in green) and 42 plots (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

snakes within 2.5 m to each side of the midline. All transects were sampled twice during the wet season (September–October 2014 and July–August 2015), and conducted between 1900 h–2300 h (exploratory surveys during the dry season showed very few encounters).

### 2.3. Statistical analysis

#### 2.3.1. Classification and preparatory calculations

We classified bird species by their habitat preferences using the Handbook to the Birds of the World (HBW) Alive, online repository (http://www.hbw.com) and followed the taxonomy proposed by HBW website. Bird species were categorized as forest interior (FI) species, open area (OA) species, and generalists (Appendix 1). Both resident and migrant bird species were included in the analysis, because the data were collected over two years and covered both migratory and off-migratory periods.

We used Distance software version 6 (Thomas et al., 2010) to calculate detection probabilities for each species, and thereby estimated the density of birds within 50 m of the plot. For details of this analysis, please see Supplementary Methods.

#### 2.3.2. Explanatory and response variables

Explanatory variables were grouped as either ‘fragmentation’ or ‘location’ factors. The fragmentation factors included: fragment size ($\log_{10}$ transformed), fragment area/perimeter ratio ($\log_{10}$ transformed), distance from the edge (Euclidian distance from the center of the point count to the nearest edge of the fragment) and isolation. We calculated mean proximity index as an index for isolation (see Supplemental Methods for more details). For all calculations, we used the land cover map created for the previous study by Liu and Slik (2014). Location factors included: soil type (classified into limestone [n = 10] and non-limestone [n = 32]), and topography (as three categories; valley [n = 13], mid-slope [n = 13] and ridge [n = 16]); see methods in Liu and Slik (2014). Topography was strongly associated with elevation, so we did not include elevation as a separate factor. We also measured some ‘degradation-related’ factors of the plot in the fragment, including disturbance (plots were considered disturbed if we observed logging and/or ginger planted in them) and whether the plot was in a nature reserve or not. The characteristics of plots of different fragment sizes, in terms of their fragmentation, location and degradation variables, are summarized in Table S1.

As response variables, we considered aspects of species diversity, abundance, and composition. We ran separate analyses for total birds, the two habitat specialist groups of birds (FI and OA), for amphibians and for retiles. For birds, species accumulation graphs were essentially flat between the fourth and fifth visits (Fig. S1), suggesting that almost all bird species in this area were detected. We found species richness to be highly correlated with Shannon-Wiener diversity, as well as with jackknifed estimates of species richness, and used species richness itself as the primary response variable. For herpetofauna, species accumulation graphs did not reach an asymptote (Fig. S2), so as a metric of diversity we calculated 1st order Jackknife species estimates (Chao and Lee, 1992) separately for amphibians and reptiles with the ‘*vegan*’ package (Oksanen, 2013). For abundance, we used the DISTANCE-adjusted density for birds only, judging that we did not have enough individuals of herpetofauna to measure abundance accurately. For composition, we used non-metric multidimensional scaling (NMDS; Oksanen, 2013) to summarize species abundance data, and extracted the scores on the first axis to then analyze using our modeling framework (although the second axis also explained substantial variation, there were no strong visual patterns related to location or fragmentation patterns; see Fig. S3). Plots with zero species richness were not included in the composition analysis.

#### 2.3.3. Modeling

All the analyses were carried out on R statistical software, version 3.1.3 (R Core Team, 2015). We built generalized linear mixed models (GLMM), using the ‘lme4’ package (Bates et al., 2014). In these models, the identity of the fragment was included as a random factor. Normal distributions were used to model total bird species richness, the densities of the three bird groups, and the compositional analyses (NMDS scores). Preliminary analyses demonstrated that modeling with normal distributions for the species richness of total bird species produced smaller residuals than Poisson distributions for that variable. For other models (species richness of FI, OA birds; estimated species richness of amphibians and reptiles), the counts per point were lower and we used Poisson distributions.

Before building the GLMMs, we first checked whether the residuals of the global models were spatially autocorrelated, since spatial autocorrelations can affect model selection as well as violate the independence of samples. We used Moran's I test in the '*ape*' package (Paradis et al., 2004) and found spatial autocorrelation to be insignificant ($P < 0.12$ for all cases, except for FI bird species composition where the value was 0.06). We found area perimeter ratio ($\log_{10}$), and isolation were highly correlated with fragment area ($r > 0.70$), and consequently we removed area perimeter ratio and isolation from the model. All remaining variables had variance inflation factors below 4.0, suggesting multicollinearity did not affect the models.

Due to the many variables included in the models, we had little power to include many interactions, so we considered only interactions between location and fragmentation factors. The interaction between fragment area and topography was found to be important and retained in the modeling, whereas that between fragment area and distance to the edge was never important and dropped from the models. Soil type had limited sample size and was not equally distributed in relation to other factors (e.g., most limestone plots were in mid-slope fragments, see Table S1), so we did not include interactions including this variable.

To assess the best models, we applied a multi model inference approach (Burnham and Anderson, 2002) with the '*MuMIn*' package (Barton, 2015), which gives all possible combinations of explanatory variables and grades the models according to their Akaike Information Criterion (AIC) with a correction for finite sample sizes (AIC*c*) and AIC weights (Burnham and Anderson, 2002). Then we conducted model averaging to make inferences on the relationship between explanatory and response variables from a subset of models with $\Delta AICc < 4$, using the zero method of calculating coefficients in order to determine which explanatory factors have the strongest effects (Grueber et al., 2011). The 95% confidence intervals, calculated from the distributions of the standardized coefficient estimates, were employed to highlight terms for which there was high confidence in the direction of the effect. The fit of the full (all variables) GLMM models were assessed following Nakagawa and Schielzeth (2013), where $R^2$ marginal represents the variance explained by the fixed factors, and $R^2$ conditional represents the variance explained by the whole model (including the random variable). To visualize the effects of the interactions between topography and fragment area, we plotted the conditional plots following the method employed in the "*visreg*" package and described in Breheny and Burchett (2017), showing the partial residuals when the rest of the variables in the averaged models are held constant.

## 3. Results

We observed 135 bird species in 4697 detections, including 54 species categorized as FI species and 18 species categorized as OA species. Species richness averaged 35.6 ± 9.4 (SD) species per plot and ranged from 22 to 61 species. For amphibians, we identified 25 species in 133 observations of individuals; species richness averaged 2.0 ± 1.9 species per transect and ranged from 0 to 6 species. For reptiles, 17 species were identified in 153 observations; species richness averaged 2.0 ± 1.5 species per transect and ranged from 0 to 7. For more details on the species, including the number of migrant birds, common families and threatened species, see the Supplementary Results.

The averaged regression models indicate that location and fragmentation factors interact to determine the diversity of total bird species, as well as FI species in particular (Table 1, Fig. 2). In these analyses, the largest coefficients are for the interaction terms: valley

**Table 1**

Model averaged estimates (coefficients) of variables that explained differences in species richness of all birds, forest interior birds (FI) and open area birds (OA) among plots. Model averaged estimates (A, standardized coefficients), confidence intervals (CI) and relative importance (RI) values are shown for all variables; shaded cells are those where the 95% CI does not include zero. For categorical variables with different levels, positive coefficients show that the first level designated had higher values than the second. NA = Not appeared; variable not in the models with $\Delta AICc < 4.0$. Fit statistics are shown for the full GLMM models (all variables included), following Nakagawa and Schielzeth (2013).

| | | Total bird species richness | | | | FI species richness | | | | OA species richness | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $R^2$marginal, $R^2$conditional | 0.63, 0.70 | | | | 0.67, 0.77 | | | | 0.37, 0.37 | | | |
| | | A | CI 2.5% | CI 97.5% | RI | A | CI 2.5% | CI 97.5% | RI | A | CI 2.5% | CI 97.5% | RI |
| Location factors | Topography (valley vs. ridge) | 0.630 | −0.043 | 1.303 | 1.00 | 0.096 | 0.012 | 0.180 | 1.00 | NA | NA | NA | NA |
| | Topography (valley vs. mid-slope) | 0.398 | −0.287 | 1.084 | | 0.031 | −0.057 | 0.118 | | NA | NA | NA | |
| | Topography (mid-slope vs. ridge) | 0.211 | −0.420 | 0.843 | | 0.064 | −0.021 | 0.149 | | NA | NA | NA | |
| | Soil type (limestone vs. non-limestone) | 0.042 | −0.150 | 0.235 | 0.25 | 0.005 | −0.018 | 0.027 | 0.24 | 0.005 | −0.044 | 0.056 | 0.16 |
| Fragmentation factors | Distance to edge (log) | 0.221 | −0.103 | 0.544 | 0.77 | 0.039 | 0.015 | 0.063 | 1.00 | −0.119 | −0.279 | 0.041 | 0.82 |
| | Fragment size (log) | 0.769 | 0.326 | 1.211 | 1.00 | 0.104 | 0.050 | 0.158 | 1.00 | −0.090 | −0.260 | 0.080 | 0.68 |
| Degradation factors | Within nature reserve or not (in vs. out) | 0.009 | 0.116 | −0.098 | 0.09 | 0.001 | 0.013 | −0.015 | 0.12 | 0.017 | 0.108 | −0.073 | 0.28 |
| | Disturbance (no vs. yes) | 0.001 | −0.062 | 0.063 | 0.08 | −0.001 | −0.011 | 0.009 | 0.14 | 0.003 | −0.043 | 0.051 | 0.17 |
| Interaction term | Fragment size: Topography (valley vs. mid-slope) | −0.751 | −1.408 | −0.094 | 1.00 | −0.054 | −0.129 | 0.021 | 1.00 | NA | NA | NA | NA |
| | Fragment size: Topography (valley vs. ridge) | −1.242 | −1.902 | −0.581 | | −0.138 | −0.215 | −0.060 | | NA | NA | NA | |
| | Fragment size: Topography (mid-slope vs. ridge) | −0.425 | −1.080 | 0.229 | | −0.079 | −0.161 | 0.003 | | NA | NA | NA | |

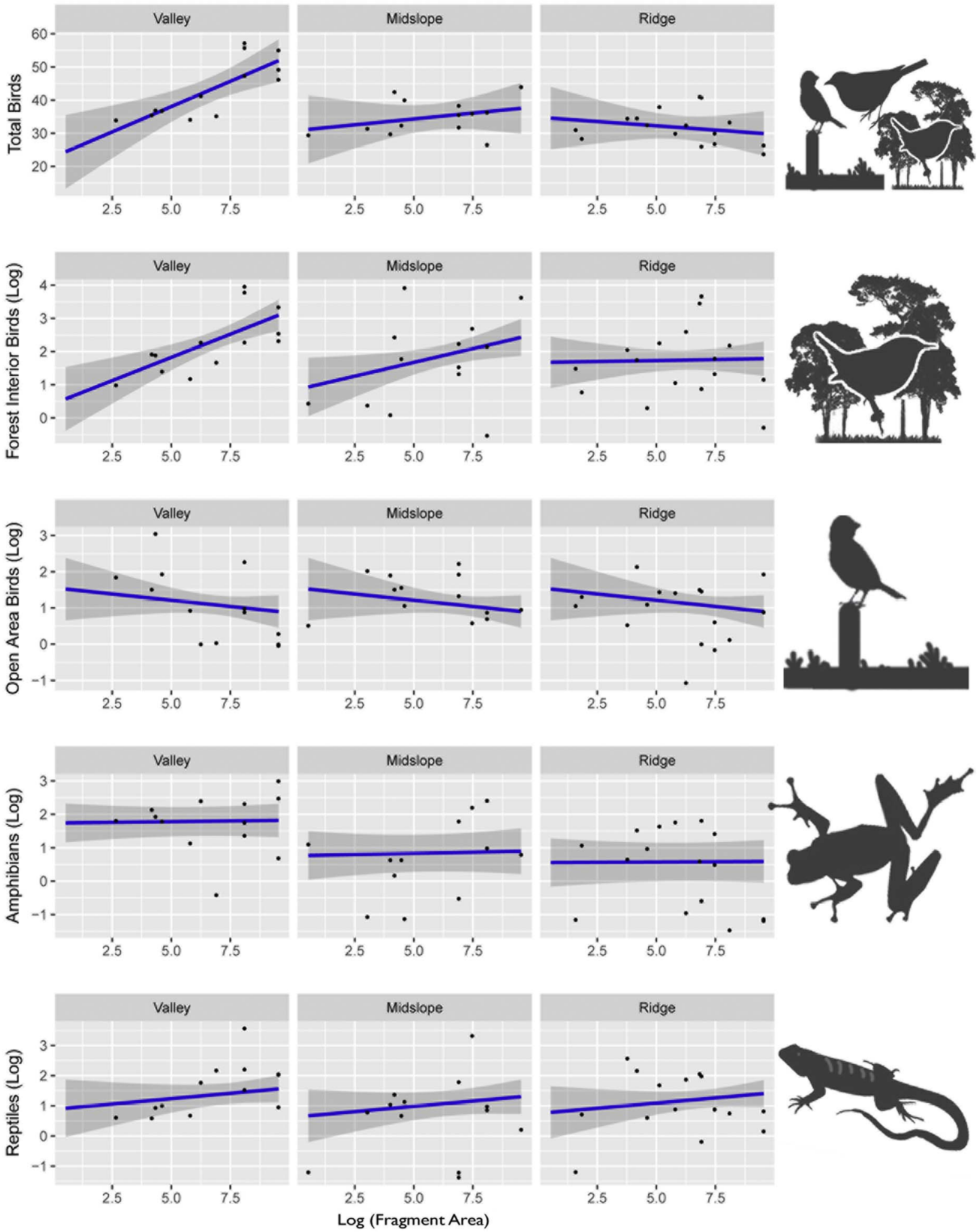

**Fig. 2.** The varying effect of fragment area for plots at different topographical locations, for the different taxa. The regression lines represent the model coefficients (Tables 1 and 2), with the shaded area being the 95% confidence interval for the line. Data points represent the partial residuals, calculated using predictions from the model and keeping all factors other than topography and fragment size constant.

plots had a strong effect of fragment area, with diversity rising with larger areas, whereas the area-diversity relationship becomes less strong for midslope plots and close to nonexistent for ridge ones. Indeed, for total bird species and FI species the diversity curves in valleys only go higher than mid-slopes and ridges once those valley fragments are > 1000 ha. In contrast, for OA species, the strongest influence was distance to the edge (though the confidence interval for this coefficient included zero), and there was neither interaction term nor any impact of topography (note the overall model fit was low, $R^2$ marginal $< 0.40$). The same qualitative trends are also seen for bird density (Table S2): total species and FI species were dominated by the fragment area vs. topography interaction, and OA species by fragmentation factors (as well as presence in a nature reserve). Bird composition, however, had a different mix of location and fragmentation influences (Table S3, Fig. S3), with total species showing the largest impact from fragmentation factors, FI species being shaped most by soil type (although $R^2$ marginal was only 0.35, and there was a substantial effect of the random variable, fragment identity), and OA species being poorly explained ($R^2$ marginal $= 0.25$).

In general, the models for amphibians and reptiles were simpler than those for birds and often only weakly explained the variation (Table 2, Table S4; $R^2$ marginal $< 0.40$ for reptile diversity, and amphibian and reptile composition). Amphibian diversity was the exception ($R^2$ marginal $= 0.54$), and here topography was the largest factor. When all variables in the model, besides fragment size and topography, were held constant, the predicted species richness for valley plots was on average 3.14 higher than midslope ones, and 3.98 higher than ridge ones. Soil type was the second most influential factor on amphibian diversity, although the confidence interval for the coefficient included zero; 5 of 10 (50%) limestone plots had zero amphibians, whereas only 6 of 32 (19%) non-limestone plots had this result. For reptilian diversity, fragment area was the most important factor, for amphibian composition, distance to the edge was, and for reptile composition, both locations factors (topography and soil type) had high relative importance ($> 0.85$); yet in all of these models the confidence intervals for the coefficients included zero.

## 4. Discussion

We found that aspects of the location of forest fragments were critical to predicting the bird and herpetofaunal communities that persist in them, either as direct influences (such as topography on amphibian diversity, or soil type on FI bird composition), or as a mediating factor shaping the effect of fragment area. The results were mixed in their support for our hypotheses. Amphibians had the strongest response to location factors: the topography and soil type coefficients for them were larger than those for fragmentation and interactions. The results for reptiles, although the models had poor fit, were often different from amphibians in which factors were most influential. While there were no clear effects of location factors on bird diversity, topography was important because it affected how fragment area affected diversity (i.e., the interaction term). Although we hypothesized guilds of disturbance sensitive or resistant species would be most affected by fragmentation, we found FI species to be similar in terms of their diversity and density to the total species analysis, and sensitive to soil type in their composition. OA species were, as expected, most influenced by fragmentation factors (distance to edge and area), and also some degradation factors.

Before we discuss the mechanisms that underlie the fragmentation and location factors in this study, and their interaction, however, we should acknowledge limitations of the study. Chief among these is the small sample size of plots (42), inside an even smaller set of fragments (18). The random factor of fragment in general did not explain a high proportion of the variation (compare $R^2$ marginal to $R^2$ conditional in the Tables), except in the case of FI bird composition, where the pattern of species presence and absence was largely similar for plots within the same fragment (this was also shown by a marginally significant spatial autocorrelation result for this category of birds). The low sample size issue limited the number of variables that we included in the model, as

**Table 2**

Model averaged estimates of variables that explained differences among sampling sites in species richness of amphibian and reptiles. Statistics as in Table 1; shaded cells are those where the 95% confidence interval does not include zero.

| | | Amphibian estimated species richness | | | | Reptile estimated species richness | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $R^2$marginal, $R^2$conditional | 0.54, 0.66 | | | | 0.32, 0.32 | | | |
| | | A | 2.5% CI | 97.5% CI | RI | A | 2.5% CI | 97.5% CI | RI |
| Location factors | Topography (valley vs. ridge) | −0.204 | −0.312 | −0.096 | 1.00 | −0.031 | −0.143 | 0.080 | 0.51 |
| | Topography (valley vs. mid-slope) | −0.160 | −0.267 | −0.054 | | −0.057 | −0.195 | 0.082 | |
| | Topography (mid-slope vs. ridge) | −0.036 | −0.185 | 0.113 | | 0.027 | −0.079 | 0.134 | |
| | Soil type (limestone vs. non-limestone) | 0.072 | −0.067 | 0.210 | 0.65 | 0.002 | −0.032 | 0.037 | 0.14 |
| Fragmentation factors | Distance to edge (log) | 0.0002 | −0.024 | 0.024 | 0.10 | 0.041 | −0.068 | 0.150 | 0.49 |
| | Fragment size (log) | 0.007 | −0.051 | 0.065 | 0.19 | 0.081 | −0.065 | 0.228 | 0.70 |
| Degradation factors | Within nature reserve or not (in vs. out) | −0.009 | 0.053 | −0.070 | 0.19 | −0.013 | 0.060 | −0.086 | 0.24 |
| | Disturbance (no vs. yes) | 0.010 | −0.043 | 0.063 | 0.21 | −0.002 | −0.037 | 0.033 | 0.14 |
| Interaction term | Fragment size: Topography (valley vs. mid-slope) | 0.006 | −0.066 | 0.078 | 0.04 | −0.001 | −0.045 | 0.042 | 0.02 |
| | Fragment size: Topography (valley vs. ridge) | −0.005 | −0.075 | 0.065 | | −0.003 | −0.067 | 0.060 | |
| | Fragment size: Topography (mid-slope vs. ridge) | −0.012 | −0.137 | 0.113 | | −0.002 | −0.056 | 0.051 | |

more complex models failed to converge. Because of this issue, and the unequal distribution of plots (e.g., lack of limestone sites in small fragments), we were unable to look at interactions that could be important, such as between soil type and the fragmentation factors. Further, some factors removed because of their collinearity to other variables, such as isolation, might in their own right be better predictors of some of the response variables. These missing factors and interactions might explain how some of our models had poor model fit ($R^2$ marginal $< 0.40$) especially for those taxa with small numbers of species (e.g., OA birds, reptiles).

Another different kind of limitation is that our study only observed the distribution of animals and not their survival and reproduction. Adding information about fitness in this landscape is likely to increase the value of large forests over small fragments, as small fragments may act like ecological traps or ecological sinks (Battin, 2004). From the results of other fragmentation studies, populations in small fragments could ultimately end up with genetically diluted, shrinking populations due to poor carrying capacity, increased predator pressure, hindered inter-patch movement and increased brood parasitism (Athrey et al., 2011; Harrison, 1991).

### 4.1. The mechanisms of location effects

A major mechanism that may underlie the direct effects of location factors in this study are differences between different topographies and soil types in forest structure. Topography has a direct influence on forest structure and height in our study area (Liu et al., 2014): tall trees with high foliage density are concentrated in valley areas (canopy height in fragments was estimated as > 15 m), while the ridge-tops are covered by shorter forest (canopy height estimated as < 8 m). The proximate mechanisms behind such structural differences include high soil/water resource availability in valley areas and high wind on ridge tops (Bohlman et al., 2008; Nagamatsu and Miura, 1997). Differences among soil types in such structural attributes is less, but because limestone forests in this region are dominated by one large canopy and two understory tree species, they are thus structurally different from other forests, which have more complex layers and denser understory (Tang et al., 2011). Amphibians in particular may respond to dense vegetation and thick canopy covers, crucial for sustaining the microclimatic conditions that facilitate their movement (Andrew and Mark, 2008; Baldwin et al., 2006), and this might be a factor increasing their abundance in non-limestone forests. Microclimatic conditions might also be important for forest specialist birds, which showed differences between limestone and non-limestone plots (although this result was partially explained by spatial autocorrelation). For example, avian understory specialists often require specific low-light conditions (Stratford and Stouffer, 2015).

Beyond the connection to forest structure, location effects can also have a direct effect on the environmental conditions in the forest. Topography is obviously important to water collection: valley areas collect and absorb surface rain water and gently release the water into springs and slow-flowing streams. Topography thus controls the availability of moist, thick and damp leaf layers that are an essential feature for the survival of amphibians (Beebee, 1996). Amphibians especially use leaf litter and other damp microhabitats as diurnal shelter sites, and these retreats are especially important to survive during the dry season (Seebacher and Alford, 2002), again explaining why topography strongly influenced their diversity.

### 4.2. The influence of fragmentation factors in the Xishuangbanna landscape and their interaction with location factors

One aspect of fragmentation in Xishuangbanna that may be different from fragmentation elsewhere is that the matrix is not an open, tree-less ecosystem. The predation risk for animals that is provided by rubber may be more similar to a forest, even though the matrix may not have rich sources of food. Thus, this matrix may be particularly permeable for some species like birds, reducing the ordinary symptoms of fragmentation such as area effects.

Despite the potential for rubber monoculture to be a permeable matrix, we found evidence of the strong influence of fragmentation variables for some taxa in some locations. In a separate study working at the same sites, we found that nocturnal predatory birds (owls) respond positively to the area of fragments (Dayananda et al., 2016). In this study, total species of birds and FI species in particular displayed strong area effects in valleys and midslopes; OA species and reptiles had less steep slopes in all topographical locations (see Fig. 2). We should point out that these effects that we attribute to fragment area here could also be due to correlated variables such as isolation.

Our results can be compared to those of Chang et al. (2013), who also studied the impact of fragmentation of birds in the same landscape, but emphasized the conservation value of very small fragments (size < 6 ha). Their fragment sizes were in general much smaller than ours (median fragment size: 3.0 ha for Chang et al. vs. 518.31 ha for this study). The birds they found in these small fragments were mostly considered generalists here. For example, they recorded a total of 15 FI species, compared to 54 found in this study. While small fragments of the size Chang et al. studied (i.e. < 10 ha) may be important for continuing populations of generalist birds, our results show that larger fragments (and especially those > 1000 ha in the valleys) are necessary for the survival of FI birds in this landscape. Another recent fragmentation study in Xishuangbanna, Zhang et al. (2017), has found the greatest predictor of avian diversity is distance to fragments > 100 ha, and the proportion of natural forest at the landscape scale.

What mechanisms are behind the fragment area/topography interaction, in which the fragment area effect was strongest for valleys in predicting bird diversity and density (total species and FI species)? We believe that there may be more human disturbance in small fragments in valley areas because such fragments are simply closer to human settlements. Specific mechanisms may include structural simplification of the forest through activities such as firewood and polewood collection, and hunting, which has been a strong driver of extirpation in this area (Sreekar et al., 2015). This subject illustrates that although we attempted to disconnect degradation from fragmentation factors, the two are really inseparably intertwined.

### 4.3. Conservation implications

The results of our study demonstrate that in an environmentally diverse landscape it is important to consider where fragments should be prioritized (their topography and soil conditions) as much as aspects related to their size or relative position to other fragments. A choice based purely on size would not be sufficient, as not all large fragments are equal, and in this landscape large fragments in valleys have more diversity than those elsewhere. Nor would a choice based purely on topography be fully informed, as for birds, including FI species, fragment size is important, especially in valleys where species diversity is highest.

Given that valley fragments of all sizes are important for amphibians in Xishuangbanna, we recommend preserving even small fragments of such type in this landscape. Fragments of both limestone and non-limestone soils are important because, although amphibians tended to avoid the limestone points, FI bird composition was distinct there, and such differences should be preserved. In general, large fragments > 1000 ha are already protected. Nevertheless, a strategy to improve the amount of biodiversity these reserves protect would be to connect smaller fragments to them, increasing their size and value for bird conservation. Unfortunately, valley bottoms are where the threat from farming is highest, due to farmers selecting the most accessible locations. As both agriculture and biodiversity prefer the same locations, policy makers are needed to intervene to ensure the protection of any remaining fragments in those specific locations.

We finally emphasize the importance of using multiple taxa to prioritize what lands in a landscape should be conserved (Croci et al., 2008; Kotze and Samways, 1999). The best designs for tree species (Liu and Slik, 2014), nocturnal avian predators (Dayananda et al., 2016), diurnal non-predaceous birds, amphibians and reptiles are different from each other, and hence multiple strategies are required (i.e. prioritization of some location characteristics as well as increasing connectivity). In particular, pooling data on amphibians and reptiles together (as herpetofauna) could obscure important differences about how these taxa are responding to human disturbance in a changing landscape.

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## Appendix 1. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.08.034.

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