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BIODIVERSITY RESEARCH

The use of species–area relationships to partition the effects of hunting and deforestation on bird extirpations in a fragmented landscape

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ABSTRACT

Aim Forest fragmentation is often accompanied by an increase in hunting intensity. Both factors are known drivers of species extirpations, but understanding of their independent effects is poor. Our goal was to partition the effects of hunting and fragmentation on bird species extirpations and to identify bird traits that make species more vulnerable to these two stressors.

Location Menglun, Yunnan, SW China

Methods We studied the landscape within 10 km radius of Menglun town, where forests have become highly fragmented by monoculture rubber plantations. We compiled data on birds recorded between 1954 and 1983 before forest loss and compared it with a checklist prepared between 2011 and 2014. We used countryside and matrix-calibrated species–area models (SAMs) to estimate the observed slope of forest bird extirpations in Menglun and compared it with the slope expected in the absence of hunting. We also investigated six ecological traits to determine those that best explained bird extirpation probability (EP).

Results We found that 34% of the bird fauna had been extirpated from the study landscape, and the estimated slopes of countryside and matrix-calibrated SAMs for forest birds were around 1.4 and 1.7 times higher, respectively, than the 0.35 expected without hunting. Bird EP was strongly associated with size, and understorey insectivores that are known to be susceptible to fragmentation were less susceptible to hunting than frugivores. Given evidence of past and present hunting activity in the area, and the lack of support for alternative explanations, we suggest that hunting increased forest bird extirpations by around 1.3- to 1.6-fold.

Conclusions This study highlights the importance of using species–area relationships to separate area effects from the impacts of hunting. Our results suggest that hunting substantially increases species extirpations in tropical fragmented landscapes and conservation interventions that only target deforestation will therefore be inadequate.

Keywords
Bird traits, defaunation, forest loss, frugivores, rubber plantations, tropical extinctions.

INTRODUCTION

The modification of tropical landscapes by human exploitation and the consequent forest fragmentation is causing severe depletion of native species (Sodhi & Ehrlich, 2010; Gibson *et al.*, 2011). Increases in roads and trails associated with fragmentation also increase forest accessibility to hunters, further intensifying species loss (Peres & Lake, 2003; Sodhi *et al.*,

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2004; Bregman *et al.*, 2014). Although biodiversity in most parts of the tropics is affected by both forest fragmentation and hunting, many studies only address fragmentation (Galetti & Dirzo, 2013), which is inadequate due to the cascading effects caused by multiple stressors (Brook *et al.*, 2008). Here, we ask how to partition the effects of multiple stressors. Knowing the answer is crucial for conservation policy, as different threats have different solutions. For example, policies aimed at only deforestation might prioritize increasing the area protected, whereas policies aimed at hunting might focus on management of existing reserves.

The classic power function model ($S = cA^z$; Arrhenius, 1920) is widely used to project species extirpations and extirpation debts due to habitat fragmentation (e.g. Pimm & Askins, 1995; Brooks *et al.*, 1999; Wearn *et al.*, 2012; Olivier *et al.*, 2013). Recently, this model was adapted to better predict species extirpations due to the alteration of habitats through human exploitation (e.g. Pereira & Daily, 2006; Koh & Ghazoul, 2010; Hanski *et al.*, 2013). However, in situations where extirpations are driven by multiple stressors (e.g. hunting and deforestation), species–area models (SAMs) are likely to underestimate them (Laurance, 2008; Fattorini & Borges, 2012). In such situations, incorporating past and present species lists and forest cover into a species–area model can be used to estimate the inflation in the slope (z) by comparing the measured slope with the expected species–area slope of the taxon due to area effects alone. Recognition of slope inflation can help identify the presence of an additional threat, such as hunting, and provide an estimate of the increase in extirpations resulting from the additional threat.

Although several recent studies have discussed the effects of hunting on mammal extirpations (e.g. Corlett, 2007; Abernethy *et al.*, 2013; Benchimol & Peres, 2013), few have explored effects on birds and most of these on selected large species only (e.g. Bennett *et al.*, 1997; Datta, 2009). Birds make useful tools for biodiversity investigations because of their diversity, available literature and their role in provision of ecosystem services (Bregman *et al.*, 2014). Among tropical forest birds, large frugivores and understorey insectivores are severely affected by anthropogenic disturbance (Bregman *et al.*, 2014). Understorey insectivores have poor dispersal abilities and high habitat specificity, making forest fragmentation the key factor affecting their survival (Sodhi *et al.*, 2004; Bregman *et al.*, 2014). However, they are not usually hunted. Large forest frugivores, on the other hand, are affected by both fragmentation and hunting (McConkey *et al.*, 2012; Bregman *et al.*, 2014). Local people hunting for meat or traditional ornamentation often take large frugivores (Bennett *et al.*, 1997; Sodhi *et al.*, 2004; Datta, 2009). Lack of adequate food or nesting sites, low reproductive output, and requirement of large home ranges are also potentially important factors increasing their extirpation probability (EP) in fragmented landscapes (Sodhi *et al.*, 2004). However, studies in landscapes without hunting have shown that medium to large frugivores such as pigeons, parrots, toucans and hornbills often track their food resources, cross non-forest matrices and visit smaller forest fragments and agroforests (Lees & Peres, 2008; Lenz *et al.*, 2011; Mueller *et al.*, 2014). This suggests that although deforestation may contribute to frugivore population declines, hunting may be the key factor affecting their survival (Datta, 2009; Bregman *et al.*, 2014).

In this study, we examined the influence of both hunting and forest fragmentation on birds in a species-rich region of SW China (Ding *et al.*, 2006), where tropical forests are hunted and have been recently fragmented by expanding monoculture rubber plantations (Wang, 1991; Yi *et al.*, 2014). This landscape was largely forested in the mid-20th century (Fig. 1), when the area was previously surveyed for birds between 1954 and 1983 (Yang, 1993; Yang *et al.*, 1995; Xu *et al.*, 2006; see 'Bird surveys' section for details). To separate the effect of hunting from that of forest loss, we used matrix-calibrated and countryside SAMs (Pereira & Daily, 2006; Koh & Ghazoul, 2010) to estimate the slope (z) of forest bird extirpations in the landscape and compared it with the expected species–area slope for birds in the absence of hunting ($z = 0.35$; Koh & Ghazoul, 2010; Pereira *et al.*, 2014; see 'Species–area models' section for details). It should be noted that this expected species–area slope was derived from a review of fragmentation studies and, because it is likely that many landscapes studied were also exposed to hunting, use of this figure may still inflate the role of habitat loss. However, as we were interested in the role of hunting, this was a conservative approach for our study.

We predicted that the slopes of the matrix-calibrated and countryside SAMs calculated for forest birds in the study landscape would be higher than the expected slope ($z = 0.35$) in an unhunted landscape, because of the evidence for past and current hunting in the area and no support for the influence on birds of other forms of human disturbance (see Discussion). In addition, we predicted that hunting would lead to a slope increase that would be higher for the forest frugivores favoured by hunters than forest understorey insectivores. Furthermore, we used a comparative macroecological modelling approach to determine the bird life history and ecological traits that influence extirpation risk, emphasizing the independent effects of size and diet.

METHODS

Study area

We conducted our study in Menglun (21°55′N, 101°15′E; 335 km^2), Xishuangbanna Prefecture, Yunnan Province, tropical SW China. We focused on the area within a 10-km radius of the Xishuangbanna Tropical Botanical Garden (XTBG), which covers 93% of the total area (335 km^2) within the political boundaries of Menglun. In this area, rubber plantations expanded from 12% to 46% of the land area between 1988 and 2006 (Hu *et al.*, 2008), after a change in land tenure regulations resulted in a massive expansion of smallholder rubber farms (Yi *et al.*, 2014). Hunting has also

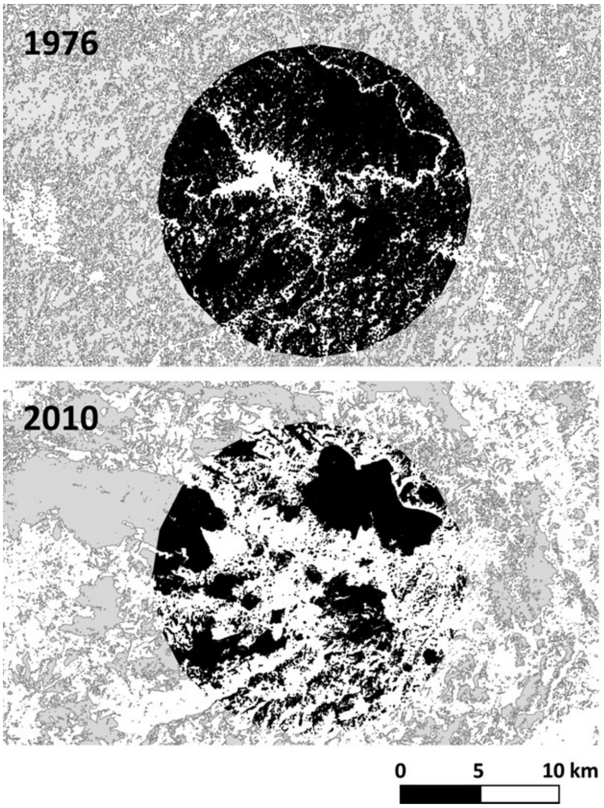

Figure 1 Maps of the Menglun landscape, Xishuangbanna Prefecture, Yunnan, China, in 1976 (above) and 2010 (below). In the Menglun landscape, the highlighted ellipse is the current and historical survey area for birds, black indicates forests, and white indicates rubber plantations and human settlements. The radius of the circle is 10 km.

historically been prevalent in the area (Wang, 1991; Yang, 1993). Currently, four large fragments (> 1000 ha each; three are protected areas) contribute > 90% of the total forest cover in Menglun (Fig. 1). Most of the other, smaller fragments (mean = 18 ha) are on steep slopes, along streams or rivers, or on soils that cannot be cultivated (e.g. limestone karsts; Liu & Slik, 2014). The landscape was covered in tropical seasonal lowland rain forest before the recent expansion of rubber (Yi *et al.*, 2014).

Forest cover

We produced forest-cover maps for the landscape within a 10-km radius of Menglun by calculating the Normalized Difference Vegetation Index (NDVI) of multispectral data from Landsat-2 Multi Spectral Scanner (MSS) and Landsat-5 Thematic Mapper (TM) images (30-m spatial resolution) acquired in February 1976 and 2010. These images were selected because they had the least cloud cover and rubber trees are briefly leafless at this time, enhancing the contrast with the largely evergreen rain forest (Yi *et al.*, 2014). The Landsat images were downloaded from the Earth Resources Observation and Science (EROS) Centre, U.S. Geological Survey (USGS). NDVI values > 0.1 were converted into 1 and everything else into 0. The resulting raster was converted to a vector shape file as a forest map to calculate the total forest area in the landscape.

Bird surveys

Xishuangbanna had 37% of China's bird species, and many early Chinese and Russian expeditions visited the region (1954–1983; Xu *et al.*, 2006). Most surveys included the collection of bird skins. From this data, a series of books on the bird species of Yunnan Province (Yang *et al.*, 1995) and Xishuangbanna (Yang, 1993) were prepared. Another study listed the species observed in the nature reserves (Xu *et al.*, 2006). This literature specifies the township where the species was collected, so we were able to construct a list of bird species that were recorded or collected from Menglun Township before 1983.

We exhaustively resurveyed the whole study landscape between 2011 and 2014 by repeatedly walking through remaining forest fragments, nature reserves, along roads/trails and in a densely planted botanical garden and recorded all birds seen or heard. The current checklist was prepared by R. Sreekar, J. Zhao and X. Wang, each of whom has >3 years of experience identifying birds in tropical Asia by sight and calls. All three lived in the study site (XTBG, Menglun) for more than 3 years, watched birds, compiled checklists for the region and collectively logged over 3000 h in the field. We used different methods to study different bird families and selected sites according to the birds' natural history and habitat use. Examples of methods used to compile the current checklist included: (1) point counts from a cliff overlooking the canopy for large frugivores, aerial insectivores and raptors, (2) counts under fruiting trees for frugivorous birds, (3) playbacks for understorey insectivores and (4) line-transects and acoustic sampling for others. Such methodologically unconstrained surveys are an efficient way to obtain a complete coverage of the fauna because of sampling bias in using a restricted set of methods, especially when compiling checklists (Bibby *et al.*, 2000). We constructed a species accumulation curve to assess the completeness of our inventories (see Fig. S1 in Supporting Information). Furthermore, by sharing sightings and observations with other amateur and professional ornithologists who visit Menglun in large numbers (*c.* 400 birdwatchers annually), we were further able to assess the completeness of our inventories. Migrants, water birds and nocturnal species were excluded from analyses because migrants may be affected by factors acting outside the area, and systematic surveys were not conducted for nocturnal and water bird species. Resident diurnal terrestrial species in the historical list that were not sighted during our bird surveys were considered extirpated (see Appendix S1). We only sighted five species that were not reported in historical lists, which supports the notion that historical surveys were of good quality. We assumed these five species were present during the earlier period (see Appendix S1).

Bird ecological data and classifications

To investigate the correlates of extirpation among bird species, we measured six life history and ecological traits using data from Yang *et al.* (1995) and Robson (2000). These were forest specialization (specialist or non-specialist), mean body size (bill to tail length), habitat breadth (observed number of habitats a species occurs in; range 1–8), primary diet type (frugivore, insectivore, carnivore, granivore, nectarivore), diet breadth (number of items recorded in its diet; range 1–5) and minimum clutch size. We further divided forest insectivores into three vertical niche use categories: understorey, bark gleaning and canopy. Understorey insectivores predominantly forage within 4 m of the ground. Bark-gleaning insectivores predominantly forage on the trunks of trees by gleaning or excavating wood. The remaining species that forage in the mid-storey, canopy and emergent layers were categorized as canopy insectivores.

Species–area models

The classic species–area model is described by the power law $S = cA^z$ (Arrhenius, 1920), where S is species richness; A is area of the habitat; c and z are two fitted parameters (Rosenzweig, 1995). In log–log space, c and z represent the intercept and slope of the species–area regression, respectively. When the original forest area (A_{org}) is reduced to its current size (A_{new}) due to anthropogenic activities, we can calculate the steepness of the slope (z value) if we know the original species richness (S_{org}) and current species richness (S_{new}).

$$S_{\mathrm{org}} = c.A^z_{\mathrm{org}} \tag{1}$$

$$S_{\mathrm{new}} = c.A^z_{\mathrm{new}} \tag{2}$$

From equation 1 and 2, we get

$$z = (\log S_{\mathrm{org}} - \log S_{\mathrm{new}})/(\log A_{\mathrm{org}} - logA_{\mathrm{new}}) \tag{3}$$

In situations where a proportion of the forest area is converted into agroforests, such as rubber, some forest biodiversity is supported by these with varying degrees of suitability and permeability for different taxa (Ricketts, 2001; Gibson *et al.*, 2011). Therefore, we use both matrix-calibrated and countryside SAMs, which incorporate surrounding matrix effects into the traditional SAM (equation 3). Matrix-calibrated SAM is expressed as

$$z = (\log S_{\mathrm{org}} - \log S_{\mathrm{new}})/(\sigma(\log A_{\mathrm{org}} - \log A_{\mathrm{new}})) \tag{4}$$

Countryside SAM is expressed as

$$z = (\log S_{\mathrm{org}} - \log S_{\mathrm{new}})/(\log A_{\mathrm{org}} - \log(A_{\mathrm{new}} + h.A_{\mathrm{rubber}})). \tag{5}$$

The component σ is the sensitivity of the taxon to the transformed habitat, which is monoculture rubber in our study area; A_{rubber} is the area covered by rubber (13,157 ha); and $h = (1 - \sigma)^{2.86}$ (see Pereira *et al.*, 2014 for details). The component σ is the proportional decrease in the number of species between forests and transformed habitats ($0 < \sigma < 1$). If the fragments are surrounded by water (e.g. land bridge islands), the σ value for forest birds is equal to one because water is a completely inhospitable habitat (see Koh & Ghazoul, 2010 for details).

We derived S_{new} and S_{org} from the current (2011–2014) and past (1954–1983) bird species lists, while A_{new} (6850 ha) and A_{org} (20,007 ha) were calculated from current (2010) and past (1976) forest-cover maps (Fig. 1). The current forest cover (A_{new}) was quantified by summing the areas of four large forest fragments (protected areas) in the landscape, which is *c.* 90% of the total forest cover. Smaller forest fragments were ignored, as these tend to be affected by edge effects and habitat degradation (Laurance, 2008). We also removed 100-m forest strips on the edges of the four remaining fragments from the forest-cover calculation to compensate for edge effects (Koh *et al.*, 2010). The four fragments that were used to calculate the current forest cover (2010) were also fragmented in the past (1976) by the Lancang River and agriculture, but with smaller interpatch distances (Hu *et al.*, 2008). The forests in the past (1976) did not have strict edges, and to be conservative as to the role of hunting, we did not remove such strips from the past forest-cover calculation. To determine the sensitivity of birds to habitat conversion (σ), we calculated the mean percentage decrease in bird species richness when primary forest is converted to agricultural land in tropical East Asia using the data analysed by Koh & Ghazoul (2010); data from Sodhi *et al.*, 2009; $\sigma = 0.68 \pm 0.05$ SE, $n = 17$). To account for uncertainty in the σ parameter, we calculated the confidence intervals of the mean σ value using 10,000 bootstrap resamples.

We estimated the number of extirpated forest species due to deforestation (loss of forest area) only ($ES_{\mathrm{deforestation}}$), by assigning slope ($z$) value of 0.35 (Koh & Ghazoul, 2010) to matrix-calibrated and countryside SAMs, and calculated $S_{\mathrm{deforestation}}$ from equation 6 (matrix-calibrated SAM) and equation 7 (countryside SAM).

$$S_{\mathrm{deforestation}} = \exp(\sigma.z.(\log A_{\mathrm{new}} - \log A_{\mathrm{org}}) + \log S_{\mathrm{org}}) \tag{6}$$

$$S_{\mathrm{deforestation}} = [(A_{\mathrm{new}} + h.A_{\mathrm{rubber}})/A_{\mathrm{org}}]^z.S_{\mathrm{org}} \tag{7}$$

The difference between $S_{\mathrm{deforestation}}$ and S_{new} is the additional number of species extirpated by hunting (ES_{hunting}; see Discussion about other potential anthropogenic drivers of extirpation that do not appear significant for birds in the region). See Panel S2 for R code.

Data analysis

To determine whether the slope of bird extirpations in Menglun was significantly greater than expected in the absence of hunting ($z = 0.35$; Koh & Ghazoul, 2010; Pereira *et al.*, 2014), an approximate, one-tailed one-sample *P*-value was estimated as $P = 1 - (x/n)$, where '*x*' is the number of resamplings greater than the expected slope in the absence of hunting (0.35), and '*n*' is the number of bootstrap resamples. To test whether the *z* values of forest frugivores were greater than forest understorey insectivores, we estimated one-tailed two-sample *t*-test as $P = 1 - (x/n)$, where '*x*' is the number of resamplings where the slope for frugivores was greater than the slope for understorey insectivores, and '*n*' is the number of bootstrap resamples.

We used a generalized linear model (GLM) with a binomial error distribution to model the effect of the six life history traits on the EP of birds, and an ANOVA (type III sum of squares) to determine the variance explained by each variable. In separate models, we further examined the effect of body size on the EP of forest frugivores and the effect of vertical niche use categories on the EP of forest insectivores. We checked for phylogenetic autocorrelation among residuals by building strict consensus phylogenetic trees for all species, forest insectivores and frugivores, using 5000 dated phylogenies that are available for download at http://birdtree.org/ (Jetz *et al.*, 2012). We found no evidence for phylogenetic autocorrelation among the residuals in the models ($P > 0.1$), so no corrections were made to the original models.

RESULTS

A total of 153 resident diurnal terrestrial species were recorded between 2011 and 2014, in contrast to the 231 species before 1983. Thus, we estimate that 78 (34%) species have been extirpated from the Menglun landscape in the last 60 years (1954–2014). Considering forest birds only, 36% (54 of the 150 recorded in the past) were extirpated.

The median slope (*z*) of forest bird extirpations was 0.61 (95% CIs = 0.54–0.72) for matrix-calibrated SAM and 0.48 (95% CIs = 0.44–0.53) for countryside SAM, which were *c.* 1.7 and *c.* 1.4 times higher, respectively, than expected for fragmentation effects alone (0.35; $P < 0.001$ for both models; Figs 2 & S2). Forest frugivores had much higher slopes (matrix-calibrated SAM median = 0.84, 95% CIs = 0.74–0.99; countryside SAM median = 0.67, 95% CIs = 0.61–0.74) than forest understorey insectivores (matrix-calibrated SAM median = 0.39, 95% CIs = 0.34–0.46; countryside SAM median = 0.31, 95% CIs = 0.29–0.34; $P < 0.001$ for both models; Figs 2 & S2). These results from matrix-calibrated and countryside SAMs suggest that hunting resulted in an increase in the number of the forest birds extirpated in Menglun landscape by *c.* 1.6-fold and *c.* 1.3-fold, respectively (Fig. 3; Table S1). Similarly, the extirpated numbers of forest frugivores for matrix-calibrated and countryside SAMs were *c.* 2.1 and *c.* 1.7 times higher, respectively, than

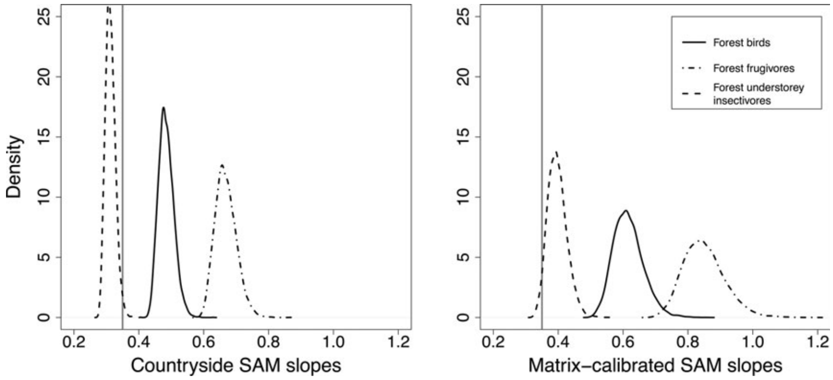

Figure 2 Observed (black lines: forest birds – solid line, forest frugivores – dot-dashed line and forest understorey insectivores – dashed line) distributions of countryside (left) and matrix-calibrated (right) species–area model (SAM) slopes in Menglun landscape. Vertical solid grey line is the expected species–area slope for birds ($z = 0.35$).

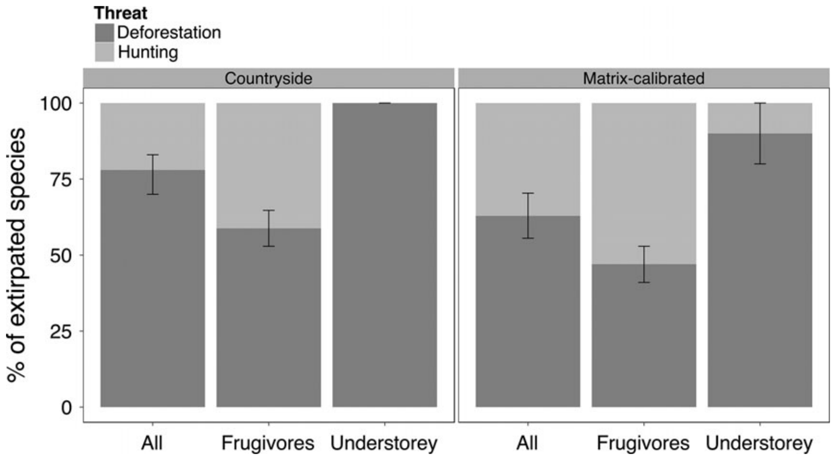

Figure 3 Proportion of total extirpations of all forest birds (All), forest frugivores (Frugivores) and forest understorey insectivores (Understorey) partitioned into estimated species extirpated by deforestation only (dark grey), and the estimated additional species extirpated by hunting (light grey) using countryside (left) and matrix-calibrated (right) species–area models. Bar heights show medians, and error bars represent 95% confidence intervals. See Table S1 for details.

expected in the absence of hunting (Fig. 3; Table S1). On the other hand, the extirpated numbers of forest understorey insectivores for matrix-calibrated and countryside SAMs were *c.* 1.1 times higher and *c.* 0.9 times higher, respectively, than expected in the absence of hunting (Fig. 3; Table S1).

Extirpation probability of birds in the Menglun landscape increased with body size ($\chi^2_{(1,223)} = 16.5$, $P < 0.001$; Fig. 4) and minimum clutch size ($\chi^2_{(1,223)} = 5.35$, $P = 0.02$). EP also varied slightly across primary diet types ($\chi^2_{(4,223)} = 8.42$, $P = 0.07$; Fig. 4). Frugivores had higher EPs than insectivores ($\beta \pm \text{SE} = -0.92 \pm 0.35$, $P = 0.008$; Fig. 4). EP did not change with diet breadth ($\chi^2_{(1,223)} = 0.01$, $P = 0.91$), and the EP of forest-dependent birds was similar to non-forest birds ($\chi^2_{(1,223)} = 0.05$, $P = 0.82$).

We recorded 46 frugivore and 142 insectivore species in the study area, of which 37 frugivores and 90 insectivores preferred forests. Seventeen forest frugivores (45.9%) and 28 forest insectivores (31%) were extirpated. As with the overall analysis, the EP of forest frugivores significantly increased with body size ($\chi^2_{(1,35)} = 8.52$, $P = 0.003$; Fig. 5). The EP of forest insectivores varied across vertical niche use categories ($\chi^2_{(2,89)} = 14.35$, $P < 0.001$; Fig. 5). Bark gleaners (intercept) had higher EPs than understorey ($\beta \pm \text{SE} = -2.34 \pm 0.75$; $P = 0.002$) and canopy ($\beta \pm \text{SE} = -2.52 \pm 0.76$, $P = 0.001$) insectivores (Fig. 5).

DISCUSSION

Our resident bird accumulation curve had flattened (Fig. S1), and given our high sampling effort, we are confident our inventories were nearly complete. However, in comparing species lists, there are inevitably some differences in sampling techniques, and the historical surveys collected specimens, which would not be permitted now (Yang, 1993; Yang *et al.*, 1995). Nevertheless, the best direct evidence of species extirpations from a landscape comes by comparing past and present species lists (Brook *et al.*, 2003; Sodhi & Ehrlich, 2010; Sodhi *et al.*, 2010).

By comparing current and historical species lists, we found that in a landscape affected by both fragmentation and hunting, 34% of the bird species had been extirpated. As predicted, the estimated slopes (*z*) for forest birds in the study landscape were much steeper than the expected slope from fragmentation effects alone (Figs 2 & S2). We suggest this reflects the high prevalence of hunting in the area (for more details see Panel S1, and later in the discussion). Moreover, in line with our second prediction, the estimated slopes were steeper for forest frugivores than for forest understorey insectivores (Fig. 2).

Ecological correlates of extirpation probability

Extirpation probability of birds increased with body size (Fig. 3). Most large-bodied species, including corvids, hornbills, woodpeckers, laughingthrushes, parakeets and pigeons, have been lost (see Appendix S1). Moreover, although a few large birds, such as the red jungle fowl (*Gallus gallus*), silver pheasant (*Lophura nycthemera*) and grey-headed woodpecker (*Picus canus*), still persist, they were rare (< 10 sightings in 4 years),

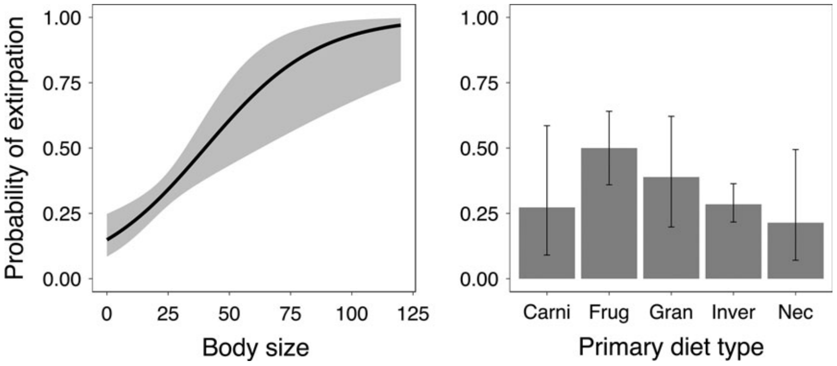

Figure 4 Extirpation probability of Menglun birds as a function of body size (left) and primary diet type (bottom right; Carni – Carnivores, Frug – Frugivores; Gran – Granivores, Inver – Insectivores; Nec – Nectarivores). The line in left plot and bars in the right plot are the predictions of the models fitted to the data with their 95% confidence intervals.

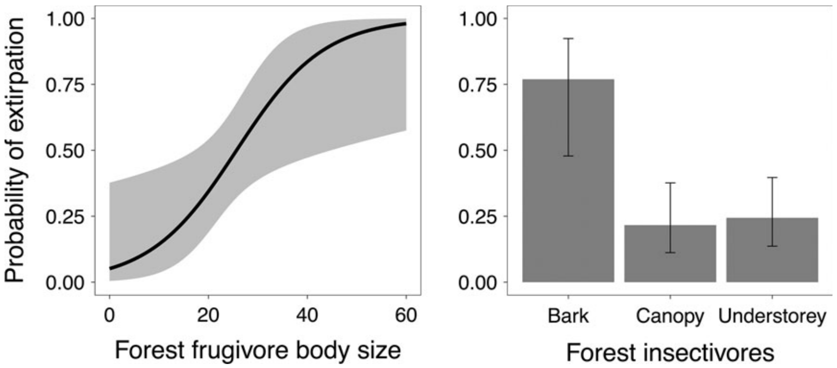

Figure 5 Extirpation probability (EP) of forest frugivorous birds as a function of body size (left) and EP of forest insectivorous birds as a function of niche use (right). The line in the left plot and the bars in the right plot are the predictions of the models fitted to the data with their 95% confidence intervals.

and, although common in non-hunted, non-fragmented landscapes, are likely to be extirpated in the near future if conservation measures are not taken. We were surprised to find that the EP of forest and non-forest birds was similar, but this probably reflects the extirpation by hunting of the larger, more conspicuous, non-forest birds, such as starlings, bee-eaters and corvids (see Appendix S1).

Large home range requirements and a need for adequate food and nesting sites may increase the EP of large-sized birds in fragmented landscapes (Sodhi *et al.*, 2004), but other studies suggest that body size is not an important predictor of EPs in birds (e.g. Castelletta *et al.*, 2000; Lees & Peres, 2008; Sodhi *et al.*, 2010). Frugivorous birds had higher EPs than insectivores in our study area (Fig. 4), independent of body size, which did not differ significantly between the two feeding guilds ($t = 1.62$, $P = 0.11$). Among forest birds, frugivores with larger body sizes and bark-gleaning insectivores (woodpeckers and nuthatches) had higher EP (Fig. 5). Thirteen species of bark-gleaning forest insectivores were recorded in the past, of which only three (23%) were extant: two small woodpeckers (< 10 cm) and the velvet-fronted nuthatch (*Sitta frontalis*) that was sighted once in 4 years. All the extirpated woodpecker species were also absent during the 1988 survey (see Wang, 1991), before the rapid expansion of rubber. Although woodpeckers are sensitive to habitat degradation (Kumar *et al.*, 2011), this history suggests that hunting caused their decline (Wang, 1991). Woodpeckers tend to be noisy, conspicuous species and therefore vulnerable to hunting.

It is known that forest understorey insectivores are vulnerable to fragmentation (Bregman *et al.*, 2014), but they had shallower species–area slopes (z) and EP than others (Figs 2 & 5; Table S1; Fig. S2). This is probably because of the relatively large fragments (*c.* 14,000 ha) in our study area have maintained their populations. Hunting doubled frugivore extirpations (Fig. 3; Table S1). We suggest this is because frugivores are more sensitive to hunting because they are preferred for the quality of their flesh and most species are conspicuous canopy birds, which assemble predictably at fruiting trees (Sreekar *et al.*, 2010; Naniwadekar *et al.*, 2013). The extirpation of large frugivores, which are mostly also excellent seed dispersal agents, is likely to reduce the diversity of the seed-rain, increasing spatial clustering among saplings of bird-dispersed species and reducing their survival probability by increasing density-dependent mortality (García & Martínez, 2012; Harrison *et al.*, 2013). All long-distance seed dispersers, such as elephants, rhinoceroses, gibbons, flying foxes, hornbills and imperial pigeons (*Ducula* spp.), have been extirpated from the Menglun and indeed much of the region.

Past and current hunting pressure in the study area

An earlier review of threats to Chinese vertebrates concluded that overexploitation was a more significant threat to species persistence than habitat loss (Yiming & Wilcove, 2005). Hunting was a major source of animal protein in Menglun before the provincial government banned hunting in 1996 (Wang, 1991; Hu *et al.*, 2008), and many vertebrates were also used in traditional medicine and as additives to local liquor (Yang, 1993). The hunting ban has not been effectively enforced in many parts of Yunnan, and hunting still occurs in the Menglun landscape (see Panel S1), although the current hunting pressure (0.06 hunters h^{-1}) was much lower than in the neighbouring Bulong Nature Reserve (100 km east; 0.55 hunters h^{-1}; R. Sreekar and R. D. Harrison, unpublished data). Hunting has also been reported to be common in the neighbouring township of Mengla (30 km south), where 33 gunshots were heard and five hunters sighted in 5 days (Fan *et al.*, 2014). In contrast, sightings of hunters in the non-forested landscape and small forest fragments of Menglun were rare (Fig. S3), possibly reflecting stricter management practices and regular police patrols in the non-forested matrix. Hunters may also be more discrete in Menglun, reducing detection probability. Ironically, hunting in the study area mostly occurs in larger fragments under legal protection (Fig. S3) and it is in these that better enforcement and regular patrols will have most impact on future vertebrate extirpations.

Other possible drivers of species extirpations

Forest fragmentation is not a tidy process, and the forest in the resulting fragments has often been degraded by additional impacts, including fire, logging and edge effects. These impacts may increase extirpations above the level expected from area-related fragmentation effects alone, but the expected matrix-calibrated slope used (0.35) was derived from a review of fragmentation studies (Koh & Ghazoul, 2010) in which these additional impacts are probably included. Moreover, our method of estimating current forest cover using only the large fragments, with edges removed in the recent map, should minimize the possibility of forest degradation being an additional, confounding factor. Long-term ecological monitoring in these large fragments also suggests they are not degraded. The disproportionate loss of lowland forests could be another cause of enhanced extirpations, as a large proportion of remaining forests in the study area were on steeper slopes, in montane areas and over poor soils (e.g. limestone; Liu & Slik, 2014). However, the lowland forests were already severely degraded in the past due to the long history of shifting cultivation and human activities (Fig. 1; Hu *et al.*, 2008).

Alien species, climate change and pesticide drift from the rubber plantation matrix could potentially be additional causes of enhanced extirpations. However, alien species have been reported to be a minor threat to China's vertebrates (Yiming & Wilcove, 2005), and no alien vertebrate species have been reported from forests in Xishuangbanna. Multiple species extirpations due to climate change over just a few decades (1960–2010) are also not plausible. Almost all species occurring in the study landscape have wide distributions and broad climatic envelopes, suggesting that they may be insensitive to minor changes in climate. The landscape is also topographically complex, which should provide local cool refuges and low velocities of climate change, making it easier for species to stay within their climate envelopes (Corlett & Westcott, 2013). The impact of pesticide drift could not be assessed, but it is only likely to significantly affect the smallest fragments and would be expected to have most impact on insectivores. In sum, we suggest that causes other than deforestation and hunting are unlikely to have any substantial impact on the results.

Why our approach is likely to be a conservative estimate of the role of hunting

Our results, which suggest a 1.3- to 1.6-fold increase in the number of extirpated birds as a consequence of hunting, may underestimate hunting's role for three reasons. Firstly, the expected species–area slope ($z = 0.35$) was derived from a review of fragmentation studies (see Koh & Ghazoul, 2010) and, because it is likely that many of the landscapes studied were also exposed to hunting, use of this figure may still inflate the role of habitat loss (forest area). Secondly, the half-life of the total bird extirpations in 1000-ha forest fragments was estimated to be around 50 years (Brooks *et al.*, 1999), while forest loss in our study area is more recent and still ongoing (< 30 years; Yi *et al.*, 2014). Therefore, our models might overestimate deforestation effects and underestimate hunting effects. Finally, our SAMs assume that deforestation is entirely responsible for extirpations up to the number predicted by the model, with hunting only implicated in extirpations above that number. In our study area, however, hunting probably preceded fragmentation as a major threat. For example, past studies in Menglun showed extirpation of around 50% of non-passerine species before large-scale fragmentation occurred (Wang, 1991), attributed primarily to hunting.

Conservation implications

The combined effect of reducing forest cover and increasing hunting pressure has been reported in tropical forests world-wide (Peres, 2001; Peres & Lake, 2003; Corlett, 2007; Abernethy *et al.*, 2013; Harrison *et al.*, 2013). Nevertheless, conservation interventions still tend to be area focused. For example, programmes to connect all the protected areas in Xishuangbanna with forest corridors have been initiated (Xi, 2009), although increasing connectivity alone will clearly not be enough to ensure conservation goals are achieved. Our results suggest a 1.3- to 1.6-fold increase in the forest birds extirpated in Menglun as a consequence of hunting (Fig. 2; Table S1), and the situation is similar or worse in other parts of Xishuangbanna (Fan *et al.*, 2014; R. Sreekar and R. D. Harrison, unpublished data). Most medium to large vertebrates (> 30 cm body length) have been extirpated, and the critical ecosystem functions they perform, such as seed dispersal, are likely to have been affected. To restore these functions, extirpated birds and mammals will need to be reintroduced, which can only be successful if hunting is controlled. Understanding how hunting increases vertebrate extirpations and skews ecosystem processes is a considerable challenge for the future. Finally, we suggest that considering the separate roles of hunting and habitat loss is important from a conservation perspective, because it may suggest a different focus for interventions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Observed number of extirpated forest bird species, and the estimated number of extirpated forest species due to deforestation.

Panel S1. Current hunting pressure in Menglun.

Panel S2. Calculation of estimated slopes and species extirpated due to deforestation only using matrix-calibrated and countryside species-area models in R.

Figure S1. Species accumulation curve of extant birds.

Figure S2. Model fits of countryside and matrix calibrated species–area relationships for loss of forest birds (all species, frugivores and understorey insectivores).

Figure S3. Relationship between forest fragment size and the number of hunters sighted.

Figure S4. Photographs showing (a) hunter with his home-made shotgun, (b) a recently shot black-crested bulbul (*Pycnonotus flaviventris*), and (c) a black-throated laughingthrush (*Ianthocincla chinensis*) in a cage, in Menglun.

Appendix S1 Summary information of species recorded in Menglun landscape, including their taxonomic information, extirpation status, and their ecological traits.

BIOSKETCH

Rachakonda Sreekar is a master's student at the Xishuangbanna Tropical Botanical Garden, China. He is interested in understanding the synergistic effects of threats on natural ecosystems and wildlife.

Author contributions: R.S., E.G., R.T.C and R.D.H designed the research; R.S., G.H., J.Z., B.O.P., I.P. and X.W. collected the data; R.S. analysed the data and led the writing. All authors contributed to manuscript writing.

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