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Scriven *et al.*

Protected area effectiveness for tropical butterflies

**ASSESSING THE EFFECTIVENESS OF PROTECTED AREAS FOR CONSERVING
RANGE-RESTRICTED RAINFOREST BUTTERFLIES IN SABAH, BORNEO**

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1 **ABSTRACT**

2 Rainforests on Borneo support exceptional concentrations of endemic insect biodiversity, but
3 many of these forest-dependent species are threatened by land-use change. Totally protected
4 areas (TPAs) of forest are key for conserving biodiversity, and we examined the effectiveness of
5 the current TPA network for conserving range-restricted butterflies in Sabah (Malaysian
6 Borneo). We found that mean diurnal temperature range and precipitation of the wettest quarter
7 of the year were the most important predictors of butterfly distributions ($N = 77$ range-restricted
8 species), and that species richness increased with elevation and aboveground forest carbon. On
9 average across all species, TPAs were effective at conserving ~43% of species' ranges, but
10 encompassed only ~40% of areas with high species richness (i.e. containing at least 50% of our
11 study species). The TPA network also included only 33-40% of areas identified as high priority
12 for conserving range-restricted species, as determined by a systematic conservation prioritization
13 analysis. Hence, the current TPA network is reasonably effective at conserving range-restricted
14 butterflies, although considerable areas of high species richness (6565 km²) and high
15 conservation priority (11,152-12,531 km²) are not currently protected. Sabah's remaining forests,
16 and the range-restricted species they support, are under continued threat from agricultural
17 expansion and urban development, and our study highlights important areas of rainforest that
18 require enhanced protection.

19

20

21 **KEY WORDS**

22 Insects; conservation prioritization; reserve design; Southeast Asia; species distribution
23 modelling; tropical biodiversity

24 **1 INTRODUCTION**

25 Tropical rainforests constitute many of the world’s biodiversity hotspots and contain
26 disproportionately high concentrations of rare and endemic species (Mittermeier, Turner,
27 Larsen, Brooks, & Gascon, 2011; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent,
28 2000). Conversion of rainforest to agriculture greatly reduces tropical biodiversity (Laurance,
29 Sayer, & Cassman, 2014; Meijaard et al., 2018), and high concentrations of endemism in the
30 tropics mean that loss of species through anthropogenic environmental changes could result in
31 widespread extinctions and biodiversity losses globally (Brook, Sodhi, & Ng, 2003; Koh &
32 Sodhi, 2010; Mittermeier et al., 2011). With demand for cropland expected to increase in
33 future (Laurance et al., 2014), there is a pressing need to better understand biodiversity
34 distributions in rainforest ecosystems in order to locate and protect important areas of high
35 diversity that may face increased pressure from continued agricultural expansion.

36 A large component of tropical biodiversity is comprised of insects, which perform
37 important ecological functions in rainforests (e.g. herbivory, pollination, dung removal,
38 decomposition; Ewers et al., 2015; Noriega et al., 2018; Slade, Mann, & Lewis, 2011; Weissflog,
39 Markesteijn, Lewis, Comita, & Engelbrecht, 2018; Wikelski et al., 2010), yet we lack
40 information on factors affecting the distributions of insects in the tropics. Given that many
41 rainforest species are vulnerable to extinction from land-use and climate change (Brook *et al.*
42 2003; WWF, 2018), and that insect biomass is declining globally (Hallmann et al., 2017), it is
43 important to map species’ ranges and determine the effectiveness of protected areas (PAs) at
44 conserving rainforest insects. Data on insect species ranges are limited in the tropics (Cheng &
45 Bonebrake, 2017), and so museum collections are an important resource for supporting insect
46 conservation (Kharouba, Lewthwaite, Guralnick, Kerr, & Vellend, 2018; Ponder, Carter,

47 Flemons, & Chapman, 2001; Tarli, Grandcolas, & Pellens, 2018). Museum records have been
48 used to document insect population declines (Grixti, Wong, Cameron, & Favret, 2009), predict
49 species' distributions (Klorvuttimontara, McClean, & Hill, 2011), and measure phenological
50 shifts (Kharouba et al., 2018); hence, they are an important source of baseline data for
51 conservation planning (Ponder et al., 2001; Tarli et al., 2018), especially in tropical regions
52 where detailed information on species' distributions is generally lacking.

53 The rainforests of Southeast Asia contain exceptionally high levels of diversity and
54 endemism (Myers et al., 2000), much of which is now restricted to montane regions as a
55 consequence of palaeogeographical range shifts (Gathorne-Hardy, Syaokani, Davies, Eggelton,
56 & Jones, 2002; Lohman et al., 2011; Sodhi, Koh, Brook, & Ng, 2004), combined with recent loss
57 of forest at low elevations (Carlson et al., 2013; Miettinen, Shi, & Liew, 2011). It is important to
58 focus conservation strategies on range-restricted species in remaining areas of forest because
59 these species can be particularly sensitive to disturbance (Bonebrake et al., 2016; Cleary &
60 Mooers, 2006; Hill, Hamer, Tangah, & Dawood, 2001; Koh, Sodhi, & Brook, 2004) and because
61 local extirpations could lead to extinction (Mittermeier et al., 2011). However, we currently
62 know little about where range-restricted insects occur in biodiverse tropical systems (Myers et
63 al., 2000), and so understanding the climatic limits to species' ranges may facilitate conservation
64 planning in areas threatened by land-use change (Cheng & Bonebrake, 2017; Klorvuttimontara et
65 al., 2011). Knowledge about range-restricted insect distributions in relation to aboveground
66 forest carbon could also be important by linking species conservation to climate change
67 mitigation strategies from avoided deforestation. Although we currently lack information on
68 whether range-restricted insect richness is related to forest carbon stocks.

69 Conserving range-restricted species requires an effective network of PAs, which now
70 comprise the remaining strongholds of biodiversity in many tropical regions (Boakes, Fuller, &
71 McGowan, 2018; Curran et al., 2004). However, PAs have become increasingly isolated within
72 human-modified landscapes (DeFries, Hansen, Newton, & Hansen, 2005), and there is little
73 research on the effectiveness of tropical PAs for conserving range-restricted invertebrates
74 (Cheng & Bonebrake, 2017). We addressed this issue by modelling the distributions of range-
75 restricted butterflies on Borneo and examining whether the current network of totally protected
76 areas (TPAs; a state governmental land designation) in Sabah overlaps with butterfly species
77 ranges and areas of high species richness. We assessed range-restricted butterflies, defined as
78 species restricted to Sundaland, because butterflies in this region are highly diverse (>900
79 species on Borneo), with many endemic to Borneo (~50 species) (Otsuka, 1988). A large number
80 of butterflies on Borneo are also dependent on closed-canopy forest and hence threatened by
81 forest loss in areas that do not fall within existing PAs (Benedick et al., 2006; Scriven, Beale,
82 Benedick, & Hill, 2017). In addition, there are good records of butterfly ranges compared to
83 many other insect groups (e.g. see Corbet & Pendelbury, 1992; D’Abrera, 1985; Otsuka, 1988,
84 2001), including information from museum collections (Klorvuttimontara et al., 2011).

85 We collated distribution records for 77 range-restricted butterflies on Borneo from
86 published data sources and museum collections, and ran species distribution models (SDMs) to
87 project butterfly distributions within forest habitat in relation to climate factors. From overlaying
88 the species’ distributions, we determined the locations of current forest areas in Sabah projected
89 to have high species richness. We also used systematic conservation prioritization methods to
90 determine the most important (i.e. the most climatically suitable) areas of remaining rainforest
91 for conserving the distributions of our study species in Sabah. We focus on Sabah because of the

92 high density of butterfly records, combined with availability of ancillary data, particularly for
93 aboveground carbon (Asner et al., 2018) and TPA coverage (Sabah Forestry Department, 2016).
94 Our main aims were to: (1) determine the most important climatic factors limiting the
95 distributions of range-restricted butterflies on Borneo, in order to improve our understanding of
96 the bioclimatic limits underpinning the ranges of tropical insects; (2) assess whether elevation
97 and aboveground carbon predict areas with high species richness; and (3) quantify the
98 effectiveness of the TPA network in Sabah for conserving range-restricted butterflies.

99

100 **2 METHODS**

101 **2.1 Butterfly locality records**

102 We obtained butterfly records from the ‘Borneo Butterfly Distribution Database (B₂D₂)’
103 retrieved from: <http://www-users.york.ac.uk/~jkh6/index.htm> (accessed 10th September 2018).

104 This database was compiled from museum specimens, published papers, field reports and
105 University PhD theses dating from 1878 to 2006; see Ghani, 2012 for more details). Overall, the
106 database contains over 22,000 records from more than 300 butterfly species belonging to the
107 families Papilionidae, Pieridae and Nymphalidae. We filtered records to include only those
108 collected after 1950, to try to balance ensuring that our butterfly records were relevant to the
109 current climate (i.e. 1970-2000; see below), while not discarding too many historical records.

110 This resulted in 7661 records at 398 unique sampling localities for all butterfly species across
111 Borneo (Figure 1a). We selected records for species that are restricted to Sundaland, including 15
112 species that are endemic to Borneo (see Otsuka, 2001 for details). Only one Sundaland species,
113 *Papilio iswaroides*, had fewer than 10 locality records and so was excluded from the analysis.

114 We therefore ran SDMs for 77 species, based on 2277 presence records from 289 unique
115 sampling locations.

116

117 **2.2 Climate and elevation data**

118 To project the potential distributions of the 77 study species, 19 climate variables representing
119 average monthly temperature and precipitation data for 1970-2000 were downloaded from the
120 WorldClim database (<http://worldclim.org/version2>; accessed 9th June 2018) (see Fick &
121 Hijmans, 2017) at ~1 km² (30 arc-second) resolution for Borneo. Elevation data were
122 downloaded from the CGIAR-CSI GeoPortal (<http://srtm.csi.cgiar.org/>; accessed 1st October
123 2018) at 250 m resolution and then aggregated by a factor of four to 1 km grid-cells. To assess
124 whether climate variables were correlated, we performed a pairwise Spearman's rank correlation
125 analysis on the 19 WorldClim variables and elevation. Analyses revealed that many
126 environmental variables were collinear (see Dormann et al., 2013) (Table S1 in Appendix S1);
127 for those variables with a regression coefficient value greater than 0.7, the variable from the pair
128 most correlated with other variables was included. Thus, five climate variables were included in
129 the SDMs: (1) annual mean temperature (°C); (2) mean diurnal temperature range (°C); (3)
130 temperature seasonality (standard deviation in monthly temperatures × 100; a measure of
131 temperature variation within years) (°C); (4) precipitation of the driest month of the year (mm);
132 and (5) precipitation of the wettest quarter of the year (mm) (Figure S1 in Appendix S1). We did
133 not include forest cover data within the SDMs because of land-use change since many of the
134 locality records were collected (Gaveau et al., 2014; Figure S3a in Appendix S1) (also see
135 Appendix S1 for additional details and implications of land-use change following record
136 collection). Instead, we used our SDMs to characterize the location of suitable climate space

137 between 1970-2000 for our study species in areas of remaining forest in 2016. We applied
138 outputs from the SDMs and *prioritizr* software (see below) to forested areas (excluding
139 mangrove forests) that contained more than 40 metric tons of aboveground carbon per hectare
140 (Mg C ha^{-1}) (mean across 1 km grid-cells resampled from 30 m grid-cells; Asner et al., 2018). In
141 this way, we tried to ensure that areas of degraded and/or regenerating forest were included in
142 our projections of species' potential ranges while production plantations were not (Rosoman,
143 Sheun, Opal, Anderson, & Trapshah, 2017).

144

145 **2.3 Species distribution models**

146 We modelled the distributions of 77 butterfly species across Borneo using R (R Core Team,
147 2017) with the *biomod2* package (Thuiller, Georges, Engler, Georges, & Thuiller, 2016). We
148 used an ensemble modelling approach to create a consensus of the predictions across three
149 algorithms (see Cheng & Bonebrake, 2017; Marshall et al., 2017; Singh, McClean, Bükler,
150 Hartley, & Hill, 2017; Thuiller, Lafourcade, Engler, & Araújo, 2009), comprising: (1) a
151 generalized linear model (GLM), with linear effects and stepwise selection based on Akaike
152 information criteria (AIC); (2) a random forest (RF) model, using the default settings (no. trees =
153 501; node size = 5); and (3) maximum entropy modelling (MAXENT), including only linear and
154 quadratic features (e.g. see Marshall et al., 2017). Maximum entropy modelling can perform well
155 with few locality records (Phillips, Anderson, & Schapire, 2006; Platts et al., 2014; Wisz et al.,
156 2008), whilst GLM and RF algorithms have also been used successfully in other insect studies
157 (e.g. see Cheng & Bonebrake, 2017; Marshall et al., 2017).

158 We determined 'absences' in our GLMs and RF models as locations (post 1950) where
159 other butterfly species had been recorded but the focal species had not. Whilst we assumed for

160 our analyses that butterfly surveys were complete at any given sampling locality (e.g. see
161 McPherson, Jetz, & Rogers, 2004; Platts, McClean, Lovett, & Marchant, 2008), some locality
162 records will have been from opportunistic encounters rather than from full site surveys (i.e. in
163 localities where few or single species were recorded; Figure S2 in Appendix S1). In MAXENT,
164 we specified that the background ('absence') data could only be calculated from the areas that
165 we had specified as absences (Marshall et al., 2017; Thibaud, Petitpierre, Broennimann, Davison,
166 & Guisan, 2014, but see Guillera-Arroita, Lahoz-Monfort, & Elith, 2014). We used equal
167 weightings for both the presence (P) and absence (A) data points by weighting the absence data
168 by a factor of P/A (<1 for all species) and standardizing the prevalence to 0.5; this tilts the
169 balance of errors from false negatives towards false positives (e.g. see Platts et al., 2008). All
170 SDMs were trained on 75% of the occurrence data and tested on the remaining 25% (Franklin,
171 2010), and this was repeated 10 times per model (Marshall et al., 2017; Platts et al., 2014). We
172 assessed model performances based on AUC (area under curve) values from the ROC (receiver
173 operating characteristic) curve (Marzban, 2004; Singh et al., 2017). Only models with AUC
174 values greater than 0.6 were included in the ensemble model analysis to generate maps of species
175 occurrence (probability of occurrence maps for GLMs and RF models and relative suitability
176 maps for MAXENT models) (Cheng & Bonebrake, 2017). The ensemble model outputs reported
177 the mean butterfly occurrence (i.e. averaged across the three algorithms) for all 1 km grid-cells
178 on Borneo, which for some analyses we subsequently transformed into binary data of
179 presence/absence using the default settings in *biomod2* (see Thuiller et al., 2016). In this way, we
180 ran 30 models per species, corresponding to 2310 models in total (77 species × 3 algorithms × 10
181 repeat model runs), and then cropped the SDM outputs to include only forested areas in mainland
182 Sabah (i.e. excluding offshore islands).

183

184 **2.4 Climate variables related to butterfly distributions**

185 To examine the importance of the five environmental variables included in our SDMs for
186 determining species' distributions across Borneo (Aim 1), we recorded the number of species for
187 which each predictor climate variable was most important, based on *biomod2* outputs for all
188 models with AUC values greater than 0.6. We also used Spearman's rank correlations to
189 determine the direction of any relationships (i.e. positive or negative) between environmental
190 variables and species occurrence (i.e. grid-cells representing the probability of occurrence or
191 relative suitability summed across all 77 study species and for just the 15 endemic species).

192

193 **2.5 Species' ranges and areas of high species richness**

194 Species' ranges in Sabah were defined as climatically-suitable forested areas from
195 presence/absence SDM output maps. We calculated the proportion of each species' range that
196 fell within each 200 m elevation band, and the proportion of each species' range that was
197 protected in each elevation band. We summed distribution maps for all 77 species, to produce a
198 combined layer of species richness, and used Spearman's rank correlations to examine the
199 relationship between species richness, elevation and aboveground carbon (Aim 2). To examine
200 the effectiveness of the TPA network for conserving richness (Aim 3), we compared species
201 richness of forested grid-cells within and outside the TPA network using a Mann-Whitney U test.
202 In order to determine areas of high species richness that did not fall within the existing TPA
203 network, we also calculated the number of grid-cells with at least 50% of species (i.e. $N > 38$
204 species, or $77/2$) that did not fall within the TPA network.

205

206 **2.6 Prioritization of remaining forest**

207 We used the systematic conservation prioritization package *prioritizr* (Hanson et al., 2018) in R
208 (R Core Team, 2017) to prioritize areas for protection in Sabah. This approach identifies areas
209 that cover input features (in our case, the continuous species occurrence maps from the 77 study
210 species), based on specification of the conservation problem, targets, budget and an objective
211 function. We used the ‘maximize features’ objective, which aims to cover a target proportion of
212 as many input features as possible (i.e. to optimize species richness and complementarity),
213 without surpassing a specified land area budget (i.e. the area of TPAs in Sabah). Our area
214 available for selection consisted of 1 km² planning units (formatted as raster grid-cells) covering
215 the forested area of mainland Sabah (40,259 km²). Using the species occurrence outputs allowed
216 us to harness the range of variation in each raster (i.e. as opposed to using presence/absence
217 data), thus providing increased parameter space to find optimal overlap across input features.
218 The total land area that was available to select for protection corresponded to the amount of land
219 area covered by the existing TPA network (18,622 km²; Fig 1b). We also included a penalty in
220 half of our prioritization scenarios, in the form of a boundary length modifier (BLM), which
221 promoted spatial clustering of the prioritized area to mirror the same number of clusters as the
222 existing TPA network (see Appendix S1 for additional BLM details). We calculated the extent of
223 the prioritized area that fell within and outside the TPA network, and determined the number of
224 TPAs in Sabah that did not contain any prioritized grid-cells (Aim 3). Finally, we re-ran our
225 prioritization analyses for only the 15 endemic species, but as results were similar to those for all
226 species, results for endemic species are only presented in the supporting information (Table S2 in
227 Appendix S2; Figure S5 in Appendix S2). All analyses were carried out in R version 3.4.0 or
228 newer (R Core Team, 2017).

229

230 **3 RESULTS**

231 **3.1 Climate variables related to butterfly distributions**

232 We modelled 77 range-restricted species using the SDM ensemble approach, and model outputs
233 for all species comprised at least two ‘useful’ models (where AUC >0.6, based on 30 SDMs per
234 species; range = 2-28 ‘useful’ models per species). These model outputs were used to create the
235 final distribution maps for each species, and represented mean occurrence across all ‘useful’
236 models. Across all 77 butterfly species, mean diurnal range in temperature and precipitation of
237 the wettest quarter of the year were the most important climate variables in predicting butterfly
238 distributions across Borneo (Table 1). The summed occurrences of all 77 study species (Figure
239 1a) increased with increasing mean diurnal range in temperature ($r_s = 0.51$, $N = 745,076$, $P <$
240 0.0001) and decreased with precipitation of the wettest quarter of the year ($r_s = -0.42$, $N =$
241 $745,076$, $P < 0.0001$). Hence, in general, our study species were more likely to occur in locations
242 with greater daily fluctuations in temperature (i.e. at high elevation; Figures S1 and S3 in
243 Appendix S1; Table S1 in Appendix S1) and in areas that were relatively dry during the wettest
244 part of the year (Figure S1 in Appendix S1). For Borneo endemics ($N = 15$ species), not only
245 was there a strong positive correlation between mean diurnal range in temperature and species
246 occurrence ($r_s = 0.73$, $N = 745,076$, $P < 0.0001$), but occurrence also increased with decreasing
247 annual mean temperature ($r_s = -0.52$, $N = 745,076$, $P < 0.0001$) (Table 1), hence endemic species
248 were also more likely to be found in high elevation areas (Figures S1 and S3 in Appendix S1;
249 Table S1 in Appendix S1).

250

251 **3.2 Areas of high species richness**

252 About 56% of Sabah is currently forested (Figure 1b; Figure S3 in Appendix S1), and even
253 though about half of the land area in Sabah occurs under 200 m asl (Figure 2a), high elevation
254 areas are more likely to be forested and protected. Across all species, TPAs were effective at
255 conserving between 30.3-72.3% of species' ranges (mean = 42.8%; SE \pm 0.89) (Figure 1b). Our
256 species' ranges were more likely to fall within TPAs at higher elevation, and in the highest
257 elevation band (>2000 m asl) 99% of projected species' ranges (mean across 77 species) fell
258 within the TPA network (Figure 2b). Species richness increased with elevation (Spearman
259 correlation: $r_s = 0.813$, $N = 40,184$, $P < 0.0001$) and to a lesser extent with aboveground carbon
260 (Spearman correlation: $r_s = 0.376$, $N = 40,259$, $P < 0.0001$) (Figure 1b; Figure S3 in Appendix
261 S1). Species richness was higher in TPA grid-cells ($N = 16,595$) than in non-TPA grid-cells ($N =$
262 $23,664$) (Mann-Whitney U test: $W = 201,400,000$; $P < 0.0001$) (Figure 1b), although the mean
263 difference was small (mean species richness per TPA and non-TPA grid-cells = 29.6 and 28.9
264 species, respectively). Areas of high richness (defined as grid-cells with at least 39 study species;
265 i.e. 50% of species) covered 11,217 km² (Figure 1b), of which 41.5% (4652 grid-cells) fell
266 within the TPA network. Hence, 58.5% of areas with high species richness of range-restricted
267 butterflies are not currently protected, corresponding to a land area of 6565 km².

268

269 **3.3 Prioritization of remaining forest**

270 We identified an area the size of the current Sabah TPA network (i.e. 18,622 km²), from a total
271 forested area of 40,259 km², as priority areas for butterfly conservation, comprising ~46% of the
272 total forested area on mainland Sabah. For all study species ($N = 77$), 32.7% (6091/18,622 grid-
273 cells) of highly prioritized areas overlapped with the TPA network in the no-BLM scenario.
274 When the BLM was included, slightly more (40.1%; 7470/18,622 grid-cells) of the TPA network

275 was prioritized (Figure 3; Table S2 in Appendix S2; Figure S5 in Appendix S2). Hence, between
276 59.9-67.3% of prioritized grid-cells did not fall within the TPA network (11,152 and 12,531 km²,
277 respectively, for the BLM and no-BLM scenarios). Locations of the prioritized grid-cells
278 corresponded with areas of high richness (Figures 1b and 3; Figures S4 and S5 in Appendix S2),
279 particularly in the Southwest of Sabah close to the Kalimantan boarder (Figure 1b). Across the
280 whole TPA network in Sabah, 84 (34%; 84/248) and 80 (32%; 80/248) TPAs contained at least
281 one highly prioritized grid-cell for the no-BLM and BLM prioritization scenarios, respectively,
282 whereas 164 (66%; 164/248) and 168 (68%; 168/248) TPAs contained no prioritized grid-cells
283 for these two scenarios (Figure 3).

284

285 **4 DISCUSSION**

286

287 **4.1 Climate variables relating to butterfly distributions**

288 Mean diurnal range in temperature and precipitation of the wettest quarter of the year were the
289 most important climate variables predicting range-restricted butterfly distributions across
290 Borneo. Mean diurnal range in temperature increased strongly with elevation (Table S1 in
291 Appendix S1), and so species occurrence also increased with elevation (below ~2000 m asl;
292 Figure S7 in Appendix S2). Temperature is a major determinant of species' distributions and
293 range boundaries (Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018) and cool tropical mountains
294 harbour many ecological specialists, often with narrow altitudinal ranges (Chen et al., 2011;
295 Laurance et al., 2011; Merckx et al., 2015; Rodríguez-Castañeda et al., 2010). We focused our
296 analyses on range-restricted butterflies, which primarily occur at mid-high elevation (Otsuka,

297 1988, 2001), and this likely drove the strong relationship we found between the mean diurnal
298 range in temperature and species occurrence.

299 Precipitation is an important predictor of species' distributions (Bush & Hooghiemstra,
300 2005), but relationships can be complex (Condit, Engelbrecht, Pino, Pérez, & Turner, 2013;
301 Lewis, Malhi, & Phillips, 2005). We included precipitation of the wettest quarter of the year in
302 our SDMs, which was strongly collinear with annual precipitation (Table S1 in Appendix S1).
303 Precipitation commonly increases with elevation (McCain & Grytnes, 2010), although on
304 Borneo this relationship was fairly weak when considering precipitation of the wettest quarter of
305 the year (Table S1 in Appendix S1), indicating that elevational precipitation trends may be
306 influenced by other factors such as monsoons or proximity to the ocean (Corlett, 2014). We
307 found that butterflies were most likely to occur in areas that were driest during the wettest part of
308 the year (i.e. most of Sabah and Eastern Borneo; Figure 1; Figure S1 in Appendix S1), and hence
309 receive low annual rainfall, indicating that our study species may be directly or indirectly (i.e.
310 through larval host plant quality and food availability) affected by periods of very high rainfall
311 during the wet season. Rainfall patterns can also alter net primary productivity (Schuur, 2003),
312 and a reduction in rainfall has been shown to affect larval host plants and butterfly abundance in
313 rainforests during El Niño-Southern Oscillation (ENSO) drought events (Hill, 1999; Srygley,
314 Dudley, Oliveira, & Riveros, 2013). However, some tropical butterflies have been found to
315 decline during very severe droughts (Hill, 1999), whilst heavy rainfall may also be detrimental
316 for some other forest taxa (e.g. see Ryan et al., 2015). Few studies have examined the
317 distributions of tropical insects in relation to climate across Southeast Asia (e.g. see Cheng &
318 Bonebrake, 2017; Klorvuttimontara et al., 2011), and so more research is needed to determine

319 the causes and patterns in abiotic range limits across different insect taxa. Such information is
320 vital for understanding the responses of insect species to climate change.

321

322 **4.2 Areas of high species richness**

323 Species richness of range-restricted butterflies in Sabah increased with elevation and to a lesser
324 extent aboveground carbon in forested areas. In Sabah, higher elevation areas contain more
325 aboveground carbon (Asner et al., 2018), likely due to less human disturbance in these remote
326 areas (Miettinen et al., 2011). Whilst data for aboveground carbon is currently limited to Sabah,
327 this pattern is likely found across the rest of Borneo due to similar topography (e.g. see Miettinen
328 et al., 2011; Scriven, Hodgson, McClean, & Hill, 2015). There is little empirical research
329 surrounding relationships between insect diversity and aboveground carbon density in tropical
330 regions, but disturbance-sensitive mammal diversity has been shown to be related to forest
331 carbon stocks (Deere et al., 2018, but see Beaudrot, Kroetz, & Alvarez-Loayza, 2016). However,
332 undisturbed (primary) forests across Southeast Asia contain higher levels of aboveground carbon
333 than logged forests or agroforests (Ziegler et al., 2012) and can support more range-restricted
334 insects than disturbed forests (e.g. butterflies: Cleary & Mooers, 2006; dungbeetles: Edwards et
335 al., 2011), which may account for the relationship we observed between aboveground carbon and
336 butterfly species richness. Nevertheless, many rainforest butterflies are sensitive to forest
337 disturbance, and so changes in canopy cover and light penetration may directly impact butterfly
338 distributions through microclimate effects on survival (of adults or larvae), or on larval food
339 plants (Hill, 1999). Hence, disturbed forest habitats that contain lower levels of aboveground
340 carbon (e.g. due to the removal of large trees) may support fewer insect species of conservation
341 concern. However, more research is needed to explicitly test the relationship between insect

342 richness and aboveground carbon in remaining forested areas, to determine whether any
343 relationship is likely to be causative.

344

345 **4.3 Efficiency of the TPA network**

346 The TPA network was reasonably effective at conserving areas with high species richness.
347 Nonetheless, a considerable amount of area (~60%; 6565 km²) with high species richness
348 occurred outside the existing TPA network. Similarly, only 33-40% of high priority areas fell
349 within the TPA network. Our results are similar to those of Cheng and Bonebrake (2017), who
350 found that ~60% of butterfly distributions in Hong Kong fell outside fully protected areas.
351 Equally, Fajardo, Lessmann, Bonaccorso, Devenish, & Muñoz (2014) showed that 43% of
352 butterfly species occurred within the current PA network of continental Peru, although this was
353 considerably lower for mammals and birds (20% and 22% protected, respectively). Thus, whilst
354 the current TPA network in Sabah may conserve the distributions of some range-restricted
355 species, in line with findings from other tropical regions, our results are worrying because many
356 areas of high species richness and high priority are not currently protected. Our results are also
357 likely to be relevant across the rest of Borneo, whereby large areas of remaining forest currently
358 persist outside of PAs and hence are under threat from continued agricultural expansion (Runting
359 et al., 2015). Given the projected growth in palm oil demand (Carrasco, Larrosa, Milner-Gulland,
360 & Edwards, 2014), as well as the negative impact of oil palm agriculture on tropical insects
361 (Brühl & Eltz, 2010; Scriven et al., 2017), these unprotected forest areas should be a priority for
362 future legislative protection. In Sabah, there are still large expanses of intact, high-carbon forest
363 that are unprotected (Figure S3 in Appendix S1), and our results highlight areas in Southwest

364 Sabah as being particularly important for range-restricted species that are not well protected by
365 the existing TPA network.

366 Over half of all TPAs (164 and 168 for the no-BLM and BLM prioritization scenarios,
367 respectively) in Sabah did not contain any high priority areas important for our study species and
368 these were primarily, small, low-lying TPAs close to the coast (Figure 3). These TPAs often
369 contain little high quality forest cover (Scriven et al., 2015), and so many degraded areas within
370 these lowland reserves will not have been classified as ‘forest’ based on our 40 Mg C ha⁻¹
371 threshold for delimiting forest areas. These degraded areas may include very young, regenerating
372 forests or areas of scrubland (Rosoman et al., 2017). Many lowland forests in Southeast Asia do
373 contain high species richness (Ashton, 2010; Curran et al., 2004; Lambert & Collar, 2002;
374 MacKinnon, Hatta, Halim, & Mangalik, 1996), but our range-restricted butterflies generally
375 occur at high elevation, and so will not be protected by low-lying TPAs. Mount Kinabalu, for
376 example, supports the highest concentration of butterfly species across Borneo, where more than
377 ~70% (625 species) of the Bornean butterfly fauna have been recorded, including many endemic
378 species (Häuser, Schulze, & Fiedler, 1997; Otsuka, 1988).

379 Tropical insects may be sensitive to changes in climate and are expected to shift their
380 distributions in response to climate change (Chen et al., 2009; Colwell, Brehm, Cardelús,
381 Gilman, & Longino, 2008). Despite limited data for the tropics, several studies predict that
382 insects will shift uphill in response to rising temperatures (e.g. moths: Chen et al., 2009;
383 butterflies: Molina-Martínez et al., 2016; dung beetles: Moret, Aráuz, Gobbi, & Barragán, 2016),
384 and this may lead to a decline in the effectiveness of current PAs if species’ ranges shift out of
385 reserve networks (i.e. because these locations become too hot or too dry) (Cheng & Bonebrake,
386 2017; Klorvuttimontara et al., 2011). We did not examine the efficiency of the TPA network to

387 conserve species under future climate change, but our results indicate that the distributions of
388 range-restricted butterflies on Borneo are limited by abiotic factors such as temperature and
389 rainfall, and thus are likely to shift to track climate. Whilst future rainfall projections are
390 uncertain (IPCC, 2014), in order to protect species from rising temperatures, increased protection
391 of forest areas at high elevation should be a conservation priority, to conserve species shifting
392 uphill from lower elevation. However, PAs are often not well connected, and so conserving
393 forest connections that link up PAs along elevational gradients may facilitate range shifting for
394 low and mid-elevation species (Feeley & Silman, 2016; Scriven et al., 2015). Montane species,
395 such as many of the species modelled in this study, which are already restricted to high elevation
396 areas, may have little opportunity to shift to cooler locations as climates warm (Colwell et al.,
397 2008). Thus, without specific conservation measures, these species may face climate-driven
398 extinctions.

399

400 **4.4 Sampling localities and biases**

401 In our study, we used a large butterfly dataset comprising museum records and published data
402 that provides reasonable spatial and temporal coverage across Sabah (Figure 1). However, as
403 with many species distribution modelling studies that rely on museum data (e.g. see Anderson,
404 2012), some of our sampling points are clustered around specific locations (e.g. Mount Kinabalu
405 National Park). Hence, our presence/absence data may reflect site-specific environmental
406 conditions and our projections of species richness may be more robust in these well-sampled
407 areas. Nonetheless, despite some clustering of sample sites, sampling localities were generally
408 well spread across the range of values in our five climate surfaces for Borneo (Figure S6 in
409 Appendix S2). Moreover, some areas in the lowlands with a high density of sampling localities

410 were predicted to have low species occurrence (e.g. coastal Brunei; Figure 1), and this indicates
411 that it is unlikely that uneven sampling effort had a large impact on our SDM outputs. It is
412 possible to account for geographical sampling biases in SDM studies (e.g. by incorporating
413 observer effort: see Beale, Brewer, & Lennon, 2014; Hill, 2012), and such strategies warrant
414 further research for capitalising on the types of data we used for examining tropical biodiversity.

415 We did not consider temporal bias in our dataset or biases from different sampling
416 regimes. If records had been collected during a particular part of the year (i.e. during drier
417 months due to ease of sampling) species that peak in abundance during the wet season (i.e. due
418 to new foliage; Novotny & Basset, 1998) may be less well represented. However, butterfly
419 diversity has been shown to peak in the dry season within primary forest (Hamer et al., 2005),
420 and so it is unlikely that temporal bias will have greatly influenced the reliability of our results.
421 In addition, for many of our sampling localities (i.e. museum records) there was no information
422 on the sampling strategy used and so some butterfly species, particularly those in the canopy,
423 may have been under-represented at certain sites. Hence, if our localities had low sampling
424 effort, were sampled at the wrong time of year, or if only one sampling method was used (such
425 as fruit-baited trapping), these biases may have resulted in false absence records for certain
426 species. In our models, we standardized the prevalence to 0.5, so that absences were weighted
427 equally to presences (resulting in false positives being more likely than false negatives) and this
428 shift was desirable because an absence record could be a consequence of limited sampling effort
429 (e.g. see Platts et al., 2008).

430

431 **4.5 Conservation implications**

432 Overall, we found that the TPA network was reasonably effective, and may protect at least 40%
433 of areas with high richness of range-restricted butterflies in Sabah. This number is reasonable,
434 considering that this reserve network was not designated primarily to conserve range-restricted
435 insects. However, more than half of all areas with high species richness and almost two thirds of
436 high priority areas fell outside TPAs, and so the current distribution of reserves may not provide
437 sufficient protection for many range-restricted species under threat from forest loss, assuming
438 our results for butterflies are similar to those for other insects. Butterfly distributions correlate
439 well with observed patterns in other taxonomic groups (e.g. see Gardner et al., 2008; Schulze et
440 al., 2004), and so many other insect species may also occur outside TPAs and will be at threat
441 from further deforestation and forest degradation. Conversely, butterfly distributions may not be
442 representative of some taxa such as large vertebrates, which may have much larger home ranges
443 and hence require more forest habitat for survival. Diverse insect communities are integral for
444 the functioning of rainforests, and their abundance and diversity can contribute to the resilience
445 of these habitats; loss of insects from rainforest ecosystems can also disrupt ecosystem processes
446 at other trophic levels (Ewers et al., 2015). Thus, insects need to be conserved in order to
447 preserve ecosystem functioning, provide stability to ecosystem processes and maintain resilience
448 of tropical rainforest habitats. The Sabah Forestry Department plans to extend TPA coverage
449 from ~25% in 2016 to ~30% in 2020 (i.e. an increase of ~3050 km²) (Sabah Forest Policy 2018;
450 see <http://www.forest.sabah.gov.my/discover/policies/sabah-forestry-department-policy>), and our
451 study emphasizes the need for creating additional TPAs, to complement the existing network, in
452 areas that contain high numbers of range-restricted and endemic species.

453

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461

462 **DATA AVAILABILTY STATEMENT**

463 Data available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.74p77q7> (Scriven
464 et al., 2019).

465

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774

775 **SUPPORTING INFORMATION**

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

778 **TABLE 1.** Importance of environmental predictor variables across Borneo for (1) all butterfly species ($N = 77$) and (2) only endemic
 779 species ($N = 15$), and for all species distribution models with AUC values greater than 0.6.

Environmental variable	No. of species for which predictor variable was most important		Total mean score ^a		Spearman's Rho (r_s) ^b	
	All ($N = 77$)	Endemic ($N = 15$)	All ($N = 77$)	Endemic ($N = 15$)	All ($N = 77$)	Endemic ($N = 15$)
Annual mean temperature (°C)	12	4	13.56	2.76	-0.34	-0.52
Mean diurnal temperature range (°C)	24	5	19.64	3.64	0.51	0.73
Temperature seasonality (°C)	10	2	13.81	2.73	-0.39	0.10
Precipitation of driest month (mm)	11	2	13.23	1.71	-0.04	0.13
Precipitation of wettest quarter (mm)	19	2	17.83	3.02	-0.42	-0.26

780

781 ^a Calculated from variable importance values for each variable involved in each model run where AUC > 0.6; the higher value, the more influence
 782 the variable has on the model (i.e. a value of 0 assumes no influence of that variable on the model).

783 ^b Calculated by correlating each environmental variable with the overall maps of species occurrence for Borneo (i.e. the probability of occurrence
 784 or relative suitability summed across all species).

785 **FIGURE LEGENDS**

786 **FIGURE 1.** (a) Map of Borneo showing summed occurrences of all 77 range-restricted butterfly
787 species from species distribution model (SDM) outputs. Black circles represent locality records
788 for all species records used in the analyses, and comprised a total of 398 sampling locations; this
789 included non Sundaland-restricted species that were used as absences. There were 2277 locality
790 records at 289 different sampling locations for all range-restricted species ($N = 77$) modelled in
791 the analyses. (b) Inset map of Sabah showing species richness (i.e. the 77 summed species'
792 ranges calculated from binary presence/absence maps and projected onto current areas of forest).
793 The outline of the existing totally protected area (TPA) network is overlaid.

794

795 **FIGURE 2.** (a) Land area in different elevation bands (m asl) in Sabah, expressed as a
796 percentage of total land area (black bars), percentage of land in each elevation band that is
797 protected (grey bars), and percentage of land in each elevation band that is forested (white bars).
798 (b) Percentage area of range-restricted butterfly distributions (species' ranges were calculated
799 from binary presence/absence maps and projected onto current areas of forest) in different
800 elevation bands (m asl) in Sabah (grey bars), and percentage area of species' ranges in each
801 elevation band that is protected (white bars). Bars represent means across all 77 study species
802 and error bars represent standard errors.

803

804 **FIGURE 3.** Maps of Sabah showing the final prioritized area (18,622 km²; blue shading) for all
805 species ($N = 77$) with: (a) no boundary length modifier (BLM) included (no-BLM scenario), and
806 (b) with the inclusion of a BLM (BLM scenario), which was used to aggregate the output grid-
807 cells (Appendix S1). The total area available for selection by the prioritization analyses

808 represents the forested area on mainland Sabah (40,259 km²; grey and blue shading combined).

809 The outline of the existing totally protected area (TPA) network is overlaid.

810 **FIGURE 1**

811





