



UNIVERSITY OF LEEDS

This is a repository copy of *Assessing the effectiveness of protected areas for conserving range-restricted rain forest butterflies in Sabah, Borneo*.

White Rose Research Online URL for this paper:
<http://eprints.whiterose.ac.uk/152959/>

Version: Accepted Version

Article:

Scriven, SA, Williams, SH, Ghani, MA et al. (7 more authors) (2019) Assessing the effectiveness of protected areas for conserving range-restricted rain forest butterflies in Sabah, Borneo. *Biotropica*. ISSN 0006-3606

<https://doi.org/10.1111/btp.12708>

© 2019 The Association for Tropical Biology and Conservation. This is the peer reviewed version of the following article: Scriven, SA, Williams, SH, Ghani, MA, et al. Assessing the effectiveness of protected areas for conserving range-restricted rain forest butterflies in Sabah, Borneo. *Biotropica*. 2019; 00: 000– 000. <https://doi.org/10.1111/btp.12708>, which has been published in final form at <https://doi.org/10.1111/btp.12708>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving. Uploaded in accordance with the publisher's self-archiving policy.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>

Scriven et al.

Protected area effectiveness for tropical butterflies

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

Sarah A. Scriven^{1*}; Sara H. Williams²; Mazidi A. Ghani^{1,3}; Agnes L. Agama⁴; Suzan
Benedick⁵; Jedediah F. Brodie²; Keith C. Hamer⁶; Colin J. McClean⁷; Glen Reynolds⁴ and Jane
K. Hill¹

¹ Department of Biology, University of York, York, YO10 5DD, UK

² Division of Biological Sciences and Wildlife Program, University of Montana, Missoula, MT
59812, U.S.A.

³ WWF-Malaysia Sabah Office, 6th Floor, CPS Tower, Centre Point Complex No. 1, Jalan
Centre Point 88800, Kota Kinabalu, Sabah, Malaysia.

⁴ The South East Asia Rainforest Research Partnership (SEARRP), Lahad Datu, Sabah,
Malaysia

⁵ Faculty of Sustainable Agriculture, Universiti Malaysia Sabah, Beg Berkunci No. 3, 90509,
Sandakan, Sabah, Malaysia

⁶ Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK

⁷ Department of Environment and Geography, University of York, York, YO10 5NG, UK

*Corresponding author; email: sarah.scriven@york.ac.uk; sarah_scriven@hotmail.co.uk

Received _____; revision accepted _____.

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 \times 3 algorithms \times 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
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205

2.4 Climate variables related to butterfly distributions

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

2.5 Species' ranges and areas of high species richness

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

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 border (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

454 **ACKNOWLEDGMENTS**

455 The project was funded by the Rainforest Trust via the South East Asia Rainforest Research
456 Partnership (SEARRP). Butterfly data were collated by MAG and SB, who were funded by a UK
457 Darwin Initiative (DEFRA) project (14-022). We thank Sabah Forestry Department for providing
458 information on TPAs, and Prof. David Burslem and Dr Luke Evans for helpful advice and
459 comments. We also thank Drs Colin Maycock, Phillip Platts, and Kuntal Singh for their help
460 with species distribution modelling.

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

466 **REFERENCES**

- 467 Anderson, R. P. (2012). Harnessing the world's biodiversity data: promise and peril in ecological
468 niche modelling of species distributions. *Annals of the New York Academy of Sciences*,
469 1260, 66-80. <https://doi.org/10.1111/j.1749-6632.2011.06440.x>
- 470 Ashton, P. S. (2010). Conservation of Borneo biodiversity: do small lowland parks have a role,
471 or are big inland sanctuaries sufficient? Brunei as an example. *Biodiversity and
472 Conservation*, 19, 343–356. <https://doi.org/10.1007/s10531-009-9717-0>
- 473 Asner, G. P., Brodrick, P. G., Philipson, C., Vaughn, N. R., Martin, R. E., Knapp, D. E., ... D. A.
474 Coomes. 2018. Mapped aboveground carbon stocks to advance forest conservation and
475 recovery in Malaysian Borneo. *Biological Conservation*, 217, 289–310.
476 <https://doi.org/10.1016/j.biocon.2017.10.020>
- 477 Beale, C. M., Brewer, M. J., & Lennon, J. J. (2014). A new statistical framework for the

478 quantification of covariate associations with species distributions. *Methods in Ecology and*
479 *Evolution*, 5, 421–432. <https://doi.org/10.1111/2041-210X.12174>

480 Beaudrot, L., Kroetz, K., Alvarez-Loayza, P., Amaral, I., Breuer, T., Fletcher, C., ... Andelman,
481 S. (2016). Limited carbon and biodiversity co-benefits for tropical forest mammals and
482 birds. *Ecological Applications*, 26, 1098-1111. <https://doi.org/10.1890/15-0935>

483 Benedick, S., Hill, J. K., Mustaffa, N., Chey, V. K., Maryati, M., Searle, J. B., ... Hamer, K. C.
484 (2006). Impacts of rain forest fragmentation on butterflies in northern Borneo: species
485 richness, turnover and the value of small fragments. *Journal of Applied Ecology*, 43, 967–
486 977. <https://doi.org/10.1111/j.1365-2664.2006.01209.x>

487 Boakes, E. H., Fuller, R. A., & McGowan, P. J. K. (2018). The extirpation of species outside
488 protected areas. *Conservation Letters*, 12, e12608. <https://doi.org/10.1111/conl.12608>

489 Bonebrake, T. C., Pickett, E. J., Tsang, T. P. N., Tak, C. Y., Vu, M. Q., & Vu, L. V. (2016).
490 Warming threat compounds habitat degradation impacts on a tropical butterfly community
491 in Vietnam. *Global Ecology and Conservation*, 8, 203–211.
492 <https://doi.org/10.1016/j.gecco.2016.09.003>

493 Brook, B. W., Sodhi, N. S. & Ng, P. K. L. (2003). Catastrophic extinctions follow deforestation
494 in Singapore. *Nature*, 424, 420–426. <https://doi.org/10.1038/nature01795>

495 Brühl, C. A., & Eltz, T. (2010). Fuelling the biodiversity crisis: species loss of ground-dwelling
496 forest ants in oil palm plantations in Sabah, Malaysia (Borneo). *Biodiversity Conservation*,
497 19, 519–529. <https://doi.org/10.1007/s10531-009-9596-4>

498 Bush, M. B., & Hooghiemstra, H. (2005). Tropical biotic response to climate change. In T. E.
499 Lovejoy & L. Hannah (Eds.), *Climate Change and Biodiversity* (pp. 125–137). New Haven,
500 USA: Yale University Press.

501 Carlson, K. M., Curran, L. M., Asner, G. P., Pittman, A. M., Trigg, S. N. & Adeney, J. M..
502 (2013). Carbon emissions from forest conversion by Kalimantan oil palm plantations.
503 Nature Climate Change, 3, 283–287. <https://doi.org/10.1038/nclimate1702>

504 Carrasco, L. R., Larrosa, C., Milner-Gulland, E. J., & Edwards, D. P. (2014). A double-edged
505 sword for tropical forests. Science, 346, 38–40. <https://doi.org/10.1126/science.1256685>

506 Chen, I.-C., Hill, J. K., Shiu, H.-J., Holloway, J. D., Benedick, S., Chey, V. K. ... Thomas, C. D.
507 (2011). Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of
508 climate warming. Global Ecology and Biogeography, 20, 34–45.
509 <https://doi.org/10.1111/j.1466-8238.2010.00594.x>

510 Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., ... Thomas,
511 C. D. (2009). Elevation increases in moth assemblages over 42 years on a tropical
512 mountain. Proceedings of the National Academy of Sciences of the United States of
513 America, 106, 1479–1483. <https://doi.org/10.1073/pnas.0809320106>

514 Cheng, W., & Bonebrake, T. C. (2017). Conservation effectiveness of protected areas for Hong
515 Kong butterflies declines under climate change. Journal of Insect Conservation, 21, 599–
516 606. <https://doi.org/10.1007/s10841-017-9998-7>

517 Cleary, D. F. R., & Mooers, A. Ø. (2006). Burning and logging differentially affect endemic vs.
518 widely distributed butterfly species in Borneo. Diversity and Distributions, 12, 409–416.
519 <https://doi.org/10.1111/j.1366-9516.2006.00256.x>

520 Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global
521 warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science,
522 322, 258–261. <https://doi.org/10.1126/science.1162547>

523 Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., & Turner, B. L. (2013). Species

524 distributions in response to individual soil nutrients and seasonal drought across a
525 community of tropical trees. *Proceedings of the National Academy of Sciences of the United*
526 *States of America*, 110, 5064–5068. <https://doi.org/10.1073/pnas.1218042110>

527 Corbet, A. S., & Pendelbury, H. M. (1992). *The butterflies of the Malay Peninsula*. Kuala
528 Lumpur, Malaysia: Malayan Nature Society.

529 Corlett, R. T. (2014). *The ecology of tropical East Asia*. Oxford, UK: Oxford University Press.

530 Curran, L. M., Trigg, S. N., McDonald, A. K., Astiani, D., Hardiono, Y. M., Siregar, P., ...
531 Kasischke, E. (2004). Lowland forest loss in protected areas of Indonesian Borneo. *Science*,
532 303, 1000–1003. <https://doi.org/10.1126/science.1091714>

533 D’Abrera, B. (1985). *Butterflies of the Oriental Region Part II*. London, UK: Hill House
534 Publishers.

535 Deere, N. J., Guillera-Arroita, G., Baking, E. L., Bernard, H., Pfeifer, M., Reynolds, G., ...
536 Struebig, M. J. (2018). High Carbon Stock forests provide co-benefits for tropical
537 biodiversity. *Journal of Applied Ecology*, 55, 997–1008. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2664.13023)
538 [2664.13023](https://doi.org/10.1111/1365-2664.13023)

539 DeFries, R., Hansen, A., Newton, A. C., & Hansen, M. C. (2005). Increasing isolation of
540 protected areas in tropical forests over the past twenty years. *Ecological applications*, 15,
541 19–26. <https://doi.org/10.1890/03-5258>

542 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S.
543 (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating
544 their performance. *Ecography*, 36, 27–46. [https://doi.org/10.1111/j.1600-](https://doi.org/10.1111/j.1600-0587.2012.07348.x)
545 [0587.2012.07348.x](https://doi.org/10.1111/j.1600-0587.2012.07348.x)

546 Edwards, D. P., Larsen, T. H., Docherty, T. D. S., Ansell, F. A., Hsu, W. W., Derhé, M. A., ...

547 Wilcove, D. S. (2011). Degraded lands worth protecting: the biological importance of
548 Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B*, 278, 82–90.
549 <https://doi.org/10.1098/rspb.2010.1062>

550 Ewers, R. M., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H. ...
551 Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical
552 rainforest. *Nature Communications*, 6, ncomms7836. <https://doi.org/10.1038/ncomms7836>

553 Fajardo, J., Lessmann, J., Bonaccorso, E., Devenish, C., & Muñoz, J. (2014). Combined use of
554 systematic conservation planning, species distribution modelling, and connectivity analysis
555 reveals severe conservation gaps in a megadiverse country (Peru). *PLoS ONE*, 9, e114367.
556 <https://doi.org/10.1371/journal.pone.0114367>

557 Feeley, K. J., & Silman, M. R. (2016). Disappearing climates will limit the efficacy of
558 Amazonian protected areas. *Diversity and Distributions*, 22, 1081-1084.
559 <https://doi.org/10.1111/ddi.12475>

560 Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces
561 for global land areas. *International Journal of Climatology*, 37, 4302-4315.
562 <https://doi.org/10.1002/joc.5086>

563 Franklin, J. (2010). *Mapping species distributions: spatial inference and prediction*. Cambridge,
564 UK: Cambridge University Press. <https://doi.org/10.1017/CBO9780511810602>

565 Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018). Expanding, shifting
566 and shrinking: The impact of global warming on species' elevational distributions. *Global*
567 *Ecology and Biogeography*, 27, 1268–1276. <https://doi.org/10.1111/geb.12774>

568 Gardner, T. A., Barlow, J., Araújo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., ... &
569 Peres, C. A. (2008). The cost-effectiveness of biodiversity surveys in tropical forests.

570 Ecology Letters, 11, 139–150. <https://doi.org/10.1111/j.1461-0248.2007.01133.x>

571 Gathorne-Hardy, F. J., Syauckani, , Davies, R. G., Egelton, P., & Jones, D. T. (2002).
572 Quaternary rainforest refugia in Southeast Asia: using termites (Isoptera) as indicators.
573 Biological Journal of the Linnean Society, 75, 453–466. <https://doi.org/10.1046/j.1095->
574 8312.2002.00031.x

575 Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., ... Meijaard, E.
576 (2014). Four decades of forest persistence, clearance and logging on Borneo. PLoS ONE, 9,
577 e101654. <https://doi.org/10.1371/journal.pone.0101654>

578 Ghani, M. A. (2012). Assessing the conservation value of protected areas of Borneo in relation
579 to the diversity of butterflies. MSc Dissertation, Insitute for Tropical Biology and
580 Conservation, Universiti Malaysia Sabah, Sabah, Malaysia.

581 Grixti, J. C., Wong, L. T., Cameron, S. A., & Favret, C. (2009). Decline of bumble bees
582 (*Bombus*) in the North American Midwest. Biological Conservation, 142, 75–84.
583 <https://doi.org/10.1016/j.biocon.2008.09.027>

584 Guillera-Aroita, G., Lahoz-Monfort, J. J., & Elith, J. (2014). Maxent is not a presence-absence
585 method: a comment on Thibaud et al. Methods in Ecology and Evolution, 5, 1192–1197.
586 <https://doi.org/10.1111/2041-210X.12252>

587 Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., ... de Kroon, H.
588 (2017). More than 75 percent decline over 27 years in total flying insect biomass in
589 protected areas. PLoS ONE, 10, e0185809. <https://doi.org/10.1371/journal.pone.0185809>

590 Hamer, K. C., Hill, J. K., Mustaffa, N., Benedick, S., Sherratt, T. N., Chey, V. K., & Maryat, M.
591 (2005). Temporal variation in abundance and diversity of butterflies in Bornean rain forests:
592 opposite impacts of logging recorded in different seasons. Journal of Tropical Ecology, 21,

593 417–425. <https://doi.org/10.1017/S0266467405002361>

594 Hanson, J. O., Schuster, R., Morrell, N., Strimas-Mackey, M., Watts, M. E., Arcese, P., ...

595 Possingham, H. (2018). prioritizr: Systematic conservation prioritization in R. R package

596 version 4.0.2 Retrieved from <https://cran.r-project.org/web/packages/prioritizr/index.html>

597 (accessed 30th September 2018).

598 Häuser, C. L., Schulze, C. H., & Fiedler, K. (1997). The butterfly species (Insecta: Lepidoptera:

599 Rhopalocera) of Kinabalu park, Sabah. *The Raffles Bulletin of Zoology*, 45, 281–304.

600 Hill, J. K. (1999). Butterfly spatial distribution and habitat requirements in a tropical forest:

601 impacts of selective logging. *Journal of Applied Ecology*, 36, 564–572.

602 <https://doi.org/10.1046/j.1365-2664.1999.00424.x>

603 Hill, J. K., Hamer, K. C., Tangah, J., & Dawood, M. (2001). Ecology of tropical butterflies in

604 rainforest gaps. *Oecologia*, 128, 294–302. <https://doi.org/10.1007/s004420100651>

605 Hill, M. O. (2012). Local frequency as a key to interpreting species occurrence data when

606 recording effort is not known. *Methods in Ecology and Evolution*, 3, 195–205.

607 <https://doi.org/10.1111/j.2041-210X.2011.00146.x>

608 Intergovernmental Panel on Climate Change (IPCC). (2014). Asia. In *Climate Change 2014 -*

609 *Impacts, adaptation, and vulnerability: Part B: Regional aspects: Working group II*

610 *contribution to the fifth assessment report* (pp. 1327–1370), Cambridge, UK: Cambridge

611 University Press. <https://doi.org/10.1017/CBO9781107415386.004>

612 Kharouba, H. M., Lewthwaite, J. M. M., Guralnick, R., Kerr, J. T., & Vellend, M. (2018). Using

613 insect natural history collections to study global change impacts: challenges and

614 opportunities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374:

615 20170405. <https://doi.org/10.1098/rstb.2017.0405>

616 Klorvuttimontara, S., McClean, C. J., & Hill, J. K. (2011). Evaluating the effectiveness of
617 Protected Areas for conserving tropical forest butterflies of Thailand. *Biological*
618 *Conservation*, 144, 2534–2540. <https://doi.org/10.1016/j.biocon.2011.07.012>

619 Koh, L. P., & Sodhi, N. S. (2010). Conserving Southeast Asia’s imperiled biodiversity:
620 scientific, management, and policy challenges. *Biodiversity Conservation*, 19, 913–917.
621 <https://doi.org/10.1007/s10531-010-9818-9>

622 Koh, L. P., Sodhi, N. S., & Brook, B. W. (2004). Ecological correlates of extinction proneness in
623 tropical butterflies. *Conservation Biology*, 18, 1571–1578. [https://doi:10.1111/j.1523-](https://doi:10.1111/j.1523-1739.2004.00468.x)
624 [1739.2004.00468.x](https://doi:10.1111/j.1523-1739.2004.00468.x)

625 Lambert, F. R., & Collar, N. J. (2002). The future of Sudanic lowland forest birds: long-term
626 effects of commercial logging and fragmentation. *Forktail*, 18, 127–146. Retrieved from
627 <http://birdingasia.org/wp-content/uploads/2012/09/Lambert-Sundaic.pdf>

628 Laurance, W. F., Sayer, J. & Cassman, K. G. (2014). Agricultural expansion and its impacts on
629 tropical nature. *Trends in Ecology and Evolution*, 29, 107–116.
630 <https://doi.org/10.1016/j.tree.2013.12.001>

631 Laurance, W.F., Useche, D. C., Shoo, L. P., Herzog, S. K., Kessler, M., Escobar, F., ... Thomas,
632 C. D. (2011). Global warming, elevational ranges and the vulnerability of tropical biota.
633 *Biological Conservation*, 144, 548–557. <https://doi.org/10.1016/j.biocon.2010.10.010>

634 Lewis, S. L., Malhi, Y., & Phillips, O. L. (2005). Predicting the impacts of global environmental
635 changes on tropical forests. In Y. Malhi and O. L. Phillips (Eds.), *Tropical forests and*
636 *global atmospheric change* (pp. 41-56). Oxford, UK: Oxford University Press.
637 <https://doi.org/10.1093/acprof:oso/9780198567066.001.0001>

638 Lohman, D. J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P. K. L., ... von Rintelen,

639 T. (2011). Biogeography of the Indo-Australian Archipelago. *Annual Review of Ecology,*
640 *Evolution, and Systematics*, 42, 205–226. [https://doi.org/10.1146/annurev-ecolsys-102710-](https://doi.org/10.1146/annurev-ecolsys-102710-145001)
641 145001

642 MacKinnon, K., Hatta, G., Halim, H., & Mangalik, A. (1996). *The ecology of Kalimantan.*
643 Oxford, UK: Oxford University Press.

644 Marshall, L., Biesmeijer, J. C., Rasmont, P., Vereecken, N. J., Dvorak, L., Fitzpatrick, U., ...
645 Dendoncker, N. (2017). The interplay of climate and land use change affects the distribution
646 of EU bumblebees. *Global Change Biology*, 24, 101–116.
647 <https://doi.org/10.1111/gcb.13867>

648 Marzban, C. (2004). The ROC curve and the area under it as performance measures. *Weather*
649 *and Forecasting*, 19, 1106–1114. <https://doi.org/10.1175/825.1>

650 McCain, C. M., & Grytnes, J.-A. (2010). *Elevational Gradients in Species Richness.*
651 *Encyclopedia of Life Sciences.* Chichester, UK: John Wiley & Sons.
652 <https://doi.org/10.1002/9780470015902.a0022548>

653 McPherson, J. M., Jetz, W., & Rogers, D. J. (2004). The effects of species' range sizes on the
654 accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of*
655 *Applied Ecology*, 41, 811–823. <https://doi.org/10.1111/j.0021-8901.2004.00943.x>

656 Meijaard, E., Garcia-Ulloa, J., Sheil, D., Wich, S.A., Carlson, K.M., Juffe-Bignoli, D., & Brooks,
657 T. (2018). Oil palm and biodiversity: a situation analysis by the IUCN Oil Palm Task Force.
658 <https://doi.org/10.2305/IUCN.CH.2018.11.en>

659 Merckx, V. S. F. T., Hendriks, K. P., Beentjes, K. K., Mennes, C. B., Becking, L. E.,
660 Peijnenburg, K. T. C. A., ... Schilthuizen, M. (2015). Evolution of endemism on a young
661 tropical mountain. *Nature*, 524, 347–350. <https://doi.org/10.1038/nature14949>

662 Miettinen, J., Shi, C., & Liew, S. C. (2011). Deforestation rates in insular Southeast Asia
663 between 2000 and 2010. *Global Change Biology*, 17, 2261–2270.
664 <https://doi.org/10.1111/j.1365-2486.2011.02398.x>

665 Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C (2011). Global
666 biodiversity conservation: the critical role of hotspots. In F. E. Zachos and J. C. Habel
667 (Eds.), *Biodiversity hotspots. Distribution and protection of conservation priority areas*.
668 (pp. 3–22), Berlin, Germany: Springer. <https://doi.org/10.1007/978-3-642-20992-5>

669 Molina-Martínez, A., León-Cortés, J. L., Regan, H. M., Lewis, O. T., Navarrete, D., Caballero,
670 U., & Luis-Martínez, A. (2016). Changes in butterfly distributions and species assemblages
671 on a Neotropical mountain range in response to global warming and anthropogenic land use.
672 *Diversity and Distributions*, 22, 1085–1098. <https://doi.org/10.1111/ddi.12473>

673 Moret, P., Aráuz, M. de los Á., Gobbi, M., & Barragán, Á. (2016). Climate warming effects in
674 the tropical Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador.
675 *Insect Conservation and Diversity*, 9(4), 342–350. <https://doi.org/10.1111/icad.12173>

676 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000).
677 Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
678 <https://doi.org/10.1038/35002501>

679 Noriega, J. A., Hortal, J., Azcárate, F. M., Bergd, M. P., Bonada, N., Briones, M. J. I., ...
680 Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. *Basic*
681 *and Applied Ecology*, 26, 8–23. <https://doi.org/10.1016/j.baae.2017.09.006>

682 Novotny, V., & Basset, Y. (1998). Seasonality of sap-sucking insects (Auchenorrhyncha,
683 Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea.
684 *Oecologia*, 115, 514–522. <https://doi.org/10.1007/s004420050549>

685 Otsuka, K. (1988). *Butterflies of Borneo*. Tokyo, Japan: Tobishima Corporation,

686 Otsuka, K. (2001). *A field guide to the butterflies of Borneo and Southeast Asia*. Kota Kinabalu,

687 Malaysia: Hornbill Books.

688 Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species

689 geographic distributions. *Ecological Modelling*, 190, 231–259.

690 <https://doi.org/10.1016/j.ecolmodel.2005.03.026>

691 Platts, P. J., Garcia, R. A., Hof, C., Foden, W., Hansen, L. A., Rahbek, C., & Burgess, N. D.

692 (2014). Conservation implications of omitting narrow-ranging taxa from species distribution

693 models, now and in the future. *Diversity and Distributions*, 20, 1307–1320.

694 <https://doi.org/10.1111/ddi.12244>

695 Platts, P. J., McClean, C. J., Lovett, J. C., & Marchant, R. (2008). Predicting tree distributions in

696 an East African biodiversity hotspot: model selection, data bias and envelope uncertainty.

697 *Ecological Modelling*, 218, 121–134. <https://doi.org/10.1016/j.ecolmodel.2008.06.028>

698 Ponder, W. F., Carter, G. A., Flemons, P., & Chapman, R. R. (2001). Evaluation of museum

699 collection data for use in biodiversity assessment. *Conservation Biology*, 15, 648–657.

700 <https://doi.org/10.1046/j.1523-1739.2001.015003648.x>

701 R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation

702 for Statistical Computing, Vienna, Austria. Retrieved from <http://www.r-project.org/>

703 Rodríguez-Castañeda, G., Dyer, L. A., Brehm, G., Connahs, H., Forkner, R. E., & Walla, T. R.

704 (2010). Tropical forests are not flat: how mountains affect herbivore diversity. *Ecology*

705 *Letters*, 13, 1348–1357. <https://doi.org/10.1111/j.1461-0248.2010.01525.x>

706 Rosoman, G., Sheun, S. S., Opal, C., Anderson, P., & Trapshah, R. (Eds.) (2017). *The HCS*

707 *approach toolkit*. Singapore: HCS Approach Steering Group. Retrieved from

708 <http://highcarbonstock.org/wp-content/uploads/2018/04/Def-HCSA-Module-5->
709 [16_04_2018_Web.pdf](http://highcarbonstock.org/wp-content/uploads/2018/04/Def-HCSA-Module-5-16_04_2018_Web.pdf)

710 Runting, R. K., Meijaard, E., Abram, N. K., Wells, J. A., Gaveau, D. L. A., Ancrenaz, M., ...
711 Wilson, K. A. (2015). Alternative futures for Borneo show the value of integrating
712 economic and conservation targets across borders. *Nature Communications*, 6, 6819.
713 <https://doi.org/10.1038/ncomms7819>

714 Ryan, M. J., Scott, N. J., Cook, J. A., Willink, B., Chaves, G., Bolaños, F., ... Koerner, S. E.
715 (2015). Too wet for frogs: changes in a tropical leaf litter community coincide with La
716 Niña. *Ecosphere*, 6, 1–10. <https://doi.org/10.1890/ES14-00352.1>

717 Sabah Forestry Department. (2016). Annual Report 2016. Sandakan, Sabah, Malaysia. Retrieved
718 from <http://www.forest.sabah.gov.my/publication/annual-reports>

719 Scriven, S. A., Beale, C. M., Benedick, S., & Hill, J. K. (2017). Barriers to dispersal of rain
720 forest butterflies in tropical agricultural landscapes. *Biotropica*, 49, 206–216.
721 <https://doi.org/10.1111/btp.12397>

722 Scriven, S. A., Hodgson, J. A., McClean, C. J., & Hill, J. K. (2015). Protected areas in Borneo
723 may fail to conserve tropical forest biodiversity under climate change. *Biological*
724 *Conservation*, 184, 414–423. <https://doi.org/10.1016/j.biocon.2015.02.018>

725 Scriven, S. A., Williams, S. H., Ghani, M. A., Agama, A. L., Benedick, S., Brodie, J. F., ... Hill,
726 J. K. (2019). Data from: Assessing the effectiveness of protected areas for conserving
727 range-restricted rainforest butterflies in Sabah, Borneo. Dryad Digital Repository,
728 <https://doi.org/10.5061/dryad.74p77q7>

729 Schuur, E. A. G., (2003). Productivity and global climate revisited: the sensitivity of tropical
730 forest growth to precipitation. *Ecology*, 84, 1165–1170. <https://doi.org/10.1890/0012->

731 9658(2003)084[1165:PAGCRT]2.0.CO;2

732 Singh, K., McClean, C. J., Bükér, P., Hartley, S. E., & Hill, J. K. (2017). Mapping regional risks
733 from climate change for rainfed rice cultivation in India. *Agricultural Systems*, 156, 76–84.
734 <https://doi.org/10.1016/j.agsy.2017.05.009>

735 Slade, E. M., Mann, D. J., & Lewis, O. T. (2011). Biodiversity and ecosystem function of
736 tropical forest dung beetles under contrasting logging regimes. *Biological Conservation*,
737 144, 166–174. <https://doi.org/10.1016/j.biocon.2010.08.011>

738 Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K. L. (2004). Southeast Asian biodiversity: an
739 impending disaster. *Trends in Ecology & Evolution*, 19, 654–660.
740 <https://doi.org/10.1016/j.tree.2004.09.006>

741 Srygley, R.B., Dudley, R., Oliveira, E. G. & Riveros, A. J. (2013). El Niño, host plant growth,
742 and migratory butterfly abundance in a changing climate. *Biotropica*, 46, 90–97.
743 <https://doi.org/10.1111/btp.12081>

744 Tarli, D. V., Grandcolas, P., & Pellens, R. (2018). The informative value of Museum collections
745 for ecology and conservation: a comparison with target sampling in the Brazilian Atlantic
746 forest. *PLoS ONE*, 13, e0205710. <https://doi.org/10.1371/journal.pone.0205710>

747 Thibaud, E., Petitpierre, B., Broennimann, O., Davison, A. C., & Guisan, A. (2014). Measuring
748 the relative effect of factors affecting species distribution model predictions. *Methods in*
749 *Ecology and Evolution*, 5, 947–955. <https://doi.org/10.1111/2041-210X.12203>

750 Thuiller, A. W., Georges, D., Engler, R., Georges, M. D., & Thuiller, C. W. (2016). The biomod2
751 package: the updated object-oriented version of BIOMOD package. R package version 3.3-
752 7. Retrieved from <https://cran.r-project.org/web/packages/biomod2/index.html> (accessed 1st
753 October 2018)

754 Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M. B. (2009). BIOMOD - A platform for
755 ensemble forecasting of species distributions. *Ecography*, 32, 369–373.
756 <https://doi.org/10.1111/j.1600-0587.2008.05742.x>

757 Weissflog, A., Markesteijn, L., Lewis, O. T., Comita, L. S., & Engelbrecht, B. M. J. (2018).
758 Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall
759 gradient. *Biotropica*, 50, 302–311. <https://doi.org/10.1111/btp.12513>

760 Wikelski, M., Moxley, J., Eaton-Mordas, A., Lopez-Uribe, M. M., Holland, R., Moskowicz, D.,
761 ... Kays, R. (2010). Large-range movements of neotropical orchid bees observed via radio
762 telemetry. *PLoS ONE*, 5, e10738. <https://doi.org/10.1371/journal.pone.0010738>

763 Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., NCEAS
764 Predicting Species Distributions Working Group. (2008). Effects of sample size on the
765 performance of species distribution models. *Diversity and Distributions*, 14, 763–773.
766 <https://doi.org/10.1111/j.1472-4642.2008.00482.x>

767 World Wide Fund for Nature (WWF) (2018). Living planet report - 2018: Aiming higher. M.
768 Grooten and R. E. A. Almond (Eds.). WWF, Gland, Switzerland. Retrieved from
769 https://wwf.panda.org/knowledge_hub/all_publications/living_planet_report_2018/

770 Ziegler, A. D., Phelps, J., Yuen, J. Q., Webb, E. L., Lawrence, D., Fox, J. M., ... Koh, L. P.
771 (2012). Carbon outcomes of major land-cover transitions in SE Asia: great uncertainties and
772 REDD+ policy implications. *Global Change Biology*, 18, 3087–3099.
773 <https://doi.org/10.1111/j.1365-2486.2012.02747.x>

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





