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

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**ABSTRACT**

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

**KEY WORDS**

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

1. **INTRODUCTION**

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

A large component of tropical biodiversity is comprised of insects, which perform important ecological functions in rainforests (e.g. herbivory, pollination, dung removal, decomposition; Ewers et al., 2015; Noriega et al., 2018; Slade, Mann, & Lewis, 2011; Weissflog, Markesteijn, Lewis, Comita, & Engelbrecht, 2018; Wikelski et al., 2010), yet we lack information on factors affecting the distributions of insects in the tropics. Given that many rainforest species are vulnerable to extinction from land-use and climate change (Brook *et al.* 2003; WWF, 2018), and that insect biomass is declining globally (Hallmann et al., 2017), it is important to map species’ ranges and determine the effectiveness of protected areas (PAs) at conserving rainforest insects. Data on insect species ranges are limited in the tropics (Cheng & Bonebrake, 2017), and so museum collections are an important resource for supporting insect conservation (Kharouba, Lewthwaite, Guralnick, Kerr, & Vellend, 2018; Ponder, Carter, Flemons, & Chapman, 2001; Tarli, Grandcolas, & Pellens, 2018). Museum records have been used to document insect population declines (Grixti, Wong, Cameron, & Favret, 2009), predict species’ distributions (Klorvuttimontara, McClean, & Hill, 2011), and measure phenological shifts (Kharouba et al., 2018); hence, they are an important source of baseline data for conservation planning (Ponder et al., 2001; Tarli et al., 2018), especially in tropical regions where detailed information on species’ distributions is generally lacking.

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

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

We collated distribution records for 77 range-restricted butterflies on Borneo from published data sources and museum collections, and ran species distribution models (SDMs) to project butterfly distributions within forest habitat in relation to climate factors. From overlaying the species’ distributions, we determined the locations of current forest areas in Sabah projected to have high species richness. We also used systematic conservation prioritization methods to determine the most important (i.e. the most climatically suitable) areas of remaining rainforest for conserving the distributions of our study species in Sabah. We focus on Sabah because of the high density of butterfly records, combined with availability of ancillary data, particularly for aboveground carbon (Asner et al., 2018) and TPA coverage (Sabah Forestry Depertment, 2016). Our main aims were to: (1) determine the most important climatic factors limiting the distributions of range-restricted butterflies on Borneo, in order to improve our understanding of the bioclimatic limits underpinning the ranges of tropical insects; (2) assess whether elevation and aboveground carbon predict areas with high species richness; and (3) quantify the effectiveness of the TPA network in Sabah for conserving range-restricted butterflies.

1. **METHODS** 
   1. **Butterfly locality records**

We obtained butterfly records from the ‘Borneo Butterfly Distribution Database (B2D2)’ retrieved from: http://www-users.york.ac.uk/~jkh6/index.htm (accessed 10th September 2018). This database was compiled from museum specimens, published papers, field reports and University PhD theses dating from 1878 to 2006; see Ghani, 2012 for more details). Overall, the database contains over 22,000 records from more than 300 butterfly species belonging to the families Papilionidae, Pieridae and Nymphalidae. We filtered records to include only those collected after 1950, to try to balance ensuring that our butterfly records were relevant to the current climate (i.e. 1970-2000; see below), while not discarding too many historical records. This resulted in 7661 records at 398 unique sampling localities for all butterfly species across Borneo (Figure 1a). We selected records for species that are restricted to Sundaland, including 15 species that are endemic to Borneo (see Otsuka, 2001 for details). Only one Sundaland species, *Papilio iswaroides,* had fewer than 10 locality records and so was excluded from the analysis. We therefore ran SDMs for 77 species, based on 2277 presence records from 289 unique sampling locations.

* 1. **Climate and elevation data**

To project the potential distributions of the 77 study species, 19 climate variables representing average monthly temperature and precipitation data for 1970-2000 were downloaded from the WorldClim database (http://worldclim.org/version2; accessed 9th June 2018) (see Fick & Hijmans, 2017) at ~1 km2 (30 arc-second) resolution for Borneo. Elevation data were downloaded from the CGIAR-CSI GeoPortal (http://srtm.csi.cgiar.org/; accessed 1st October 2018) at 250 m resolution and then aggregated by a factor of four to 1 km grid-cells. To assess whether climate variables were correlated, we performed a pairwise Spearman’s rank correlation analysis on the 19 WorldClim variables and elevation. Analyses revealed that many environmental variables were collinear (see Dormann et al., 2013) (Table S1 in Appendix S1); for those variables with a regression coefficient value greater than 0.7, the variable from the pair most correlated with other variables was included. Thus, five climate variables were included in the SDMs: (1) annual mean temperature (°C); (2) mean diurnal temperature range (°C); (3) temperature seasonality (standard deviation in monthly temperatures × 100; a measure of temperature variation within years) (°C); (4) precipitation of the driest month of the year (mm); and (5) precipitation of the wettest quarter of the year (mm) (Figure S1 in Appendix S1). We did not include forest cover data within the SDMs because of land-use change since many of the locality records were collected (Gaveau et al., 2014; Figure S3a in Appendix S1) (also see Appendix S1 for additional details and implications of land-use change following record collection). Instead, we used our SDMs to characterize the location of suitable climate space between 1970-2000 for our study species in areas of remaining forest in 2016. We applied outputs from the SDMs and *prioritizr* software (see below) to forested areas (excluding mangrove forests) that contained more than 40 metric tons of aboveground carbon per hectare (Mg C ha-1) (mean across 1 km grid-cells resampled from 30 m grid-cells; Asner et al., 2018). In this way, we tried to ensure that areas of degraded and/or regenerating forest were included in our projections of species’ potential ranges while production plantations were not (Rosoman, Sheun, Opal, Anderson, & Trapshah, 2017).

* 1. **Species distribution models**

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

We determined ‘absences’ in our GLMs and RF models as locations (post 1950) where other butterfly species had been recorded but the focal species had not. Whilst we assumed for our analyses that butterfly surveys were complete at any given sampling locality (e.g. see McPherson, Jetz, & Rogers, 2004; Platts, McClean, Lovett, & Marchant, 2008), some locality records will have been from opportunistic encounters rather than from full site surveys (i.e. in localities where few or single species were recorded; Figure S2 in Appendix S1). In MAXENT, we specified that the background (‘absence’) data could only be calculated from the areas that we had specified as absences (Marshall et al., 2017; Thibaud, Petitpierre, Broennimann, Davison, & Guisan, 2014, but see Guillera-Arroita, Lahoz-Monfort, & Elith, 2014). We used equal weightings for both the presence (P) and absence (A) data points by weighting the absence data by a factor of P/A (<1 for all species) and standardizing the prevalence to 0.5; this tilts the balance of errors from false negatives towards false positives (e.g. see Platts et al., 2008). All SDMs were trained on 75% of the occurrence data and tested on the remaining 25% (Franklin, 2010), and this was repeated 10 times per model (Marshall et al., 2017; Platts et al., 2014). We assessed model performances based on AUC (area under curve) values from the ROC (receiver operating characteristic) curve (Marzban, 2004; Singh et al., 2017). Only models with AUC values greater than 0.6 were included in the ensemble model analysis to generate maps of species occurrence (probability of occurrence maps for GLMs and RF models and relative suitability maps for MAXENT models) (Cheng & Bonebrake, 2017). The ensemble model outputs reported the mean butterfly occurrence (i.e. averaged across the three algorithms) for all 1 km grid-cells on Borneo, which for some analyses we subsequently transformed into binary data of presence/absence using the default settings in *biomod2* (see Thuiller et al., 2016). In this way, we ran 30 models per species, corresponding to 2310 models in total (77 species × 3 algorithms × 10 repeat model runs), and then cropped the SDM outputs to include only forested areas in mainland Sabah (i.e*.* excluding offshore islands).

* 1. **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).

* 1. **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.

* 1. **Prioritization of remaining forest**

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

1. **RESULTS**

**3.1 Climate variables related to butterfly distributions**

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

**3.2 Areas of high species richness**

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

* 1. **Prioritization of remaining forest**

We identified an area the size of the current Sabah TPA network (i.e*.* 18,622 km2), from a total forested area of 40,259 km2, as priority areas for butterfly conservation, comprising ~46% of the total forested area on mainland Sabah. For all study species (*N =* 77), 32.7% (6091/18,622 grid-cells) of highly prioritized areas overlapped with the TPA network in the no-BLM scenario. When the BLM was included, slightly more (40.1%; 7470/18,622 grid-cells) of the TPA network was prioritized (Figure 3; Table S2 in Appendix S2; Figure S5 in Appendix S2). Hence, between 59.9-67.3% of prioritized grid-cells did not fall within the TPA network (11,152 and 12,531 km2, respectively, for the BLM and no-BLM scenarios). Locations of the prioritized grid-cells corresponded with areas of high richness (Figures 1b and 3; Figures S4 and S5 in Appendix S2), particularly in the Southwest of Sabah close to the Kalimantan boarder (Figure 1b). Across the whole TPA network in Sabah, 84 (34%; 84/248) and 80 (32%; 80/248) TPAs contained at least one highly prioritized grid-cell for the no-BLM and BLM prioritization scenarios, respectively, whereas 164 (66%; 164/248) and 168 (68%; 168/248) TPAs contained no prioritized grid-cells for these two scenarios (Figure 3).

1. **DISCUSSION**

**4.1 Climate variables relating to butterfly distributions**

Mean diurnal range in temperature and precipitation of the wettest quarter of the year were the most important climate variables predicting range-restricted butterfly distributions across Borneo. Mean diurnal range in temperature increased strongly with elevation (Table S1 in Appendix S1), and so species occurrence also increased with elevation (below ~2000 m asl; Figure S7 in Appendix S2). Temperature is a major determinant of species’ distributions and range boundaries (Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018) and cool tropical mountains harbour many ecological specialists, often with narrow altitudinal ranges (Chen et al., 2011; Laurance et al., 2011; Merckx et al., 2015; Rodríguez-Castañeda et al., 2010). We focused our analyses on range-restricted butterflies, which primarily occur at mid-high elevation (Otsuka, 1988, 2001), and this likely drove the strong relationship we found between the mean diurnal range in temperature and species occurrence.

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

**4.2 Areas of high species richness**

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

* 1. **Efficiency of the TPA network**

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

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

Tropical insects may be sensitive to changes in climate and are expected to shift their distributions in response to climate change (Chen et al., 2009; Colwell, Brehm, Cardelús, Gilman, & Longino, 2008). Despite limited data for the tropics, several studies predict that insects will shift uphill in response to rising temperatures (e.g. moths: Chen et al., 2009; butterflies: Molina-Martínez et al., 2016; dung bettles: Moret, Aráuz, Gobbi, & Barragán, 2016), and this may lead to a decline in the effectiveness of current PAs if species’ ranges shift out of reserve networks (i.e. because these locations become too hot or too dry) (Cheng & Bonebrake, 2017; Klorvuttimontara et al., 2011). We did not examine the efficiency of the TPA network to conserve species under future climate change, but our results indicate that the distributions of range-restricted butterflies on Borneo are limited by abiotic factors such as temperature and rainfall, and thus are likely to shift to track climate. Whilst future rainfall projections are uncertain (IPCC, 2014), in order to protect species from rising temperatures, increased protection of forest areas at high elevation should be a conservation priority, to conserve species shifting uphill from lower elevation. However, PAs are often not well connected, and so conserving forest connections that link up PAs along elevational gradients may facilitate range shifting for low and mid-elevation species (Feeley & Silman, 2016; Scriven et al., 2015). Montane species, such as many of the species modelled in this study, which are already restricted to high elevation areas, may have little opportunity to shift to cooler locations as climates warm (Colwell et al., 2008). Thus, without specific conservation measures, these species may face climate-driven extinctions.

* 1. **Sampling localities and biases**

In our study, we used a large butterfly dataset comprising museum records and published data that provides reasonable spatial and temporal coverage across Sabah (Figure 1). However, as with many species distribution modelling studies that rely on museum data (e.g. see Anderson, 2012), some of our sampling points are clustered around specific locations (e.g*.* Mount Kinabalu National Park). Hence, our presence/absence data may reflect site-specific environmental conditions and our projections of species richness may be more robust in these well-sampled areas. Nonetheless, despite some clustering of sample sites, sampling localities were generally well spread across the range of values in our five climate surfaces for Borneo (Figure S6 in Appendix S2). Moreover, some areas in the lowlands with a high density of sampling localities were predicted to have low species occurrence (e.g. coastal Brunei; Figure 1), and this indicates that it is unlikely that uneven sampling effort had a large impact on our SDM outputs. It is possible to account for geographical sampling biases in SDM studies (e.g. by incorporating observer effort: see Beale, Brewer, & Lennon, 2014; Hill, 2012), and such strategies warrant further research for capitalising on the types of data we used for examining tropical biodiversity.

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

**4.5 Conservation implications**

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

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**DATA AVAILABILTY STATEMENT**

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

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**SUPPORTING INFORMATION**

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

**TABLE 1.** Importance of environmental predictor variables across Borneo for (1) all butterfly species (*N* = 77) and (2) only endemic 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 scorea | | Spearman’s Rho (*rs*)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 |

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

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

**FIGURE LEGENDS**

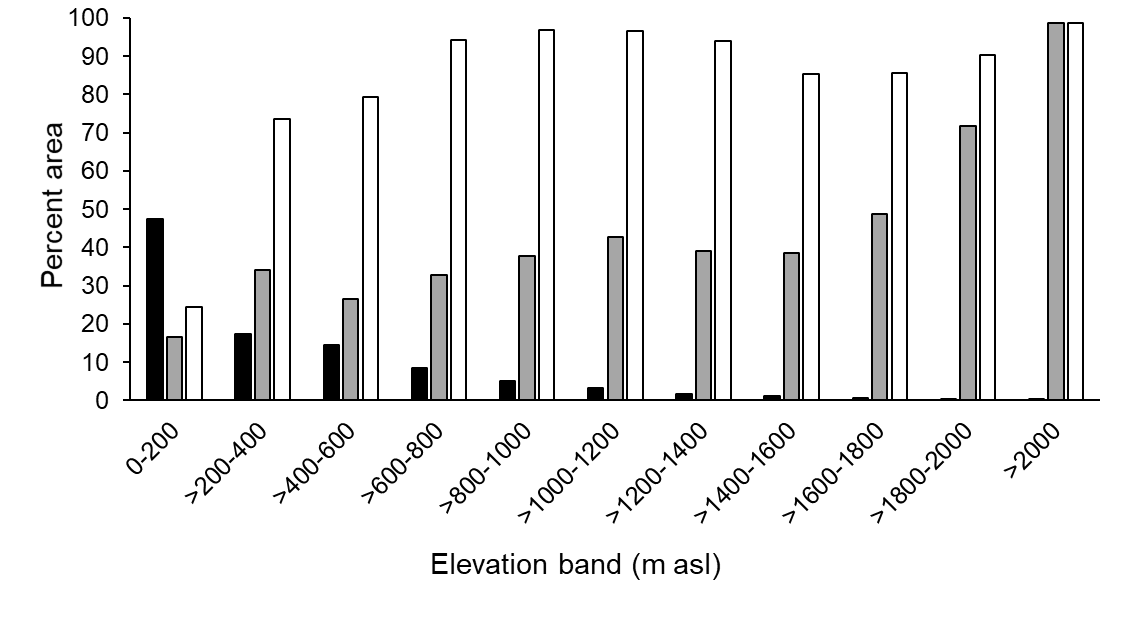
**FIGURE 1.** (a) Map of Borneo showing summed occurrences of all 77 range-restricted butterfly species from species distribution model (SDM) outputs. Black circles represent locality records for all species records used in the analyses, and comprised a total of 398 sampling locations; this included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

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

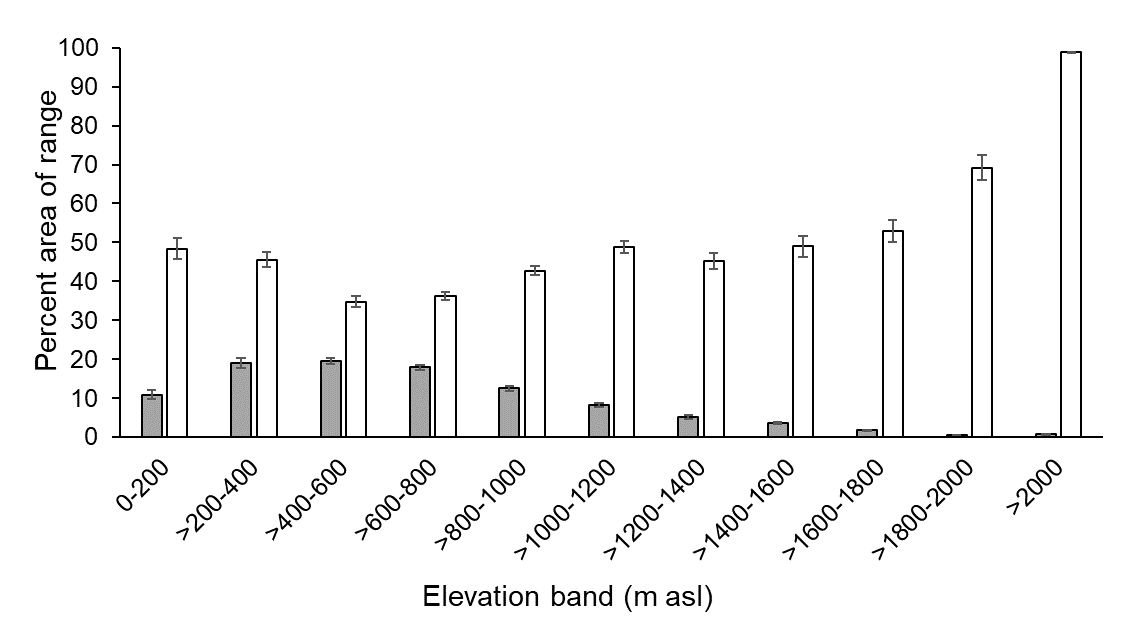
**FIGURE 3.** Maps of Sabah showing the final prioritized area (18,622 km2; blue shading) for all species (*N =* 77) with: (a) no boundary length modifier (BLM) included (no-BLM scenario), and (b) with the inclusion of a BLM (BLM scenario), which was used to aggregate the output grid-cells (Appendix S1). The total area available for selection by the prioritization analyses represents the forested area on mainland Sabah (40,259 km2; grey and blue shading combined). The outline of the existing totally protected area (TPA) network is overlaid. **FIGURE 1**

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**FIGURE 2**



**(a)**



**(b)**

G:\Rainforest Trust Project\SDM Biotropica Manuscript\Manuscript Drafts\Accepted Final Version July 2019\Final Figures\To Upload\Figure3Map_600dpi_crop.tif**FIGURE 3**