Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change

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ABSTRACT

Protected areas (PAs) are key for conserving rainforest species, but many PAs are becoming increasingly isolated within agricultural landscapes, which may have detrimental consequences for the forest biota they contain. We examined the vulnerability of PA networks to climate change by examining connectivity of PAs along elevation gradients. We used the PA network on Borneo as a model system, and examined changes in the spatial distribution of climate conditions in future. A large proportion of PAs will not contain analogous climates in future (based on temperature projections for 2061–2080), potentially requiring organisms to move to cooler PAs at higher elevation, if they are to track climate changes. For the highest warming scenario (RCP8.5), few (11–12.5%; 27–30/240) PAs were sufficiently topographically diverse for analogous climate conditions (present-day equivalent or cooler) to remain in situ. For the remaining 87.5–89% (210–213/240) of PAs, which were often situated at low elevation, analogous climate will only be available in higher elevation PAs. However, over half (60–82%) of all PAs on Borneo are too isolated for poor dispersers (<1 km per generation) to reach cooler PAs, because there is a lack of connecting forest habitat. Even under the lowest warming scenario (RCP2.6), analogous climate conditions will disappear from 61% (146/240) of PAs, and a large proportion of these are too isolated for poor dispersers to reach cooler PAs. Our results suggest that low elevation PAs are particularly vulnerable to climate change, and management to improve linkage of PAs along elevation gradients should be a conservation priority.

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1. Introduction

Protected areas (PAs) have been established globally to help conserve biodiversity, and now cover over 10% of the Earth's land surface (Chape et al., 2005; Soutullo, 2010). Targets under the Convention on Biological Diversity (CBD) aim to expand this protection to 17% by 2020 (CBD, 2010). In tropical regions, current conversion of natural habitat to other land uses is particularly high, and PAs are especially important for protecting high levels of biodiversity (Curran et al., 2004; Klorvuttimontara et al., 2011; Laurance et al., 2012), but PAs are becoming increasingly isolated within human-modified landscapes (Curran et al., 2004).

Climate change drives geographic range shifts in plants and animals (Thomas, 2010; Thomas et al., 2012), and tropical species are shifting to higher elevations in response to warming temperatures (Chen et al., 2011, 2009; Colwell et al., 2008; Feeley et al., 2011;

Forero-Medina et al., 2011; Freeman and Class Freeman, 2014; Laurance et al., 2011; Pounds et al., 1999). Rainfall may also affect the responses of tropical species to climate change (Colwell et al., 2008; Corlett, 2012), although future projections are more uncertain for precipitation than for temperature (Corlett, 2012, 2011; IPCC, 2013). Species' abilities to shift their ranges will also be limited by the availability and distribution of suitable habitat (Chen et al., 2009; Feeley and Silman, 2010; Hodgson et al., 2009), and species that fail to shift their ranges may face increased likelihood of extinction (Thomas et al., 2004). The effectiveness of PAs to conserve tropical species under climate change has been questioned (Klorvuttimontara et al., 2011; Marini et al., 2009; Vieilledent et al., 2013), and if the connectivity of PAs is reduced due to land-use change, it may become difficult for species to track climate changes and move between PAs. In temperate regions, PAs have been shown to be effective in facilitating latitudinal range expansions (Thomas et al., 2012), but the effectiveness of PAs to conserve tropical biota responding to climate changes along elevation gradients has received little attention.

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We address this issue by studying PAs on Borneo. As is typical of tropical regions across Southeast Asia, Borneo is extremely biologically diverse but facing severe pressure due to loss of forest habitats. Rainforest now covers only approximately 50% of Borneo, with most extensive areas of remaining forest occurring in the central montane region and many coastal forest areas now fragmented and isolated due to conversion to oil palm (*Elaeis guineensis* Jacq.) plantations (Proctor et al., 2011). Lowland Dipterocarpaceae forests support exceptionally high levels of species diversity, and in many low-lying areas remaining dipterocarp forest is confined to PAs, which are therefore vital for conserving rainforest species within human-modified landscapes (Curran et al., 2004). Protection is clearly important to prevent habitat conversion, but the extent to which PAs are sufficiently well connected to allow biota to move between them in order to track climate change is unknown.

We examined the connectivity of PAs along elevation gradients using a spatially-explicit metapopulation model (Incidence Function Model (IFM); Hanski, 1994). We focus specifically on temperature changes, based on current empirical evidence from tropical studies (e.g. Laurance et al., 2011; Freeman and Class Freeman, 2014) and the limited understanding of species' responses to other climate variables. We do not model responses of individual species because distribution data are very incomplete for tropical taxa, and often available only for iconic species (e.g. Struebig et al., 2015), and so we describe changes in the distribution of climate conditions within PAs and the connectivity of PAs (e.g. see Ackerly et al., 2010; Ohlemüller et al., 2006). We determined which PAs will not retain analogous climate conditions (present-day temperature or cooler) in future and the characteristics of these PAs (area, mean elevation and amount of forest in the surrounding landscape). Organisms in these PAs may need to reach cooler PAs if they are to keep track of climate, and we modelled whether or not PAs are sufficiently well connected for organisms to successfully reach cooler PAs at higher elevation (for different dispersal abilities, population densities and forest covers within PAs). We ran models primarily for the highest ('business-as-usual') warming scenario (IPCC Fifth Assessment Report (AR5), RCP8.5), but compared our results with the lowest ('mitigation') warming scenario (RCP2.6), to highlight common patterns.

2. Materials and methods

2.1. Data sources

The locations of PAs on Borneo (IUCN; World Conservation Union) were downloaded from the World Database of Protected Areas (WDPA; http://www.protectedplanet.net; including designated and proposed PAs, but excluding offshore islands). Only PAs that had complete boundaries were used, and PAs that were duplicated or overlapping other PAs were excluded. Forest cover was obtained at a grid cell resolution of 250 m (Miettinen et al., 2012). We extracted data for peatswamp forest, lowland forest, and lower and upper montane forest, subsequently termed 'forest', and all other remaining land categories were termed 'non-forest'. Our 'forest' category included selectively logged forests that have reached structural characteristics similar to those of primary forest. Elevation data as well as current and future annual climate data for 1950–2000 and 2061–2080 were obtained (http://www.worldclim.org) at a 30 arc-second grid cell resolution. We used a nearest neighbour interpolation method to convert gridded climate and elevation data from 30 arc second resolution (approx. 0.86 km grid cells) to 1 km grid cells. Future climate data were for IPCC AR5 Representative Concentration Pathways (RCP) 8.5 and 2.6, HadGEM2-AO general circulation model (GCM). RCP8.5

represents the most severe ('business-as-usual') IPCC scenario, and projects global mean surface temperature to increase between 2.6 and 4.8 °C in 2081–2100, relative to 1986–2005; whilst RCP2.6 represents the least severe ('mitigation') scenario (0.3–1.7 °C increase) (IPCC, 2013). RCP8.5 predicts mean temperature for Borneo to rise by 3.2 °C (mean difference between 1950 and 2000 annual mean temperature and 2061–2080 predicted annual mean temperature at a 1 km grid cell resolution), whereas RCP2.6 predicts a rise of only 0.9 °C (Appendix A) (Appendix B shows precipitation projections for Borneo for these scenarios).

Gridded annual temperature data from 1950–2000 (current) and 2061–2080 (future) were used in our model simulations (see Section 2.3 below) at a 1 km grid cell resolution. Forest grid cells at 250 m resolution were also converted to 1 km grid cells, and assigned a value between 0 and 16 representing the number of aggregated 250 m forest cells within each 1 km grid cell. Each 1 km forest grid cell was also specified as 'protected' or 'not protected' depending on whether or not it fell within a PA polygon. Small PAs < 1 km^2 (29 PAs in total) were represented by a single 1 km grid cell. For PAs that contained no forest according to Miettinen et al. (2012), we added one 250 m forest grid cell to the centre of each PA so that all PAs could be included in our simulations.

2.2. PA characteristics

All spatial data were analysed in ArcGIS Version 10. WDPA listed 223 PAs, corresponding to 240 spatially independent polygons, and so we based our subsequent analyses on these 240 PA units (henceforth termed PAs). For each PA we calculated the area (km^2), the percentage of forest it contained, mean elevation (m a.s.l.), elevation range (m), current (1950–2000) mean temperature range (°C) and percentage of forest in a surrounding 10 km buffer ('surrounding forest'), all at a 250 m (62,500 m^2) grid cell resolution.

2.2.1. Source and refuge PAs

We described the spatial distribution of climate conditions within PAs, and categorised PAs into 'source', 'refuge' or 'target' PAs in relation to whether or not analogous climate conditions were projected to remain in PAs in future (using predicted temperature of forested grid cells within PAs in 2061–2080). The current (1950–2000) mean temperature of forested grid cells within each PA was used as our measure of climate conditions. If a PA contained at least one forested grid cell in future that was cooler than, or the same as, the current mean temperature of forested grid cells within the PA, we assumed that analogous climate conditions remained in situ and so we did not examine connectivity of these PAs (termed 'refuge' PAs) to other PAs. For all other PAs, termed 'source' PAs, we carried out simulations to determine whether or not organisms from these PAs could reach cooler 'target' PAs. Target PAs were defined as PAs containing analogous climate conditions in future; i.e. protected and forested grids cells with temperatures that were cooler than, or the same as, the current mean temperature of the focal source PA. In this way, each source PA had its own specific set of target PA grid cells. Thus, our approach focused on whether PAs were projected to lose analogous climate conditions in future, and if so, whether connectivity of PAs was sufficient to facilitate organisms moving from source PAs to cooler target PAs. Therefore, we examined the connectivity and relative vulnerability of PAs to climate change impacts, based on changes in the locations of analogous climate conditions, and in the absence of species-specific information required for climate-envelope modelling (e.g. Thomas et al., 2004).

2.3. Modelling PA connectivity with the IFM

We used a patch-based metapopulation model (IFM; Hanski, 1994) (R code in Appendix C) to examine connectivity of source and target PAs. The IFM assumes that (a) extinction risk of populations in grid cells is inversely related to population size and habitat patch area (amount of forest cells at a 250 m grid cell resolution contained within a 1 km grid cell), and (b) colonisation probability of forest habitat patches within grid cells is positively related to habitat patch connectivity; where connectivity is a function of the distance to other occupied forest cells and the amount of forest they contain (Hanski, 1994). Specifically, connectivity (S_i) for a habitat patch (a spatially discrete forest grid cell(s)) i, is defined as:

$$A_i \frac{R\alpha^2}{2\pi} \sum_{j \neq i} p_j A_j e^{-\alpha d_{ij}}.$$

where A = area of habitat (km^2) in cell i or j, R = population density (number of emigrants produced per generation per occupied km^2 grid cell), α = slope of a negative exponential dispersal kernel, p_j = occupancy of j (1 if cell j is occupied, 0 if not) and d_{ij} is the Euclidean distance between the centre of cells i and j. As our measure of PA connectivity, we simulated the likelihood of individuals successfully reaching cooler target PAs from every source PA, at a 1 km grid cell resolution.

Model simulations were run separately for each source PA, with the focal source PA initially occupied (i.e. seeding all forest grid cells at maximum carrying capacity) at the start of each simulation. Movement of organisms from source PAs could potentially occur in any direction, organisms could reproduce in forest grid cells on route to the target PA regardless of whether or not the forest was protected, but we constrained reproduction to occur only in forested cells that were cooler than, or the same as, the current (1950–2000) mean temperature of forest grid cells in the focal source PA (Fig. 1). Thus, organisms were constrained to disperse to target PAs through forest habitats that were not hotter than the PA they were leaving. We assumed that dispersal could occur across non-forest areas, but that organisms did not survive if they landed in a non-forest grid cell. For each source PA the model simulation could be unsuccessful, when a target PA was not reached (Fig. 1a), or successful, when a target PA was reached (Fig. 1b).

2.3.1. Future climate scenarios, dispersal, and model parameter values

Using RCP8.5 temperature projections, we varied population density in occupied habitat and dispersal ability (representing plausible parameter ranges for winged invertebrates, e.g. tropical butterflies; Benedick et al., 2007, 2006). Population density was set as either 12.5, 125 or 1250 individuals per 250 m forest grid cell (corresponding to 2, 20 and 200 individuals per ha^{-1}). Dispersal ability was varied by altering α (the slope of a negative exponential dispersal kernel) within the model (Hodgson et al., 2011). We examined 10 dispersal values corresponding to maximum dispersal distances from 0.5 to 10 km per generation, spanning a wide range of mobilities. Tropical butterflies can develop through 6 generations y^{-1} (Azerefegne et al., 2001), and so we ran models for 600 generations to represent approximately 100 y of climate warming. Whilst we assume six generations per year, species with fewer
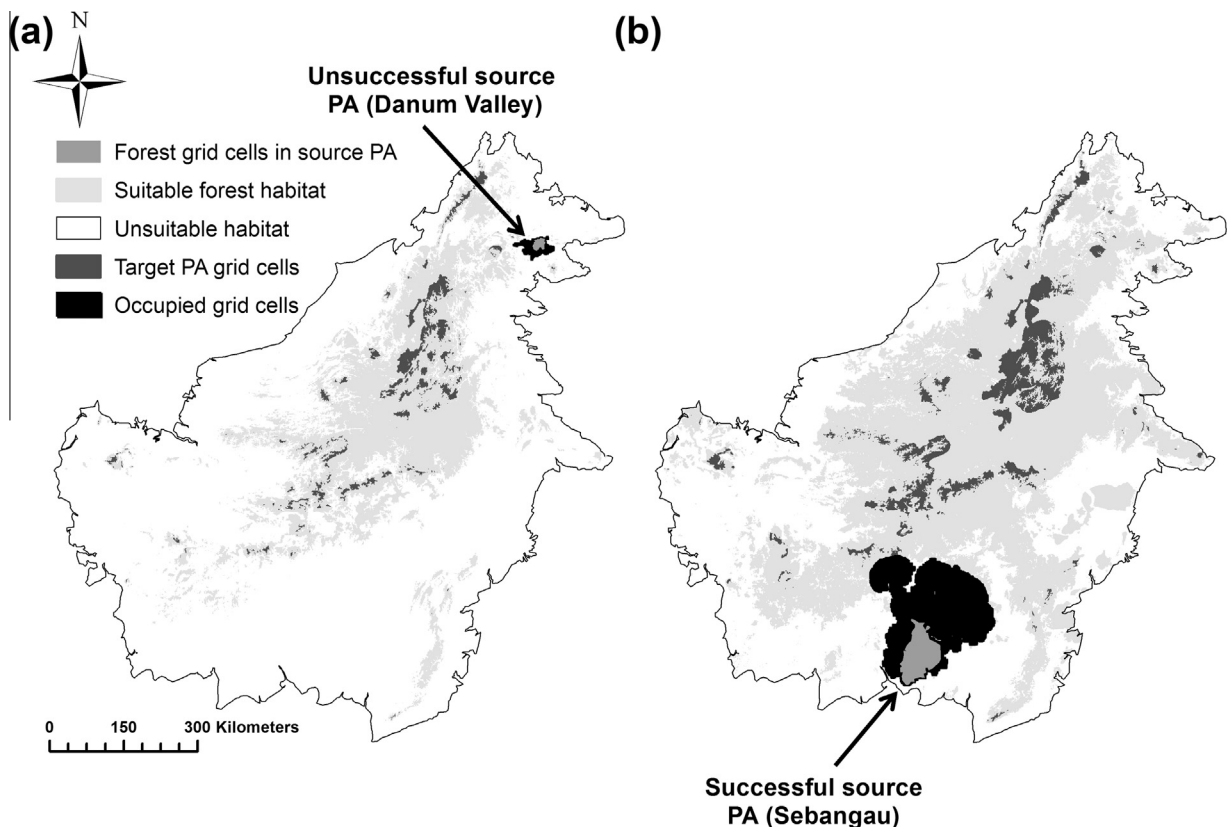
Fig. 1. Examples of simulations illustrating the connectedness of two source PAs (RCP8.5 temperature projections). In (a) individuals did not reach a cooler target PA grid cell within 600 generations, whilst in (b) individuals reached a target PA grid cell after 55 generations. Simulations assumed 1 km dispersal ability, a population density of 125 individuals per 250 m forest grid cell and 100% forest cover within all PAs. Medium grey shading = forested grid cells within the source PA from which populations were seeded; light grey = forested grid cells containing analogous climate conditions, i.e. that were the same temperature, or cooler, than the current (1950–2000) mean temperature of the PA, and through which organisms could potentially disperse to reach a target PA; white = unsuitable habitat, either non-forest grid cells, or forested grid cells that were too warm; dark grey = target PA grid cells, and black = occupied grid cells.

generations per year are likely to take much longer to reach target PAs, and so our findings may be conservative for these types of organisms. The amount of forest within each 1 km grid cell was multiplied by the population density to estimate the carrying capacity of each cell, and the extinction probability was 1/carrying capacity of each habitat patch at each time step (generation). In order to assess the degree to which forest management within PAs might benefit conservation we examined two forest cover scenarios; assuming current levels of forest cover within PAs, and assuming forest cover in all PAs was improved to 100%. Increasing forest cover to 100% caused three source PAs to become refuge PAs. A total of 34,873 km^2 (in 250 m grid cells) was added to PAs to increase forest cover to 100%; this corresponded to 10% of existing forest cover on Borneo.

In total, for each source PA, we ran models for 10 dispersal scenarios, three population densities and two forest cover scenarios (i.e. 60 treatments in total per source PA). Our model is stochastic and so we ran five repeat runs for each treatment (i.e. 300 simulations per source PA in total). Model simulations were terminated once any individual reached a target PA grid cell, or if the seed population failed to expand, or went extinct, or after a maximum of 600 generations (i.e. 100 y). Only when a target PA had been reached in three or more of the five repeat runs, did we consider the outcome 'successful'. To assess the impact of different warming scenarios, we also ran models using RCP2.6 temperature projections. We simulated expansion from source PAs for all dispersal distances, but only one population density (125 individuals per 250 m forest grid cell), and one landcover scenario (100% forest cover in PAs; i.e. 10 treatments per source PA for RCP2.6). The number of source and refuge PAs was dependant on the RCP scenario (RCP8.5 and 100% forest cover; refuge PAs = 30, source PAs = 210; RCP2.6 and 100% forest cover; refuge PAs = 94, source PAs = 146).

2.4. Analysis of model outputs

All statistical analyses were performed in R statistical software, version 3.0.2. We used a Generalised Linear Model (GLM, binomial logistic regression), with a logit link function and binomial error distribution to analyse whether individuals successfully reached target PAs from source PAs for each of the 60 model treatments for the RCP8.5 warming scenario. Population density (3 categories), forest cover in PAs (current/100%) and dispersal distance (10 values, continuous variable) were included as predictor variables of connectivity success/failure. To evaluate the importance of each parameter on connectivity, we calculated partial McFadden's r^2 values (Menard, 2000) for each predictor by sequentially removing the variable of interest from the model and comparing the change in the r^2 between the full model and reduced model. For each source PA in the RCP2.6 warming scenario, we ran models for 10 dispersal distances, one population density and one forest cover scenario (i.e. 10 treatments and 50 simulations per source PA). To examine the importance of RCP scenario in relation to dispersal ability on connectivity success/failure, we used a GLM (binomial logistic regression), with a logit link function and binomial error distribution. We included 20 model treatments, comprising RCP scenario (2 categories) and dispersal distance (10 values, continuous variable), which were both included as predictor variables of success/failure. We calculated partial McFadden's r^2 values to determine the importance of each parameter.

We also used GLMs (binary logistic regression) to examine the probability of a source PA being connected to a target PA ('successful' versus 'unsuccessful' movement of individuals; RCP8.5 scenario) in relation to PA elevation, area, and percentage cover of forest within a 10 km buffer zone surrounding the source PA boundary (termed 'surrounding forest'). We computed the

percentage of forest within a 10 km buffer zone to coincide with maximum dispersal distance examined in our models. We also included the straight-line distance (km) of the source PA to the nearest target PA to account for the spatial locations of source and target PA grid cells. We analysed the characteristics of successful versus unsuccessful source PAs separately for each dispersal distance (0.5–10 km). We used a binomial error distribution and a probit link function, which consistently provided the lowest AIC and residual deviances. We also square root transformed data for surrounding forest cover to improve model parsimony. In order to improve the interpretation of regression coefficients, all predictor variables were centred and standardised (Schielzeth, 2010), and 95% confidence intervals were calculated for each coefficient estimate. To control for effects of variation in forest cover within PAs, we only analysed data from simulations with 100% forest cover in all PAs ($n = 210$ source PAs). We also only analysed outputs for models with intermediate population density (125 individuals per 250 m forest grid cell). To evaluate the importance of each parameter on determining the connectivity of PAs, we calculated partial McFadden's r^2 values for each predictor.

3. Results

3.1. PA characteristics

There is considerable variation in the topography of PAs on Borneo; mean elevation range of the 10% of PAs ($n = 24$) with the lowest topographical heterogeneity is 3.1 m, but 1536.8 m for the most heterogeneous 10% of PAs (Fig. 2). The 10% of PAs with the lowest topographical heterogeneity had a current mean temperature range of 0.1 °C, compared with 8.4 °C for the most heterogeneous 10% of PAs. As mean elevation of all PAs (including both sources and refuges) increased, surrounding forest around each PA increased (Spearman correlation: $r_s = 0.53$, $n = 240$, $p < 0.0001$), as did percentage forest within PAs ($r_s = 0.58$, $n = 240$, $p < 0.0001$) and PA area (km^2) ($r_s = 0.18$, $n = 240$, $p = 0.004$), consistent with the fact that higher elevation forests on Borneo are more likely to be intact and protected (Appendix D).

3.1.1. Source and refuge PAs

Our analyses of the RCP8.5 temperature projections revealed that only 11–12.5% (27–30/240; current and 100% forest cover in PAs, respectively) of PAs were refuges and the vast majority of PAs (87.5–89%; 210–213/240) were source PAs (Fig. 2b), which will not retain analogous climate conditions in future, and from which individuals may need to move if they are to track future climate change and reach cooler locations. Under the RCP2.6 scenario (assuming 100% forest cover in PAs), slightly more PAs were refuges (39%; 94/240), but again the majority of PAs were source PAs. Source PAs were generally much smaller than refuge PAs, situated at lower elevation, and with low topography (Appendix E).

3.2. Simulations of PA connectivity

Dispersal ability was the most important factor determining whether or not a source PA was connected to a target PA (partial McFadden $r^2 = 0.843$), and forest cover within PAs (current or 100% cover; partial McFadden $r^2 = 0.095$), population density (partial McFadden $r^2 = 0.029$) and RCP scenario (partial McFadden $r^2 = 0.978$ for dispersal versus $r^2 = 0.003$ for RCP) were less important. The relationship between PA connectivity and dispersal ability was non-linear for both RCP scenarios, initially increasing rapidly with increased dispersal, but then reaching an asymptote where further increased dispersal ability had little additional impact on the success of dispersers (Fig. 3).
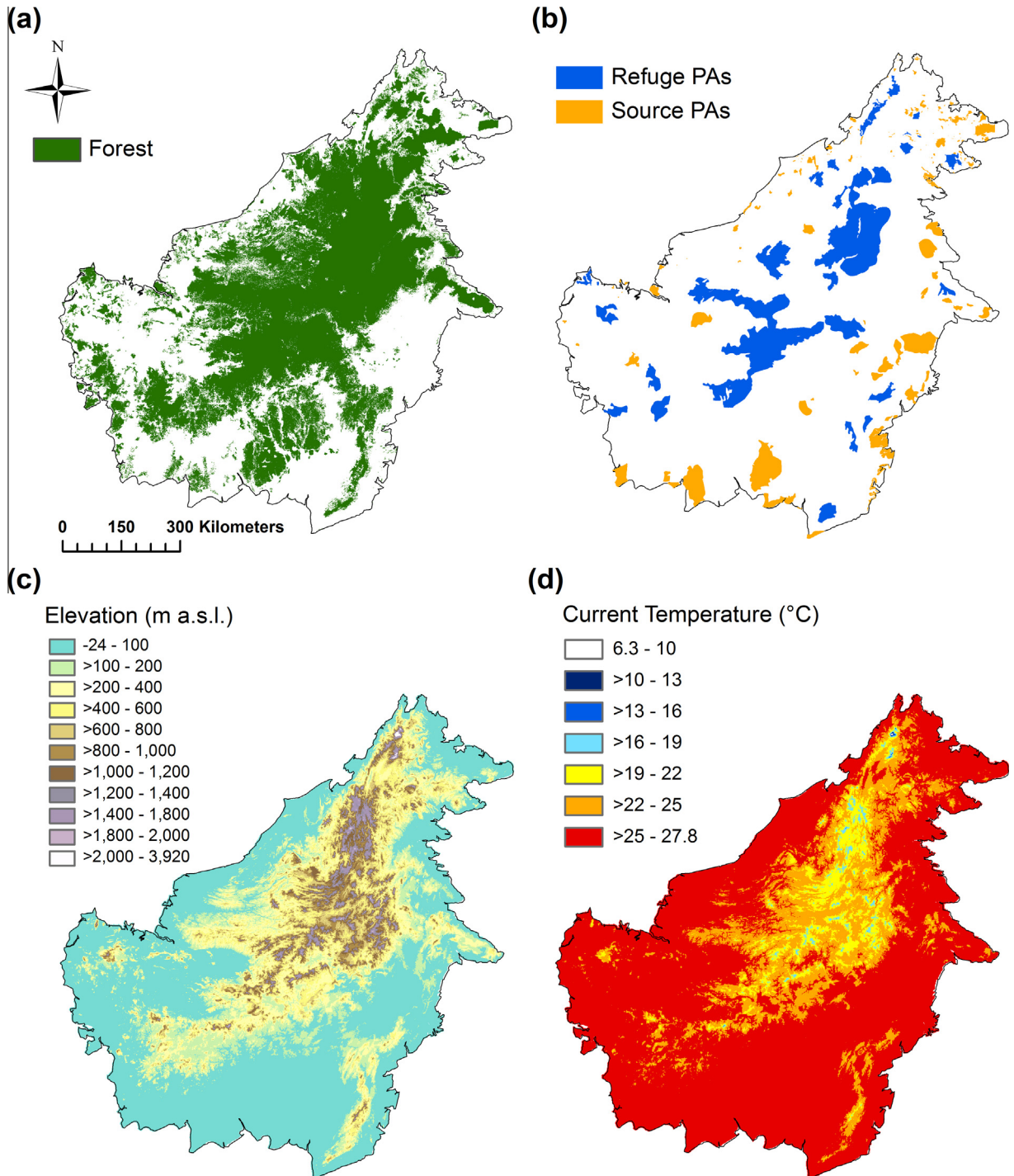
Fig. 2. Maps of Borneo showing baseline data for simulations. (a) Distribution of forest cover (250 m grid cell resolution), where approximately 48% remains; (b) locations of refuge and source PAs (see main text for definitions; assuming current forest cover within PAs and using RCP8.5 temperature projections), which cover approximately 16% of Borneo's total land area; (c) elevation (1 km grid cell resolution); and (d) current (1950–2000) temperature (1 km grid cell resolution).

Across all RCP8.5 model scenarios (60 treatments) the percentage of source PAs connected to target PAs ranged from a minimum of 18% (n = 39/213 PAs; lowest forest cover, dispersal and density treatments) to a maximum of 99% (n = 208/210 PAs; highest forest cover, dispersal and density treatments) (Fig. 3a). Across these scenarios, 60–82% of source PAs were not successfully connected to target PAs for the poorest dispersers (<1 km dispersal ability), depending on forest cover and population density values (Fig. 3a; Appendix F, Table F.1). Fig. 4 shows the minimum dispersal ability required for organisms to reach a target PA from each source PA,

and shows the three PAs which were never connected to target PAs even at the highest (10 km per generation) dispersal ability. The time taken (in generations) to reach target PAs generally decreased with increasing dispersal ability (Fig. 3b). Improving forest cover within PAs to 100% increased the percentage of source PAs connected to target PAs by 6–30%, depending on population density and dispersal ability (Fig. 3a). Reforestation within PAs had the greatest benefit on source PA connectedness when organisms with low population densities and/or intermediate dispersal abilities were used (Fig. 3a).
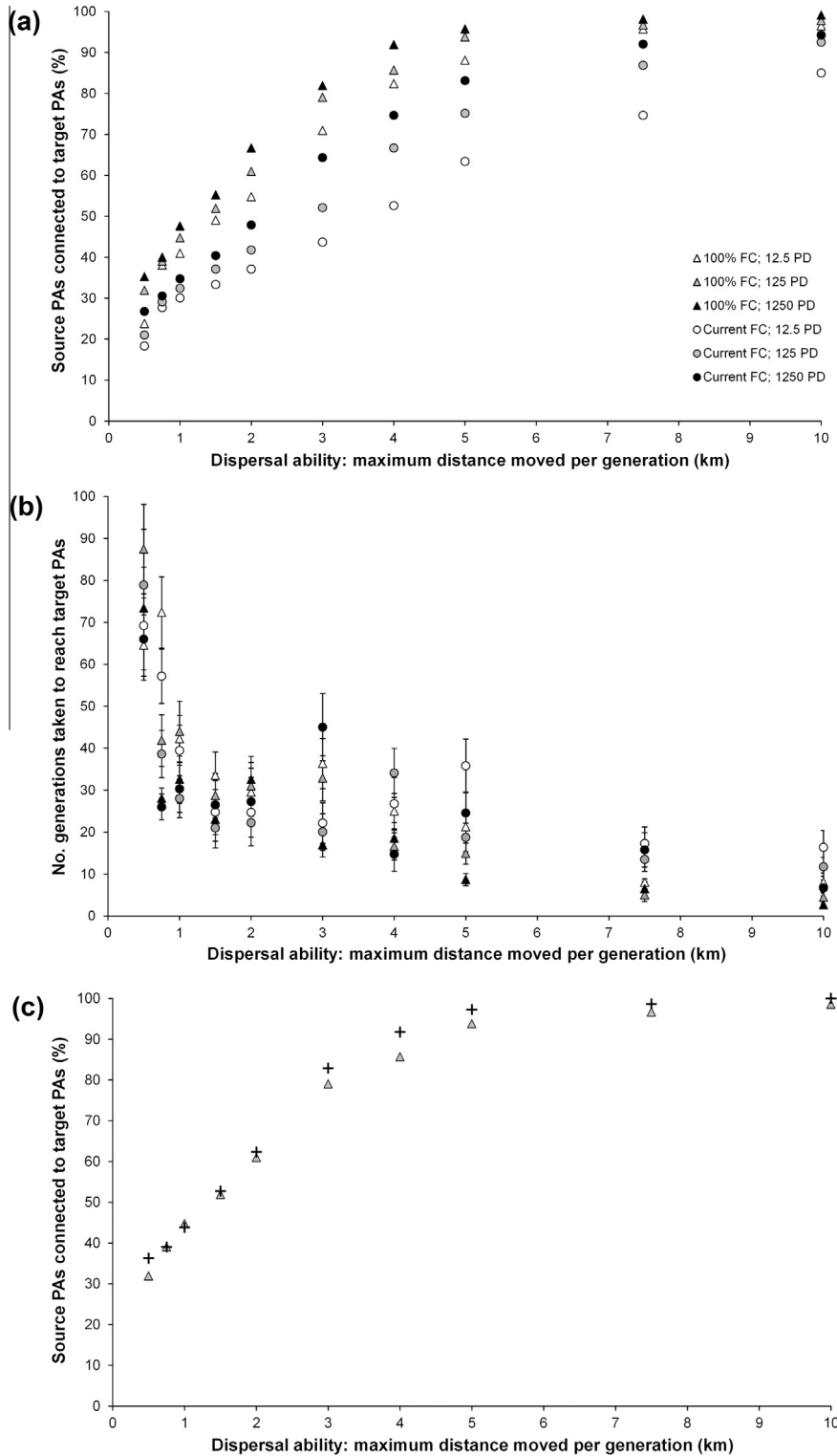
Fig. 3. Incidence function model (IFM) outputs. (a) Percentage of source PAs (current forest cover (FC): n = 213; 100% forest cover: n = 210) connected to cooler target PAs for organisms with different dispersal abilities and population densities (PD) (individuals per 250 m forest grid cell) (RCP8.5 temperature projections); (b) mean number of elapsed generations for organisms at each dispersal distance to reach cooler target PAs (of those successful in Fig. 3a); standard error bars illustrate the error across all successful source PAs at each dispersal distance; and (c) percentage of source PAs (100% forest cover; 125 individuals per 250 m forest grid cell) connected to cooler target PAs for organisms with different dispersal abilities under the low (RCP2.6) (crosses; n = 146) and high (RCP8.5) (triangles; n = 210) warming scenarios. Ten dispersal distances were examined (see Table 1; 0.5–10 km per generation).

In the RCP2.6 scenario, the percentage of source PAs connected to target PAs ranged from a minimum of 36% (n = 53/146 PAs; lowest dispersal treatment) to a maximum of 100% (n = 146/146 PAs; highest dispersal treatments) (Fig. 3c). However, the majority

(61–64%) of source PAs were not connected to target PAs for poor dispersers (<1 km dispersal ability; Fig 3c), highlighting the vulnerability of many PAs under even the lowest warming scenario. Overall, there was little difference in success rates of dispersers
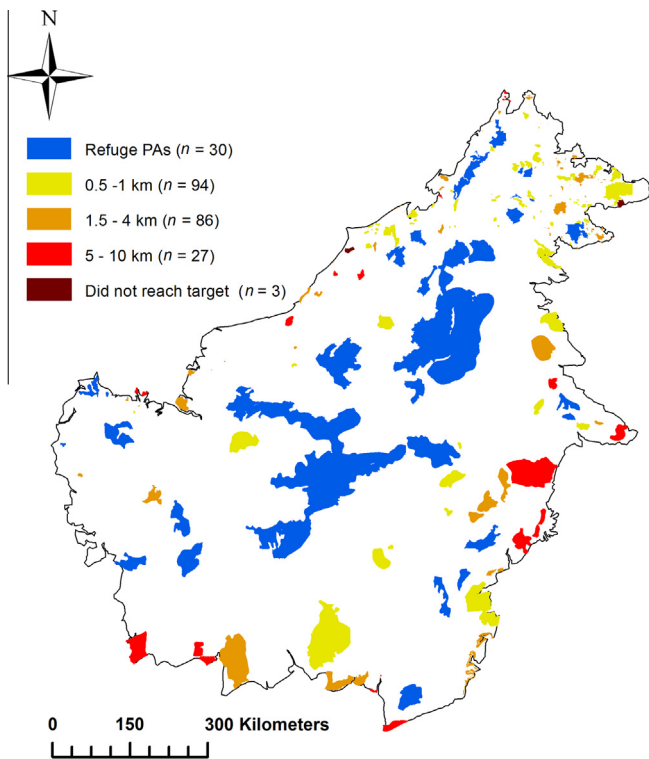
Fig. 4. Map of Borneo showing location of refuge (n = 30) and source PAs (n = 210). Source PAs are shaded according to the minimum dispersal ability required for individuals to successfully reach target PAs (assuming 100% forest cover in PAs, a population density of 125 individuals per 250 m forest grid cell and using RCP8.5 temperature projections).

between the lowest or highest RCP scenarios (Fig. 3c; difference ranged from −0.9% to +6%), or the time taken to reach target PAs (Appendix F; Fig. F.1).

3.3. Characteristics of successful and unsuccessful source PAs (RCP8.5 scenario)

The relative importance of elevation, area, distance to nearest target PA and surrounding forest on the likelihood of a source PA

being connected to a target PA (n = 210 source PAs) differed according to dispersal ability. For organisms with low-medium dispersal abilities (⩽4 km per generation) surrounding forest was most important for source PA connectivity, followed by distance to target PA, while elevation and area of source PAs were of less importance (Table 1). Thus, for organisms with poorer dispersal ability, source PAs were more likely to be connected if they were surrounded by high forest cover and the target PA was nearby. At intermediate dispersal distances, surrounding forest became less important for connectivity, and straight-line distance to target PA increased in importance. In simulations with highly mobile organisms (⩾5 km per generation), source PAs were nearly always connected regardless of the characteristics of the PAs (Table 1).

4. Discussion

4.1. Characteristics of PAs

Climate change is resulting in the distributions of tropical species shifting to higher elevations (Corlett, 2012, 2011; Freeman and Class Freeman, 2014). Protected areas are vital for in situ biodiversity conservation (Chape et al., 2005), but our Borneo study highlights the isolation of many low-lying PAs. The majority (60–82%) of source PAs under the highest warming scenario (RCP8.5) were not connected to target PAs for poor dispersers (i.e. <1 km per generation), meaning that poor dispersers may fail to reach cooler PAs at higher elevation from these PAs. Broadly similar findings were also evident for the lowest scenario (RCP2.6), despite a much lower predicted temperature change. Even though more than 16% of Borneo's land area is currently protected, and more than 48% still covered in forest (Fig. 2), our study reveals that populations of forest species within many lowland PAs on Borneo may be isolated from cooler locations in future and so could be vulnerable to climate change (Appendix G). Poor dispersers, which may represent a high proportion of tropical species, may be particularly vulnerable to the consequences of low connectivity of PAs.

Assuming full forest cover in PAs, our study suggests that 61–87.5% of PAs on Borneo may not be sufficiently topographically diverse to retain analogous climate conditions in future, even under low levels of warming. These source PAs with low topographic diversity were primarily in low-lying areas, often close to the coast and in regions where most conversion to oil palm plantations has occurred (Reynolds et al., 2011). Thus, in order to track

Table 1
Standardised regression coefficients and McFadden's partial r^2 values from binary logistic regression models of whether or not source PAs (n = 210) were connected to target PAs for organisms with different dispersal abilities. The analysis assumed 100% forest cover in PAs, a population density of 125 individuals per 250 m forest grid cell and used RCP8.5 temperature projections.

Dispersal[a]	α[b]	No. of connected source PAs (/210)	Predictors in model							
			Area (km²)		Surrounding forest (%)		Mean elevation (m a.s.l.)		Distance to target (km)	
			Coefficient	r^2	Coefficient	r^2	Coefficient	r^2	Coefficient	r^2
0.5	9.40	67	0.168	0.008	1.059*	0.309	−0.213*	0.016	−0.300*	0.023
0.75	6.27	82	0.203	0.010	1.203*	0.337	−0.226*	0.015	−0.543*	0.066
1	4.70	94	0.170	0.007	1.244	0.334	−0.283*	0.020	−0.676*	0.096
1.5	3.13	109	0.327*	0.019	1.386*	0.335	−0.286*	0.016	−1.005*	0.171
2	2.35	128	0.197	0.009	1.210*	0.280	−0.362*	0.027	−0.896*	0.168
3	1.57	166	0.076	0.001	1.538*	0.271	−0.524*	0.032	−0.879*	0.186
4	1.18	180	0.068	0.002	1.113*	0.188	−0.419*	0.027	−0.652*	0.145
5	0.94	197	0.032	0.001	0.844*	0.127	−0.476*	0.058	−0.602*	0.163
7.5[c]	0.63	203	–	–	–	–	–	–	–	–
10[c]	0.47	207	–	–	–	–	–	–	–	–

[a] Maximum dispersal distance (km).
[b] Slope of negative exponential dispersal kernel.
[c] Results from GLMs not computed due to small number of unsuccessful source PAs (i.e. very high connectivity in all simulations).
* 95% confidence intervals that do not overlap with zero.

climate, we predict that populations of forest species within these PAs will have to cross large expanses of inhospitable agricultural habitat, which may be barriers to dispersal for many species. Failure of organisms to track climate may result in local extinctions of range-restricted species as climate conditions become unsuitable for them (Deutsch and Tewksbury, 2008). Low connectivity of PAs may also reduce gene flow and genetic diversity of populations, and/or reduce the distribution extent of species depending on their thermal limits in relation to the location of source and target PAs (Appendix G). Our study has focussed on temperature, but other climate variables such as precipitation may also determine the viability of populations of tropical species in PAs (Colwell et al., 2008; Corlett, 2012), and species in locations that become both too hot and too dry may be particularly vulnerable, although future precipitation changes are uncertain (Appendix B). Thus, biodiversity may decline in many low-lying regions, especially if there is no pool of colonising species adapted to higher temperatures/drier conditions to replace species shifting uphill (Colwell et al., 2008). If species fail to extend their leading-edge range margins uphill, the species richness of sites at intermediate and higher elevation may also decline as trailing-edge margins of montane species retract upslope (Chen et al., 2009; Freeman and Class Freeman, 2014); therefore, improving linkage of PAs along elevation gradients may help conserve regional tropical diversity.

4.2. Factors affecting PA connectivity

The amount of forest surrounding source PAs was important in influencing whether or not they were connected to cooler target PAs, and neither PA size nor mean elevation strongly influenced connectivity if the PA had little surrounding forest habitat (Table 1). Therefore, whilst cooler, higher elevation PAs appeared to be well located to receive organisms from warmer habitats, many low-lying PAs were topographically homogeneous and too isolated from tracts of continuous forest or patches of stepping stone habitats linking to cooler habitats. Whilst our analysis specifically focused on Borneo, similar patterns are likely elsewhere. In Thailand for example, extensive areas of forest at high elevation are protected, but organisms in low-lying areas are likely to experience similar difficulties reaching higher elevations from isolated PAs (Klorvuttimontara et al., 2011); similarly, PAs in Sumatra also tend to be at higher elevations (Gaveau et al., 2009). Other studies in Southeast Asia have shown that upland and montane rainforests have encountered relatively low levels of deforestation compared with lowland areas (Margono et al., 2014; Miettinen et al., 2014, 2011), and so our findings concerning low connectivity of low-lying PAs are likely to be relevant throughout the region.

4.3. Conservation implications

Source PAs that were not connected to cooler target PAs were primarily located around the coastal regions of Borneo. This finding is worrying because low-lying forests not only contain high numbers of endemics, but also contain the majority of vertebrate species (Curran et al., 2004); species richness of some taxa can also peak at low elevation (Ashton, 2010). For example, 50% of the 40 endemic Bornean bird species and over 35% of endemic mammal species depend upon lowland forests (Lambert and Collar, 2002; MacKinnon et al., 1996). Highest tree diversity is also found at low elevation (<300 m a.s.l.) along with high levels of dipterocarp endemism (Ashton, 2010). In many lowland landscapes, little forest habitat now remains outside of PAs and so they are increasingly important strongholds for biodiversity in these regions (Curran et al., 2004).

The inaccessibility and remoteness of central Borneo means that extensive tracts of relatively undisturbed forest remain at high elevation, of which a large proportion is protected (Appendix D). Thus, the future prospects for conserving low-mid elevation species under threat from climate change that reside within, or are well connected to, this central montane region remain promising, as long as current levels of forest cover outside PAs remain. An analysis to examine consequences of loss of all forest outside current PAs, suggests that connectivity of source PAs could decrease by up to 50% under a worse-case deforestation scenario (Appendix H). Species with high dispersal abilities (>5 km) may still be able to track climate, providing that the agricultural matrix does not prevent dispersal across the landscape, but most lowland species with poor dispersal abilities will fail to track climate due to lack of forest. Therefore, conservation efforts should also focus on the preservation of remaining forest outside PAs, which often retains high biodiversity value (Edwards et al., 2011), including the increased protection of forest 'corridors' that play an important role in linking forest areas along elevation gradients.

Replanting and forest management may be required to improve connectivity in some very heavily degraded landscapes, and our study suggested that improving forest cover within existing PAs increased PA connectivity by up to 30% in some instances (Fig. 3a). Improving habitat quality and increasing population growth rates of species within PAs may help promote dispersal (Mair et al., 2014). Thus, forest management within existing PAs may be more cost-effective in the immediate term given the high economic returns from oil palm plantations. However, certification criteria for sustainable oil palm agriculture require riparian forest strips and 'High Conservation Value' (HCV) forest areas to be retained within plantations (RSPO, 2013). Such forest fragments may help link PAs in human-dominated landscapes; although studies that address this issue are lacking.

5. Conclusions

Assuming our findings for Borneo are typical for many parts of Southeast Asia, we conclude that analogous climate conditions will disappear from a large number of tropical PAs, particularly those in the lowlands, even under modest warming. PAs are crucial for preserving tropical biodiversity in human-modified landscapes, but low connectivity of PAs will mean that many forest-dependent species, particularly poor dispersers, may fail to track climate. Increasing demand for agricultural lands, especially in tropical lowlands is likely to further increase the isolation of lowland PAs; thus, the connectivity of PAs along elevation gradients should be increased in order to enhance the effectiveness of tropical PA networks for conserving biodiversity under climate change.

Appendix A. Supplementary data

Temperature maps of Borneo with current and future temperature, and temperature change for both RCP2.6 and RCP8.5 warming scenarios (Appendix A); precipitation maps of Borneo with current and future precipitation and precipitation change for both RCP2.6 and RCP8.5 (Appendix B); R code and help for running (IFM) simulations (Appendix C); land area and the proportion of protected land in different elevation bands (Appendix D); source and refuge PA summary data and location (Appendix E); additional IFM simulation outputs (Appendix F); schematic diagram illustrating the potential consequences of lack of connectivity between source and target PAs for different types of species tracking climate changes (Appendix G); and methods, results and summary data for a landcover scenario where all forest outside of PAs was removed (Appendix H), are available online. Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.02.018.

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