Diversity and Distributions, (Diversity Distrib.) (2014) 1–14

Diversity and Distributions A Journal of Conservation Biogeography

BIODIVERSITY RESEARCH

Forecasts of habitat suitability improve habitat corridor efficacy in rapidly changing environments

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ABSTRACT

Aim Habitat fragmentation threatens species' persistence by increasing subpopulation isolation and vulnerability to stochastic events, and its impacts are expected to worsen under climate change. By reconnecting isolated fragments, habitat corridors should dampen the synergistic impacts of habitat and climate change on population viability. Choosing which fragments to reconnect is typically informed by past and current environmental conditions. However, habitat and climate are dynamic and change over time. Habitat suitability projections could inform fragment selection using current and future conditions, ensuring that corridors connect persistent fragments. We compare the efficacy of using current-day and future forecasts of breeding habitat to inform corridor placement under land cover and climate-change mitigation and no mitigation scenarios by evaluating their influence on subpopulation abundance, and connectivity and long-term metapopulation abundance. Our case study is the threatened orangutan metapopulation in Sabah.

Location Sabah, Malaysian Borneo.

Methods Using coupled niche–population models that capture a metapopulation distribution and its major processes, we forecast the effect of current-day and future-informed habitat corridor implementations under two scenarios where (1) land cover and climate change continue unabated (no mitigation) and (2) local and international cooperation mitigates their synergistic impact (mitigation).

Results We show that Future-informed corridor placement maximizes long-term metapopulation abundance when human-driven land cover and climate change alter the spatio-temporal composition of suitable habitat. By contrast, there is no apparent benefit in using future forecasts of breeding habitat to inform corridor placement if conditions remain comparatively stable. For the Sabah orangutan under unabated land cover and climate change, habitat corridors should connect current-day populated eastern habitat fragments with vacant fragments in the state's west.

Main conclusions The efficacy of habitat corridors can be improved by using habitat-suitability model projections to inform corridor placement in rapidly changing environments, even for long-lived, low-fecundity, philopatric species such as orangutan.

Keywords

Climate change, coupled niche–population model, habitat corridors, habitat fragmentation, metapopulation, orangutan, scenario analysis.

DOI: 10.1111/ddi.12208
http://wileyonlinelibrary.com/journal/ddi

INTRODUCTION

Habitat fragmentation is a major threat to forest-dependent tropical biodiversity in Southeast Asia (Sodhi & Brook, 2006). Forest fragments are generally small, isolated, exposed and irregularly shaped, increasing their susceptibility to a unique suite of threats (Fahrig, 2003). Populations in smaller fragments are more prone to extinction from stochastic weather events and can be driven extinct deterministically or by altered ecological pressures such as increased predation or changing food availability (Swift & Hannon, 2010). As continuing habitat modification renders fragments more isolated, dispersal among them decreases resulting in reduced gene flow and inbreeding, loss of ecosystem function, and higher direct and indirect mortality among dispersing individuals (Fahrig, 2003).

There is growing evidence that the tropical climate is changing (Corlett, 2012) and that shifts in climate will act synergistically with habitat fragmentation to further increase species' threat of extinction (Mantyka-Pringle *et al.*, 2012). Changes in mean climate conditions can reduce habitat suitability, while climate extremes can render otherwise suitable habitat as uninhabitable, and fragmentation prevents individuals from reaching alternative suitable habitat (Thomas, 2011).

By connecting habitat fragments, corridors should help avert population extirpation and even species extinction, by augmenting dispersal and promoting genetic admixing, movement out of unsuitable habitat and recolonization of extirpated subpopulations (Heller & Zavaleta, 2009). Based on this belief, corridors have been established to safeguard populations of many tropical species, including chimpanzees in Guinea (Matsuzawa *et al.*, 2011) and a variety of vertebrates in Vietnam (Cu & Vy, 2006). Evidence that corridors are a measurably effective means to mitigate extinction threat is, however, mixed (Beier & Gregory, 2012). A key problem seems to be deciding which fragments to connect to best mitigate extinction threat (Beier *et al.*, 2008). In this respect, few studies have provided any insight beyond common-sense reasoning, assuming that, for example, the most populated habitat fragments will be the most important under future environmental conditions (Heller & Zavaleta, 2009).

Beier *et al.* (2011) reviewed habitat corridor studies in the light of experiences learnt from six global projects. They classified seven methods to decide which fragments to connect. These ranged in emphasis from habitat features to species requirements and movements. For example, Theobald *et al.* (2000) advocated connecting swathes of ecologically intact habitat away from human disturbance, such as road networks. In contrast, the Washington Habitat Connectivity Workgroup estimated the habitat requirements and least-cost corridors of 16 focal species using observations and biological knowledge (Beier *et al.*, 2011). However, none of these approaches considered the importance of habitat fragments under future environmental change. Other studies have explored this additional complexity. Phillips *et al.* (2008) used graph theory to calculate network flow to inform corridor locations under climate change. Carroll *et al.* (2010) used species distribution forecasts with zonation analysis to inform reserve locations under future climate conditions.

We assess whether habitat-suitability forecasts should be used to inform the placement of habitat corridors under different land cover and climate-change scenarios. Our focal species is the threatened orangutan (*Pongo pygmaeus morio*) metapopulation of Sabah, Malaysian Borneo, chosen for two reasons. First, forest fragmentation is one of the greatest threats to tropical Southeast Asian biodiversity (Kinnaird *et al.*, 2003) – particularly to mammals on Borneo (Laidlaw, 2000) and to orangutan (Bruford *et al.*, 2010) – and its effects are likely to be worsened by climate change (Corlett, 2012). As a low-fecundity, long-lived, forest-dependent species, the orangutan is particularly susceptible to the negative effects of habitat fragmentation (Gregory *et al.*, 2012). Second, in an attempt to combat the threat of habitat degradation, the Sabah government has agreed to commit resources to implement sustainable forest management (SFM) in all its commercial forest reserves in the near future (Sabah Forestry Department, 2010) [SFM includes reduced impact logging to preserve standing forest; Reynolds *et al.* (2011)], presenting us with a real-world situation in a challenging environment that contextualizes our comparison of corridor efficacy under different forest management scenarios. The orangutan is a forest-dependent species that could be an umbrella species for other forest-dependent animals.

Beier *et al.* (2008) reviewed model-based approaches to corridor planning and noted several deficiencies. Among their remedial recommendations, they highlighted the need to: (1) identify breeding habitat and use dynamic landscape models to ensure corridors will connect habitat fragments critical for the species' persistence under climate (and presumably land cover) change; (2) assess the effectiveness of proposed corridors at facilitating movement between habitat fragments and maximizing long-term metapopulation persistence; and (3) to run uncertainty and scenario analyses to evaluate alternative corridor placements and their consequences for management targets, such as extinction risk.

Here, we heed these recommendations and used a coupled niche–population model to investigate whether by promoting connectivity among persistent habitat fragments, habitat-suitability forecasts can improve the efficacy of habitat corridor to reduce extinction risk under global change. We addressed this question by simulating long-term dynamics of the Sabah orangutan metapopulation under two land cover and climate-change scenarios and measuring the effect of *Current-informed* and *Future-informed* habitat corridors on their persistence. Current-informed corridors connect future breeding habitat identified from current-day landscape configurations. Future-informed corridors connect future breeding habitat identified from forecast future changes in habitat suitability. We measured the change in metapopulation and subpopulation abundance and connectivity due to the addition of Current-informed and Future-informed corridors relative to No corridor scenarios under two land cover and climate-change scenarios, chosen to represent the extremes of a range of possible realistic scenarios.

METHODS

Habitat suitability projections

To measure average orangutan habitat suitability, we modelled aerial nest counts in 6 years between 2000 and 2010 (Ancrenaz *et al.*, 2010) using climate, habitat and anthropogenic predictors thought to influence their distribution and abundance (Gregory *et al.*, 2012). The model was fitted on time-averaged and spatially aggregated nest counts at 2.5 km^2 resolution, using a hurdle-boosted regression tree (BRT) model accounting for spatio-temporal autocorrelation and zero inflation. The data resolution approximated an average female territory size (2.5 km^2; Singleton *et al.*, 2009) and the BRT accounted for nonlinear land cover and climate-change interactions (Elith *et al.*, 2008). The final nest-count predictions were validated against independent aerial nest counts (Alfred *et al.*, 2010) and verified by 15 Sabah Wildlife Department staff (Gregory *et al.*, 2012).

We forecasted habitat suitability under two contrasting land cover and climate-change scenarios: (1) *No mitigation*, in which only six major forest reserves are under SFM and there is no effective global action on CO_2 mitigation (MiniCAM Ref.), and (2) *Mitigation*, in which SFM is fully implemented and atmospheric CO_2 concentration is stabilized at 450 p.p.m by 2100 due to reduced global carbon emissions (MiniCAM, Level 1). We chose these scenarios because (1) they represented the extremes of a plausible range of scenarios, and (2) we would not expect deforestation and CO_2 mitigation efforts to occur independently because international agreements, such as REDD+, incentivize reduced deforestation as a mechanism to slow climate change (Pistorius, 2012).

We simulated land cover and climate-change projections from patterns in 2000 to 2010 land cover observations and 1980 to 1999 climate observations using a custom-built land cover-change model (Gregory *et al.*, 2012) and MAGICC/SCENGEN 5.3 software (Fordham *et al.*, 2012). These projections were combined in annual habitat suitability projections using the habitat-suitability model (Gregory *et al.*, 2012).

Metapopulation model

Our coupled niche–population model (RAMAS GIS v5, Akçakaya & Root, 2007) simulated the fate of orangutan subpopulations inhabiting suitable habitat fragments. It included demographic and environmental stochasticity in age-specific survival and dispersal, density dependence on adult fecundity, habitat- and density-dependent dispersal and geographic dispersal barriers, environmental correlation among subpopulation dynamics and subpopulation-specific habitat-dependent fire probabilities. We modelled females only (the limiting sex) and four life stages: infant, juvenile, subadult and adults. Density dependence in adult fecundity was modelled as a Beverton–Holt function of suitable habitat fragment carrying capacity (K). Orangutans were able to survive in habitat fragments rendered unsuitable for breeding because there is growing evidence that orangutan can survive (assuming no detrimental effect on survival) in degraded landscapes in the short term (Ancrenaz *et al.*, 2010, 2014). This was achieved through a balance of density-dependent immigration and emigration. Density-dependent dispersal was modelled as the distance-dependent dispersal rate modified by a Ricker function of K. Density dependence affected sub-adult dispersal and ensured they remained in suitable fragments until the effects of overcrowding were apparent, at which point they dispersed. The probability of a dispersing individual entering a subpopulation decreased as its carrying capacity decreased, ensuring that orangutan avoided fragments in the process of being logged. Demographic parameters used in the model were collated from literature and experts (Table 1).

To estimate the initial stable age distribution and spatial distribution of subpopulations, we ran a baseline spatial metapopulation model with stable environmental conditions for 500 years and 1000 iterations (Fordham *et al.*, 2013). The resulting spatial distribution of orangutan abundance was similar to the nest counts estimated from the habitat-suitability model. This was expected because the recent decrease in Sabah orangutan abundance has been attributed largely to habitat loss suggesting that the habitat fragments are near their carrying capacity (Ancrenaz *et al.*, 2005).

Metapopulation structure and abundances

The metapopulation structure was calculated from the habitat suitability projections (Gregory *et al.*, 2012). Cells predicted to have ≥ 4 nests were buffered with a 2.5 km^2 average territory size and grouped into habitat fragments of ≥ 3 cells. Genetic studies have shown that wide rivers are barriers to orangutan dispersal (Goossens *et al.*, 2005). We imposed impassable stretches of the Sugud, Tungud, Kinabatangan, Segama and Kalabakan rivers as geographic dispersal barriers. The initial (2010) metapopulation structure was verified by experts (Fig. 1).

Initial subpopulation abundances were calculated from ecological niche models (Gregory *et al.*, 2012) and verified by experts who recommended initializing western subpopulations (see Fig. S2 in Supporting Information) at zero orangutan abundance because they have been extirpated by hunting (Caldecott & Miles, 2005). For each fragment and year, we calculated K as the annual fragment nest count from the habitat suitability projections (Gregory *et al.*, 2012). This value was – on average – 8% higher than the initial subpopulation abundance, ensuring that subpopulations started close to K and would decline concomitantly with K to reflect the Sabah orangutan population decline across several parts of its range due to habitat degradation (Ancrenaz *et al.*, 2010).

Table 1 Parameter estimates used in the calculation of habitat suitability or metapopulation models (female only), including their sources and ranges used for sensitivity analysis. Further justification of estimates and model assumptions are given in the Supporting Information

Parameter	Value	Range	Source
Mass (m)	41 kg	–	37–45; http://pin.primate.wisc.edu/
Home range (τ)	2.5 km^2	–	Average female home range size; Singleton *et al.* (2009)
Age at maturity (α)	15 year	–	Marshall *et al.* (2009)
Longevity (ω)	40 year	–	35–45; Marshall *et al.* (2009), http://pin.primate.wisc.edu/
Lambda (λ)	e0.06	e0.05–e0.07	Range for *Pan troglodytes* & *Gorilla gorilla*; Ross (1992)
Survival l_x			
$x = 0$	0.985	–	Marshall *et al.* (2009)
$x = 1–5$	0.985	–	
$x = 6–15$	0.990	–	
$x = 16+$	0.960	0.940–0.970	Adult survival equivalent to living 30 and 50 year
CV survival (CV)	0.30	–	2 × value for *Pan troglodytes schweinfurthii*; see Methods
Fecundity (b)	1/7 year	1/6–1/8 year	Marshall *et al.* (2009), Knott *et al.* (2009)
Carrying capacity (K)	Fragment-specific	$K \pm 36\%$	SDM prediction error; see Gregory *et al.* (2012)
Density feedback in b	Beverton–Holt	–	Competition for territories; Knott *et al.* (2008)
Max. dispersal ($d_{\max}$)	120 km	–	MacKinnon (1974)
Fire probability (fp)	Fragment-specific	–	Empirically derived; see Methods
Fire mortality (f)	2.5%	1.5–3.5%	Marshall *et al.* (2009)

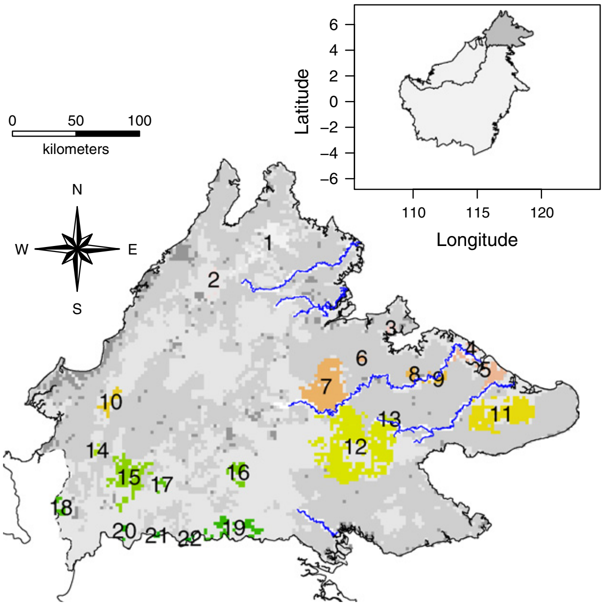

Figure 1 Map showing the location of Sabah (Malaysia) on the equatorial island of Borneo (Southeast Asia; inset) and the current-day orangutan breeding-habitat fragment structure (numbered pixel clusters) in Sabah with impassable rivers (blue). Terrestrial areas are shaded grey, and the intensity of grey represents the 'friction' of the habitat for movement from dark grey representing mostly impassable cleared areas to light grey representing optimal primary forest.

Forest fires and environmental correlation

Most fires in Southeast Asia are set deliberately to clear land for agriculture (Miettinen *et al.*, 2011). Consequently, it is difficult to predict how fire regimes might change over time (J. Miettinen, pers. comm.). Occasionally, fires burn uncontrollably and cause substantial direct orangutan mortality, usually during El Niño years when there is decreased precipitation (Marshall *et al.*, 2009). We modelled fire as a fragment-specific catastrophe killing 2.5% of animals and occurring (on average) once in every 7 years (based on historic patterns). This mortality rate approximated the estimated 2.5% of 40,000 Bornean orangutan killed in the Bornean fires of 1997 (Marshall *et al.*, 2009). The probability of fragment-specific fire outbreak was estimated from 2000 to 2012 fire-hotspot data (https://earthdata.nasa.gov/data/near-real-time-data/firms) and spatio-temporal fragment land cover composition (Fig. S3). We modelled an effect of increasing El Niño intensity (due to forecast decreases in annual precipitation) on fire intensity as a linear increase in orangutan mortality from 2.5 to 10% over 91 years, but no change in fire frequency due to their anthropogenic nature. The value of 10% was an arbitrary value representing a 4-fold increase in mortality due to fire.

Reproduction and survival of Bornean orangutan are thought to be influenced by food shortages, themselves a consequence of rainfall effects on seed masting events (Marshall *et al.*, 2009). We assumed environmental correlation in variation of demographic rates between subpopulations. Environmental correlation between subpopulations was estimated from multivariate correlograms measuring interannual synchronicity of monthly Sabah rainfall. We extracted 12,487 monthly rainfall measures between 1879 and 2011 from 50 weather stations closest to the geometric centre of Sabah (http://www.ncdc.noaa.gov/ghcnm/; Fig. S4). We estimated parameters for a negative exponential fit to characterise the spatio-temporal correlation

(Fig. S4; Keith *et al.*, 2008). This correlation captured the similarity of environmental fluctuations in vital rates among nearby populations.

Dispersal

Little is known about orangutan long-distance dispersal. Some studies suggest both sexes are philopatric (Goossens *et al.*, 2006; Van Noordwijk *et al.*, 2011), but others suggest that males move further, particularly when dispersing (Arora *et al.*, 2012). We assumed, conservatively, that females were largely philopatric. We calculated dispersal assuming a heterogeneous habitat matrix, including geographical dispersal barriers. Inter-fragment distances were calculated from a least-cost surface, based on expert-informed habitat permeability cost estimates. For example, the cost of traversing a cleared cell was 10 times more costly than traversing a primary forest cell (Table S2). The proportion of individuals dispersing from each fragment at the end of each time step was calculated from the negative exponential dispersal kernel:

$$m_{ij} = \begin{cases} \beta 1 \times \exp\left(-d_{ij}^{\beta 2}/\beta 3\right) & \text{if } d \leq d_{\max} \\ 0 & \text{if } d > d_{\max} \end{cases}, \tag{1}$$

where $\beta 1 = 0.2$, $\beta 2 = 0.69$, $\beta 3 = 8.0$, d is the least-cost distance between fragments i and j, and $d_{\max}$ is the maximum distance that an orangutan can feasibly disperse, set at 120 km (Table 1). This allowed 5% and 1% of individuals of each subpopulation to disperse 30 and 100 km through primary forest, respectively (Fig. S5). This was an upper estimate of orangutan dispersal ability because the dispersal kernel assumed homogeneous habitat, that is that d is the Euclidean distance; we calculated d using Dijkstra's algorithm to navigate the least-cost path between the closest points on the donor and recipient fragments. Consequently, the realized proportions of dispersing individuals reaching recipient fragments were substantially lower (Fig. S7). This dispersal rate was further modified by a density-dependent function of K, as explained above.

Identifying fragments to connect

To gauge a fragment's potential contribution to long-term metapopulation persistence, we calculated a *fragment value* (FV) for each fragment. FV was calculated as the ratio of the size of fragment i at time t relative to the largest fragment at time t summed over time and is given by:

$$\mathrm{FV}_i = \sum_{t=1}^{T} K_{i,t}/K_{\max,t}, \tag{2}$$

where $K_{i,t}$ is the carrying capacity of fragment i at time t and $K_{\max,t}$ is the maximum carrying capacity among all fragments present at time t. The fragment with the highest FV was the fragment with the largest average carrying capacity over the period $t = 1, \ldots, T$.

Model scenarios

To evaluate whether habitat suitability projections could improve the efficacy of habitat corridors to ameliorate extinction risk, we compared results from metapopulation models with and without corridors in the landscape. Corridors connected *donor* and *recipient* fragments. We defined the donor fragment as the largest fragment in 2010, which also had the largest subpopulation size (fragment 12 in Fig. 1). We selected the recipient fragments under two corridor scenarios: (1) *Future-informed*, in which FV was calculated over $T = 91$ annual time steps (2010–2100), and the four fragments with the highest FV (excluding the donor fragment) were designated *recipient* fragments, and (2) *Current-informed*, in which FV was calculated for $T = 1$ only, and the four fragments with the highest FV (i.e. the four largest habitat fragments from Fig. 1, excluding the donor fragment) were designated recipient fragments. Fragment selection was designed to: (1) be comparable between Future-informed and Current-informed scenarios, and (2) favour the largest fragments because large reserves should be preferred if the species' risk of extinction is high (McCarthy *et al.*, 2005).

Habitat corridors were represented as the least-cost path between the donor and recipient fragments and assumed that land managers would want to locate them where the need to create new habitat was minimized. In effect, corridors converted intervening heterogeneous habitat to a homogeneous maximum-conductance forest habitat, that is the Euclidean distance, with a corresponding increase in dispersal rate calculated from equation 1. The least-cost path was calculated using Dijkstra's algorithm as explained above. By allowing corridors to affect connectivity only, we avoided the confounding effect of an increase in suitable habitat, which is dependent on factors such as their width. Connectivity was increased gradually over 10 years intended to simulate replanting and good silviculture practices promoting fast forest regeneration (Peña Claros *et al.*, 2008). Connectivity to *non-target* fragments was increased inadvertently because they fell along proposed corridors. Fragments whose connectivity was not affected by corridors were *unlinked*.

Sensitivity analysis

Metapopulation simulations are sensitive to their chosen parameterizations. We analysed the sensitivity of our metapopulation models under the No mitigation scenario with No corridors and the Mitigation scenario with model-informed corridors to: (1) assess the effect of uncertainties in metapopulation parameter estimates, and (2) determine to which parameters the models were most sensitive. Whilst these analyses would not allow us to evaluate the influence of habitat forecasts on habitat corridor efficacy under feasible global change scenarios directly, they would highlight parameter estimates to which the metapopulation results are sensitive (Akçakaya & Root, 2007). Future research might then validate or improve our understanding of those parameters.

We varied six parameters across a uniform probability distribution, bounded by values determined from literature or expert knowledge (Table 1). We used Latin hypercube sampling that allowed us to evaluate interactions among the parameter combinations while efficiently sampling the six-dimensional parameter space (Conroy & Brook, 2003). This procedure amounted to refitting the metapopulation models with 200 combinations of our six chosen parameters selected by stratified sampling across the full range of each parameter. Given the short time-scale of our simulations (91 years) relative to orangutan generation time (33 years) and the attendant low extinction risk, we analysed mean final metapopulation abundance as a function of the parameter combinations using a BRT model with learning rate (lr) = 0.001, bag fraction (bf) = 0.75 and complex five-way interactions (tc = 5). We selected the number of trees (nt) that minimized the 10-fold cross-validation predictive deviance (Elith *et al.*, 2008). We calculated the relative importance of each parameter on variation in mean final metapopulation abundance and their partial effects.

Detailed methods are presented in Supporting Information. Unless specified, all analyses were carried out in R 2.15.2 (www.r-project.org).

RESULTS

Forecast fragmentation

The majority of suitable habitat in 2010 was predicted to occur in Eastern Sabah, the current-day orangutan stronghold (Fig. 1). Suitable habitat was spread across 22 fragments, some of which were separated by impassable river stretches, for example fragments 8 and 9. Assuming a maximum least-cost path distance of 120 km through the heterogeneous landscape, those 22 fragments were grouped into 10 suitable habitat clusters connected by 35 links (Table 2; Fig. S1). The initial metapopulation abundance was estimated to be 4204 female individuals.

Table 2 Fragmentation statistics for the start, middle and end of the simulation, showing a decrease in the mean number of links (Links), number of core cells (Core cells) and fragment area under the No mitigation scenario overtime compared to the Mitigation scenario. The number of clusters of suitable habitat fragments (Components) increases as number of links decreases. Graphs of these data are presented in the Supporting Information

Scenario	Year	Links	Components	Core cells	Fragment area
No mitigation	2010	35	10	3.421	16.965
	2055	21	13	2.156	14.625
	2100	14	10	0.295	7.262
Mitigation	2010	35	10	3.421	16.965
	2055	79	4	3.718	16.986
	2100	37	6	3.152	14.127

Under the No mitigation scenario, mean total and core fragment area and connectivity (of fragments with persisting orangutan subpopulations) was forecast to decrease by 57% and 91% and 60% by 2100, respectively (Table 2; Fig. S1). The decrease was salient in Eastern Sabah, where almost all suitable habitat disappeared by 2100. By comparison, the same measures were relatively stable under the Mitigation scenario, forecast to decrease by 29% and 8% and increase by 6% by 2100, respectively (Table 2; Fig. S1).

Current- and Future-informed corridors

Current-day corridors connected fragment 12 with fragments 7, 11, 5 and 1 (Fig. 2), which would require the creation of 98 km and protection of 179 km of forest corridor, respectively. The Current-informed corridors increased connectivity to 17 and 7 non-target habitat fragments under the No mitigation and Mitigation scenarios, respectively. All but one of the Current-informed recipient fragments were still suitable by 2055 under the No mitigation and Mitigation scenarios (fragment 9 was forecast to become unsuitable after 2020), although this dropped to three by 2100 under the No mitigation scenario.

Future-informed corridors connected fragment 12 with fragments 7, 15, 16 and 18, under the No mitigation scenario, which would require the creation of 10 km and protection of 269 km of forest corridor, respectively. In contrast, the Future-informed corridors connected fragment 12 with fragments 1, 7, 15 and 18, under the Mitigation scenario, and would require the creation of 26 km and protection of 322 km of forest corridor, respectively. These corridors increased connectivity to 14 and 8 non-target fragments under the No mitigation and Mitigation scenarios, respectively. All fragments were forecast to remain suitable until 2055, and only fragment 7 was considered unsuitable by 2100 under the No mitigation scenario.

Corridor efficacy and metapopulation abundance

Relative to their corresponding No corridor scenarios, corridors increased the mean dispersal rate between donor, recipient and non-target subpopulations (Fig. 3). Dispersal to recipient subpopulations was higher than to donor and non-target subpopulations under the No mitigation scenario and was highest to recipient subpopulations under Future-informed corridors. Dispersal by Current-informed corridors under the Mitigation scenario was similar to that observed under the No mitigation scenario but was lower to recipient subpopulations (and slightly higher to donor and non-target subpopulations) under the Future-informed corridors (Fig. 3).

In the absence of habitat corridors, metapopulation abundance decreased by 51% (mean 2028 females) under No mitigation and 16% (mean 3481 females) under the Mitigation scenarios by 2100 (Fig. 4). The increase in mean dispersal rate due to corridors resulted in a slower decline in total metapopulation abundance under all but one scenario: Current-informed corridors under a Mitigation scenario. This

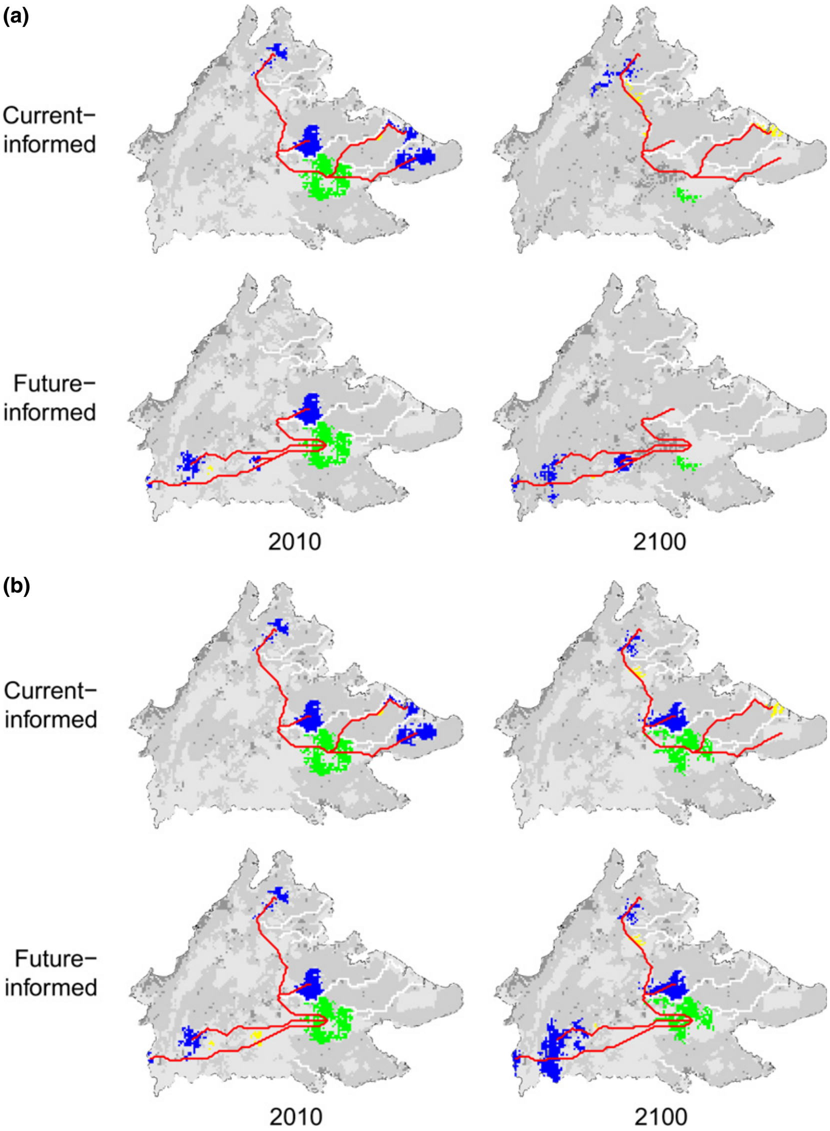

Figure 2 Current-informed and Future-informed corridors (red lines) connecting donor and recipient subpopulations in 2010 and 2100 under (a) No mitigation and (b) Mitigation scenarios, where mitigation refers to land cover and climate-change mitigation (global CO_2 emissions reductions). The Current-informed corridors are based on past and current-day information only and are therefore identical for (a) and (b). The Future-informed corridors are based on 2010–2100 habitat suitability projections and are different under the two mitigation scenarios. Donor fragments are green and recipient fragments are blue. Yellow fragments are non-target fragments whose connectivity is also increased through the corridor. The background is shaded from light to dark grey, representing high to low habitat permeability, whereby forest and open ground represent highest and lowest permeability, respectively (see Supporting Information). Recipient and non-target subpopulations that do not appear to be connected by corridors on the 2010 maps are connected during the intervening period.

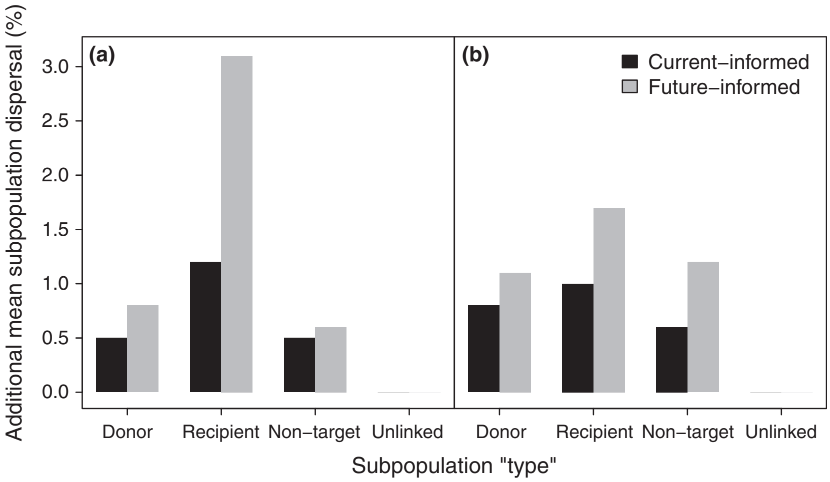

Figure 3 Panels showing the effect of Current-informed and Future-informed corridors on the mean dispersal rates of different subpopulation 'types' under the (a) No mitigation and (b) Mitigation land cover and climate-change scenarios. Subpopulation types were: recipient that were directly connected to the donor fragment, non-target that were inadvertently connected to the donor fragment and unlinked that were not connected by corridors.

slowing effect was strongest for Future-informed corridors relative to the No corridor scenario under the No mitigation scenario (a difference of 120 females or 2.3% of the 2100 No corridor metapopulation abundance). The slowdown in the relative metapopulation abundance decline was weaker for Current-informed corridors compared to Future-informed

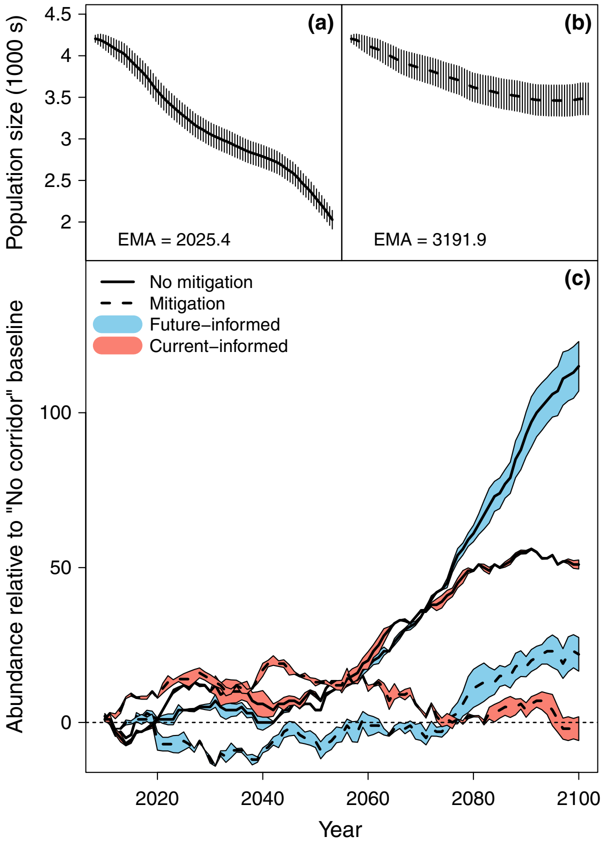

Figure 4 Total metapopulation abundance projections under the No corridor baseline scenarios for (a) No Mitigation and (b) Mitigation scenarios, and (c) metapopulation abundance projections for Current-informed and Future-informed corridors (relative to their corresponding No corridor scenarios) under No mitigation and Mitigation land cover and climate-change scenarios. Error bars and areas are 95% confidence intervals calculated from 10,000 metapopulation simulations. EMA is the expected minimum abundance. Absolute changes in abundance are given in the Results and Discussion.

corridors under both mitigation scenarios (Fig. 4). Changes in metapopulation abundance under corridor scenarios only diverged from no corridor scenarios after 2055 when suitable habitat fragments began to disappear.

The higher 2100 Sabah orangutan population size with Future-informed corridors (relative to the No corridor scenario) under the No mitigation scenario was due largely to an abundance increase in recipient and unlinked subpopulations (Fig. 5), particularly in western Sabah (Fig. 6). In contrast, Current-informed corridors promoted population increases in unlinked subpopulations (relative to the No corridor scenario; Fig. 5) and recipient and non-target subpopulations across the state increased in abundance (Fig. 6).

Model sensitivity

Mean final metapopulation abundance under the No mitigation and No corridor scenario was most sensitive to variation in K and intrinsic population growth rate ($R_{\max}$), causing it to increase as they increased (Fig. 7a). This was expected since habitat fragmentation was greatest under the No mitigation scenario and individuals could not escape shrinking habitat fragments with increasing population density that was driving a decrease in fecundity (perhaps due to competition for breeding territories). Where the effect of habitat fragmentation was minimized – under the Mitigation scenario with Future-informed corridors – mean final metapopulation abundance was most strongly affected by variation in adult survival, followed by K and $R_{\max}$. Adult survival drove a decrease in mean final metapopulation abundance as it increased (Fig. 7b), perhaps suggesting that lower fecundity was offset by increases in adult survival where habitat fragmentation was decreased. Relative to K, $R_{\max}$ and adult survival, variation in mean dispersal rate had only a minor influence on model outcomes in both cases (Fig. 7b).

DISCUSSION

Compared to Current-informed corridors, we show that Future-informed habitat corridors slowed the metapopulation abundance decline (relative to the No corridor baseline), but only when land cover and climate change continue unabated. This slowing of the population decline was a direct consequence of corridors facilitating dispersal to long-term suitable habitat fragments. This is the first time this has been shown. Hodgson *et al.* (2011b) showed that restoring habitat along model-informed corridors better promoted metapopulation persistence compared to expert-informed habitat restoration, but their analysis did not account for climate change. Gregory *et al.* (2012) recently showed that Sabah orangutan persistence would likely be maximized under deforestation and CO_2 mitigation, but they did not consider the effect of habitat corridors on population persistence.

Habitat loss and fragmentation is one of the greatest contemporary threats to the long-term persistence of tropical forest-dependent biodiversity, and its impact will be exacerbated by the synergistic effect of climate change (Mantyka-Pringle *et al.*, 2012). By reconnecting isolated habitat fragments in an effective way, corridors are expected to reduce the threat of population extinction by increasing dispersal, facilitating genetic admixing and allowing species to access future suitable habitat when current-day habitat becomes unsuitable (Gilbert-Norton *et al.*, 2010). Our results show how habitat-suitability forecasts can be used to identify the most important habitat fragments for Sabah orangutan and thereby improve the efficacy of habitat corridors for long-term metapopulation persistence, particularly in rapidly changing environments.

In contrast to the advantage of using Future-informed corridors under land cover and climate change, we show that corridors developed on the basis of current knowledge are an equal or better (and simpler) option when the amount and spatial configuration of future suitable habitat is comparable

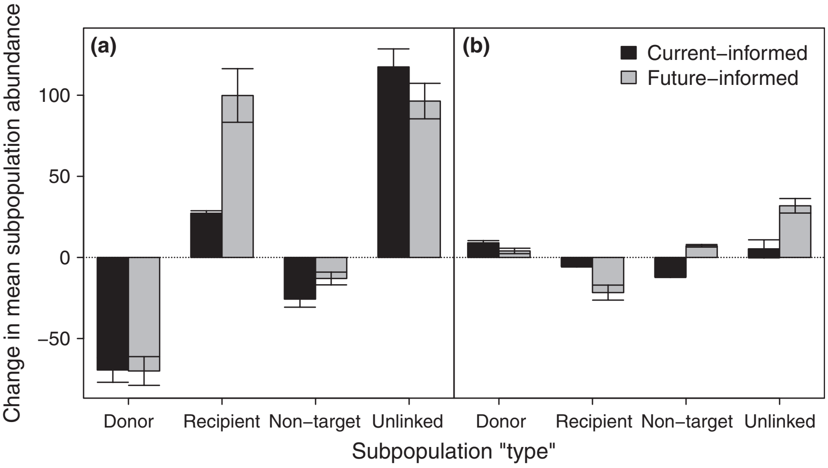

Figure 5 Panels showing the effect of Current-informed and Future-informed corridors on mean abundance of different subpopulation 'types' under the (a) No mitigation and (b) Mitigation land cover and climate-change scenarios. Subpopulation types were: recipient that were directly connected to the donor fragment, non-target that were inadvertently connected to the donor fragment, and unlinked that were not connected by corridors. Error bars are 95% confidence intervals calculated from 10,000 metapopulation simulations.

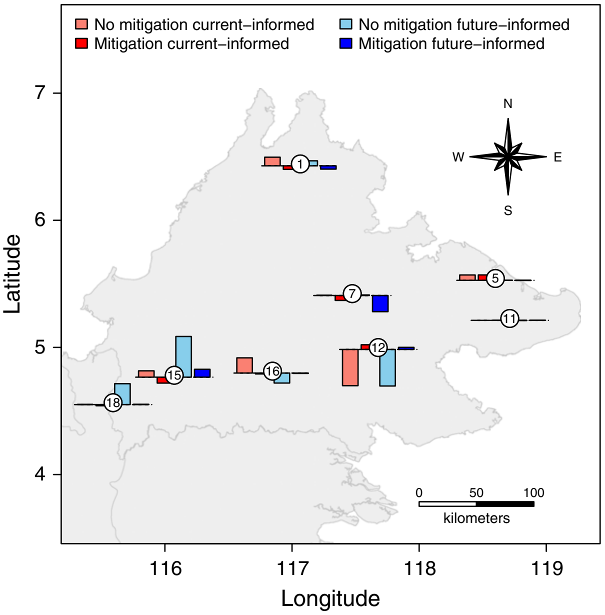

Figure 6 A map showing the difference between initial and final abundance for each corridor, and No mitigation and Mitigation land cover and climate-change scenario combination. Only donor and recipient subpopulations from all combinations are plotted. Note the relatively large increase in abundance in subpopulation 15 in western Sabah across all treatments. Terrestrial areas are shaded grey.

to that of the current-day. This is an intuitive result: if species' have colonized all available and accessible habitat in the landscape, then large and stable suitable habitat fragments would sustain large local populations that will persist into the future. Habitat suitability projections therefore serve mainly to supplement current-day knowledge by accounting for unobserved future environmental changes and their interactions. Hence, the value of future simulations is dependent entirely on the realisation of the projected land cover and climate changes. Since our sensitivity analysis highlighted that the final metapopulation abundance was sensitive to changes in *K* (based on habitat suitability projections), so these results should be considered guidance for more informed management decisions supplemented by local expert opinion.

Implications for Sabah orangutan

A recent study showed that the Sabah orangutan population would fare best if all commercial forest reserves were placed under SFM and atmospheric CO_2 concentrations were stabilized at 450 p.p.m. (Gregory *et al.*, 2012). Under this Mitigation scenario, our results suggest connecting suitable habitat fragments will have a negligible effect by 2100, slowing the metapopulation decline by 20 females or 0.4% of the 2100 No corridor metapopulation abundance. If, however, the Sabah government does not meet its commitment to adopt SFM and CO_2 emissions continue unabated, then corridors could save up to 2.3% of the 2100 No corridor metapopulation abundance, *c.* 120 animals.

Although the numbers of orangutan potentially saved by corridors is small, they should be considered relative to the study time frame, orangutan life history and the capacity to maintain landscape connectedness over long-term (evolutionary) timescales. Our simulations ran for 91 years (from 2010 to 2100). The Bornean orangutan is a long-lived, low-fecundity and philopatric species (Wich *et al.*, 2009) with a generation time of over 33 years (calculated from the Leslie matrix using estimates in Table 1). Given that our simulations were initiated with a stable age distribution, our model simulated only three generations of orangutan population dynamics and corridors only improved dispersal after 2020. While we could have run these simulations for longer (e.g. 1000 years in Marshall *et al.*, 2009), the uncertainty associated with the forecasts would likely have rendered the results meaningless (Fieberg & Ellner, 2001). Running the simulations for a shorter period would have reduced the magnitude of the observed effect because the effects of corridors were not apparent until after 2055. This suggests that corridors would not be particularly effective in the short term.

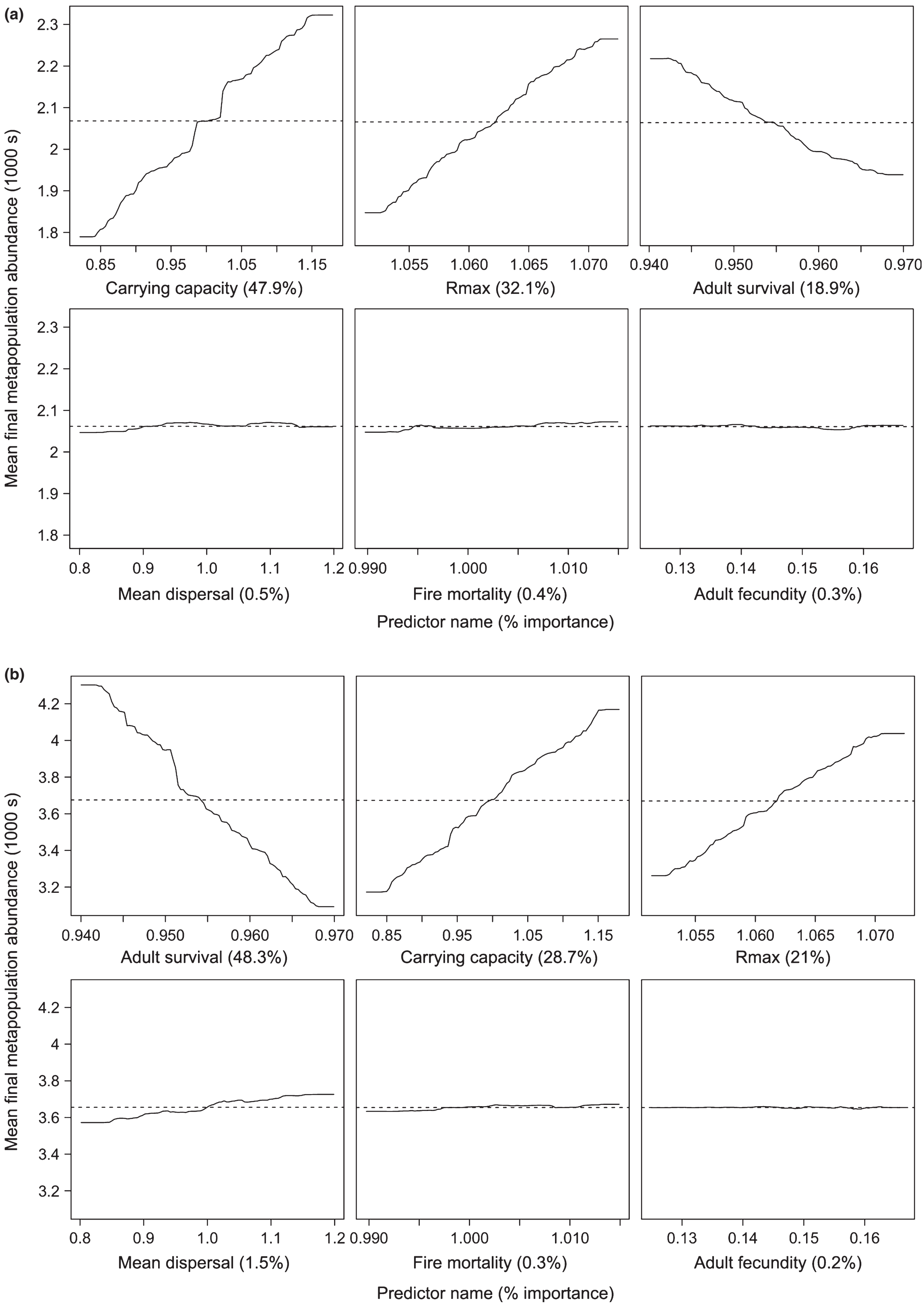

Figure 7 Partial effects plots showing the sensitivity of mean final total metapopulation abundance of persistent runs only, plotted against variation in parameter estimates after accounting for the average effects of all other variables in the model. Plots are ordered by % importance, which measures the relative model fit improvement credited to each predictor. Dashed line is the mean final metapopulation abundance. Panels group plots for (a) No mitigation scenario without corridors and (b) Mitigation scenario with Model-informed corridors.

Realities of corridor creation

Several issues would need to be addressed if corridors were to be implemented. First, both Current- and Future-informed corridors require the creation of new forest habitat, although the latter scenario requires only one tenth of the amount under the former. Whether this habitat could be created is subject to a range of socio-economic and political factors not considered here, in part because their inclusion would steer the results away from our ecological focus (Beier *et al.*, 2011). Experts suggest that they should be a minimum of 500 m wide and restored with a variety of plant species to encourage use by species other than just orangutan (M. Ancrenaz, pers. comm.), and this has been shown in other tropical ecosystems (e.g. Lees & Peres, 2008). For our purposes, we opted to increase *connectivity* between habitat fragments and not habitat per se. A more realistic model might have increased available suitable habitat together with connectivity, which would allow animals to live in corridors and disperse over several years.

Another consideration is whether corridors would serve other threatened animals and plants, and encourage genetic admixing. The Kinabatangan River in Eastern Sabah delineates the migration route for the Bornean elephant (Alfred *et al.*, 2012). Improving riverine forest habitat along the Kinabatangan could allow orangutan to escape to larger, more long-term suitable habitat fragments further west while ensuring that the elephants can continue to undertake their annual migrations (Estes *et al.*, 2012). The degree to which the Sabah orangutan population is structured as subpopulations is not known. It would be important to study the genetic distinctiveness of the subpopulations and the effects of corridors on gene flow.

Model limitations

Although our investigation was detailed in an attempt to be realistic, we were required to make some simplifying assumptions. Consequently, our findings fall short of providing a plan for habitat corridor implementation to minimize Sabah orangutan extinction risk.

First, we omitted socio-economic factors that could prevent the creation or protection of forest for corridors. Second, our population model was female only because we had more complete information on female orangutan life history and movements. Some studies suggest that intersex differences in ecology and behaviour are small (Goossens *et al.*, 2005), but others suggest that males move further, particularly when dispersing (Arora *et al.*, 2012), neglecting which could overestimate the effect of corridors. Third, our model is region-specific and neglects potential migration to and from Brunei and East Kalimantan, Indonesia, because we lacked the necessary data to estimate their suitable orangutan habitat and because cross-national-border corridor placement would need multilateral forest management. Fourth, our model neglected disease and inbreeding depression despite the potential impact of increased dispersal due to corridors could have on these factors. A model to predict more precise orangutan population dynamics (as opposed investigating corridor efficacy) should include these factors. Fifth, our study was delivered at a coarse spatial resolution that assumed all movements occurring at a finer resolution were unimportant to population dynamics. It would be interesting to repeat this study with finer resolution data to evaluate this assumption.

Regarding the habitat corridors, we made several simplifying assumptions. We assumed that corridors were implemented in their entirety in 2010 and that no further habitat management took place thereafter. We assumed that the budget existed to implement and protect the corridors into perpetuity and that money saved from implementing shorter corridors was not reinvested into additional corridors.

Finally, we did not include hunting as a threat to orangutan because it has been outlawed and is believed to be negligible (M. Ancrenaz, pers. comm.). Nevertheless, hunting was a problem in the west of the state (Caldecott & Miles, 2005) and – if still practiced – this exercise highlights the importance of eradicating hunting in the near future, to ensure that orangutan do not disperse west to their death. Similarly, for this model to be transferred to other areas of Borneo or Sumatra, hunting would be a crucial component in forecasting metapopulation abundance and persistence (Davis *et al.*, 2013).

A theme that emerges strongly from this study is that of uncertainty. We undertook a sensitivity analysis of our results to parameter values, but their uncertainties were not captured in the modelling process, preventing us evaluating their effects on our study conclusions. Rather they highlighted which parameters could be usefully refined or validated with field-based studies, such as the SAFE project (Ewers *et al.*, 2011). A second type of uncertainty is the effect of uncertainties in the forecasts themselves. Although we included K as a parameter in our sensitivity analyses and used an ensemble of seven GCMs for our climate-change predictions, uncertainty in the locations of breeding-habitat fragments was not considered despite their potential to affect our findings (Naujokaitis-Lewis *et al.*, 2013), although perhaps less than habitat quantity or quality (Hodgson *et al.*, 2011a). A more thorough analysis of these uncertainties in coupled niche–population models would be a valuable further work.

There is growing experimental evidence that corridors are an effective means to increase connectivity between habitat fragments (Gilbert-Norton *et al.*, 2010). Here, we show that using habitat-suitability model projections is likely to improve the efficacy of habitat corridors under future land cover and climate change but is no better than current knowledge if the landscape remains relatively stable. Although we have shown that Future-informed habitat corridors are a potentially useful management strategy to promote the long-term persistence of metapopulations, the Sabah orangutan metapopulation was nevertheless forecast to decline by almost half by 2100 if land cover and climate change continue unabated. This suggests that if we are to mitigate extinction risk in the long term, we must also address the drivers of habitat loss, degradation and fragmentation.

ACKNOWLEDGEMENTS

We thank the Economic Planning Unit for permission to conduct research in Sabah, the late Datuk Patrick Andau and the SFD, SWD and KOCP staff. We thank Donna Harris, Datuk Sam Mannan, Nicola Abram, Thomas Prowse, Steve Delean, Jonathan Rhodes and two anonymous referees for comments and discussions. ASTER GDEM is a product of METI and NASA, and the land cover is derived from data provided by JAXA as the ALOS sample product © JAXA, METI. We thank WWF-Malaysia for supplying spatial data. Australian Research Council (ARC) grants supported contributions of S.D.G., D.A.F. and B.W.B. (DP1096427, FT100100200 and FS110200051). Financial support to KOCP originates from Hutan's supporters.

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SUPPORTING INFORMATION

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

Appendix S1 Additional detailed methods

Table S1 Future land cover and climate-change scenarios.

Table S2 Habitat permeability values (‘conductance values’) used in dispersal calculations.

Figure S1 Graphs showing the habitat fragments, their links and their membership to habitat clusters in 2010, 2055 and 2100 under (a) No mitigation and (b) Mitigation scenarios.

Figure S2 A map showing the initially empty habitat fragments in western Sabah.

Figure S3 Plots of calculated fire-return rate and derived fire-return probability layer.

Figure S4 Plots showing rainfall record locations and derived spatial cross-correlogram used to estimate environmental correlation.

Figure S5 Dispersal kernel assuming an exponential decay function.

Figure S6 The 2010 (a) land cover and (b) transition layer used to calculate a least-cost path.

Figure S7 Maps of connected habitat fragments at 40, 70 and 100 km when assuming (a) Euclidean distance, and (b) least-cost distance.

BIOSKETCH

Stephen Gregory, a post-doctoral researcher with an expertise in modelling population dynamics, undertook this research at the Global Ecology Lab at the University of Adelaide. This study is part of a broader project supported by the Australian Research Council (DP1096427), which is developing a quantitative understanding of the demographic mechanisms underpinning range margins and incorporating this new knowledge into spatially and dynamic population-habitat models. The study capitalised on 15 years of Sabah orangutan conservation work undertaken by Hutan, the Sabah Wildlife Department and Cardiff University.

Author contributions: S.D.G., M.A., B.G. and D.A.F. conceived the ideas; M.A., B.G., R.A. and L.N.A. collected the data; S.D.G., B.W.B. and D.A.F. analysed the data; and S.D.G., M.A., B.W.B. and D.A.F. led the writing.

Editor: Mark Robertson