



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

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Keywords:	Climate change, Coupled niche-population model, Habitat change, Habitat corridors, Population viability analysis, Scenario analysis

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

4 *Running head:* Model-informed habitat corridor placement

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Abstract

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 ~~past~~, 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~~ 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

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). Our case study is the Sabah the orangutan (*Pongo pygmaeus morio*) metapopulation living in Sabah that is threatened by both future land cover and climate changes.

We show that future-informed corridor placement maximizes long-term metapopulation

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3 58 abundance when human-driven land-cover and climate change alter the spatio-temporal
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5 59 composition of suitable habitat. By contrast, there is no apparent benefit in using future forecasts
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7 60 of breeding habitat to inform corridor placement if conditions remain comparatively stable. For
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9 61 the Sabah orangutan under unabated land cover and climate change, habitat corridors should
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11 62 connect current-day populated eastern habitat fragments with vacant fragments in the state's
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13 63 west.
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18 64 **Main Conclusions** The efficacy of habitat corridors can be improved by using habitat suitability
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20 65 model projections to inform corridor placement in rapidly changing environments, even for long-
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22 66 lived, low fecundity, philopatric species, such as orangutan.
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28 67 **Keywords** Climate change; Coupled niche-population model; Habitat change; Habitat corridors;
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30 68 Metapopulation; Orangutan; Population viability analysis; Projections; Scenario analysis
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4 **70 (A) Introduction**

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8 **71** Habitat fragmentation is a major threat to forest-dependent tropical biodiversity in Southeast
9 **72** Asia (Sodhi & Brook, 2006). Forest fragments are generally small, isolated, exposed and
10 **73** irregularly shaped, increasing their susceptibility to a unique suite of threats (Fahrig, 2003).
11
12 **74** Populations in smaller fragments are more prone to extinction from stochastic weather events
13 **75** and can be driven extinct deterministically or by altered ecological pressures such as increased
14 **76** predation or changing food availability (Swift & Hannon, 2010). As fragments become more
15 **77** isolated due to greater clearance of once-continuous habitats, dispersal among them decreases,
16 **78** resulting in reduced gene flow and inbreeding, loss of ecosystem function, and higher direct and
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18 **79** indirect mortality in individuals moving between them (~~Watling et al., 2011~~Fahrig, 2003).
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32 **81** There is growing evidence that the tropical climate is changing (Corlett, 2012) and that shifts in
33 **82** climate will act synergistically with habitat fragmentation to further increase species' threat of
34 **83** extinction (Mantyka-Pringle *et al.*, 2012). Changes in mean climate conditions can reduce habitat
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36 **84** suitability, while climate extremes can render otherwise suitable habitat as uninhabitable, and
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38 **85** fragmentation prevents individuals from reaching alternative suitable habitat (Thomas, 2011).
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46 **87** By connecting habitat fragments, corridors should help avert population extirpation and even
47 **88** species extinction, by augmenting dispersal and promoting genetic admixing, movement out of
48 **89** unsuitable habitat and recolonization of extirpated subpopulations (Heller & Zavaleta, 2009).
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50 **90** Based on this belief, corridors have been established to safeguard populations of many tropical
51 **91** species, including chimpanzees in Guinea (Matsuzawa *et al.*, 2011) and a variety of vertebrates
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3 92 in Vietnam (Cu & Vy, 2006). Evidence that corridors are a measurably effective means to
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5 93 mitigate extinction threat is, however, mixed (Beier & Gregory, 2012). ~~The mainA key~~ problem
6
7 94 seems to be deciding which fragments to connect to best mitigate extinction threat (Beier *et al.*,
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9 2008). In this respect, few studies have provided any insight beyond common-sense reasoning,
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11 95 assuming that, for example, the most populated habitat fragments, or those with the largest area,
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13 96 will be the most important under future environmental conditions (Heller & Zavaleta, 2009).
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19 99 Beier *et al.* (2011) reviewed habitat corridor planning studies in light of experiences learnt from
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21 six global projects. They classified seven different methods to decide which fragments to
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23 connect. These ranged from a focus on habitat features to a focus on species requirements and
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25 movements. For example, Theobald *et al.* (2000) advocated connecting swathes of relatively
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27 ecologically intact habitat, calculated using proxies of human disturbance such as road networks.
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29 100
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31 101 In contrast, the Washington Habitat Connectivity Workgroup modelled the habitat requirements
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33 and least-cost corridors for 16 focal species based on observations and biological knowledge (see
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35 references in Beier *et al.*, 2011). However, none of these approaches explicitly considered the
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37 importance of habitat fragments under future environmental change. Other studies have explored
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39 this additional complexity. Phillips *et al.* (2008) used graph theory to calculate network flow as a
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41 means of optimizing corridor locations under climate change. Similarly, Carroll *et al.* (2010)
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43 used climate change forecasts in species distribution models together with zonation analysis to
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45 optimize the location of reserves under future environmental conditions.
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3 115 species is the threatened orangutan (*Pongo pygmaeus morio*) metapopulation of Sabah,
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5 116 Malaysian Borneo, chosen for two reasons. First, forest fragmentation is one of the greatest
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7 117 threats to tropical Southeast Asian biodiversity (Kinnaird *et al.*, 2003) – particularly to mammals
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9 118 on Borneo (Laidlaw, 2000) and to orangutan (Bruford *et al.*, 2010) – and its effects are likely to
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11 119 be worsened by climate change (Corlett, 2012). As a low-fecundity, long-lived, forest-dependent
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13 species, the ~~Bornean~~-orangutan (*Pongo pygmaeus morio*) is particularly susceptible to the
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15 negative effects of habitat fragmentation (Gregory *et al.*, 2012). Second, in an attempt to combat
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17 the threat of habitat degradation, the Sabah government has agreed to commit resources to
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19 implement sustainable forest management in all its commercial forest reserves in the near future
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21 (Sabah Forestry Department, 2010) [sustainable forest management (SFM) encapsulates several
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23 management methods, including reduced impact logging, with potential to preserve standing
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25 forest; see Reynolds *et al.* (2011)], presenting us with a real-world situation in a challenging
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27 environment that contextualizes our comparison of corridor efficacy under different forest
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29 management scenarios. As a forest-dependent species, the orangutan could also be considered an
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31 umbrella or indicator species for other forest-dependent animals.

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131 Beier *et al.* (2008) reviewed model-based approaches to corridor planning and noted several
132 deficiencies. Among their remedial recommendations, they highlighted the need to: (1) identify
breeding habitat and use dynamic landscape models to ensure that 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

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3 138 management targets, such as extinction risk.
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8 140 Here, we heed these recommendations and used a coupled niche-population model (Fordham *et*
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10 *al.*, 2013^{32a}) to investigate whether by promoting connectivity among persistent habitat
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12 fragments, habitat suitability forecasts can improve the efficacy of habitat corridor to reduce
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14 extinction risk under global change. We addressed this question by simulatinge long-term
15 dynamics of the Sabah orangutan metapopulation under two land cover and climate change
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17 scenarios and measuring the effect of Current-informed and Future-informed habitat corridors on
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19 their persistence. opposing land cover and climate change scenarioss (Gregory *et al.*, 2012), with-
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21 and without current informed and future informed habitat corridors. Current-informed corridors
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23 use connect future breeding habitat identified from past and current-day landscape configurations
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25 to identify future breeding habitat. Future-informed corridors use connect future breeding habitat
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27 identified from forecast future changes in habitat suitability to identify future breeding habitat.
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30 We measured the change in metapopulation and subpopulation abundance and connectivity due
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32 to the addition of Current-informed and Future-informed corridors relative to No corridor
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34 scenarios under two land cover and climate change scenarios, chosen to represent the extremes
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36 of a range of possible realistic scenarios. To ensure our model results were robust, we also
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38 rigorously examined the sensitivity of our metapopulation models to a range parameter
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40 estimates.
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4 159 **(A) Materials and methods**
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89 160 **(B) Habitat suitability projections**
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13 161 To measure average orangutan habitat suitability, we modeled aerial nest counts collected by
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15 162 helicopter survey in ~~six~~ years between 2000-10 (Ancrenaz *et al.*, 2005; Ancrenaz *et al.*, 2010)
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17 163 using climate, habitat and anthropogenic predictors thought to influence their distribution and
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19 164 abundance ([see Gregory *et al.*, 2012 & Supporting information for more details](#)). The model was
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21 fitted on time-averaged and spatially aggregated nest counts at 2.5 km² resolution, using a two-
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23 165 step hurdle-boosted regression-tree model to account for spatiotemporal autocorrelation and
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25 166 zero-inflation, respectively. [This single type of habitat suitability model was used because: \(1\) a](#)
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27 167 [single model can be more carefully parameterized and explored compared to an ensemble of](#)
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29 168 [multiple models \(Elith *et al.*, 2008\), and \(2\) boosted regression-tree models capture non-linearity](#)
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31 169 [and interaction among predictor variables, accounting for any synergistic effects of land cover](#)
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33 170 [and climate change \(Elith *et al.*, 2008\). This](#) [The](#) spatial resolution was chosen because 2.5 km²
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35 171 is the estimated average female territory size (Singleton *et al.*, 2009), although it is arguably too
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37 172 coarse for practical application without additional local expert knowledge. The final nest-count
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39 173 predictions were validated against an independent aerial nest-count dataset (Alfred *et al.*, 2010)
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41 174 and verified [using the expert opinion of](#) 15 rangers and officers from the Sabah Wildlife
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43 175 Department ([see Gregory *et al.*, 2012 & Supporting information](#)).
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53 178 We used our model to forecast habitat suitability under two contrasting land cover and climate-
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55 179 change scenarios: (1) *No mitigation*, in which only six major forest reserves are under
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3 180 sustainable forest management (SFM) and there is no effective global action on CO₂ mitigation
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5 181 (MiniCAM Ref.), and (2) *Mitigation*, in which SFM is fully implemented promoting
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7 182 conservation of standing forest and atmospheric CO₂ concentration is stabilized at 450 ppm by
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9 183 2100 due thanks to large-scale reductions in global anthropogenic carbon emissions (MiniCAM,
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11 Level 1). We chose these land cover and climate change scenarios because (1) they represented
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13 184 the extremes of a plausible range of scenarios, and (2) we would not expect the mitigation efforts
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15 185 for deforestation and CO₂ mitigation to occur independently of one another. For example,
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17 186 deforestation mitigation without CO₂ mitigation is unlikely because international agreements,
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19 187 such as REDD+, incentivize reduced deforestation as a mechanism to slow climate change
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21 188 (Pistorius, 2012).
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32 191 To obtain The land cover and climate-change projections, patterns in 2000 to 2010 land cover
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34 192 observations and 1980 to 1999 climate observations were simulated from a custom-built land-
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36 193 cover-change model (Gregory *et al.*, 2012) and MAGICC/SCENGEN 5.3 software (Fordham *et*
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38 194 *al.*, 2012^b), respectively. See the Supporting information for more details. These projections
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40 195 were then combined into annual habitat suitability projections using the habitat suitability model
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42 196 described above, which accounts for the synergistic effects of land cover and climate change
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44 197 (Gregory *et al.*, 2012).
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50 199 **(B) Metapopulation model**

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53 200 Our coupled niche-population model (built in RAMAS GIS v5; Akçakaya & Root, 2007)
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55 201 simulated the fate of orangutan subpopulations inhabiting suitable habitat fragments and
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3 202 | included demographic and environmental stochasticity in age-specific survival and dispersal,
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5 203 | density dependence on adult fecundity, habitat- and density-dependent dispersal and geographic
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7 204 | dispersal barriers, environmental correlation among subpopulations and subpopulation-specific
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9 205 | habitat-dependent fire probabilities. We modeled females only (the limiting sex) and four life
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11 206 | stages: infant, juvenile, sub-adult and adults. Density dependence in adult fecundity was modeled
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13 207 | as a non-linear (Beverton-Holt) function based on the carrying capacity of suitable habitat
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15 208 | fragments. Orangutans were however, able to survive in habitat fragments even after they were
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17 209 | considered unsuitable for breeding because there is growing evidence that orangutans can
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19 210 | survive (but not breed assuming no detrimental effect on survival) in degraded – and even highly
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21 211 | modified agricultural – landscapes (Ancrenaz *et al.*, 2010), although it is unclear whether these
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23 212 | populations are viable in the long-term (Ancrenaz *et al.*, in press). This was achieved
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25 213 | through a balance of density-dependent immigration and emigration (see Supporting
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27 214 | information). Density dependence in dispersal was modeled by modifying the distance-
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29 215 | dependent dispersal rate by a linear (Ricker) function of habitat carrying capacity. Density
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31 216 | dependence affected sub-adults dispersal and ensured that individuals remained in suitable
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33 217 | fragments until the effects of overcrowding were apparent, at which point they dispersed.
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35 218 | Whether or not they arrived in a recipient subpopulation was dependent on its carrying capacity
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37 219 | (K); the probability of entering a subpopulation decreased as its carrying capacity decreased,
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39 220 | ensuring that orangutan avoided fragments in the process of being logged. Demographic
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41 221 | parameters used to build the model were collated from literature and experts, and are shown in
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43 222 | Table 1 and their use in the metapopulation model is explained in the Supporting information.
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3 225 spatial distribution of populated habitats As a first step, we built a baseline spatial
4 metapopulation model, parameterized using stable environmental conditions and ~~run~~ ran it as a
5 'burn in' simulation for 500 years (and 1000 iterations) ~~to estimate the equilibrium initial stable~~
6
7 227 ~~age distribution of subpopulations and to verify the spatial distribution of populated habitats~~
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9 228 (Fordham *et al.*, 2012a2013). The resulting spatial distribution of orangutan abundance was
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11 229 similar to that calculated from the fitted nest counts from the habitat suitability model, which was
12
13 230 expected since the recent decrease in Sabah orangutan abundance has been attributed largely to
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15 231 habitat loss suggesting that the habitat fragments are near their carrying capacity (Ancrenaz *et*
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17 232 al., 2005).
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30 235 **(B) Metapopulation structure, initial and threshold abundances**
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33 236 The metapopulation structure was calculated from the habitat-suitability projections from
34 ecological niche models (Gregory *et al.*, 2012). Cells predicted to have ≥ 4 nests were buffered
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36 237 with a 2.5 km^2 average territory size (Singleton *et al.*, 2009) and grouped into habitat fragments
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38 238 of ≥ 3 cells. Genetic studies have shown that wide rivers are barriers to orangutan dispersal
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40 (Goossens *et al.*, 2005). We imposed impassable stretches of the Sugud~~t~~, Tungud, Kinabatangan,
41 Segama and Kalabakan rivers as geographical dispersal barriers, which had the effect of dividing
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43 240 some fragments. The initial (2010) metapopulation structure was verified by experts (Figure 1).
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53 244 Initial subpopulation abundances were calculated using information from ecological niche
54 models (see Gregory *et al.*, 2012 for further details) and verified by experts who recommended
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56 245 initializing western subpopulations (Figure S2) at zero orangutan abundance because they have
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3 247 been extirpated by hunting (Caldecott & Miles, 2005). For each fragment, we calculated K as the
4 total fragment nest count for each year as per the ecological niche model projections (Gregory *et*
5 *al.*, 2012). This value was – on average – 8 % higher than the initial subpopulation abundance,
6 ensuring that subpopulations started close to K and would decline concomitantly with K ; a
7 reasonable assumption given that the Sabah orangutan population appears to be declining across
8 several parts of its range due to habitat loss [and degradation](#) (Ancrenaz *et al.*, 2005, 2010).
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(B) Forest fires and environmental correlation

255 Most fires in Southeast Asia are set deliberately to clear land for agriculture, ~~and so land cover is~~
256 ~~a prime determinant of fire risk~~ (Miettinen *et al.*, 2011). ~~Consequently, it is difficult to predict~~
257 ~~how fire regimes might change over time~~ (J. Miettinen, *et al.* *pers. comm.*, 2011). Occasionally,
258 ~~usually during El Niño years,~~ fires burn uncontrollably and cause substantial direct orangutan
259 mortality, ~~usually during El Niño years when there is decreased precipitation~~ (Marshall *et al.*,
260 2009). ~~For example, the 1997–8 Borneo El Niño fires may have killed up to 33 % of the island's~~
261 ~~orangutan population (Rijksen & Meijaard, 1999).~~ ~~To account for these patterns, We~~ modeled
262 fire ~~conservatively~~ as a fragment-specific catastrophe killing 2.5 % of animals from all stages of
263 the affected subpopulation ~~occurring (on average) once in every seven years (based on historic~~
264 ~~patterns).~~ ~~The mortality rate was based on the observation that 2.5 % of 40,000 Bornean~~
265 ~~orangutan were estimated to have been killed in the Bornean fires of 1997 (Marshall *et al.*,~~
266 ~~2009).~~ The probability of fragment-specific fire outbreak was estimated empirically from
267 observed 2000–12 University of Maryland fire-hotspot data (<http://firefly.geog.umd.edu/firms/>)
268 and spatio-temporal fragment land-cover-composition projections (Figure S1S3). We modeled

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3 269 | the effect of an increasing El Niño intensity (in response to a forecast decrease in annual
4 precipitation due to climate change) on fire intensity as a linear increase in orangutan mortality
5 from 2.5 to 10 % over 91 years, but no change in the frequency of these events due to their
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7 271 | anthropogenic nature (Marshall *et al.*, 2009). The value of 10 % was an arbitrary value
8 representing a substantial increase (4-fold) in mortality due to fire. As an example, under initial
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10 272 | conditions fire outbreak was most probable approximately seven years after a previous fire in an
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12 273 | area of disturbed habitat historically affected by fire and would kill 2.5 % of the orangutan in the
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14 274 | area affected.

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24 278 | It is thought that reproduction and survival of Bornean orangutans are influenced by food
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26 279 | shortages, themselves a consequence of environmental variation, notably rainfall effects on seed
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28 280 | masting events (Marshall *et al.*, 2009). We therefore assumed environmental correlation in the
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30 281 | variation of demographic rates between subpopulations in Sabah. Environmental correlation
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32 between subpopulations was estimated from multivariate correlograms measuring inter-annual
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34 282 | synchronicity of monthly rainfall from meteorological stations in and around Sabah (see
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36 283 | Supporting information). We extracted 12487 monthly rainfall measures from January 1879 to
37
38 284 | January 2011 from the 50 stations closest to the geometric center of Sabah from the Global
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40 285 | Historical Climate Network (<http://www.ncdc.noaa.gov/ghcnm/>; Figure S2S4). We then
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42 286 | estimated parameters for a negative exponential correlation function by minimizing the residual
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44 287 | error of a negative-exponential-curve fit to the spatio-temporal correlation predictions (Figure
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46 288 | S2S4; Keith *et al.*, 2008). These correlations capture the similarity of environmental fluctuations
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48 289 | in vital rates among nearby populations.
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291 (B) Dispersal

292 Little is known about orangutan movements, particularly their long-distance dispersal. It seems
 293 that both males and females occasionally disperse to find new territories (Nater *et al.*, 2011;
 294 Arora *et al.*, 2012), although other evidence suggests both sexes are relatively philopatric
 295 (Goossens *et al.*, 2006; van Noordwijk *et al.*, 2011). We adopted the conservative view that
 296 females were largely philopatric. We calculated dispersal assuming a heterogeneous habitat
 297 matrix that included geographical barriers to dispersal. Inter-fragment distances were calculated
 298 from a least-cost surface, based on expert-informed habitat permeability values-cost
 299 estimates relative to primary forest. For example, the cost of traversing a cleared cell was 10
 300 times more costly than traversing a primary forest cell; see supplementary material Supporting
 301 information for a more complete explanation and Table S2 for all habitat permeability costs).
 302 The least-cost surface was used to calculate the proportion of individuals that dispersed from
 303 each fragment at the end of each time step according to a negative exponential dispersal kernel
 304 given by:

$$m_{ij} = \begin{cases} \beta_1 \times \exp(-d_{ij}^{\beta_2} / \beta_3) & \text{if } d \leq d_{\max} \\ 0 & \text{if } d > d_{\max} \end{cases}, \quad (2)$$

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 306
 307 where $\beta_1 = 0.2$, $\beta_2 = 0.69$, $\beta_3 = 8.0$, d is the least-cost distance between populations-fragments i
 308 and j , and d_{\max} is the maximum distance that an orangutan can feasibly disperse, set at 120 km
 309 (Table 1). This allowed 5 and 1 % of individuals of each subpopulation to disperse 30 and 100
 310 km through primary forest that are not clear-felled, respectively (Figure S3S5). This should be

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 3 311 considered an upper estimate of orangutan dispersal ability, ~~which we justify using~~, because the
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 5 312 dispersal kernel assumes homogeneous habitat, i.e., that d is calculated using Euclidean distance,
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 7 313 whereas we assume heterogeneous habitat quality in the inter-patch matrix and calculate d using
 8
 9 314 Dijkstra's algorithm to navigate the least-cost path between the closest points on the donor and
 10
 11 315 recipient fragments (see Supporting information for more details). Consequently, the so that the
 12
 13 316 realized proportions of dispersing individuals reaching recipient ~~subpopulations~~fragments will
 14
 15 317 ~~was be~~ substantially lower (Figure S4S7). This distance-dependent dispersal rate was further
 16
 17 318 modified by a density dependent function of habitat fragment carrying capacity, as explained
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 19 319 above.
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 27 321 **(B) Identifying important ~~subpopulations~~fragments to connect**

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 29 322 To gauge a fragment's potential contribution to long-term metapopulation persistence, We we
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 31 323 calculated a measure, hereafter, hereafter referred to as called fragment trend value (FTFV), for
 32
 33 324 each fragment, to gauge its potential contribution to long-term metapopulation persistence. This
 34
 35 325 ~~is defined as the temporal trend in fragment carrying capacity relative to all other fragments,~~
 36
 37 326 ~~weighted by its initial condition~~ FV was calculated as the ratio of the size of fragment i at time t
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 39 327 relative to the largest fragment at time t summed over time, and is given by:
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$$FV_i = \sum_{t=1}^T K_{i,t} / K_{\max,i}, \quad (3)$$

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 45
 46 330 where $K_{i,t}$ is the carrying capacity of fragment i at time t and $K_{\max,i}$ is the maximum

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3 331 carrying capacity among all fragments present at time t . The fragment with the highest FTFV
4
5 332 was the fragment with the largest average carrying capacity over the period $t = 1, \dots, T$.
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7 333 Conversely, the fragment assigned the lowest FTFV would be the fragment with the smallest
8
9 334 average carrying capacity over the same period.
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16 336 **(B) Model scenarios**

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19 337 We evaluated whether habitat suitability projections could be used to improve the efficacy of
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21 338 habitat corridors to ameliorate extinction risk by comparing results from metapopulation models
22
23 339 with and without corridors in the landscape. To do this, we selected donor and recipient
24
25 340 fragments to connect with corridors. We defined the donor fragment as the largest fragment in
26
27 341 2010, which also had the largest subpopulation size (fragment 12 in Figure 1). We selected the
28
29 342 recipient fragments under examined two habitat corridor scenarios: (a) Future-informed, in
30
31 343 which FTFV was calculated over $T = 91$ annual time steps (2010-2100) and the four fragments
32
33 344 with the highest FTFV (not including the donor fragment) were taken to be recipient
34
35 345 subpopulationsfragments, and (b) Current-informed, in which FV was calculated for the current
36
37 346 time step only, i.e., $T = 1$, and the four fragments with the highest FV (i.e., the four largest
38
39 347 habitat fragments from Figure 1, not including the donor fragment) were taken to be the recipient
40
41 348 subpopulationsfragments. The donor fragment was the largest fragment with the largest
42
43 349 population size in 2010 (fragment 12 in Figure 1). Fragment selection was designed to: (1) be
44
45 350 comparable between Future-informed and Current-informed scenarios, and (2) favor the largest
46
47 351 fragments because large reserves should be preferred if the species' risk of extinction is high
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49 352 (McCarthy et al., 2005).

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4
5 354 Habitat corridors were represented as the least-cost path between the donor and recipient
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7 355 fragments and increased their connectivity from the dispersal rate calculated assuming a
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9
10 356 heterogeneous intervening habitat to ~~that a dispersal rate~~ calculated assuming a homogeneous
11
12 357 maximum conductance intervening forest habitat, i.e., the Euclidean distance. We aligned the
13
14 corridors with least-cost paths assuming that land managers would want to locate the corridors
15
16 where the need to create new habitat was minimized. The least-cost path was calculated using
17
18 359 Dijkstra's algorithm to navigate the least-cost path between the closest points on the donor and
19
20 recipient fragments, as explained in the Dispersal section above. By allowing corridors to affect
21
22 connectivity only, we avoided any confounding effect caused by an increase in suitable habitat,
23
24 362 which is dependent on factors such as their width, etc. Connectivity was increased gradually over
25
26 363 which is dependent on factors such as their width, etc. Connectivity was increased gradually over
27
28 364 10 years intended to simulate replanting and good silviculture practices to promote fast
29
30 365 regeneration of forest habitat (Peña Claros *et al.*, 2008). Connectivity to some habitat fragments
31
32 366 was increased inadvertently because these coincidentally fell along proposed habitat corridors,
33
34 367 and these are referred to as *non-target subpopulationsfragments*. Fragments whose connectivity
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36 368 was not affected by corridors are hereafter referred to as *unlinked subpopulationsfragments*.
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44 370 **(B) Sensitivity analysis**

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47 371 Our metapopulation simulations were based on carefully researched model parameters but their
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49 372 results will be sensitive to our chosen parameterizations. We analyzed the sensitivity of
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52 373 metapopulation models under two scenarios: the No mitigation and No corridors scenario, with-
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54 no corridors and the Mitigation scenario with Model-informed corridors. The aim of the
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3 375 sensitivity analysis was to: (1) assess the effect of uncertainties in metapopulation parameter
4 estimates, and (2) determine to which parameters the models were most sensitive. Whilst these
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6 376 sensitivity analyses would not allow us to evaluate the robustness of our findings directly (i.e.,
7
8 377 the influence of habitat forecasts on habitat corridor efficacy under feasible global change
9
10 378 scenarios), they would highlight parameter estimates to which the metapopulation results are
11
12 379 sensitive (Akçakaya & Root, 2007). Future research might then focus on validating or improving
13
14 380 our understanding of those parameters through, for example, additional field work.
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20 383 We varied six parameters across a uniform probability distribution, bounded by minimum and
21 maximum values determined from literature or expert knowledge (Table 1). We used a Latin
22 hypercube sampling design that allowed us to evaluate interactions among the parameter
23 combinations while efficiently sampling the 6-dimensional parameter space (Conroy & Brook,
24 384 2003). In effect, this procedure amounted to refitting the metapopulation models with 200 new
25
26 385 combinations of our six chosen parameters selected by stratified sampling across the full range of
27
28 386 each parameter. Given the short timescale of our simulations (91 years) relative to orangutan
29 generation time (33 years) and the attendant low extinction risk, we analyzed mean final
30
31 387 metapopulation abundance of persistent runs as a function of the parameter combinations using a
32 boosted regression tree (BRT) model with learning rate (lr) = 0.001, bag fraction (bf) = 0.75 and
33
34 388 complex 5-way interactions ($tc = 5$). We used functions provided by Elith *et al.* (2008) to select
35
36 389 the number of trees (nt) that minimized the 10-fold cross-validation predictive deviance. We
37
38 390 calculated the relative importance of each parameter on variation in mean final metapopulation
39 abundance and their partial effects.
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3 398 Detailed methods are presented in Supporting information. Unless specified, all analyses were
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5 399 carried out in Program R 2.15.2 (www.r-project.org).
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For Review Only

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4 402 **(A) Results**
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9 403 **(B) Forecast habitat fragmentation**
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13 404 The majority of present-day (year 2010) suitable habitat was predicted to occur in eastern Sabah,
14
15 405 the current-day orangutan stronghold (Figure 1). In total, the suitable habitat was spread across
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17 406 22 fragments. Assuming a maximum least-cost path distance of 120 km through the
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19 heterogeneous landscape, those 22 fragments could be grouped into 10 clusters of suitable
20
21 habitat connected by 35 links (Table 2; Figure S1; see Supporting information). As expected,
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23 409 several habitat fragments of which were separated by impassable river stretches, e.g., fragments
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25 410 8 and 9. The initial metapopulation abundance was estimated to be 4204 female individuals.
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32 412 Mean habitat total and core fragment size area and connectivity (of fragments with persisting
33
34 413 orangutan subpopulations) was forecast to decrease by 2100 under the No mitigation scenario by
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36 414 70–57 and 44–91 % and 60 %, respectively. (Table 2 and Figure S1). The decrease was
37
38 415 particularly salient in eastern Sabah, where almost all suitable habitat disappeared by 2100. By
39
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41 416 comparison, mean habitat total and core fragment size area and connectivity were relatively
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43 417 stable under the Mitigation scenario, being forecast to decrease by 25–29 and 8 % and increase by
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45 418 5–6 %, respectively (Table 2 and Figure S1).
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52 420 **(B) Current- and Future-informed corridors**
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2 422 2), which would require the creation of 98 km of new forest corridor and protection of 179 km of
3 existing forest as corridors. The Current-informed corridors increased connectivity to 17 and 7
4 423 non-target habitat fragments under the No mitigation and Mitigation scenarios respectively. All
5 424 but one of the current-informed recipient fragments were still suitable by 2055 under the No
6 425 mitigation and Mitigation scenarios (fragment 9 was forecast to become unsuitable after 2020),
7 426 although this dropped to three by 2100 under the formerNo mitigation scenario.
8 427
9 428
10 429 The Future-informed corridors connected fragment 12 with fragments 7, 15, 16 and 18, under the
11 430 No mitigation scenario. This required the creation of 10 km and protection of 269 km of forest
12 431 corridor respectively. In contrast, the Future-informed corridors connected fragment 12 with
13 432 fragments 1, 7, 15 and 18, under the Mitigation scenario, and required the creation of 26 km and
14 433 protection of 322 km of forest corridors respectively. These corridors increased connectivity to
15 434 14 and 8 non-target fragments under the No mitigation and Mitigation scenarios, respectively.
16 435 All fragments were forecast to remain suitable until 2055 and only fragment 7 was considered
17 436 unsuitable by 2100 under the No mitigation scenario.
18 437
19 438 **(B) Corridor efficacy and metapopulation abundance**
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21 439 Relative to their corresponding No corridor scenarios, corridors increased the mean dispersal
22 440 rate between donor, recipient and non-target subpopulations, but not to unlinked subpopulations
23 441 (Figure 3). Dispersal to recipient subpopulations was higher than for donor and non-target
24 442 subpopulations under the No mitigation scenario, and was highest for recipient subpopulations
25 443 under Future-informed corridors. Dispersal by Current-informed corridors under the Mitigation
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3 444 scenario was similar to that observed under the No mitigation scenario but was notably lower to
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5 445 recipient subpopulations (and slightly higher to donor and non-target subpopulations) under the
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7 446 Future-informed corridors (Figure 3).
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12 448 ~~Without~~In the absence of habitat corridors, metapopulation abundance decreased by 51 % to a
13 mean of 2028 females under No mitigation and 16 % to a mean of 3481 females under the
14
15 450 Mitigation scenarios by 2100 (Figure 4). The increase in mean dispersal rate due to Current- and
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17 451 Future-informed corridors resulted in a slower led to a long-term slowing in the decline in of the
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19 total metapopulation abundance under all but one scenario: Current-informed corridors under a
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21 452 Mitigation scenario. This slowing effect was strongest for Future-informed corridors relative to
22
23 453 the corresponding No corridor scenario under the No mitigation scenario (a difference of 120
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25 females or 2.3 % of the 2100 No corridor metapopulation abundance) and weaker for Future-
26
27 454 informed corridors under the Mitigation scenario (a difference of 20 females or 0.4% of the 2100
28
29 455 No corridor metapopulation abundance; Figure 4). The slowdown in the metapopulation
30
31 456 abundance decline was weaker for Current-informed corridors relative to the corresponding No
32
33 457 corridor scenarios than the relative difference for Future-informed corridors under both
34
35 458 mitigation scenarios, but particularly under the No mitigation scenario (Figure 4). Changes in
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37 459 metapopulation abundance under corridor scenarios only really diverged from no corridor
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39 460 scenarios after 2055 when suitable habitat fragments began to disappear.
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53 The higher total orangutan population size in Sabah in 2100 (relative to a~~the~~ no ~~No~~ corridor
54 baseline scenario) for Future-informed corridors under the No mitigation scenario was due
55 largely to an abundance increase in recipient and unlinked subpopulations (Figure 5), particularly
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3 467 in Western Sabah (Figure 6). In contrast, Current-informed corridors promoted largest
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5 468 population increases in unlinked subpopulations relative to the No corridor scenario (Figure 5),
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7 469 and recipient and non-target subpopulations across the state increased in abundance (Figure 6).
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14 471 **(B) Model sensitivity**

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17 472 Mean final metapopulation abundance under the No mitigation scenario without corridors was
18
19 473 most sensitive to variation in habitat-fragment carrying capacity and intrinsic population growth
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21 474 rate (R_{max}), causing it to increase as they increased (Figure 7a). This was expected since habitat
22
23 fragmentation was greatest under the No mitigation scenario and where no corridors were
24
25 present to allow individuals to escape from shrinking habitat fragments with increasing
26
27 475 population density that was driving a decrease in fecundity (due, for instance, to compression of
28
29 476 territory size or exclusion of some individuals from breeding territories). Where the effect of
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31 477 habitat fragmentation was minimized – under the Mitigation scenario with Future-informed
32
33 478 corridors – mean final metapopulation abundance was most strongly affected by variation in
34
35 479 adult survival, followed by K and R_{max} . Adult survival drove a decrease in mean final
36
37 480 metapopulation abundance as it increased (Figure 7b). This suggests that when habitat
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39 fragmentation was decreased, the effect of density-dependence on fecundity was offset by
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41 481 increases in adult survival. Relative to K , R_{max} and adult survival, variation in mean dispersal
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43 482 rate had only a minor influence on model outcomes in both cases (Figure 7b).
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488 (A) Discussion

489 Compared to Current-informed corridors, we show that Future-informed habitat corridors slowed
490 the metapopulation abundance decline (relative to ~~a-the N~~o corridor baseline), but only when
491 land cover and climate change continues unabated. This slowing in population decline occurred
492 as a direct consequence of facilitating dispersal through corridors to long-term suitable habitat
493 fragments. To our knowledge, this is the first time this has been shown. Hodgson *et al.* (2011b)
494 recently showed that restoring habitat along model-informed corridors connecting suitable
495 habitat clusters was a more efficient strategy to promote metapopulation persistence compared to
496 expert-informed habitat restoration strategies, although their analysis considered only current-
497 day habitat configuration and did not account for climate change. Gregory et al. (2012) recently
498 showed that Sabah orangutan persistence would likely be maximized under deforestation and
499 CO₂ mitigation but they did not consider the addition effect that habitat corridors might have on
500 population persistence.

501 These results have potentially important implications for conservation management considering
502 that habitat loss and fragmentation is one of the greatest contemporary threats to the long-term
503 persistence of tropical forest-dependent biodiversity, and its impact will be exacerbated by the
504 synergistic effect of climate change (Mantyka-Pringle *et al.*, 2012). By reconnecting isolated
505 habitat fragments in an effective way, corridors are expected to reduce the threat of population
506 extinction by increasing dispersal, facilitating genetic admixing and allowing species to access
507 future suitable habitat when current-day habitat becomes unsuitable (Gilbert-Norton *et al.*, 2010).
508 Our results show how habitat suitability forecasts coupled niche population models can be used
509 to identify the most important habitat fragments for orangutans in Sabah and thereby improve the

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3 510 efficacy of habitat corridors for long-term metapopulation persistence, particularly in rapidly
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5 511 changing environments.
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11 513 In contrast to the advantage of using Future-informed corridors under continuing land cover and
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13 514 climate change, we show that corridors developed on the basis of current knowledge are an equal
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15 515 or better (and simpler) option when the amount and spatial configuration of future suitable
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18 516 habitat is comparable to that of the current-day. This is an intuitive result; if species' native-
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20 organisms have colonized all available and accessible habitat in the landscape, then the larger
21
22 517 suitable habitat fragments would sustain larger local populations, and provided these fragments
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24 518 remain stable over time, then they should continue to be important in the future. In effect then,
25
26 519 the habitat suitability projections might serve mainly to supplement current-day knowledge by
27
28 520 accounting for unobserved future environmental changes and their interactions. Hence the value
29
30 521 of future simulations is entirely dependent on realization of the projected land cover and climate
31
32 522 changes, and since our sensitivity analysis highlighted that the final metapopulation abundance
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34 523 was sensitive to changes in carrying capacity (based on habitat suitability projections), so these
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36 524 results should only be considered guidance for more informed management decisions based on
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39 526 more comprehensive sensitivity analyses supplemented by local expert opinion.
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46 528 ~~Although we have shown that using habitat suitability projections can inform corridor placement~~
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48 529 ~~for maximum long-term conservation gain, we have not considered whether the corridors could~~
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50 530 ~~be placed at the recommended locations or how the corridors should be implemented, which are~~
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53 531 ~~management decisions that require further investigation. Both Current and Future informed~~
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55 532 ~~corridors required the creation of new forest habitat, although only latter scenario required only~~
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3 533 ~~one tenth the amount that was needed under the former. Whether this habitat can be created is~~
4 ~~subject to a range of socio-economic factors that we did not consider. If corridors are deemed a~~
5 ~~useful management action, then a more holistic analysis, at a detailed spatio-temporal resolution~~
6 ~~(at a scale of <1 km pixel size for individual patch connections), would be required.~~
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16 538 **(B) Implications for Sabah orangutan**

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19 539 A recent study showed that the Sabah orangutan population would fare best if all commercial
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21 540 forest reserves were placed under sustainable forest management and atmospheric CO₂
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23 541 concentrations were stabilized at 450 ppm due to global action on greenhouse gas emissions
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25 542 (Gregory *et al.*, 2012). Under this Mitigation scenario, our results suggest that connecting
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27 543 suitable habitat fragments will have a negligible effect, slowing the metapopulation decline by
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29
30 544 only 20 females (relative to ~~a-the no-No~~ corridor baseline) by 2100; less than 0.4 % of the
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32 545 current-day female population size. If, however, the Sabah government does not meet its
33
34 546 commitment to adopt sustainable forest management and CO₂ emissions continue to rise, then
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36 547 corridors could save up to 2.3 % of the current-day orangutan female population (relative to ~~thea~~
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38 548 ~~no-No~~ corridor baseline) by 2100, approximately 120 animals.
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46 550 Although these relative increases in final metapopulation abundance due to corridors are small,
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48 551 they should be considered relative to the timeframe of the simulations and orangutan life-history
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50 552 information, and in maintaining the capacity for landscape connectedness over long-term
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53 553 (evolutionary) time scales. Our simulations ran for 91 years (from 2010 to 2100). The Bornean
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55 554 orangutan is a long-lived, low-fecundity and philopatric species (Wich *et al.*, 2009) with a
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3 555 generation time of over 33 years (calculated from the survival estimates in Table 1). Given that
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5 556 our simulations were initiated with a stable age distribution, our model simulated only three
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7 557 generations of orangutan population dynamics and corridors only improved dispersal after 2020.
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9 558 While we could have run these simulations for longer (e.g., for 1000 years as was used in
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11 Marshall *et al.*, 2009), the uncertainty associated with the forecasts would likely have rendered
12
13 559 the results meaningless (Feiberg & Ellner, 2001). On the other hand, 91 years is a timescale
14
15 560 pertinent to simulations of land cover and climate change. Running the simulations for a shorter
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17 561 period would have reduced the magnitude of the observed effect because the effects of corridors
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19 562 weren't apparent until after 2060. This suggests that corridors would not be particularly effective
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21 563 in the short-term.

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23 564 **(B) Realities of corridor creationAdditional management considerations**

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25 565 If the corridor approach is pursued, then there are considerations on how they should be
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27 566 implemented. First, both Current- and Future-informed corridors require the creation of new
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29 567 forest habitat, although the latter scenario requires only one tenth of the amount of new forest
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31 568 habitat needed under the former scenario. Whether this habitat can be created is subject to a
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33 569 range of socio-economic and political factors that we did not consider, in part because their
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35 570 inclusion can bias the results away from an ecological focus (Beier *et al.*, 2011). Expert opinion
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37 571 Expert opinion suggests that they should be a minimum of 500 m wide and restored with a variety of plant
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39 572 species to encourage use by species other than just orangutan (M Ancrenaz, *pers. comm.*). and
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41 573 this has been shown in other tropical ecosystems (e.g., Lees & Peres, 2008). For our purposes –
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43 574 to evaluate habitat suitability forecasts as a tool for improving ~~compare~~ the ability~~efficacay~~ of
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45 575 Current and Future informed corridors to sustain the Sabah orangutan metapopulation

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3 577 abundance – we opted to increase connectivity between habitat fragments and not habitat *per se*.
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5 578 If our intention was to design the most realistic model, then we might have increased available
6 suitable habitat together with connectivity, which would allow animals to live in the corridor and
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8 579 disperse through them over more than one year.
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13 582 Another consideration is whether the corridors would serve other threatened animals and plants
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15 583 and encourage genetic admixing. For As an example of the former, the Kinabatangan River in
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17 584 eastern Sabah delineates the migration route for Bornee's forest elephantthe Bornean elephant
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19 585 (Alfred *et al.*, 2012). Although our model forecast suggests that habitat fragments along the
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21 586 Kinabatangan would become unsuitable within 10 years, improving riverine forest habitat along
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23 587 the Kinabatangan could allow orangutan to escape to larger, more long-term suitable habitat
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25 588 fragments further west while ensuring that the elephants can continue to undertake their annual
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27 589 migrations (Estes *et al.*, 2012). The degree to which the Sabah orangutan is structured as
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29 590 subpopulations is not known. A potentially important study will be to look at the genetic
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31 591 distinctiveness of the subpopulations and do a study of the effects of corridors on gene flow.
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42 593 **(B) Model assumptions and limitations**
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46 594 Although our approach to investigating corridor placement scenarios was detailed in an attempt
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48 595 to be realistic, we were required to make some simplifying assumptions. Consequently, our
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50 596 results fall short of providing a plan for habitat corridor implementation to minimize the
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52 597 extinction risk for Sabah orangutanfindings fall short of providing a plan for habitat corridor
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54 598 implementation to minimize the extinction risk for Sabah orangutan and rather set the scene for a
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3 599 more comprehensive study of the effect of uncertainties on coupled niche-population model
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5 600 findings.
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10 602 First, we omitted socio-economic factors that could prevent the creation or protection of forest
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12 603 for corridors. Second, our population model was a female-only model because we had more
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14 604 complete information on female orangutan life history and movements. What information does
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16 605 exist for males suggests that intersex differences in ecology and behavior are small (Goossens *et*
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18 606 *al.*, 2005). However, there is some evidence to suggest that males might move further,
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20 607 particularly when dispersing (Nater *et al.*, 2011; Arora *et al.*, 2013), the effects of which could
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22 608 result in an overestimated effect of corridors on the metapopulation abundance. Third, our model
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24 609 is region-specific and neglects the existence of adjoining land areas that might have suitable
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26 610 orangutan habitat. Specifically, Sabah borders Brunei and East Kalimantan, Indonesia. We were
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28 611 not able to account for possible orangutan immigration into these areas because we lacked the
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30 612 necessary information to map and forecast their suitable habitat and because cross-national-
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32 613 border corridor placement would need multi-lateral forest management protocols. Fourth, our
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34 614 population model neglected disease and inbreeding depression, despite the potential impact that
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36 615 increased dispersal due to corridors could have on these factors. A more detailed population
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38 616 model designed to predict more precise orangutan population dynamics (as opposed to a
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40 617 comparison of Current- and Future-informed corridor efficacy) should include these factors.
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42 618 Fifth, our study was delivered at a coarse spatial resolution of 2.5 km², chosen to match the mean
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44 619 reported female orangutan home range size. In effect, this decision assumed that all movements
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46 620 occurring at a finer resolution were unimportant to the population dynamics. It would be
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48 621 interesting to repeat this study with finer resolution data to evaluate this assumption.

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8 624 Regarding the habitat corridors, we made several simplifying assumptions. We assumed that
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10 625 corridors were implemented in their entirety in 2010 and that no further habitat management took
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12 626 place under any scenario thereafter. We assumed no financial constraints i.e., that the budget
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14 627 existed to implement and protect the corridors into perpetuity and that money saved from
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16 628 implementing shorter corridors was not reinvested into additional corridors. To separate the
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18 629 effect of increased connectivity from increased suitable habitat area, we assumed that corridors
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20 630 did not increase the area of suitable habitat. This is despite the recommendation that corridors
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22 631 should be at least 500 m wide (M. Ancrenaz, *pers. comm.*).

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29 633 Finally, we did not include hunting as a threat to orangutan in any part of Sabah, despite
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31 634 historical hunting problems in the west of the state (Caldecott & Miles, 2005), because it has
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33 635 been outlawed and is believed to be negligible (M. Ancrenaz, *pers. comm.*). If hunting is still a
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35 636 problem in western habitat fragments, then this exercise highlights the importance of eradicating
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37 637 hunting in those regions in the near future, to ensure that orangutan do not disperse west to their
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39 638 death. Similarly, for this model to be transferred to other areas of Borneo or Sumatra, hunting
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41 639 would be a crucial component to forecasting metapopulation abundance and persistence (Wich et
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43 640 al., 2012Davis et al., 2013).

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51 642 A strong theme that emerges from this study is that of uncertainty. While we undertook a
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53 643 sensitivity analysis of metapopulation models to select model parameters, the uncertainties were
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55 644 not captured in the modelling process and did not allow us to evaluate the effect of these

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3 645 uncertainties in our study conclusions. Rather they highlight which of those parameters could be
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5 646 usefully refined or validated with field-based studies, such as the SAFE project (Ewers *et al.*,
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7 647 2011). A second, and perhaps more important type of uncertainty inherent in this and other
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9 648 forecasting studies, is the effect of uncertainties in the forecasts themselves. Although we
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11 649 included carrying capacity as a parameter in our sensitivity analyses and used an ensemble of
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13 650 seven GCMs for our climate change predictions, uncertainty in the locations of breeding habitat
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15 651 fragments, for example, were not considered and have been shown to affect coupled niche-
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17 652 population model findings (Naujokaitis-Lewis *et al.*, 2013), although perhaps less than habitat
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19 653 quantity or quality (Hodgson *et al.*, 2011a). A more thorough analysis of these uncertainties in
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21 654 coupled niche-population models investigating corridor scenarios would be a valuable further
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23 655 work.

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32 657 Despite these limitations, this study provides a valuable contribution to the habitat corridor
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34 658 literature. By coupling a statistical model of abundance with a demographic model we were able,
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36 659 for the first time, to investigate the importance of selecting which habitat fragments to connect
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38 660 under different rates of climate and environmental change while accounting for some of the
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40 661 complexities involved in making such a decision (Beier *et al.*, 2008). With further refining, this
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42 662 approach could be used to compare competing corridor scenarios both within and between
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44 663 different mitigation scenarios applicable to real-world situations and evaluate factors involved in
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46 664 their implementation.

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4 **667 (A) Conclusions**
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668 There is growing experimental evidence that corridors are an effective means to increase
669 connectivity between habitat fragments (Gilbert-Norton *et al.*, 2010). Here, we show that using
670 habitat suitability model projections is likely to improve the efficacy of habitat corridors under
671 future land cover and climate change but is no better than current knowledge if the landscape
672 remains relatively stable. Although we have shown that Future-informed habitat corridors are a
673 potentially useful management strategy to promote the long-term persistence of metapopulations,
674 the Sabah orangutan metapopulation was nevertheless forecast to decline by almost half by 2100.
675 if land cover and climate change continue unabated. This suggests that if we are to mitigate
676 extinction risk in the long term, we must also address the drivers of habitat loss, degradation and
677 fragmentation.

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For Review Only

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4 853 **Supporting information**
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10 854 Additional Supporting Information may be found in the online version of this article:
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13 856 **Appendix S1** Additional detailed methods
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15 857 **Table S1** Future land-cover and climate-change scenarios
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17 858 **Table S2** Habitat permeability values (“conductance values”) used in dispersal calculations
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19 859 [Figure S1 Graphs showing the habitat fragments, their links and their membership to habitat](#)
20 [clusters in 2010, 2055 and 2100 under \(a\) No mitigation and \(b\) Mitigation scenarios](#)
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22 861 [Figure S2 A map showing the initially empty habitat fragments in Western Sabah](#)
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24 862 [Figure S1-S3](#) Plots of calculated fire-return rate and derived fire-return probability layer
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26 863 [Figure S2-S4](#) Plots showing rainfall record locations and derived spatial cross-correlogram used
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28 864 to estimate environmental correlation
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30 865 [Figure S3-S5](#) Dispersal kernel assuming an exponential decay function
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32 866 [Figure S6 The 2010 \(a\) land cover and \(b\) transition layer used to calculate a least-cost path](#)
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34 867 [Figure S4-S7](#) Maps of connected habitat fragments at 40, 70 and 100 km when assuming (a)
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36 868 Euclidean distance, and (b) least-cost distance
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40 870 As a service to our authors and readers, this journal provides supporting information supplied by
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3 875 Biosketch
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5 876 Stephen Gregory, a post-doctoral researcher with expertise in modeling population dynamics,
6 877 undertook this research at the Global Ecology Lab at the University of Adelaide
7
8 878 (www.adelaide.edu.au/environment/gel) who undertake world-leading multidisciplinary research
9
10 879 to mitigate the actions of human-induced biological change across all environments and develop
11 880 adaptive strategies to respond to the anticipated impacts of climate change.
12
13 881 Author contributions: S.D.G., M.A. and D.A.F. conceived the ideas; M.A., B.G., R.A. and
14 882 L.N.A. collected the data; S.D.G., B.W.B. and D.A.F. analysed the data; and S.G., M.A., B.W.B.
15 883 and D.A.F. led the writing.
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For Review Only

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4 885 **Tables**
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8 886 **Table 1:** Parameter estimates used in the calculation of habitat suitability or
9 metapopulation models (female only), including their sources and ranges used for
10 sensitivity analysis. Further justification of estimates and model assumptions are given
11 in the [Supplementary Supporting Information](#).
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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 <i>et al.</i> (2009)
age at maturity α	15 y	-	Marshall <i>et al.</i> (2009)
longevity ω	40 y	-	35 - 45; Marshall <i>et al.</i> (2009), http://pin.primate.wisc.edu/
lambda λ	e0.06	e0.05 - e0.07	range for <i>Pan troglodytes</i> & <i>Gorilla gorilla</i> ; Ross (1992)
survival I_X , $x = 0$	0.985	-	Marshall <i>et al.</i> (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 y
CV survival CV	0.30	-	2 x value for <i>Pan troglodytes schweinfurthii</i> ; see Methods
fecundity b	1/7 y	1/6 - 1/8 y	Marshall <i>et al.</i> (2009), Knott <i>et al.</i> (2009)
carrying capacity K	fragment-specific	$K \pm 36\%$	SDM prediction error; see Gregory <i>et al.</i> (2012)
density-feedback in b	Beverton-Holt	-	competition for territories; Knott <i>et al.</i> (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 <i>et al.</i> (2009)

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3 892 **Table 2:** Fragmentation statistics for the start, middle and end of the simulation,
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5 893 showing a decrease in the mean number of links (Links), number of core cells (Core
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7 894 cells) and fragment area under the No mitigation scenario over time compared to the
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9 895 Mitigation scenario. The number of clusters of suitable habitat fragments (Components)
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11 896 increases as number of links decreases. Graphs of these data are presented in the
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13 897 Supporting information.
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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

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4 899 **Figure legends**
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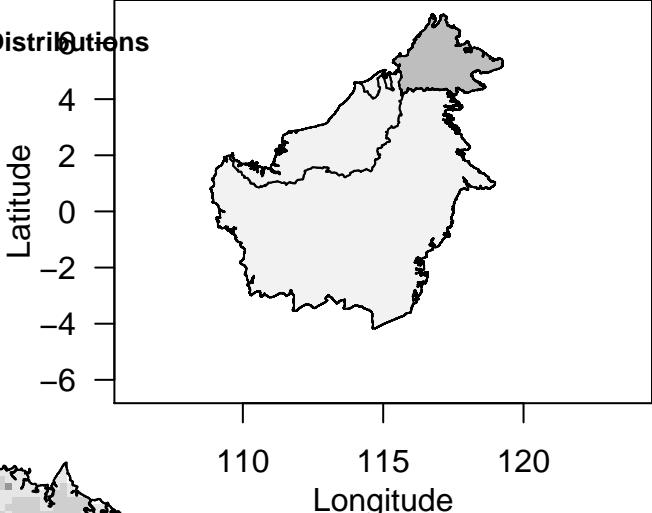
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11 900 **Figure 1:** Map showing the location of Sabah (Malaysia) on the equatorial island of
12 Borneo (Southeast Asia; inset) and the current-day orangutan breeding habitat fragment
13 structure (numbered pixel clusters) in Sabah with impassable rivers (blue). Terrestrial
14 areas are shaded grey and the intensity of grey represents the “friction” of the habitat for
15 movement from dark grey representing mostly impassable cleared areas to light grey
16 representing optimal primary forest.
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56 919 **Figure 3:** Panels showing the effect of Current-informed and Future-informed corridors
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3 920 on the mean dispersal rates of different subpopulation 'types' under the (a) No
4 mitigation and (b) Mitigation land-cover and climate-change scenarios. Subpopulation
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6 921 types were: 'recipient' that were directly connected to the donor fragment, 'non-target'
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8 922 that were inadvertently connected to the donor fragment and unlinked that were not
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10 923 connected by corridors.
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16 925 **Figure 4:** Total metapopulation abundance projections under the ~~noNo-~~ corridor
17 baseline scenarios for (a) No Mitigation and (b) Mitigation scenarios, and (c)
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19 927 metapopulation abundance projections for Current-informed and Future-informed
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21 928 corridors (~~relative to metapopulation abundance projections with their corresponding no~~
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23 929 ~~No~~ corridor scenarios) under No mitigation and Mitigation land-cover and climate
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26 930 change scenarios. Error bars and areas are 95% confidence intervals calculated from
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28 931 10,000 metapopulation simulations. EMA is the Expected Minimum Abundance.
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31 932 Absolute changes in abundance are given in the Results and Discussion.
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36 933 **Figure 5:** Panels showing the effect of Current-informed and Future-informed corridors
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38 934 on mean abundance of different subpopulation 'types' under the (a) No mitigation and
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40 935 (b) Mitigation land-cover and climate-change scenarios. Subpopulation types were:
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42 936 recipient that were directly connected to the donor fragment, non-target that were
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44 937 inadvertently connected to the donor fragment, and unlinked that were not connected by
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46 938 corridors. Error bars are 95% confidence intervals calculated from 10,000
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48 939 metapopulation simulations.
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54 940 **Figure 6:** A map showing the difference between initial and final abundance for each
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56 941 corridor and No mitigation and Mitigation land cover and climate change scenario

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3 942 combination. Only donor and recipient subpopulations from all combinations are plotted.
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5 943 Note the relatively large increase in abundance in subpopulation 15 in western Sabah
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7 944 across all treatments. Terrestrial areas are shaded grey.
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12 945 **Figure 7:** Partial effects plots showing the sensitivity of mean final total metapopulation
13 abundance of persistent runs only, plotted against variation in parameter estimates after
14 accounting for the average effects of all other variables in the model. Plots are ordered
15 by % importance, which measures the relative model fit improvement credited to each
16 predictor. Dashed line is the mean final metapopulation abundance. Panels group plots
17 for (a) No mitigation scenario without corridors, and (b) Mitigation scenario with Model-
18 informed corridors.
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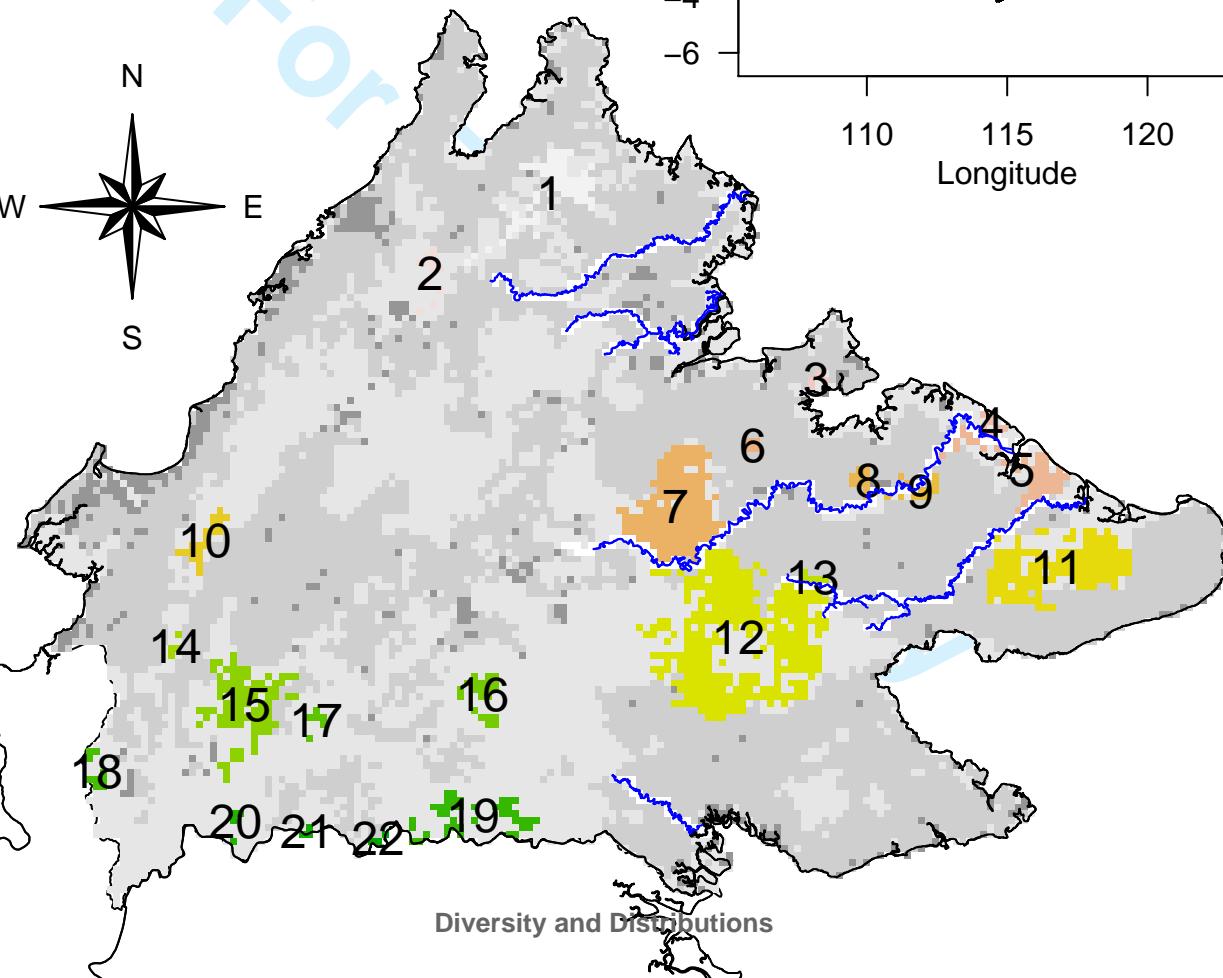


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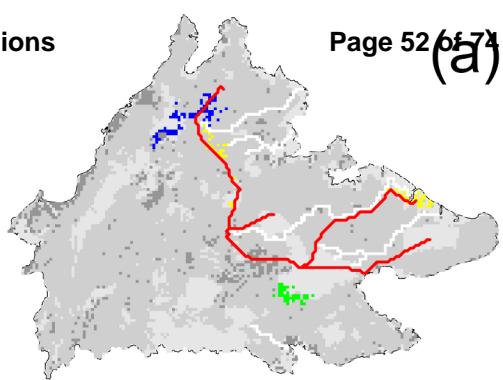
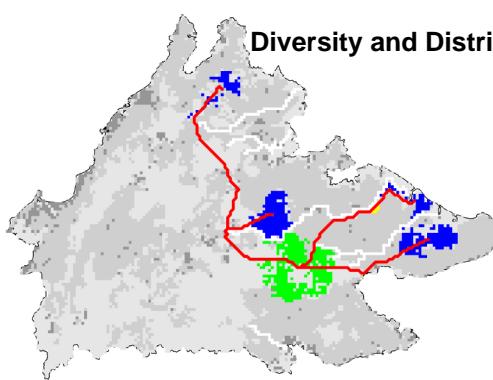
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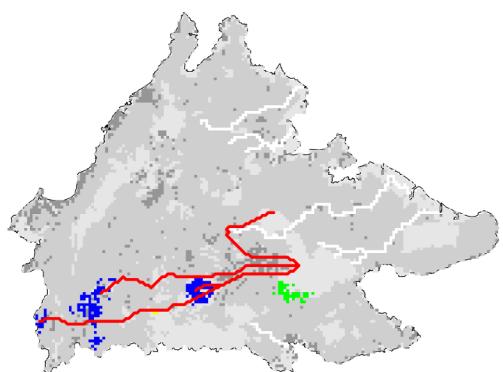
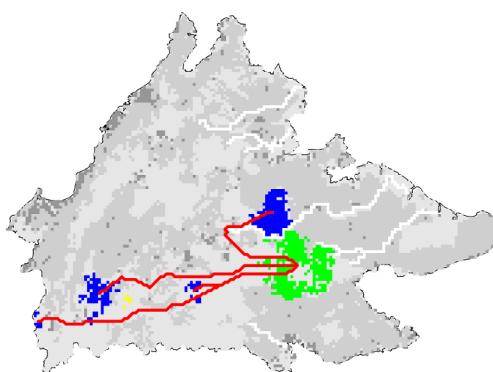
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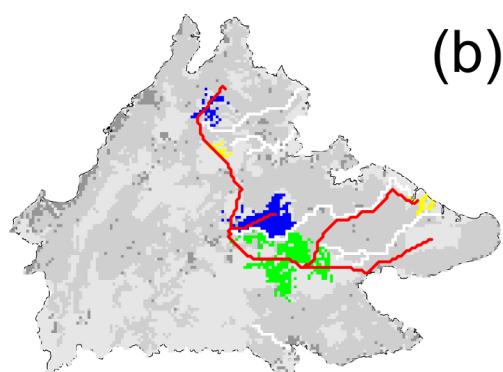
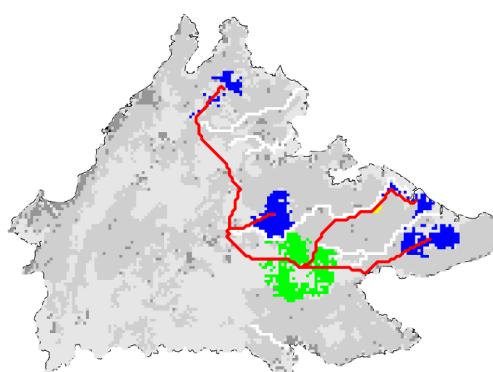
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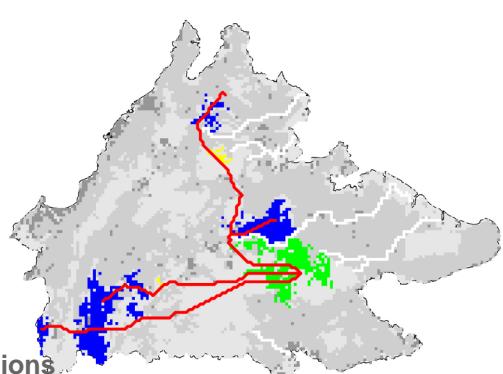
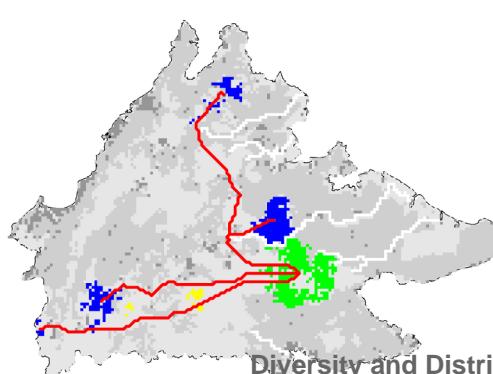
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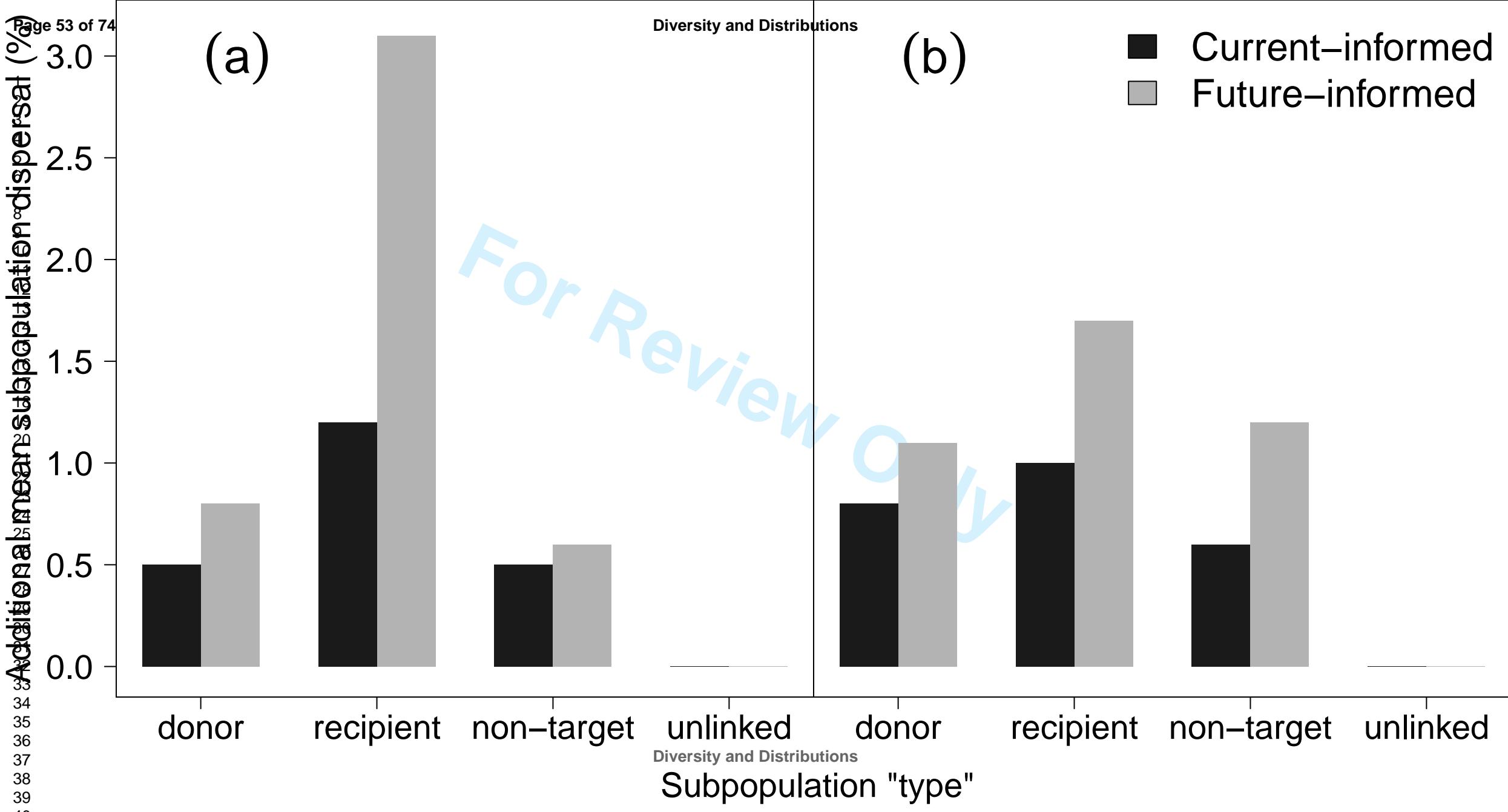
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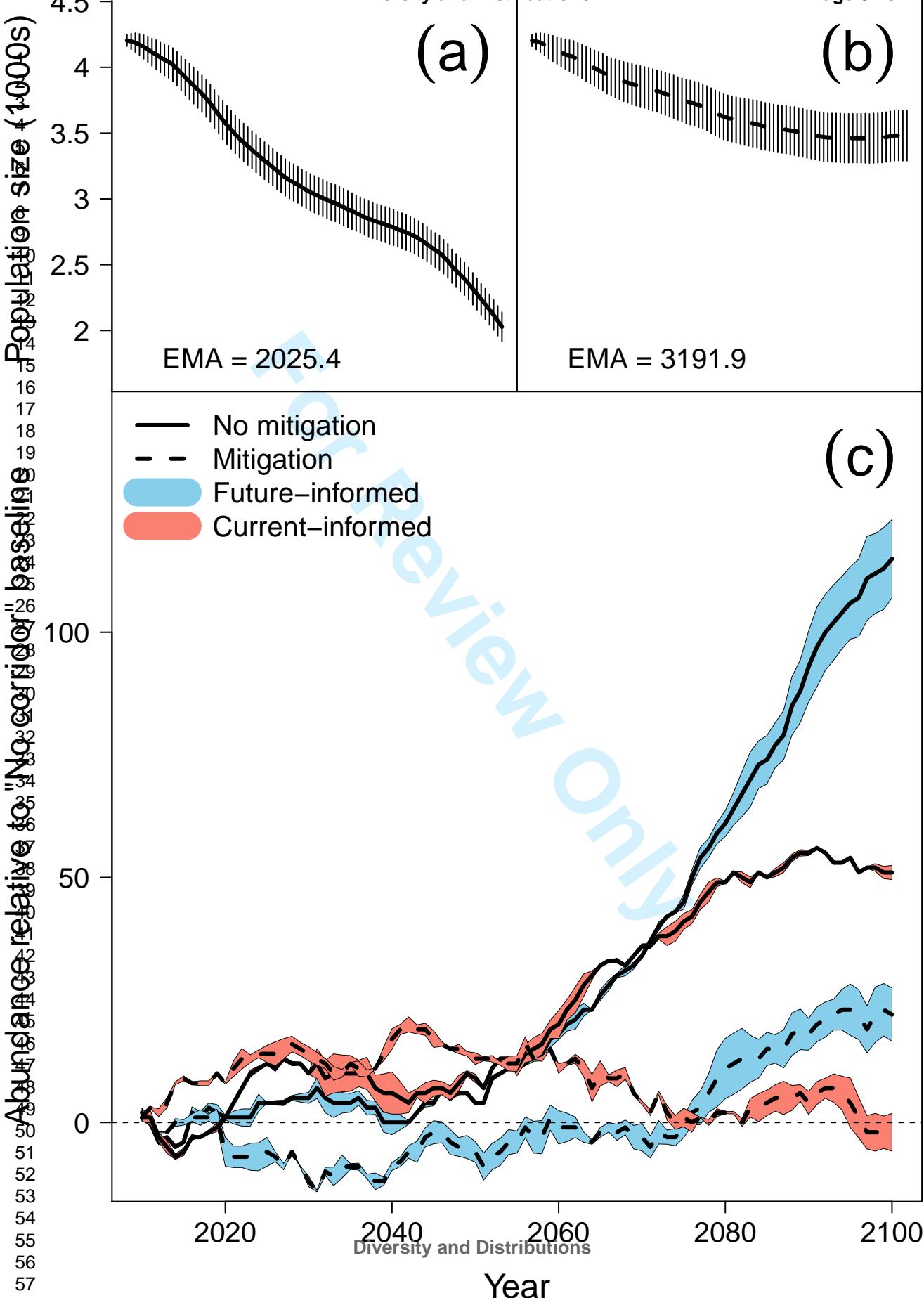
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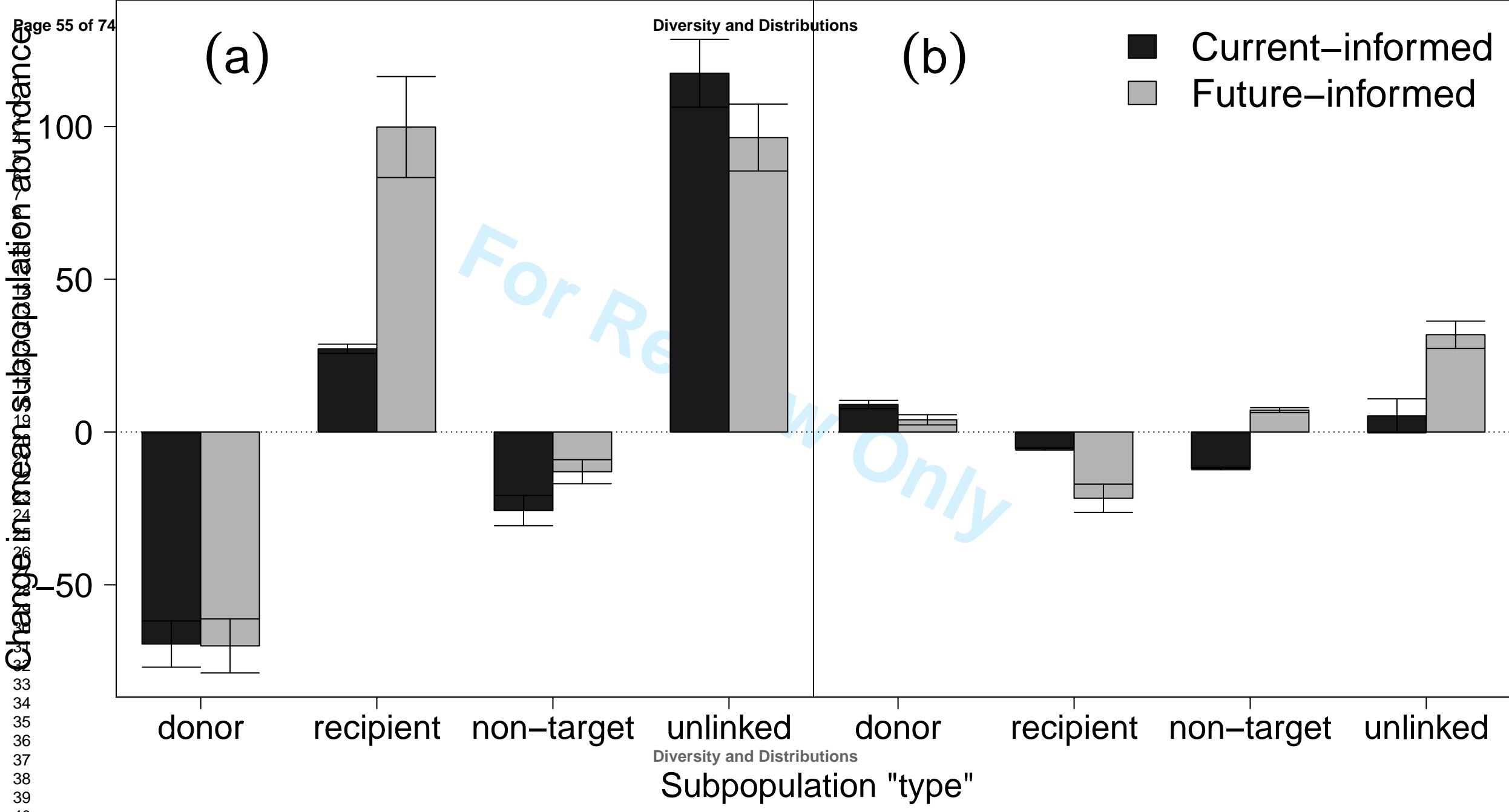


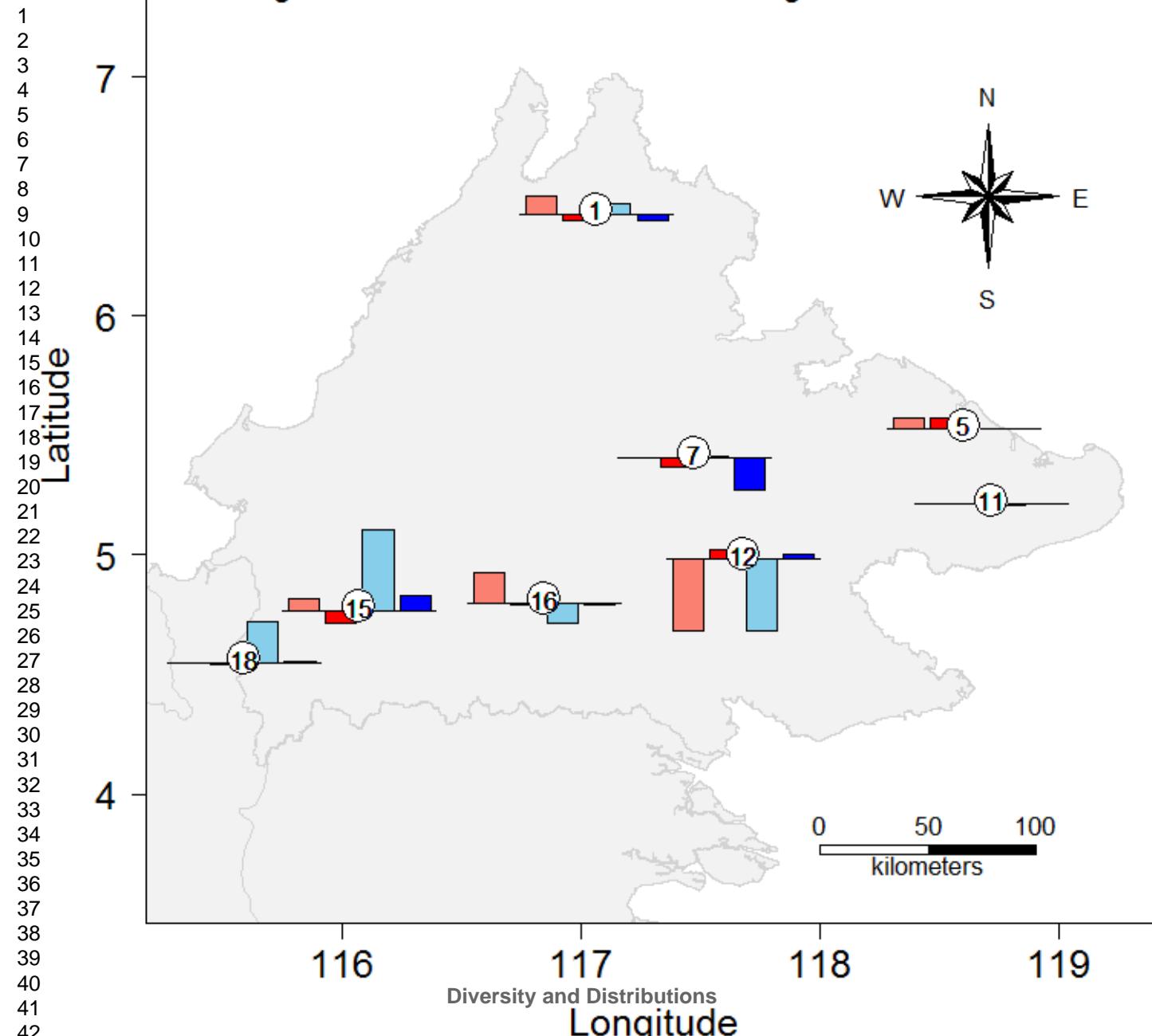
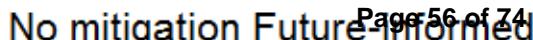
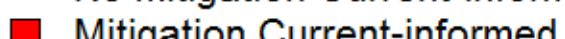
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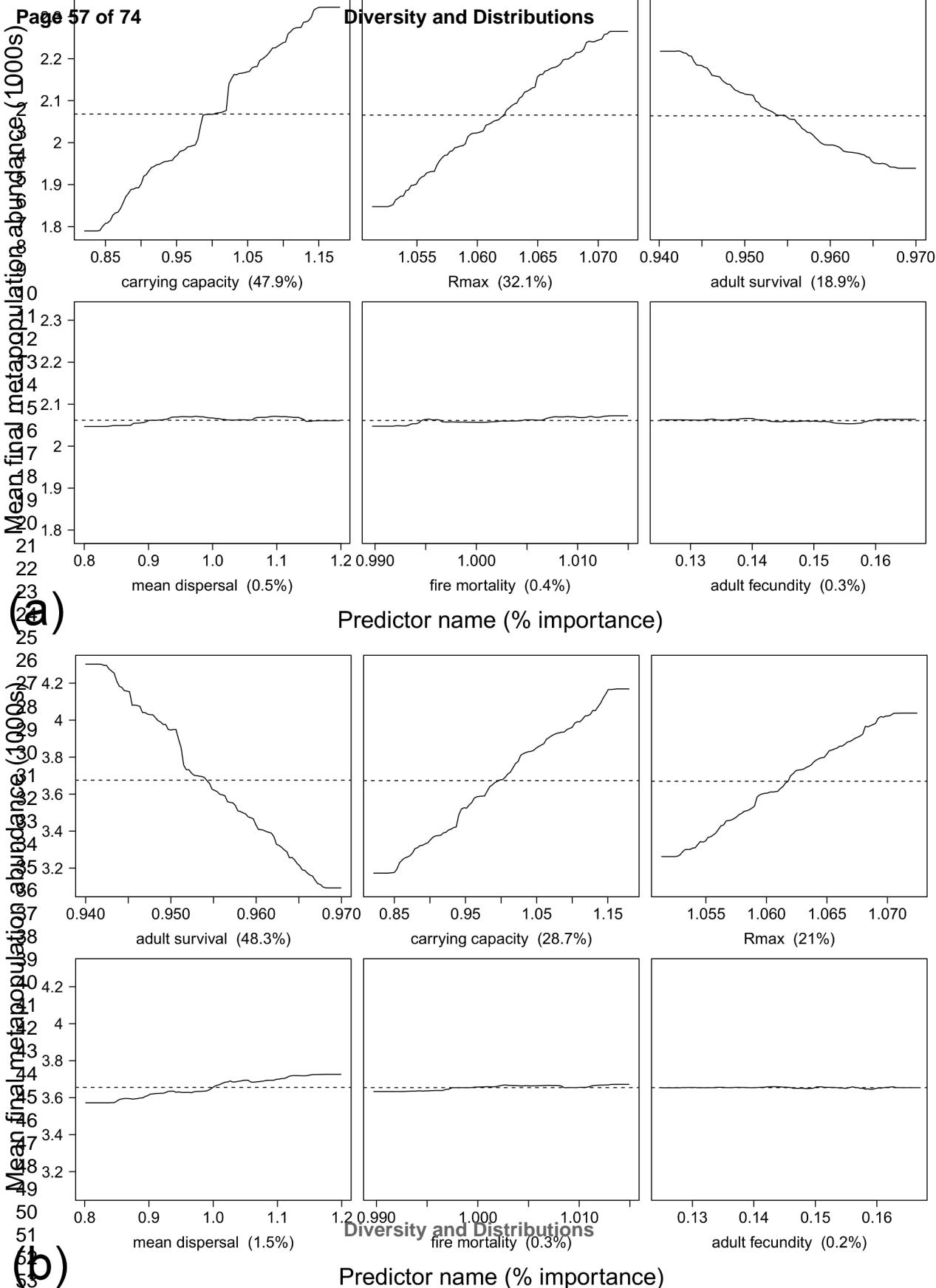












Forecasts of habitat suitability improve habitat corridor efficacy in rapidly changing environments

Stephen D. Gregory^a, Marc Ancrenaz, Barry W. Brook, Benoit Goossens, Raymond Alfred, Laurentius N. Ambu, and Damien A. Fordham

^a email: stephendavidgregory@gmail.com

Additional detailed methods

R packages

We used the following R packages: base, dismo, doMC, expm, fields, foreach, gbm, gdistance, igraph, lhs, MASS, popbio, randomForest, raster, rgdal, SDMTools, sp, spatstat, spdep, spgrass6, zoo

Habitat suitability and the metapopulation structureenvironmental forecasts

To measure average orangutan habitat suitability, we modelled aerial nest counts collected by helicopter survey in 6 years between 2000-10 (Ancrenaz *et al.*, 2005; Ancrenaz *et al.* 2010). Aerial nest counts are subject to a range of biases. For example, detecting nests, especially older nests, is difficult as they degrade into the background vegetation, and different observers might have different abilities to detect nests. In addition to detection biases, there were also biases in the methods used to collect these nest counts. Transects were flown multiple times, introducing spatio-temporal autocorrelation, and helicopter flights were limited largely to forest reserves, i.e., few survey were done over heavily degraded or cleared areas (Ancrenaz *et al.*, 2005; Ancrenaz *et al.* 2010).

Rather than attempting to correct for detection or observer bias, the model predictions were validated on an independent dataset and verified by experts (see below). To account for spatio-temporal autocorrelation, nest counts were spatially aggregated to 2.5 km² resolution and then averaged over all survey years. This had the effect of reducing spatial autocorrelation compared to spatially aggregating counts to a finer resolution (see Gregory *et al.* 2012). To account for bias in the habitats surveyed the nest count dataset was supplemented with pseudoabsences that were selected randomly from areas outside the surveyed forest reserves. We selected the same number of pseudoabsences as there were aggregated nest counts (resulting prevalence = 0.5) and we minimized the influence of pseudoabsences on the model predictions by converting fitted probabilities to Bernoulli predictions using the Maximum Sum of Specificity threshold criteria that is designed to down-weight the influence of pseudoabsences (Liu *et al.* 2005; implemented in R package SDMTools).

Treated nest counts were modelled using a two-step hurdle-boosted regression-tree model to account for zero-inflation. We implemented this model using a manual combination of a Bernoulli and Poisson boosted regression tree models fitted using R package gbm. We used the helper functions in R package dismo to fit and interrogate the gbm models. Climate,

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3 habitat and anthropogenic variables thought to influence orangutan distribution and
4 abundance were used as explanatory variables in the zero-inflated hurdle BRT. Details on the
5 explanatory variables used, their treatment using R package `raster` and the model fitting
6 are given in Gregory *et al.* (2012).
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9 Model-fitted nest counts were validated against an independent nest count dataset and
10 verified by expert opinion. There was a positive linear relationship between model-fitted nest
11 counts and independent survey data measured using Ordinary Least Square (OLS) and
12 Iteratively-Reweighted Least Squares (IWLS) (Gregory *et al.*, 2012) and consensus that the
13 model-fitted nest counts captured the distribution and abundance of orangutan as understood
14 by a group of 15 Sabah Wildlife Department Wildlife Wardens.
15

16 We extrapolated and projected the habitat suitability model under two land-cover and
17 climate-change scenarios, as detailed in Table S1.
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20 **Table S1:** Future land-cover and climate-change scenarios evaluated for their effect
21 on orangutan metapopulation abundance and occupancy in Sabah (Malaysian
22 Borneo).

23 Scenario	24 Description	25 Justification
26 No mitigation	27 Sustainable Forest Management (SFM) is implemented only in current SFM forest reserves - others are converted to degraded sequentially and regenerate after 60 years. CO ₂ emissions continue to increase under a no-climate-policy scenario and climate changes unabated	28 Current SFM is adequate to safeguard the orangutan population, which will not be affected by climate change
30 Mitigation	31 SFM is implemented in all forest reserves - the Sabah Forest Department plans to implement this scenario by 2014. CO ₂ emissions are cut and stabilize at 450 ppm under a stabilization-policy scenario and climate change slows	32 Safeguarding the orangutan population requires complete SFM implementation as climate change affects habitat suitability

33 Land-cover projections were generated from a custom-built spatially explicit land-cover-change model that projected observed 2000-10 deforestation and forest regeneration rates through to 2100. Land cover rasters for years 2000 and 2010 were obtained from CRISP (<http://www.crisp.nus.edu.sg/>) because (1) they allowed calculation of an average annual deforestation rate from 11 years of observations (2000-2010), and (2) they were found to be highly accurate (> 85%). The rasters and their preparation are described in Miettinen *et al.* (2012). The rasters were reclassified into 4 land cover classes: [1] Cleared, [2] Mangrove, [3] Primary forest, and [4] Degraded forest & large oil palm plantations, and then aggregated to 2.5 km resolution using functions in the R package `raster`. The 2010 reclassified and aggregated land cover raster is mapped in Figure S5Figure S5.

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47 Land cover transitions (i.e., change of each cell from one class to any other) between 2000 and 2010 were estimated using the `randomForest` function in R package `randomForest`. A range of spatial explanatory variables believed *a priori* to influence land cover change were used to explain observed transitions (see Gregory *et al.*, 2012 for more details). The random forest fitted estimates were validated using the inbuilt out-of-bag validation (see Gregory *et al.*, 2012 for more details). From the random forest model, we calculated the probability that cell *i* would change to land cover class *j* as the proportion of random forests model iterations that predicted membership of cell *i* to class *j* (probability of class membership). We then calculated the probability that each cell *i* of land class *j* would

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3 change to any other land cover class (*cell vulnerability to change*). These probabilities were
4 used to determine whether cell i changed and to which land cover class as explained below.
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6

7 Deforestation and forest regeneration rates were calculated as the difference in the frequency
8 of these land-cover classes between 2000 and 2010. Deforestation rate calculations were
9 restricted to areas outside nationally and internationally designated protected areas in which
10 any extraction is strictly prohibited. These rates were then projected for forest reserves and
11 unprotected forest separately, representing timber harvesting with regeneration and forest
12 conversion without regeneration, respectively. We calculated recent deforestation rates from
13 2000–10 observed land cover raster layers (Miettinen et al., 2012), restricted to areas outside
14 nationally and internationally designated protected areas in which any extraction is strictly
15 prohibited. See Gregory et al. (2012) for more details. The number of cells expected to
16 transition from forest to any other class and from any other class to forest was then calculated
17 using a Discrete Transition Markov Chain (Takada et al., 2010). Cell land cover classes were
18 then changed according to a simple competitive land cover class allocation algorithm in
19 which cell i was allocated a new land cover class with a probability given by *cell
20 vulnerability to change * probability of class membership*. Forest reserves were deforested in
21 sequence, as a decreasing function of the vulnerability of their constituent cells.
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24 Rasters of predicted land cover change were produced for all 91 years of the simulation. We
25 examined changes in the amount and connectivity between habitat fragments in three years of
26 the simulation: the start year (2010), the middle year (2055) and the end year (2100).
27 Analyses were done using the R package `igraph`. Results are presented in the main text but
28 a visual summary of the connectivity findings are presented in Figure S1Figure S1. Overall, it
29 illustrates how the number of links (graph edges) decreased under the No mitigation scenario
30 (Figure S1Figure S1a) and so the number of components (clusters of connected habitat
31 fragments or vertices) increased. In contrast, the number of links and components were
32 similar in 2010 and 2100 under the Mitigation scenario (Figure S1Figure S1b), although the
33 number of links was more in 2055 as more suitable habitat fragment arose in the west and
34 higher elevations of the north.
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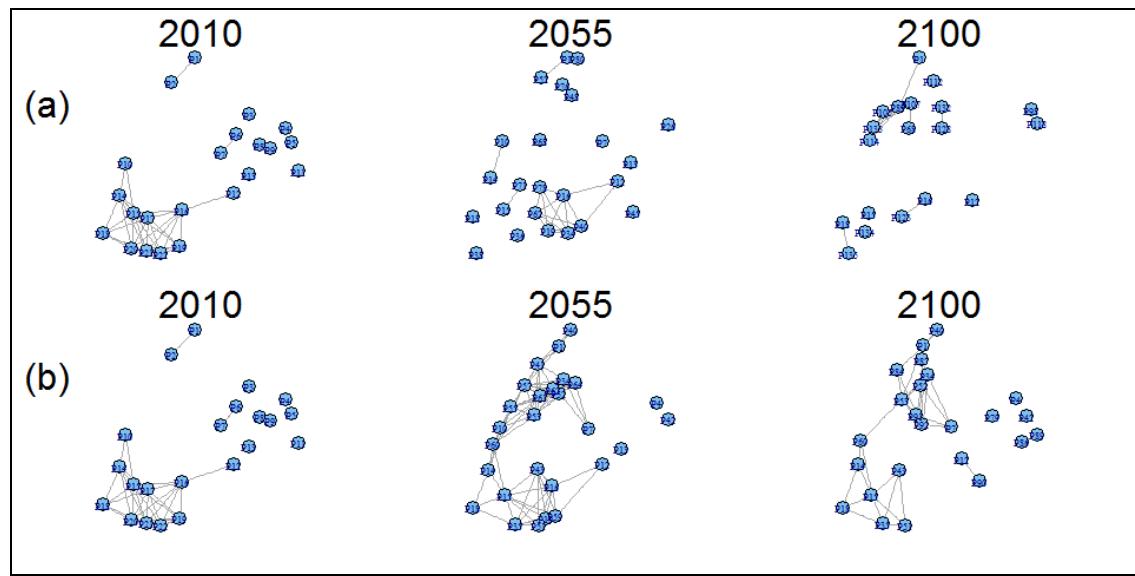


Figure S1: Graphs showing numbers of clusters of vertices (Components) and edges (Links) at the start, middle and end of the simulation period for (a) the No mitigation, and (b) the Mitigation scenarios.

Climate-change scenarios were: (1) a no-climate-policy reference scenario (MiniCAM Ref.; Clarke *et al.*, 2007), and (2) a corresponding policy (CO_2 stabilization at ~ 450 ppm) scenario (MiniCAM, Level 1; Wigley *et al.*, 2009). We used MAGICC/SCENGEN v.5.3 (<http://www.cgd.ucar.edu/cas/wigley/magicc>), a coupled gas-cycle/aerosol/climate model to generate the climate anomalies that were an ensemble of seven GCMs chosen on the basis of their skill in reproducing seasonal rainfall (1980–1999) at global and regional (Southeast Asia) scales. The GCMs were: BCCRBCM2, CCCMA-31, CSIRO-30, GFDL-CM20, MIROC-MED, CCSM-30 and UKHADGEM. We chose seven GCMs for the ensemble forecasts because any number greater than 5 tends to be more robust to GCM choice (Pierce *et al.*, 2009).

Climate anomalies were downscaled to the relevant spatial resolution (2.5 km) using the “change factor” method, where the low-resolution climate signal (anomaly) from a GCM is added directly to a high-resolution baseline observed climatology (Hulme *et al.*, 1995). Bilinear interpolation of the GCM data to a resolution of 2.5 km \times 2.5 km resolution was used to reduce discontinuities in the perturbed climate at the GCM grid box boundaries and to account for coastal cells that were assigned no data values. This was done using the R package fields.

Metapopulation structure and parameters

The metapopulation structure was derived from the habitat suitability model (HS) projections described above. HS projections were clumped into groups of cells or fragments of breeding habitat using Connected Components Labelling as implemented in the R package SDMTools. Any habitat fragments with fewer than 4 cells were set as unsuitable in each projection because they were considered too small to sustain a viable population (M. Ancrenaz, *pers. comm.*). A total of 5 rivers were verified to be impassable for some lengths of the course (B. Goossens, *pers. comm.*). Habitat fragments through which these impassable

stretches of river passed were split into separate habitat fragments. The final set of habitat fragments used for the metapopulation model is given in Figure 1 of the main text.

The initial abundances of habitat fragments were set as the sum of the underlying HS predictions. This assumes that the HS predictions correspond with the habitat fragments carrying capacity, which we considered a reasonable assumption give that recent declines in the Sabah orangutan population have been attributed to habitat loss, suggesting that most habitat fragments are at their carrying capacity. Based on expert opinion, however, we set the initial abundances of western habitat fragments 14, 15, 17, 18, 20 and 21 to zero because orangutan have been extirpated from this region from hunting (Figure S2Figure S2; M. Ancrenaz, *pers comm.*, Caldecott & Miles, 2005).

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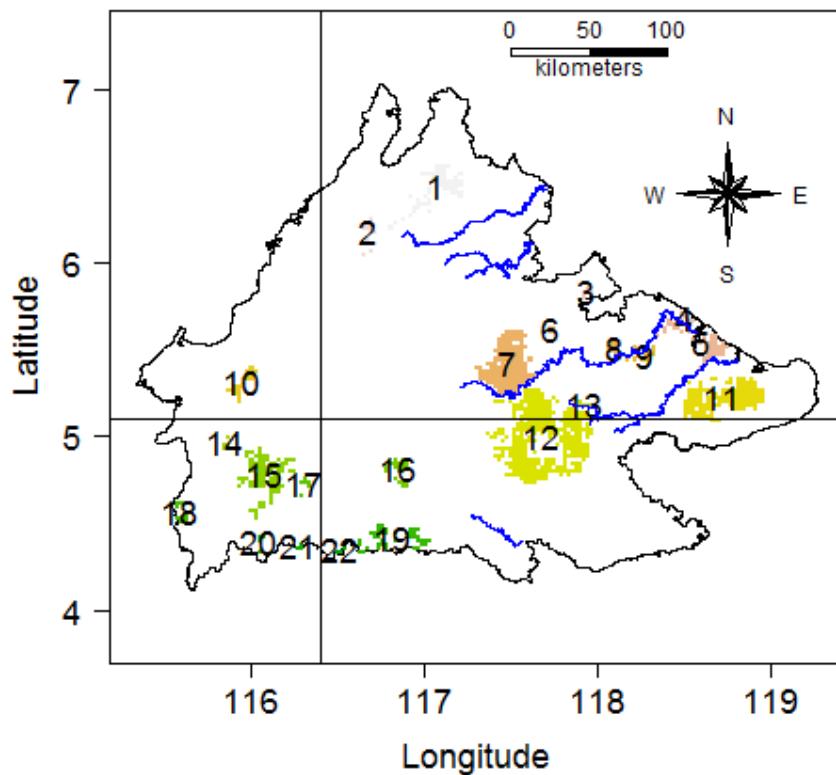


Figure S2: A map showing the western habitat fragments (those in the south western quadrant: fragments 14, 15, 17, 18, 20 and 21) that were initialised at zero abundance based on expert opinion and historical accounts of orangutan extirpation due to hunting.

The demographic models were implemented in RAMAS Metapop (Akçakaya. & Root, 2007). The template for the baseline Sabah orangutan model is given at the end of the Supporting information.

We collected demographic information from the published and grey literature and by soliciting expert advice. A list of the parameters collected, their values, ranges for the sensitivity analysis and sources are given in Table 1 in the main text.

For the population model, we defined four life stages: infant (< 1 yr), juvenile (1-5 yr), sub-adult (6-15) and adults (16+). Adult survival was parameterised so that they lived to a mean age of 40 years. Fecundity was parameterised so that the produced one offspring every 7 years. The resulting Leslie matrix is given by:

$$L = \begin{pmatrix} 0.000, 0.000, 0.000, 0.143 \\ 0.985, 0.800, 0.000, 0.000 \\ 0.000, 0.185, 0.900, 0.000 \\ 0.000, 0.000, 0.090, 0.960 \end{pmatrix}$$

Environmental and demographic stochasticity were incorporated into estimates of vital rates by sampling their values from pre-defined probability distributions at each iteration. Environmental stochasticity in st(age)-specific survival and fecundity rates was simulated by sampling each value from a lognormal distribution, parameterised by the estimated mean vital rate value ([Table 1](#)) and a coefficient of variation of 0.3 (30%). This latter value was approximately twice the CV of survival calculated from the Long-haired chimpanzee time series in the Global Populations Dynamics Database as $s = Nt / Nt + 1$ (GPDD ID 6769; www3.imperial.ac.uk/cpb/databases/gpdd). We set it at twice the Long-haired chimpanzee CV to allow for larger environmental variability. Demographic stochasticity was simulated by allowing numbers of survivors and new-born to be sampled from Binomial and Poisson distributions, respectively. The Binomial distribution was parameterised with mean survival and the number of individuals in the subpopulation. The Poisson distribution was parameterised with the product of the mean fecundity rate and number of individuals in the subpopulation. More details on these calculations and their assumptions are given in Akçakaya. & Root (2007).

Density dependence in adult fecundity (*i.e., for animals aged 16+*) was modelled as a non-linear (Beverton-Holt) function of suitable habitat fragment size, intended to approximate contest competition for territories. This meant that as the size of a suitable breeding habitat fragments reduced towards zero, so too the fecundity reduced towards zero. If the subpopulation size relative to carrying capacity in neighbouring habitat fragments was low, then orangutan in nearby habitat fragments unsuitable for breeding could move into a neighbouring habitat fragment and breed. On the other hand, if the subpopulation size relative to carrying capacity was high, then orangutan in habitat fragments unsuitable for breeding remained in those fragments unable to breed but with a high chance of dispersal (see below) and unchanging survival. These rules were implemented in RAMAS Metapop using the density-dependent fecundity, immigration and emigration options (Akçakaya. & Root, 2007).

RAMAS Metapop requires specification of a maximum intrinsic rate of population increase or R_{max} . We were unable to find an estimate of R_{max} for orangutan. Instead, we calculated an estimate as the mean between *Pan troglodytes* and *Gorilla gorilla*; a value of e0.06 or 1.062. See Table 1 in the main text for more details.

Forest fires

Due to their strong anthropogenic influence, it is not known how fire regimes will change over the coming century in Sabah (Cochrane 2009; J. Meittinen and A. Langner pers. comm.). To avoid subjectivity, we calculated fire probabilities empirically from 2000-12 fire hotspot data downloaded from the University of Maryland Fire Information for Resource Management Systems (FIRMS; <http://firefly.geog.umd.edu/firms/>). We upscaled all high confidence (“confidence” > 24 %) fire hotspots in Sabah from 1 km to 2.5 km resolution by taking the sum of fire hotspots in the constituent cells. We calculated the fire probabilities for all 2.5 km cells as the proportion of years in which a cell burned between 2000-2012 and interpolated these fire probabilities to unburned cells using thin-plate splines ([implemented in R package fields](#)) with smoothing parameter found by a generalized cross-validation search. Degraded land is fire-prone due to its high level of human activity (Miettinen *et al.*, 2011). To account for this, we calculated the proportion of degraded land cover in each fragment and used this as a multiplier for the baseline fire probabilities. Because fragments changed over space and time, we recalculated these values for each time step of the simulation. The final baseline fire probability layer is shown in [Figure S3](#)[Figure S3](#)[Figure S1](#).

We modelled fire as a fragment-specific catastrophe killing 2.5 % of orangutan in a fragment, removed across all stages in proportion to their abundances. [This value was based on the observation that 1,000 \(2.5 %\) of 40,000 Bornean orangutan were estimated to have been killed in the Bornean fires of 1997 \(Marshall *et al.*, 2009\)](#). We accounted for the increased orangutan mortality due to increasing [fire intensity during El Niño intensity events characterised by decreased precipitation](#) by increasing mortality from fire events from 2.5 % to 10.0 % of fragment abundance over 91 years (Marshall *et al.*, 2009). This was intended to simulate an increase in El Niño intensity with decreasing annual precipitation. We did not model a change in El Niño frequency.

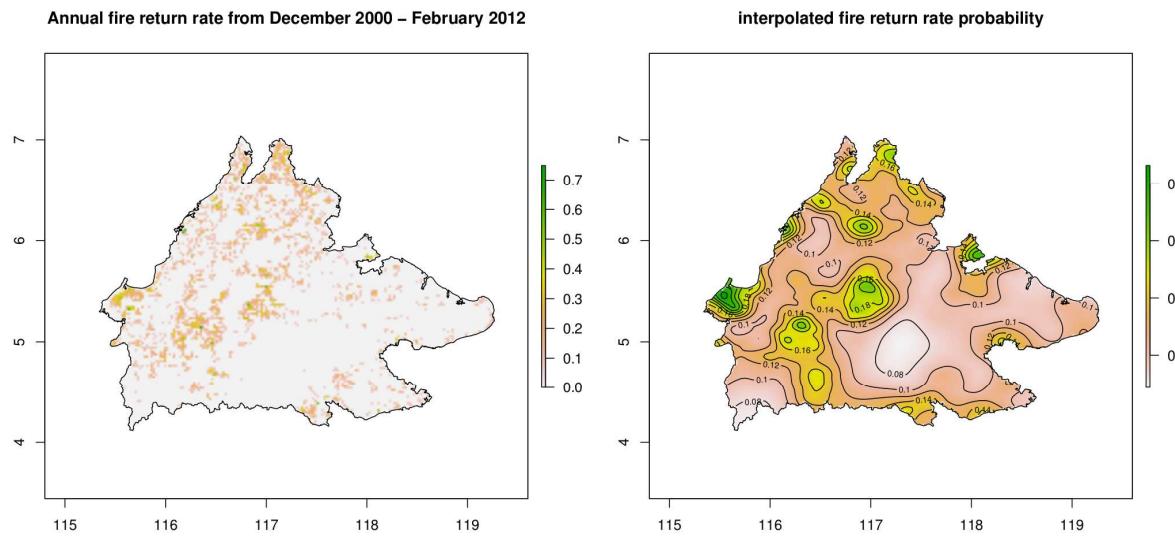
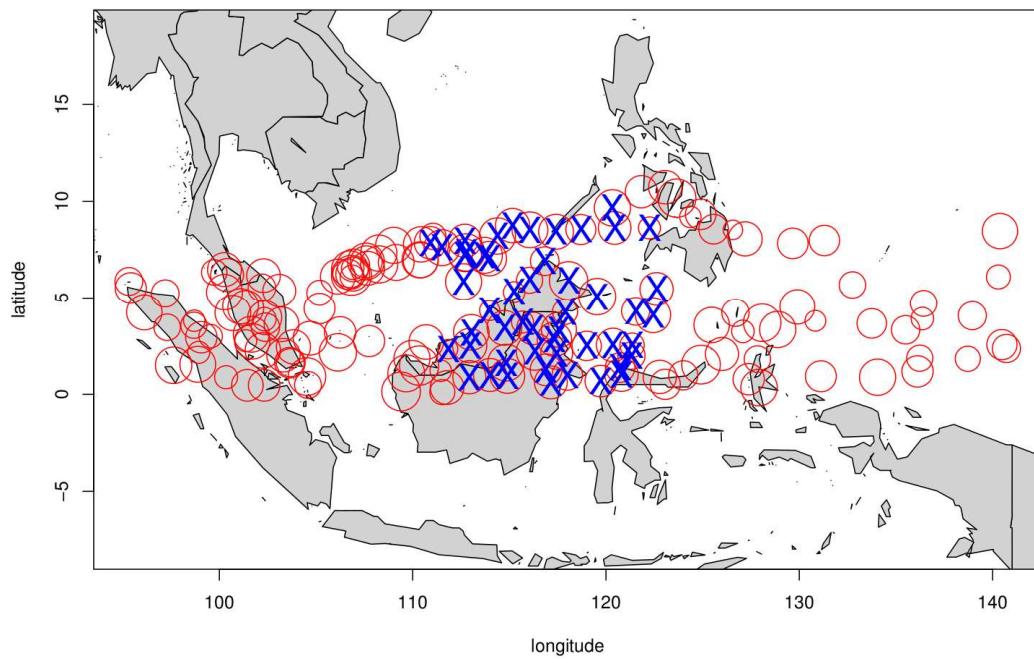


Figure S3: Plots showing (left) the empirically calculated fire-return rate, estimated from 2000-2012 fire hotspot data, and (right) the fire-return probability layer interpolated from (left) using thin-plate splines.

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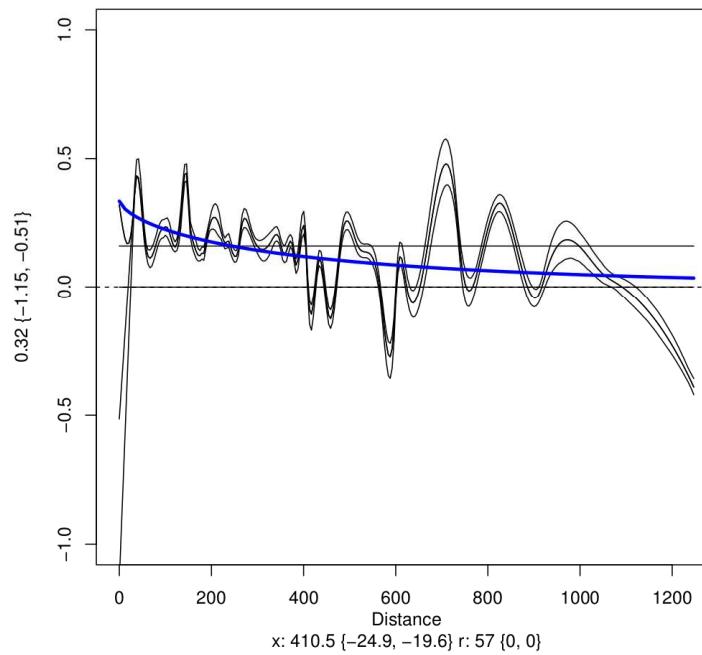


Figure S4: Plots showing (top) the $k = 50$ points (blue crosses) of available points (red circles) for which rainfall records were used to parameterise (bottom) the spatial cross-correlogram. The rainfall records - from the Global Historical Climatology Network - were from 1879 - 2011. The blue line is the optimised negative exponential fit to the spatial cross-correlogram used to estimate environmental correlation between habitat fragments.

Environmental correlation

We estimated the environmental correlation among fragments empirically. We download precipitation data from 1879-2011 from 1000 stations across Malaysia and Indonesia from the Global Historical Climatology Network (<http://www.ncdc.noaa.gov/ghcnm/v3.php>) (Figure S4Figure S4Figure S2a top). We used these data because they make up the largest observed spatio-temporal environmental dataset available. We selected $k = 50$ nearest neighbour stations to the Sabah geometric centroid and measured spatio-temporal environmental correlation among the resulting 12487 monthly rainfall measures using a non-centred (spline) spatial cross-correlogram implemented in R package ncp (Björnstad & Falck, 2001) (Figure S4Figure S4Figure S2 bottom). We ran the spline cross-correlogram with 500 bootstrap iterations to estimate 95% error bounds about the correlation. We then estimated parameters for a negative exponential correlation function (a direct input in RAMAS GIS) by minimising the residual error of a negative exponential curve fit to the spatio-temporal correlation predictions (thick blue line in Figure S4Figure S4Figure S2 bottom).

Dispersal

Data are sparse on orangutan movements, particularly their dispersal. Females are thought to be philopatric (Morrogh-Bernard et al. 2011; Goossens et al. 2005), and very little is known about males: Morrogh-Bernard et al. (2011) suggest that subadult males are the main dispersing stage, although data for these analyses were taken in relatively undisturbed habitat; Goossens et al. (2005) found no difference between male and female dispersal rates, and these data were measured in eastern Sabah, where habitat is impacted by anthropogenic disturbance. Given the uncertainty in sex-specific dispersal rates, we chose to use a female-only metapopulation model (this assumes that females are the demographically limiting sex).

Barriers to dispersal include wide river stretches, above which the canopy does not join, and open areas including urban centres, and orangutan are thought to avoid large open spaces (Goossens et al. 2005). We calculated dispersal assuming a heterogeneous habitat matrix in which different land cover classes are represented by different “conductance” values (Table S2Table S2Table S2). We parameterised the negative exponential dispersal kernel given by:

$$m_{ij} = \begin{cases} \beta_1 \times \exp(-d_{ij}^{\beta_2}/\beta_3) & \text{if } d \leq d_{\max} \\ 0 & \text{if } d > d_{\max} \end{cases},$$

where $\beta_1 = 0.2$, $\beta_2 = 0.69$, $\beta_3 = 8.0$, d is the least-cost distance between populations fragments i and j and d_{\max} is the maximum distance that an orangutan can feasibly disperse in one year, set at 120 km. This allowed 1 and 5 % of individuals of each subpopulation to disperse 100 and 30 km through primary forest, respectively (Figure S5Figure S5Figure S3). This should be considered an upper estimate of orangutan dispersal ability, but we justify its use because the dispersal kernel assumes homogeneous habitat, i.e.,

that d is calculated using Euclidean distance, whereas we assume heterogeneous habitat and calculate d using Dijkstra's algorithm to navigate the least-cost path between the closest points on the donor and recipient fragments. Dijkstra's algorithm is implemented in the shortestPath function in R package gdistance. The closest edge cells between fragments i and all other fragments were identified and used as the origin and goal in shortestPath and the transition layer was calculated from the least-cost surface assuming the cost of transitioning from one cell to the next is a mean of their cost values. The land cover raster and resulting transition layer with an example least-cost path are shown in Figure S6[Figure S6](#). See documentation for gdistance for working examples (van Etten 2012; <http://CRAN.R-project.org/package=gdistance>). Consequently, the so that the realised proportions of dispersing individuals reaching recipient fragments will be substantially lower ([Figure S7](#)[Figure S7](#)[Figure S4](#)).

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Table S2: Table of habitat permeability values (measured as “conductance values”) defined as the cost of dispersal through different habitat types relative to primary forest.

Habitat	Value	Description
Ocean	Inf	no conductance
Cleared	10	10 times less ‘permeable’ than forest
Mangrove	2	2 times less permeable than forest
Primary forest	1	complete conductance
Degraded forest & large oil palm plantations	5	5 times less permeable than forest

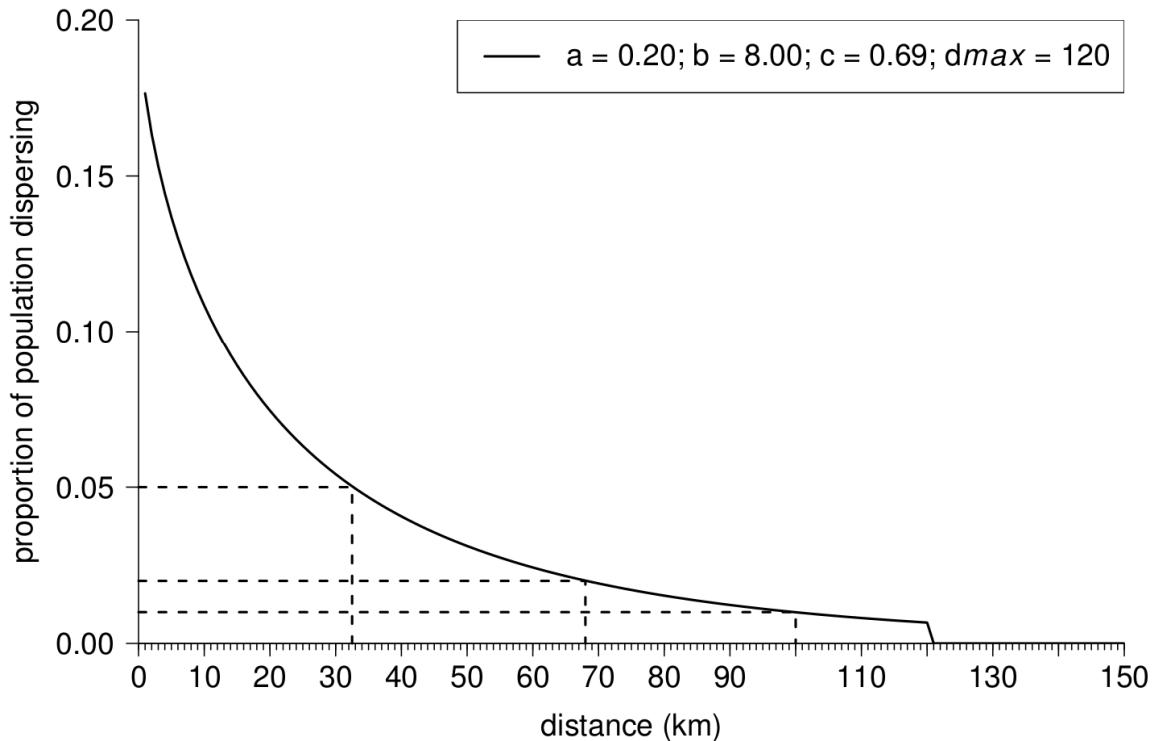


Figure S5: Proportion of individuals dispersing from each population as a function of distance and assuming an exponential decay function. Dashed lines show the distance that 1, 2 and 5% of individuals from each fragment can disperse.

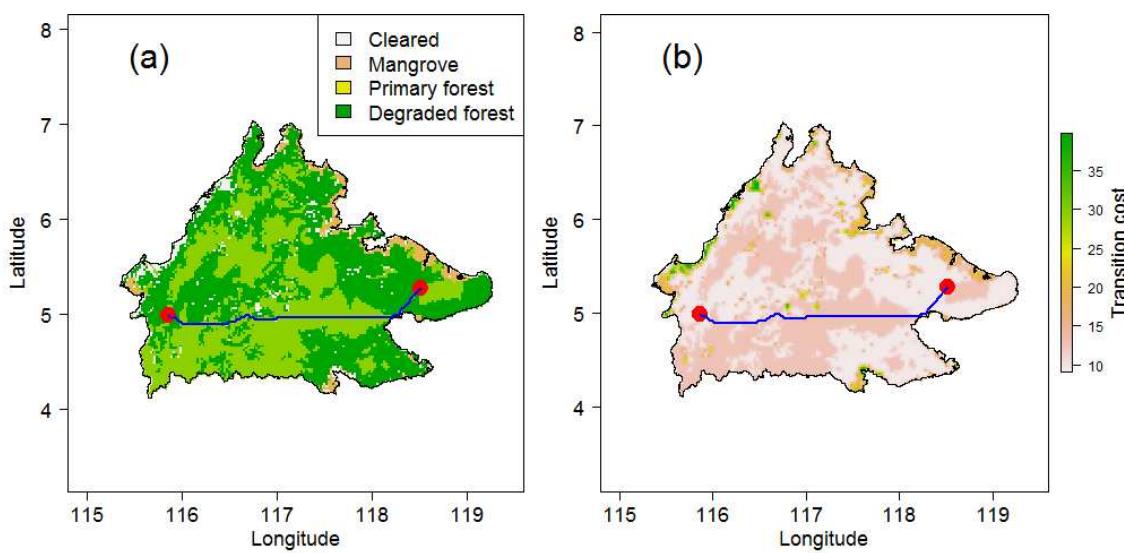


Figure S6: Maps showing (a) the 2010 land cover map for Sabah, and (b) the resulting transition layer. An example of a least-cost path is shown on each map, linking coordinates (118.5173, 5.278397) and (115.8605, 4.988159).

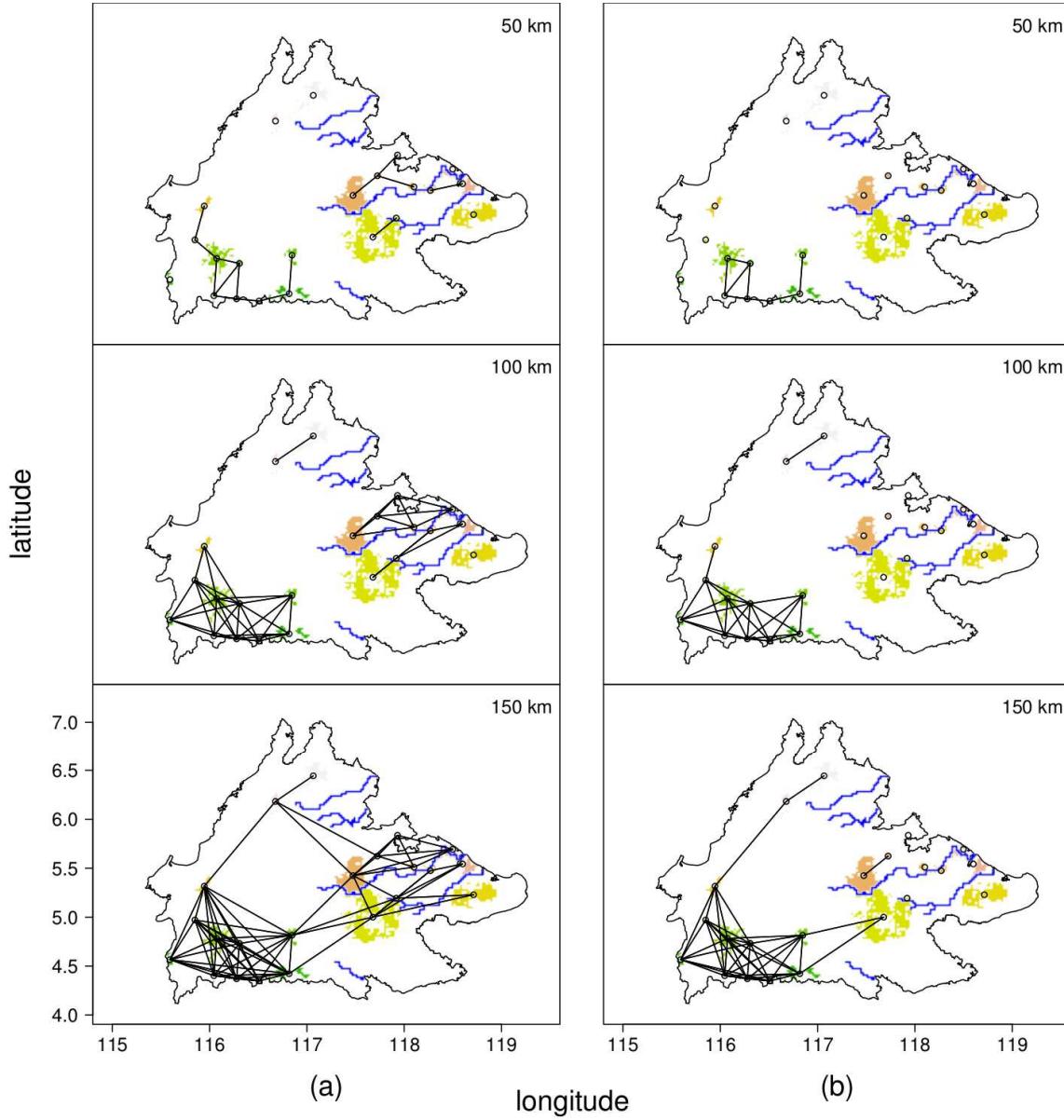


Figure S7: Maps showing connected orangutan habitat fragments in Sabah (indicated by black lines) at 40, 70 and 100 km when assuming (a) Euclidean distance, and (b) least-cost distance. Clearly, assuming a heterogeneous habitat matrix reduces the connectivity, and thus dispersal, among fragments. Note, also, using Euclidean distance does not account for dispersal barriers, such as impassable river channels, indicated by blue lines.

Selecting habitat fragments: fragment **trend**value

We calculated a measure, hereafter referred to as fragment **trend-value (FTFV)**, for each fragment to gauge its potential contribution to long-term metapopulation persistence. It is calculated as the sum over time of the ratio of the size of fragment i at time t relative to the largest fragment at time t + 1 defined as the temporal trend in fragment “carrying capacity”

relative to all other fragments, weighted by its initial condition. It is given by the following equation:

$$FVi = \sum_{t=1}^T K_{i,t} / K_{\max,t},$$

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 $t = 1, \dots, T$. Conversely, the fragment assigned the lowest FV would be the fragment with the smallest average carrying capacity over the same period, where $N_{i,0}$ is the abundance of fragment i at time 0 and $K_{\max,f}$ is the maximum carrying capacity among all fragments present at time t . The fragment with the highest FT was the largest, initially empty fragment, which increased in size over the period $t = 0, \dots, T$.

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RAMAS Metapop Sabah orangutan metapopulation file

The following code is the raw RAMAS Metapop baseline Sabah orangutan metapopulation file. The code can be copied to a text editor, saved with the extension “.mp” and then opened in RAMAS Metapop. All fields of the program will then be populated with the model parameters.

```
Metapopulation input file (5.1) map=\\
Sabah Orang mp file

5000
91
TRUE
4 FALSE
Fire

Local
Abundances
not spread
0.0000
0.0000,0.0000,0.0000,0.0000

Local
Abundances
not spread
0.0000
0.0000,0.0000,0.0000,0.0000
False,Zero
fecundities
Lognormal,0
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count in total
3 (F, S, K uncorrelated)
Yes
SelectedStages
No
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years
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Migration
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Correlation
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11 0.985 0.800 0.000 0.000
12 0.000 0.185 0.900 0.000
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46 female5-15
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49 FALSE
50 0.0
51 female15+
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