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1 **Title**

2 **Capacity for recovery in Bornean orangutan populations**

3 **when limiting offtake and retaining forest**

4 **Running title**

5 **Bornean Orangutan: Recovery Prospects**

6

7 **Abstract**

8 *Aim:*

9 We assess the potential long-term viability of orangutan populations across Borneo,

10 considering the effects of habitat loss, and various forms of population reduction,

11 including hunting, retaliatory killings, and capture and translocation.

12 *Location:*

13 The study focused on the island of Borneo, a region that has experienced substantial

14 deforestation over the past four decades, resulting in the degradation and

15 fragmentation of its lowland forests, thereby threatening the island's unique

16 biodiversity, including orangutan populations.

17 *Methods:*

18 To evaluate the long-term viability of orangutan populations, we employed a

19 spatially-explicit individual-based model. This model allowed us to simulate various

20 scenarios, including the impact of removing habitat fragments or individuals from

21 the population.

Results:

Our findings revealed that small forest fragments facilitate orangutan movement, thereby increasing the number of individuals settling in non-natal patches. Crucially, orangutan populations proved highly vulnerable to even small levels of offtake. Annual removal rates exceeding 2% diminished the positive role of small forest patches in sustaining population connectivity, the long-term viability of populations and prospects for recovery.

Main Conclusions:

Our results suggest that orangutan populations in Borneo could potentially recover from recent declines if removal of orangutans by hunting, retaliatory killings, capture and translocation is reduced, and habitat connectivity is maintained within human-modified landscapes. These findings emphasize the urgent need for conservation strategies that mitigate negative human-wildlife interactions, and/or help preserve habitat and fragments as stepping stones. Measures could include promoting coexistence with local communities and translocating orangutans only in rare cases where no suitable alternative exists, to ensure the long-term survival of orangutan populations in Borneo.

Key words: Connectivity, Human-modified landscapes, Individual-based model, Landscape ecology, Meta-population, RangeShifter 2.0

Introduction

Tropical forests support more than half of the world's terrestrial vertebrate species. However, forests in tropical regions have also experienced some of the world's highest rates of degradation and deforestation, with many species threatened by extinction (Seymour and Harris, 2019; Pillay *et al.*, 2021). Southeast Asia has experienced substantial deforestation - between 1973 and 2016, 19.5 million ha of old growth forest was cleared in Borneo alone, reducing the forest extent from 76% to 50% (Gaveau *et al.*, 2014). Now, much of the remaining lowland landscapes are extensively modified, and are increasingly characterised by plantation monocultures and scattered forest fragments (Gaveau *et al.*, 2016). Habitat fragments affect species by increasing their isolation and exposure to edge habitats, which have very different biotic and abiotic conditions (Haddad *et al.*, 2015). Nevertheless, habitat fragments in human-modified landscapes often retain some conservation value, and forest remnants serve as important refuges for many forest-dependent species (Lion *et al.*, 2016; Deere *et al.*, 2019). Fragments are also likely to be important for maintaining connectivity between forest areas, allowing species movement among metapopulations and facilitating range shifts in response to climate change (Laurance, 2004; Senior, Hill and Edwards, 2019).

Despite the potential benefits of habitat fragments as refugia and for connectivity, populations within them are likely to be at greater risk of environmental and demographic stochasticity, for example through drought, fire, or disease, as well as other fluctuations in population size. If mortality exceeds recruitment from births and emigration, fragments may become population sinks (Gilroy and Edwards, 2017). While there is a large body of research regarding the impacts of habitat fragmentation on biodiversity, the potential importance of forest

67 fragments in facilitating connectivity and species population viability in human-

68 modified tropical landscapes is not well studied (Scriven *et al.*, 2019), particularly

69 for large bodied primates (Ancrenaz *et al.*, 2021), undermining our ability to guide

70 conservation planning.

71   Despite international commitments to halt biodiversity loss, species such as

72 the orangutan (*Pongo* spp.) have been declining steeply over the past two decades

73 (Wich *et al.*, 2016; Nowak *et al.*, 2017; Voigt *et al.*, 2018). Orangutan population

74 losses in both Borneo and Sumatra have been driven by deforestation, as well as

75 hunting and retaliatory killings (Ancrenaz *et al.*, 2016; Nowak *et al.*, 2017; Singleton

76 *et al.*, 2017). Orangutans are also lost from populations through captures and

77 translocations, where individuals are removed from areas following a real or

78 perceived risk that the individual will otherwise be killed (Sherman *et al.*, 2021).

79 Orangutans depend on forest for survival and large populations and highest densities

80 are found in protected areas and other remaining forests with low anthropogenic

81 pressure (Voigt *et al.*, 2018). However, orangutans can survive in human-modified

82 landscapes in the absence of killing, where forest remnants offer sufficient food and

83 nesting opportunities (Ancrenaz *et al.*, 2021). Although typically at low population

84 densities (Seaman *et al.*, 2019), most individuals in human-modified landscapes

85 appear to be in good health (Rayadin and Spehar, 2015) and are able to survive and

86 reproduce in fragmented landscapes for extended periods of time (>20 years)

87 (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). Forest fragments may therefore play an

88 important role in connecting larger areas of orangutan habitat and preventing further

89 population segregation and decline.

90   As there is currently a dearth of orangutan data from human-dominated

91 landscapes, population viability analysis can be used to provide insights into the

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92   population dynamics and survival probability over longer periods of time. However,

93   to date, these models have not accounted for spatially explicit habitat dynamics

94   (Marshall et al 2009, Utami-Atmoko 2019) and offtake, or have assumed perfect

95   knowledge of the landscape and no inter-individual variation in dispersal behaviour

96   (Gregory et al 2014).

97   Advances in modelling and computational power have led to the

98   development of increasingly complex simulations to study dynamic environmental

99   systems (Kool, Moilanen and Treml, 2013). Individual-based models epitomise this

100 progress and are increasingly popular in ecological studies (Zurell *et al.*, 2022).

101 These modelling approaches to study species responses to environmental change or

102 management options have several advantages over other commonly used methods.

103 For example, species distribution and environmental niche models assume that

104 populations are at equilibrium and that species presence data are correlated with

105 environmental covariates, but this is rarely the case (Urban *et al.*, 2016). Individual-

106 based models on the other hand, incorporate population dynamics in space and time,

107 as well as species movement and inter-individual variation in the stochastic

108 processes that govern species distributions (Bocedi *et al.*, 2014; Urban *et al.*, 2022).

109 As such, individual-based models are likely to become increasingly important tools

110 in managing biodiversity and landscapes (Synes *et al.*, 2016).

111   As a charismatic great ape species, orangutans attract a lot of public attention

112 and are relatively well studied. We use the existing data on abundance, life history

113 and population dynamics to showcase the analytical potential of the individual-based

114 modelling approach for orangutans and predict the potential long-term consequences

115 of loss of fragments from landscapes and offtake (hunting, retaliatory killings and

116 capture and translocation) on orangutan populations across Borneo. The method and

117 conclusions, however, could be equally applicable to other species that face

118 challenges from habitat loss and offtake, and for which basic information on

119 demography and dispersal behaviour is known.

120 **Methods**

121 *Study system*

122 Bornean orangutans are found across a third (227,000 km^2) of Borneo

123 (IUCN, 2021: Figure 1a). The island is topographically complex, with the interior

124 being predominantly mountainous, giving way to lowland forest (≤500 m asl) and

125 peat swamps towards coastal areas. Borneo is governed among Indonesia

126 (Kalimantan), Malaysia (Sabah and Sarawak) and Brunei Darussalam, although

127 orangutans are absent from the latter.

128 Genetic data suggest that major rivers and mountain ranges have been a

129 significant barrier to movement across evolutionary time scales for orangutans (Jalil

130 *et al.*, 2008). This separation has resulted in sufficient genetic divergence for the

131 Bornean orangutan population to be divided into three subspecies, the largest being

132 the Southwest Bornean orangutan (*Pongo pygmaeus wurmbii*) found across

133 southern, west and central Kalimantan. The Northeast Bornean orangutan (*P. p.*

134 *morio*) ranges from Sabah to East Kalimantan, and the Northwest Bornean orangutan

135 (*P. p. pygmaeus*) remains as a small population in Sarawak and northwest of

136 Kalimantan. Although the demography of orangutans is broadly consistent across

137 Borneo (van Noordwijk *et al.*, 2018), environmental variation, such as soil type and

138 rainfall, leads to considerable differences in densities across the subspecies (Voigt *et*

139 *al.*, 2018). We capture this variation in abundance, by considering movement and

140 population dynamic separately for each subspecies.

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Modelling framework

142   We modelled orangutan population dynamics and dispersal using a customised

143   version of RangeShifter 2.0 (Bocedi *et al.*, 2021). RangeShifter is an individual-

144   based population viability and connectivity modelling platform, which allows users

145   to simulate joint population dynamics and spatially explicit dispersal, whilst

146   including inter-individual stochasticity. We used a version of the base-model that

147   included a potential management options for controlling invasive and non-native

148   species through culling (https://github.com/RangeShifter/RS_CONTAIN). However,

149   rather than simulating culling of an invasive species, we used it to model killing or

150   translocation of orangutan individuals. With the model we investigated the combined

151   long-term effects of habitat loss, removal of fragments and offtake on orangutan

152   population viability and connectivity.

153   *Landscape characterization*

154   We used a fine-scale 30 m resolution gridded system (raster) to define our study

155   landscape, to which we applied a patch-based model. Patches are aggregations of

156   suitable habitat cells forming defined spatial clusters (specified below), where each

157   patch is considered a discrete population. We developed a landcover layer based on

158   high resolution forest maps for 2017 (v1.5, Hansen *et al.*, 2013) to coincide with

159   orangutan density values from 2016 (Voigt et al 2018) that were used to populate

160   patches. Forest was defined according to Margono et al (2014) as stands >5 ha with a

161   natural composition and structure that had not been cleared in recent history (until

162   2017) and having >70% tree canopy cover. We acquired forest change data from the

163   Global Forest Change repository (v1.5; Hansen et al 2013) and applied it to forest

164   cover data from 2000. We further refined these maps by setting pixels that were

165   prominently within areas of either water (including major rivers) or urban

166   development to *no-data*, using habitat layers by Miettinen, Shi and Liew, (2016).

167   *Demographic model*

168   Male orangutans will range over large distances, often encompassing multiple

169   female home ranges and are unlikely to be a limiting factor in reproduction

170   (Nietlisbach et al., 2012). We, therefore implemented a female-only model, with

171   stage-structured demographics, comprising nine stages (Table 1).

172   Rather than reduce the fecundity to reflect female births only, we set a

173   survival probability of stage one individuals of 0.45 to represent the slight male-

174   biased sex ratio at birth (van Noordwijk *et al.*, 2018). We derived subsequent

175   survival probabilities from the most recent orangutan Population and Habitat

176   Viability Analysis report (Utami-Atmoko *et al.*, 2019; Table 1). We added density

177   dependence in both fecundity and development to the youngest breeding stage

178   (Table 1). The demographic model is described in detail in the Supplementary

179   Information SI 1. The strength of the density dependency (*1/b* parameters) for each

180   habitat type was informed by density estimates for 2016 from the most recent range

181   wide density distribution model (Voigt et al., 2018). These densities were

182   summarised across discrete landcover types and independently for each of the three

183   subspecies. As we only modelled females, we then halved density estimates (Table

184   2).

185   *Patch allocation*

186   On Borneo, orangutans predominantly occupy lowland forest areas and are generally

187   absent from, or found at very low densities at higher altitudes (Husson *et al.*, 2009).

188   Thus, we focussed our analysis on all suitable lowland habitat (≤500 m asl) having

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189 the potential to support orangutans irrespective of whether they are currently present,

190 thereby allowing for possible future colonisation and range expansion.

191 Large rivers and multi-lane highways are likely to hinder orangutan

192 movement (Utami-Atmoko *et al.*, 2019). Large rivers were derived from Abram *et*

193 *al.* (2015) and major roads were derived from OpenStreetMap (OpenStreetMap

194 Contributors, 2022b, 2022a) using the identifiers "Primary", "Primary_link",

195 "Motorway", "Motorway_link", "Trunk" and "Trunk_link". We thus divided all

196 forest blocks that were intersected by major roads and rivers to reflect potential

197 movement constraints. The current orangutan distribution crosses several large areas

198 of forest, which would otherwise be considered a continuous patch; in order to

199 initialise the model with individuals within the current range, we intersected forest

200 areas with the IUCN orangutan range polygon (Ancrenaz *et al.*, 2016).

201 In RangeShifter, local populations are modelled within forest areas, which

202 are called patches, and each patch is assigned a unique identity. Orangutan nests

203 have been observed in oil palm plantations up to 50 m from natural forest areas and

204 orangutans are regularly observed making short-distance excursions into plantations

205 (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). Therefore, small natural forest fragments

206 close to larger forested areas are likely to be incorporated into the home ranges of

207 female orangutans. To represent this in the model landscape, we placed a 50 m

208 buffer around all forest areas and considered all fragments within the buffer to be

209 part of the same patch as the larger forest area. Patches were then assigned a unique

210 ID based on the spatial arrangement of forest fragments, whereby all fragments

211 within ≤100 m (if 50 m buffers overlapped) were assigned the same identity and

212 considered a discontinuous patch. If a patch was too small to support an orangutan

213 based on the summarised densities (Table 2), we removed these patches from the

214 patch layers, but retained them for the cost and landcover layer, as even small forest

215 patches will provide resources and limit the cost of moving across the landscape.

216 *Dispersal parameters*

217 RangeShifter simulates dispersal through three distinct processes: emigration,

218 transfer, and settlement (Travis *et al.*, 2012). Female orangutans display a high

219 degree of philopatry, and it is almost exclusively males that disperse over long

220 distances (Nietlisbach et al., 2012; Ashbury et al., 2020). Therefore, range expansion

221 is limited by short distance dispersal of females. We further assumed that dispersal

222 was limited to young adult females and characterised by a strong density dependence

223 in both emigration and settlement probabilities, replicating a high degree of

224 philopatry. We parametrised density dependence in emigration so that females would

225 stay within their natal patch until the patch reached its equilibrium density, above

226 which there was a maximum probability of 0.2 that a female would leave the patch.

227 To model the transfer (movement) process, we used the stochastic movement

228 simulator, an individual-based model which simulates step-based movements across

229 a cost surface (Palmer, Coulon and Travis, 2011), nested within RangeShifter 2.0.

230 Here, movement trajectories during transfer are governed by three parameters:

231 perceptual range, directional persistence, and memory. We based these parameters

232 on previous expert judgement of visualised simulated trajectories (Seaman *et al.*,

233 2021). If a female orangutan leaves her natal patch and is unable to find suitable

234 habitat, we assumed it was likely that she would return, and as a result, we modified

235 the base version of RangeShifter 2.0 to allow individuals to return and settle in their

236 natal patch, even if it was at carrying capacity.

237   A female will usually settle close to or within the mother's home range (van

238   Noordwijk *et al.*, 2012; Ashbury *et al.*, 2020). This was approximated in the model

239   by parameterising the settlement probability at 100% with a steep density

240   dependence. This parameterisation means a female will almost certainly settle once

241   reaching a patch, unless that patch is close to or above its equilibrium density, at

242   which point there is a rapid reduction in the settlement probability (Figure SI 3).

243   Through these two independent processes, emigration and settlement, females will

244   only leave their natal patch if the patch cannot support them, because it is at or above

245   its carrying capacity and will then settle at the first available opportunity. As there is

246   limited information on orangutan dispersal within human-modified landscapes, we

247   undertook a sensitivity analysis to determine how robust our model was to changes

248   in dispersal parameters (Table 1).

249   *Cost surface*

250   We built a cost surface layer using a land-cover layer, a digital elevation model and

251   observations of terrestrial movement of orangutans and expert information. Although

252   being predominantly arboreal, terrestrial movement is a common behaviour for

253   orangutans on Borneo. However, this form of locomotion requires additional

254   energetic expenditure, as well as risks from predation and novel diseases (Ancrenaz

255   *et al.*, 2014; Ashbury *et al.*, 2015). To capture this nuance, we created a cost surface

256   based on Tobler's hiking function using the Distance Accumulation tool in ArcGIS

257   Pro (*v*2.6.0; ESRI, 2020). We used three inputs, a 30 m digital elevation model (Farr

258   *et al.*, 2007), expert informed resistance surface values based on habitat type (Table

259   SI 2), and known barriers to movement (major roads and rivers). To ensure rivers

260   and major highways were represented in the simulated landscape and to prevent

261   diagonal movement between barrier pixels, we buffered all major roads and rivers by

262 50 m and pixels were assigned a no-data value. We included all suitable forest areas

263 as starting points, i.e. where cost was assigned the lowest value of 1. The resulting

264 surface is a cost to movement layer, where the cost increases when moving away

265 from natural forest areas, mediated by the resistance of the habitat type, degree of

266 slope and barriers within the landscape (Figure SI 2).

267 *Landscape fragmentation and offtake scenarios*

268 We developed scenarios to explore the relative effects of both loss of fragments from

269 the landscape and offtake on orangutan population dynamics and connectivity. To

270 investigate the effects of fragment loss we established two landscape scenarios; the

271 "Current Landscape Configuration" scenario included all forest suitable for

272 orangutans (≤500 m asl) across Borneo and represented the landscape configuration

273 in 2017. Small forest fragments are at much greater risk of being deforested (Hansen

274 *et al.*, 2020) and any fragment ≤5,000 ha is currently considered unviable for

275 supporting an orangutan population (Utami-Atmoko *et al.*, 2019; Sherman *et al.*,

276 2020), potentially increasing its risk for clearing as a consequence of perceived

277 lower usefulness to conservation. We therefore produced a "Fragment Removal"

278 landscape, in which we removed all fragments ≤5,000 ha, representing a worst-case

279 scenario. Patch and cost surfaces were produced for the landscapes with and without

280 fragments (Figures SI 1 and SI 2).

281   For both landscape scenarios, we modelled five potential yearly offtake rates

282 from hunting, retaliatory killing and/or live capture and translocation at: 0%, 1%,

283 2%, 4% and 10% of the population, estimated from published studies and

284 extrapolations from crime data (Sherman *et al.*, 2022). These offtake rates were

285 chosen as they represent plausible real-world values based on empirical data.

286   Individuals were removed from patches selected at random and individuals could be

287   removed from all age groups, as killing and translocation affect orangutans across

288   age groups (Sherman, Ancrenaz and Meijaard, 2020).

289   *Model initialisation and metrics*

290   Before applying the model to our landscape scenarios, we calibrated the strength of

291   the density dependency (*1/b* parameter) on an artificial landscape to ensure the

292   demographic model was behaving as expected and the population reached the correct

293   density after reaching equilibrium. After calibration, we initialised the model using

294   the IUCN distribution (Ancrenaz *et al.*, 2016) for each subspecies, populating all

295   suitable patches within the range at equilibrium density. To investigate the potential

296   long-term effects of orangutan offtake and fragment removal, we ran models for 250

297   years, i.e. approximately 10 generations. Each scenario was run with 50 iterations to

298   allow for model stochasticity. We applied the five offtake rates to both landscape

299   scenarios, resulting in 10 model outcomes for each subspecies.

300   We recorded six metrics during the model runs: 1) the total population size at

301   each time step; 2) the percentage change in population compared to the starting

302   population; 3) the cumulative probability that the population becomes extinct across

303   the 50 iterations at each 10-year time interval; 4) the area occupied after 50 and 250

304   years (patch occupancy); 5) the percentage of individuals settling in non-natal

305   patches (dispersal success); 6) individual dispersal distances.

306   *Sensitivity analysis*

307   The largest degree of uncertainty in our connectivity model came from the dispersal

308   parameters, as relatively little is known about dispersal behaviour of female

309   orangutans. Therefore, we undertook a sensitivity analysis to determine the

310   robustness of the model to these parameters, mostly pertaining to orangutan

311   movement (Table 1), by increasing and decreasing baseline values by 5%. In

312   particular, we varied perceptual range between 24 and 26, directional persistence

313   between 2.6 and 2.4 and memory between 11 and 8. In addition, we tested the

314   model's sensitivity to 5% variations of other model parameters, specifically in the

315   maximum number of steps, maximum total number of steps, per step mortality,

316   maximum emigration probability (α_S), and the slope of the density dependency in

317   settlement (d_0). For each permutation we ran a baseline model (Current Landscape

318   Configuration and no offtake) for 250 years and 50 iterations. We assessed the model

319   sensitivity by comparing the proportion of patches occupied at 250 years to the

320   model parametrisation used in our main analysis, for the same landscape and no

321   offtake.

322   **Results**

323   Our demographic model revealed that in both landscape scenarios (Current

324   Landscape Configuration and Fragment Removal) the populations of all three-

325   orangutan subspecies increased from their initial size and expanded their range over

326   the duration of the model run when no additional mortality was applied (Figures 1

327   and 2). All three subspecies increased in population size over the first 50 years of the

328   model run (80% − 82%), and continued to increase thereafter, although at a slower

329   rate until the final population size at 250 years (123% - 159% increase from starting

330   population). Although there was a similar percentage increase in population between

331   landscape scenarios, total abundance was on average 4% higher (1.8-5.4% or 724

332   individuals for *P. p . pygmaeus* and 10,150 for *P. p. wurmbii*) under the Current

333   Landscape Configuration and when no offtake was applied. In both scenarios, the

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334 population growth had not reached an asymptote, suggesting the population would

335 continue to increase after 250 years (Figures 1 and 2). When no offtake was applied,

336 the extinction probability was zero for all model outcomes among subspecies and

337 landscape scenarios over the modelled time frame (Figure 2).

338   Even the lowest modelled offtake rate had a substantial effect on the

339 projected population size. When a 1% offtake rate was applied, the population

340 increased, but substantially less at 50 years than under no offtake (16-19% from

341 starting population) and after 250 years populations had only increased by 60-71%

342 (Figures 1 and 2). This difference in population growth compared to no offtake was

343 most severe for *P. p. wurmbii*, which was projected to grow by 60% (from an initial

344 population of 128,000 to 205,000; ±120 s.e. at 250 years) when the Current

345 Landscape Configuration was maintained and by 61% (from 124,000 to 199,000, ±

346 121) under the Fragment Removal scenario, a final abundance that was 28% lower

347 than when no offtake was applied.

348   For both landscape scenarios, a 2% offtake rate led to marked declines in

349 abundance across subspecies of 76% on average after 250 years (73 – 79% Figure 1

350 and Table SI 3 – 5). When we applied a 4% offtake rate, the population loss was

351 substantial, with a >99% decrease in abundance for all model outcomes after 250

352 years.

353   Despite these large abundance declines, offtake rates until 4% did not lead to

354 an extinction of any subspecies within 250 years. However, at an offtake rate of 4%

355 and higher, overall numbers were reduced in a way that would likely lead to a

356 functional extinction of many of the populations (with 4 - 68 individuals of *P. p.*

357 *pygmaeus,* 28 - 106 individuals of *P. p. morio* and 183 - 284 individuals of *P. p*

wurmbii after 4% offtake was applied for 250 years for the entire landscape, in both

landscape scenarios). The highest offtake modelled of 10% resulted a 100%

extinction probability for all subspecies under both landscape configuration

scenarios before 250 years (Figure 2).

Orangutan dispersal for different scenarios

The percentage and number of dispersing individuals being able to use non-natal

patches was higher under the Current Landscape Configuration than under the

Fragment Removal scenario. For example, annually for *P. p. morio* 14% (±0.10) of

dispersing individuals or 28 (± 1.6) orangutans were able to successfully settle in a

non-natal patch and 69% (±0.15) or 133 individuals (±3.8) remined in their natal

patch, when no offtake was applied. However, in the Fragment Removal scenario

only 9% (±0.11) of dispersers or 16 (±1.2) individuals were able to use non-natal

patches, and 73% (±0.90) or 127 (±3.8) individuals remined in their natal patch. In

both the scenario a similar number of individuals died during dispersal, 18% (±0.15)

or 31 individuals when fragments were removed and 16% (±0.11) or 32 individuals

under the Current Landscape Configuration. Generally, a similar pattern was

observed when offtake was applied, but with a smaller majority remaining in their

natal-patches and a slightly higher percentage settling in non-natal patches (Figure

3). This was likely due to reduced densities after offtake was applied, thus allowing

the settlement probability to increase. Despite these differences, there was a

consistent pattern among all scenarios, with a similar number of individuals dying

during dispersal, but a higher percentage of individuals moving to non-natal patches

and fewer remaining in natal patches under the Current Landscape Configuration,

when fragments were retained.

382   For all offtake scenarios, the median dispersal distance (from the natal patch

383   to the non-natal patch where individuals successfully moved) was generally greater

384   when fragments had been removed (i.e. the Fragment Removal scenario, Figure 3),

385   although this difference was generally < 2 km. The greatest difference in dispersal

386   distances between landscape scenarios was without removal of orangutans. This

387   difference was particularly true for *P. p. wurmbii*, which had a median dispersal

388   distance of 8.5 km under the Current Landscape Configuration compared to 11 km in

389   the Fragment Removal scenario. When offtake was applied this difference generally

390   decreased (Figure 3).

391   *Orangutan occupancy in different scenarios*

392   There was a substantial increase in the area occupied by the subspecies through

393   dispersal after the first 50 years of the model run, although with some variation

394   among species (Figure 4). The greatest increase was observed with *P. p. pygmaeus*

395   which expanded from 21,858 km^2 at year zero to 59,670 km^2 ($\pm$ 305) in the Current

396   Landscape Configuration scenario and from 21,486 km^2 to 59,835 km^2 ($\pm$ 610) in the

397   Fragment Removal scenario (or a 173% and 178% increase respectively). *P. p.*

398   *wurmbii* had a much smaller percentage increase after the first 50 years from 90,624

399   km^2 to 172,574 km^2 in the Current Landscape Configuration scenario and from

400   87,445 km^2 to 167,560 km^2 ($\pm$ 26) in the Fragment Removal scenario (or a 90% and

401   92% increase respectively) (Table SI 6 – 8).

402   Under the different rates of offtake, the area occupied was smaller than

403   without offtake. When the highest offtake of 10% was applied, the area occupied

404   initially increased over the first 50 years, although at a much smaller rate than with

405   no or less offtake (ranging from 24 – 45% increase from starting area). After 80

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406   years however, occupied areas had decreased from the starting population under all

407   landscape configuration scenarios with a 10% offtake rate.

408   *Sensitivity analysis*

409   Our sensitivity analysis on dispersal parameters led to only small variations in model

410   outcomes for both patch occupancy and final abundance, suggesting our model is

411   relatively robust to dispersal parameters (Figure SI 6). For all three subspecies,

412   changing the maximum emigration probability had the largest effect on patch

413   occupancy, and although outside the standard error of the baseline scenario (Current

414   Landscape Configuration and no offtake), the proportion of occupied patches

415   differed by no more than 0.4% or an average of 4.3 patches, with this largest

416   deviation from *P. p. morio* (Figure SI 6).

417   **Discussion**

418   We modelled spatially explicit population dynamics for Bornean orangutans under

419   landscape and offtake scenarios, revealing that in the absence of non-natural offtake

420   by killing, orangutan populations are likely to increase in number and distribution.

421   Although orangutan numbers increased regardless of whether fragments were

422   removed from the current landscape, the largest population size was observed when

423   the current forest cover, including all fragments under 5,000 ha, was maintained, and

424   no orangutan was lost due to additional mortality (Figure 2). Conversely, even a low

425   offtake rate of 1% led to markedly reduced population sizes compared to when no

426   offtake was applied (16-19% vs 80 – 82% growth after 50 years respectively). These

427   results corroborate earlier research using a non-spatially explicit approach (Marshall

428   *et al.*, 2009). Given that estimates of current annual offtake rates on Borneo likely

429   exceed 5% (Sherman *et al.*, 2022), our results imply that a drastic reduction of

430 orangutan killing or removal from the landscape is necessary to allow orangutans to

431 persist and recover from past losses.

432   Here, we have assumed spatially homogenous levels of offtake. Information

433 on killings and translocations are geographically dispersed and quite variable across

434 the orangutan range (Sherman et al., 2022). Hunting, retaliatory killing and

435 translocation are driven by different factors, including human presence, cultural

436 norms and belief systems (Meijaard *et al.*, 2011). While spatial data on translocation

437 and orangutan crime exist for Kalimantan (Sherman *et al.*, 2022; Massingham *et al.*,

438 2023), these likely underrepresent hunting in the interior, and there is no information

439 from Sarawak and Sabah. Consequently, we have modelled offtake rates found in

440 Sherman *et al.* (2022) for Borneo uniformly in space and time to understand general

441 impacts across the subspecies. Future modelling work could examine the

442 implications of considering covariates of killing and translocations, and would refine

443 recommendations for local population management and conservation actions.

444   We found that when no offtake was applied orangutan populations increased,

445 regardless of the landscape configuration scenario. Although the percentage increase

446 in population was often greater when fragments were removed, the total population

447 size was always greatest when fragments were maintained in the landscape, although

448 these differences were marginal. While this may suggest habitat fragments are of

449 limited importance, we caution against this view for several reasons. Although

450 fragments under 5,000 ha make up only 4.3% of the total forest suitable for

451 orangutans, these patches may still support considerable numbers of individuals (e.g.

452 >10,000 individuals for *P. p. wurmbii* when no offtake was applied in our models).

453 As well as supporting individual orangutans, fragments will also likely serve as

454 stepping-stones or corridors, aiding range expansion, as suggested by the larger

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number of individuals settling in non-natal patches when fragments were present in the landscape. The use of fragments connecting larger habitat patches is also supported by direct observations from the Kinabatangan region in Sabah, Borneo (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). Thus, despite their lower impact on total modelled orangutan numbers compared to offtake, maintaining forest fragments in the landscape will likely be crucial for allowing species to recover and for maintaining genetic connectivity. Furthermore, such fragments may act as microrefugia and aid in facilitating range shifts in response to climate change (Struebig *et al.*, 2015).

Under the Current Landscape Configuration scenario, a higher proportion of dispersing individuals settled in non-natal patches and dispersed over shorter distances than under the Fragment Removal scenario, although this difference was relatively small (Figure 3). Shorter dispersal distances are likely an important factor in facilitating natural movement in anthropogenic landscapes for highly philopatric female orangutans (Goossens *et al.*, 2006; van Noordwijk *et al.*, 2012). The longer dispersal distance predicted by the model when fragments were removed not only would result in increased energy expenditure during dispersal and likely limit success, but also expose dispersing individuals to increased incidences of negative human-orangutan interactions and heightened risk of contact with novel diseases (Russon, 2009; Ancrenaz *et al.*, 2015). The difference in dispersal distances between landscape scenarios became smaller as offtake rates increased (Figure 4). When individuals are removed from the landscape, the resulting empty or low-density patches likely provide additional opportunities for dispersing individuals to settle. There is a risk however, that under high levels of offtake, fragments may become population sinks if emigration and additional mortality exceeds birth or immigration

rates. Interestingly, for *P. p. pygmaeus* when no offtake was applied the area
occupied after 50 years was slightly larger when fragments were removed, although
the opposite was true for the other two subspecies or when offtake was applied. This
is likely due to lack of fragments - as well as having to travel longer distances, when
orangutans find suitable habitat to settle in these areas are larger and may indicate *P.
p. pygmaeus* habitat is less isolated than for *P. p. wurmbii and P. p. morio.*

A growing body of literature is showing that even small or isolated terrestrial
fragments can support species occupancy (Lion *et al.*, 2016; Scriven *et al.*, 2019).
Similarly, remnant forest patches in anthropogenic landscapes have been shown to
support a large proportion of forest-dependent species (Mitchell *et al.*, 2018; Deere
et al., 2019). Increasing zero-deforestation commitments, uptake of certification
schemes and growing levels of corporate environmental and social responsibility, are
providing opportunities for maintaining and restoring areas of forest within
agricultural landscapes (Morgans *et al.*, 2018). Orangutans are a flagship species that
receive high public support and regularly bring in large amounts of conservation
funding, such as approximately USD 1 billion of conservation funding over 20 years
from 2000 (Santika *et al.*, 2022). Investment in habitat protection, patrolling, and
public outreach has already been shown to be effective in conserving orangutan
populations (Santika *et al.*, 2022). The research we present here adds to the growing
evidence that maintaining forest in anthropogenic landscapes is crucial for species
survival, bringing positive conservation outcomes for biodiversity in general.

A benefit of our approach compared to previous orangutan population viability
assessments is the incorporation of stochastic movement, inter-individual variability
and naivety to the overall landscape within the dispersal process. Through this
approach not all forest patches have equal probability of receiving emigrants, but

505 instead this is highly dependent not only on their spatial arrangement and the cost of

506 moving through the landscape, but also the stochastic movement of individuals. This

507 reflects the process of natural dispersal much better than more correlative models

508 (Coulon *et al.*, 2015). However, the approach relies heavily on the assumptions used

509 to parametrise the models. We based parameters on orangutan behavioural ecology

510 from available data drawn from relatively undisturbed areas, expert opinion and

511 observations from anthropogenic landscapes (Ancrenaz *et al.*, 2021; Oram *et al.*,

512 2022). To capture the influence of those assumptions on model outcomes, we ran a

513 sensitivity analysis that asserted the robustness of the model. This analysis revealed

514 the emigration probability (i.e. the willingness of a female to leave her natal patch)

515 had the greatest effect on the model outcome, although overall effect on patch

516 occupancy was small (≤0.4 %). This is unsurprising, as emigration would directly

517 affect the number of individuals moving across the landscape and impact the

518 probability of patches to be colonised. We know from field observations that females

519 exhibit a high degree of home range fidelity and generally settle close to their

520 mother's home range (Goossens *et al.*, 2006; Ashbury *et al.*, 2020). However, these

521 observations are mostly from areas with very low disturbance and high landscape

522 connectivity. In highly modified (i.e. non-forest dominated) landscapes where small

523 fragments will contain finite resources, individuals are likely to have greater

524 incentive to leave and fewer opportunities to settle close to their mother's home

525 range, which may impact the emigration process, as is reflected in our simulations.

526 Similarly, we initiated our models with patches being at their assumed density

527 equilibrium. Although the starting density may not represent current abundances,

528 which are also driven by ongoing offtake (Marshall *et al.*, 2006) and can vary

529 through time and space (Marshall *et al.*, 2021), we aimed to address this by

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530 summarising densities across broad habitat types (Table 2). However, starting at

531 density equilibrium may lead to a higher level of emigration earlier in the model run

532 or, conversely, may extend the point at which the offtake initially impacts the

533 populations and this should be considered when interpreting our results.

534   The results from the RangeShifter model presented here arise from information

535 on individual behaviour based on assumptions about the animal's interaction with

536 the landscape. The resulting patterns where verified by experts and seem to match

537 broad orangutan dynamics observed in anthropogenic landscapes (e.g. Ancrenaz *et*

538 *al.*, 2015, 2021; Oram *et al.*, 2022). However, an intensification of research efforts

539 to collect more orangutan data from human-modified landscapes and on orangutan

540 movement and dispersal patterns therein, will allow us to refine models further,

541 improving their ability to predict local population responses to management and

542 land-use change.

543 **Conclusion**

544 There is growing recognition of the potential conservation value of forest fragments

545 in human-modified tropical landscapes for forest-dependent species (e.g. Lion *et al.*,

546 2016; Deere *et al.*, 2018). Our research demonstrates the potential importance of

547 these fragments in facilitating movement of a critically endangered vertebrate

548 species across anthropogenic landscapes. This movement is vital to allow dispersal,

549 which is the basis to ensure populations remain genetically connected, can recover in

550 the event of a disturbance and facilitate range shifts in response to future climate

551 change (Årevall *et al.*, 2018; Lino *et al.*, 2019). However, removal of individuals

552 from the landscape via hunting, retaliatory killings and capture and translocation is

553 likely to be a more insidious threat for long-lived, slow reproducing species such as

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554 orangutans, even if connectivity is maintained. Conservation initiatives aimed at

555 retaining and restoring forest areas for the benefit of species like the orangutan,

556 should also address offtake. Broadly, this could be achieved by promoting tolerance

557 of species amongst human populations and thus enhancing co-existence with the

558 species that share these landscapes.

559

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741 **Data Accessibility Statement**

742 The data that support the findings of this study are openly available in Zenodo at

743 https://doi.org/10.5281/zenodo.8386166, reference number 10.5281/zenodo.8386166

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749 **Conflict of interest statement**

750 The authors have no conflict of interest to declare.

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Table 1: Demographic and dispersal parameters of Bornean orangutan populations used in the RangeShifter model, their description, values used and sources. The fecundity ([1]) uses a customised function described in SI1.1. Survival probability at birth ([2]) represents male bias in birth ratio. Survival probability of adolescent and young adult age classes (10-13 years) was implemented with density dependence ([3]). Certain dispersal parameters ([†]) were tested for sensitivity.

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| Parameter	Description	Value	Reference
Demographic			
Fecundity ϕ	Yearly probability of a reproductive female giving birth	0.167^{1}	(van Noordwijk, Atmoko, et al., 2018)
Age-stages & Survival probabilities	Age range (years) and annual survival probability of each age stage		
At birth		0.45^{2}	(van Noordwijk, et al., 2018)
Infant	1-2 years	0.97	(Utami-Atmoko et al., 2019)
Juvenile	3-9 years	0.99	
Adolescent	10-11 years	0.98	
Young adult	12+ years	0.99^{3}	
Adult	13-41 years	0.99^{3}	
Mature adult	42-45 years	0.95	
Senior adult	46-51 years	0.85	
Senescent	52-55+ years	0.75	
Max. age (years)		55	
Dispersal			
Emigration			Expert informed
d_0 Max Emigration probability		$0.2^{†}$	
α_0 (slope)		10	
β_0 (inflection point)		1	
Transfer parameters			Expert informed
Directional persistence		$2.5^{†}$	
Perceptual range (cells)		$25^{†}$	
Memory size (cells)		$10^{†}$	
Max. steps per year		$3,000^{†}$	(Singleton et al., 2009)
Total max. no. of steps		$12,000^{†}$	
Per step mortality		$0.001^{†}$	
Settlement			Expert informed
S_0 Max. Settlement probability		1	
α_S (slope)		$-50^{†}$	
β_S (inflection point)		1	
Offtake rates	Mean precent of the population killed or rescued at different estimated detection rates		
At 62.4% detection rate		0%	(Sherman et al., 2022)
At 10.0% detection rate		1%	
At 6.2% detection rate		2%	
At 3.2% detection rate		4%	
At 1.2% detection rate		10%	

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Table 2: Habitat specific orangutan equilibrium density.
Estimates derived by summarising a density distribution (sensu Voigt *et al*., 2018) by
landcover type (*sensu* Miettinen, Shi and Liew, 2016), and halved to represent the female
only population.

| Habitat type	Subspecies max. carrying capacity (females/km^2)		
	P. p. morio	*P. p . pygmaeus*	*P. p. wurmbii*
Water	0.00	0.00	0.00
Mangrove	0.88	0.05	0.41
Peat swamp	1.50	1.67	2.79
Lowland evergreen	2.81	0.82	2.57
lowland montane evergreen	0.40	0.31	0.49
Upper montane evergreen	0.03	0.01	0.01
Regrowth/plantation	0.25	0.25	0.25
lowland mosaic	2.01	0.67	1.98
Montane mosaic	0.17	0.00	0.01
Lowland open	2.03	1.04	1.84
Montane open	0.17	0.00	0.00
Urban	0.00	0.00	0.00
Large scale oil palm plantation	0.00	0.00	0.00

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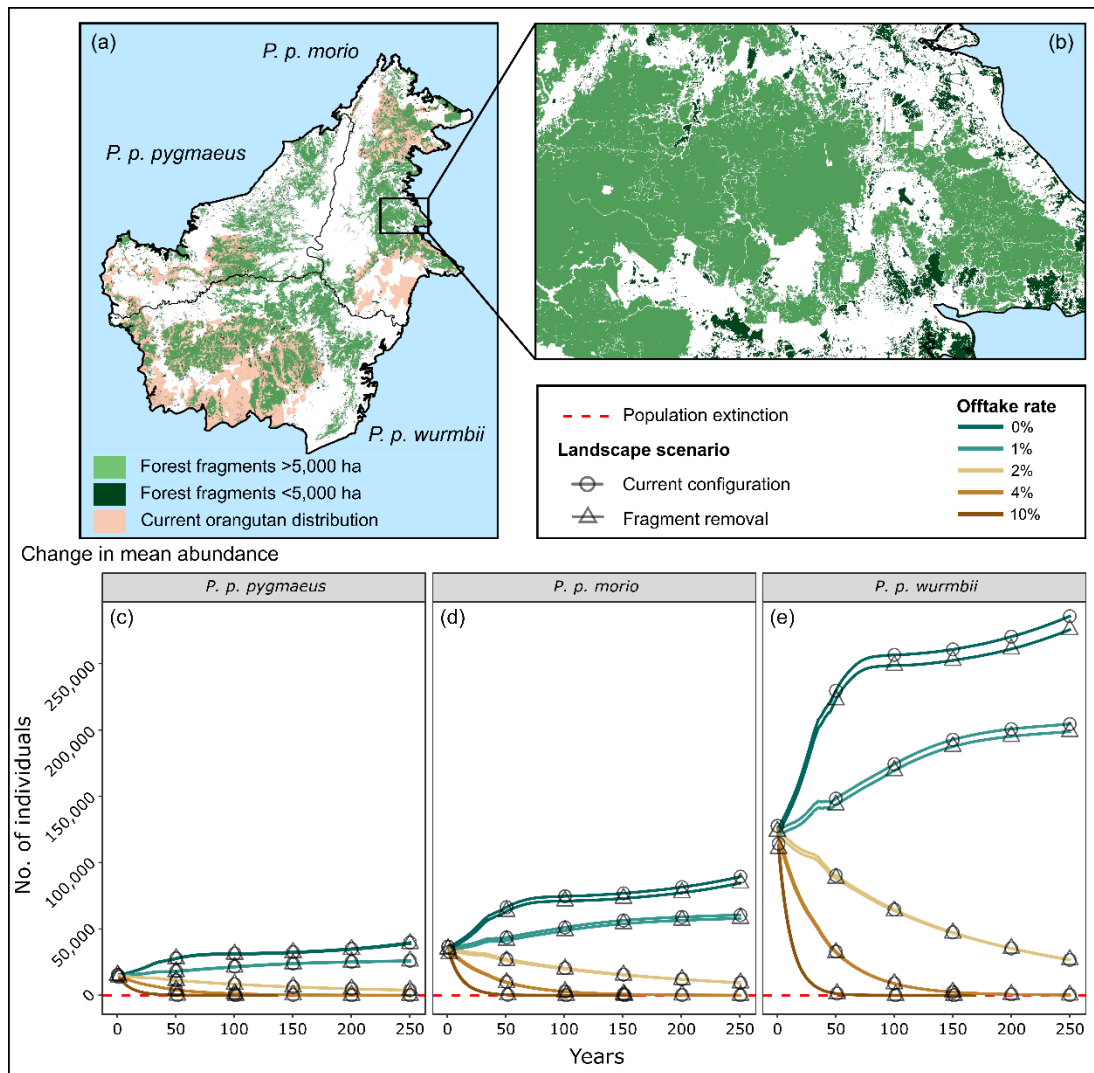
Figure 1 The impact of the Current Landscape Configuration and Fragment Removal scenarios on the Bornean orangutan population size, and under different levels of orangutan off-take.

Simulated population size over time for each orangutan subspecies. (a) Distribution of current forest across Borneo. (b) Example of landscape with fragments ≤ 5,000 ha shown in dark green. (c-e) Subspecies specific changes in abundance after offtake was applied, for the two landscape scenarios (circles: Current Landscape Configuration; triangles: Fragment Removal scenario). Results are from 50 iterations for each of the offtake rates, subspecies and landscape scenarios. Confidence intervals are not shown as they fall within the line.

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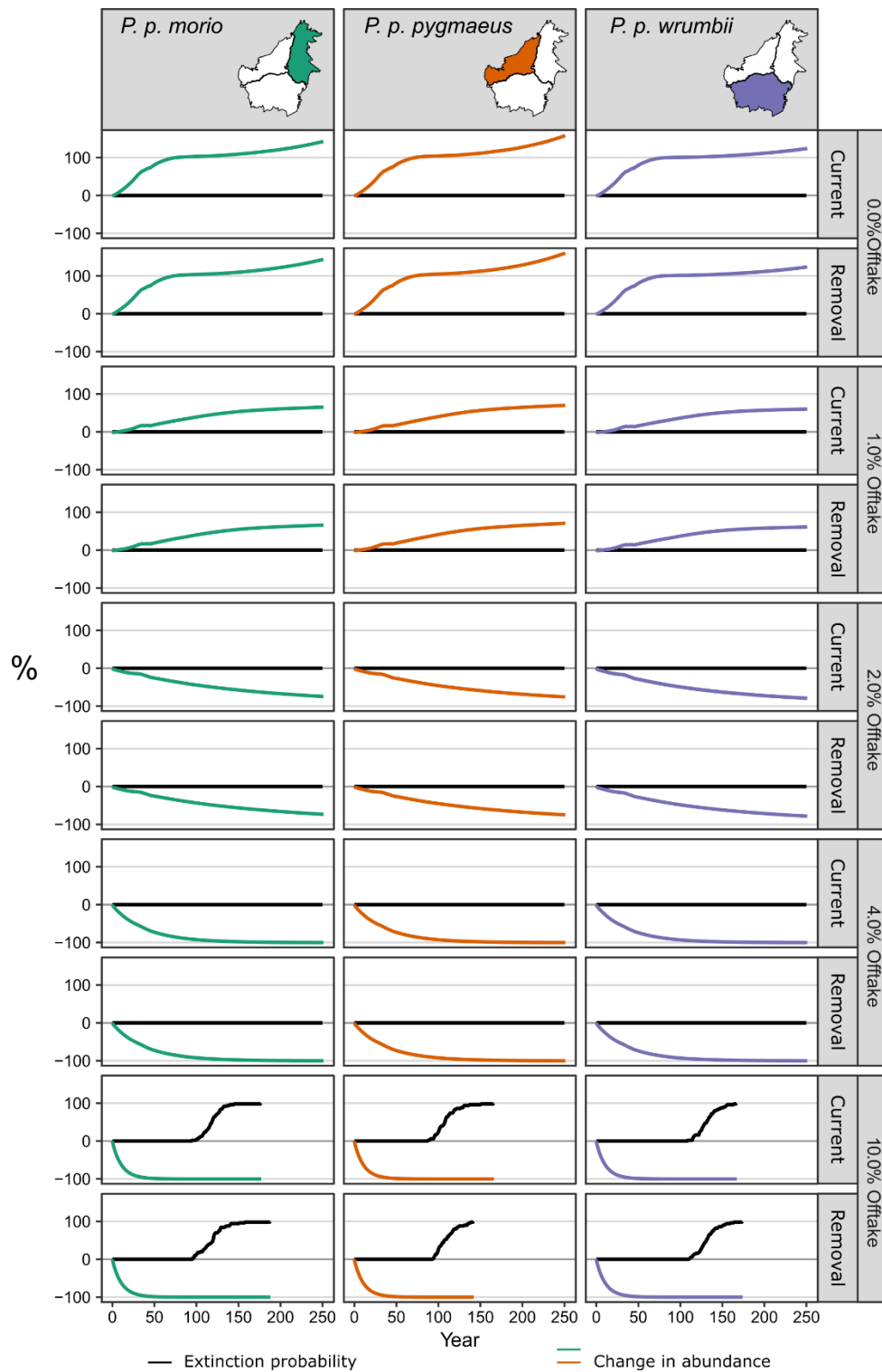
Figure 2 Extinction probability and percentage change in abundance over time from model initiation.

The black lines show the cumulative extinction probability averaged across the 50 iterations for each of the three subspecies, landscape scenarios (Current: Current Landscape Configuration with all existing forest cover suitable for orangutans retained in the landscape; Removal: Fragment Removal scenario with all fragments ≤5,000 ha removed) and offtake rates. Percentage change in abundance is shown in solid coloured lines. We do not show standard error, as it falls within the lines.
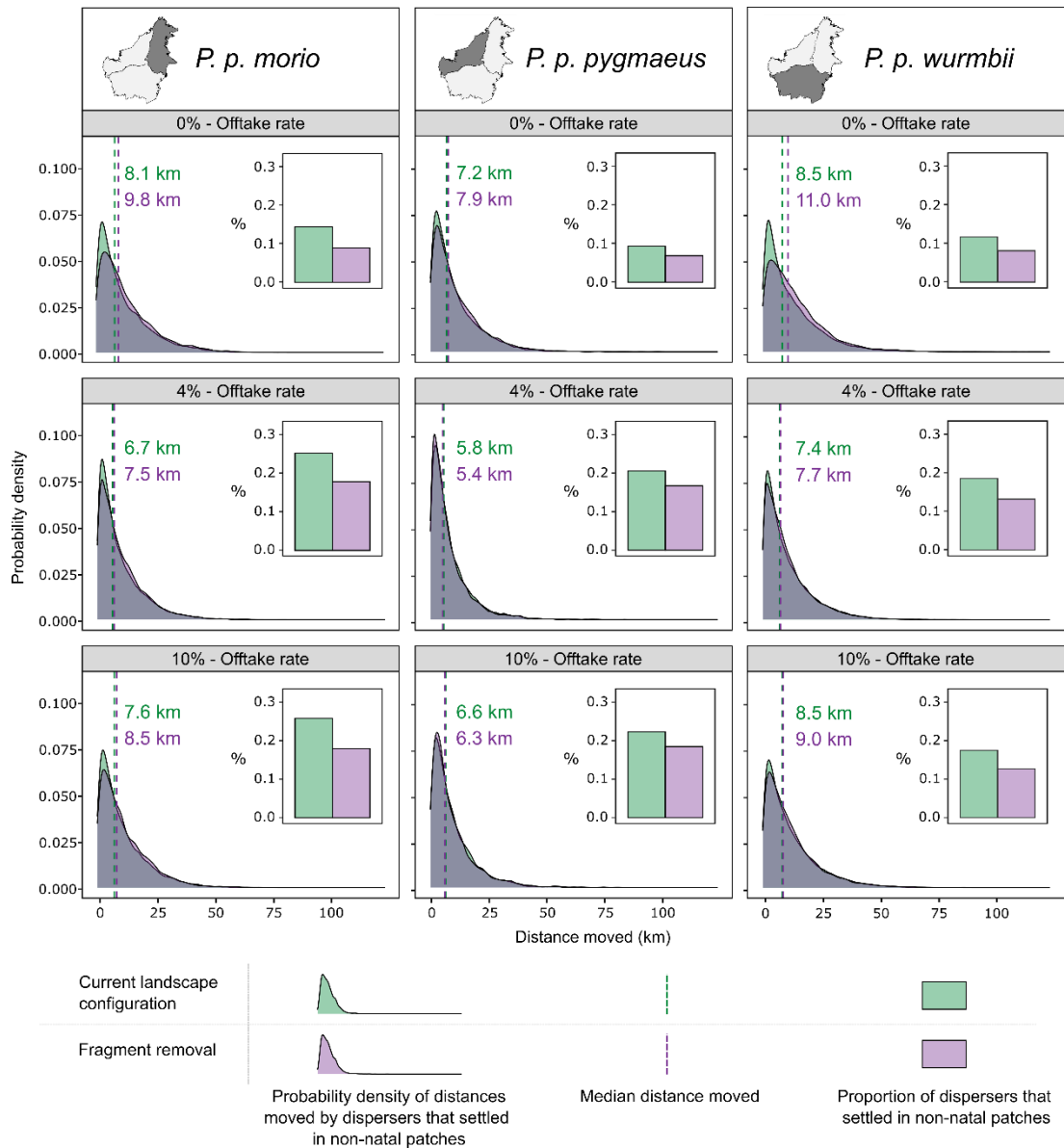
Figure 3: Dispersal distance and success under different landscape and offtake scenarios.

The probability density plots show the distribution of distances taken by successful dispersers (individuals that have settled in non-natal patches) for each subspecies, landscape, and offtake scenario, with dashed lines denoting the median distance travelled. Embedded bar charts show the proportion of dispersing individuals which settled in non-natal patches. We did not plot standard error as they were too fine to display.

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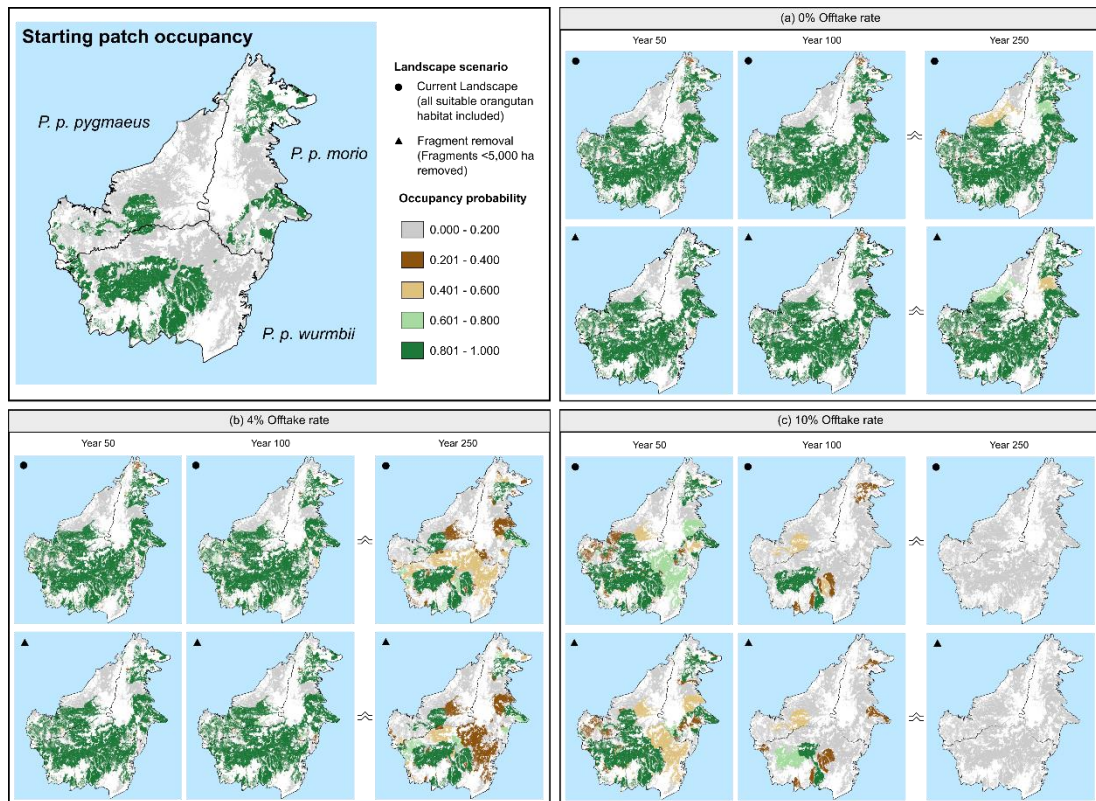
801 **Figure 4. Occupancy probability different fragmentation and offtake scenarios.**

802 Cumulative patch occupancy (proportion of the simulations where each patch was

803 occupied), under the Current Fragmentation and Extreme fragmentation scenario and three

804 offtake (annual proportion of the population removed) rates, (a) no offtake, (b) 4% offtake

805 and (c) 10% offtake.

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