

Capacity for recovery in Bornean orangutan populations when limiting offtake and retaining forest

Abstract

Aim:

We aim to assess the potential long-term viability of orangutan populations across Borneo, considering the effects of habitat loss, fragmentation, and various forms of population reduction, including hunting, retaliatory killings, and capture and translocation.

Location:

Our study focused on the island of Borneo, a region that has experienced substantial deforestation over the past four decades, resulting in the degradation and fragmentation of its lowland forests, thereby threatening the island's unique biodiversity, including orangutan populations.

Methods:

To evaluate the long-term viability of orangutan populations, we employed a spatially-explicit individual-based model. This model allowed us to simulate various scenarios, including the impact of removing habitat fragments and of individuals.

Results:

Our findings revealed that small forest fragments were found to facilitate orangutan movement, thereby increasing the number of individuals settling in non-natal patches. However more crucially, orangutan populations proved highly vulnerable to even small levels of offtake. Annual removal rates exceeding 2% diminish the positive role of small forest patches in sustaining population connectivity, their long-term viability and population 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 prioritize preservation of habitat and fragments as stepping stones, and mitigate negative human-wildlife interactions. 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

35 **Introduction**

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

51 Despite the potential benefits of habitat fragments as refugia and for connectivity,
52 populations within them are likely to be at greater risk of environmental and demographic
53 stochasticity, such as caused by drought, fire, disease, or other fluctuations in population size. If
54 mortality exceeds recruitment from births and emigration, fragments may become population
55 sinks (Gilroy and Edwards, 2017). While there is a large body of research regarding the impacts
56 of habitat fragmentation on biodiversity, the potential importance of forest fragments in
57 facilitating connectivity and species population viability in human-modified tropical landscapes
58 is not well studied (Scriven *et al.*, 2019), particularly with large bodied primates (Ancrenaz *et*
59 *al.*, 2021), undermining our ability to guide conservation planning.

60 Despite international commitments to halt biodiversity loss, species such as the orangutan
61 (*Pongo* spp.) have been declining steeply over the past two decades (Wich *et al.*, 2016; Nowak *et*
62 *al.*, 2017; Voigt *et al.*, 2018). Orangutan population losses in both Borneo and Sumatra have
63 been driven by deforestation, as well as hunting and retaliatory killings (Ancrenaz *et al.*, 2016;
64 Nowak *et al.*, 2017; Singleton *et al.*, 2017). Orangutans are also lost from populations through
65 captures and translocations, where individuals are removed from areas following a real or
66 perceived risk that the individual is killed otherwise (Sherman *et al.*, 2021). Orangutans depend
67 on forest for survival and large populations and highest densities are found in protected areas and
68 other remaining forests with low anthropogenic pressure (Voigt *et al.*, 2018). However,
69 orangutans can survive in human-modified landscapes in the absence of killing, where forest
70 remnants offer sufficient food and nesting opportunities (Ancrenaz *et al.*, 2021). Although
71 typically at low population densities (Seaman *et al.*, 2019), most individuals are in good health
72 (Rayadin and Spehar, 2015) and appear to be able to survive and reproduce in fragmented

73 landscapes for extended periods of time (>20 years) (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022).
74 Forest fragments may therefore play an important role in connecting larger areas of orangutan
75 habitat and preventing further population segregation and decline.

76 As there is currently a dearth of orangutan data from human-dominated landscapes,
77 population viability analysis can be used to provide insights into the population dynamics and
78 survival probability. However, to date, these models have failed to account for spatially explicit
79 habitat dynamics (Marshall *et al.* 2009, Utami-Atmoko 2019) and oftaken or have assumed
80 perfect knowledge of the landscape and no inter-individual variation in dispersal behaviour
81 (Gregory *et al.* 2014).

82 Advances in modelling and computational power have led to the development of
83 increasingly complex simulations to study dynamic environmental systems (Kool, Moilanen and
84 Treml, 2013). Individual-based models epitomise this progress and are increasingly popular in
85 ecological studies (Zurell *et al.*, 2022). The use of individual-based modelling approaches to
86 study species responses to environmental change or management options, has several advantages
87 over other commonly used methods. For example, species distribution and environmental niche
88 models assume that populations are at equilibrium and that species presence data are correlated
89 with environmental covariates, but this is rarely the case (Urban *et al.*, 2016). Individual-based
90 models can address several of these limitations by incorporating population dynamics in space
91 and time, as well as species movement and inter-individual variation in the stochastic processes
92 that govern species distributions (Bocedi *et al.*, 2014; Urban *et al.*, 2022). As such, individual-
93 based models are likely to become increasingly important tools in managing biodiversity and
94 landscapes (Synes *et al.*, 2016).

95 Here we employ a spatially explicit individual-based model, integrating demography and
96 spatially explicit dispersal behaviour, to predict the potential long-term consequences of
97 deforestation, loss of fragments in anthropogenic landscapes and oftaken (hunting, retaliatory
98 killings and capture and translocation) on orangutan populations across Borneo. As a charismatic
99 great ape species, orangutans attract a lot of public attention and are relatively well studied. We
100 use the existing data on abundance, life history and population dynamics to showcase the
101 analytical potential of the Individual Based approach for this species, but the method and
102 conclusions could be equally applicable to other species that face challenges from habitat loss
103 and oftaken.

104 **Methods**

105 *Study system*

106 Bornean orangutans are found across approximately 30% (227,000 km²) of Borneo (IUCN,
107 2021: Figure 1a). The island is topographically complex, with the interior being predominantly
108 mountainous, giving way to lowland forest (≤ 500 m asl) and peat swamps towards coastal areas.

109 Borneo is governed among Indonesia (Kalimantan), Malaysia (Sabah and Sarawak) and Brunei
110 Darussalam, although orangutans are absent from the latter.

111 Genetic data suggest that major rivers and mountain ranges have been a significant
112 barrier to movement across evolutionary time scales for orangutans (Jalil *et al.*, 2008). This
113 separation has resulted in sufficient genetic divergence for the Bornean orangutan population to
114 be divided into three subspecies, the largest being the Southwest Bornean orangutan (*Pongo*
115 *pygmaeus wurmbii*) found across southern, west and central Kalimantan. The Northeast Bornean
116 orangutan (*P. p. morio*) ranges from Sabah to East Kalimantan, and the Northwest Bornean
117 orangutan (*P. p. pygmaeus*) remains as a small population in Sarawak and northwest of
118 Kalimantan. Although the demography of orangutans is broadly consistent across Borneo (van
119 Noordwijk *et al.*, 2018), environmental variation, such as soil type and rain fall, leads to
120 considerable differences in densities across the subspecies (Voigt *et al.*, 2018). We capture this
121 variation in abundance, by considering movement and population dynamic separately for each
122 subspecies.

123 *Modelling framework*

124 We modelled orangutan population dynamics and dispersal using a customised version of
125 RangeShifter 2.0. RangeShifter is an individual-based population viability and connectivity
126 modelling platform, which allows users to simulate joint population dynamics and spatially
127 explicit dispersal, whilst including inter-individual stochasticity (Bocedi *et al.*, 2021). We used a
128 version of the base-model that included a potential management options for controlling invasive
129 and non-native species through culling (https://github.com/RangeShifter/RS_CONTAIN).
130 However, rather than simulating culling of an invasive species, we used it to model killing or
131 translocation of orangutan individuals. With the model we investigated the combined long-term
132 effects of habitat loss, removal of fragments and offtake on orangutan population viability and
133 connectivity.

134 *Landscape characterization*

135 We used a fine-scale 30 m resolution gridded system (raster) to define our study landscape, to
136 which we applied a patch-based model. Patches are aggregations of suitable habitat cells forming
137 defined spatial clusters (specified below), where each patch is considered a discrete population.
138 We developed a landcover layer based on high resolution forest maps for 2017 (v1.5, Hansen *et*
139 *al.*, 2013) to coincide with orangutan density values from 2016 (Voigt *et al* 2018) that were used
140 to populate patches. Forest was defined according to Margono *et al* (2014) as stands >5 ha with a
141 natural composition and structure that had not been cleared in recent history (until 2017) and
142 having >70% tree canopy cover. We acquired forest loss data from the Global Forest Change
143 repository (v1.5; Hansen *et al* 2013) and applied it to forest cover data from 2000. We further
144 refined these maps by setting pixels which were prominently within areas of either water

145 (including major rivers) or urban development to *no-data*, using habitat layers by Miettinen, Shi
146 and Liew, (2016).

147 *Demographic model*

148 Male orangutans will range over large distances, often encompassing multiple female home
149 ranges and are unlikely to be a limiting factor in reproduction (Nietlisbach et al., 2012). We,
150 therefore implemented a female-only model, with stage-structured demographics, comprising
151 nine stages (Table 1). Rather than reduce the fecundity to reflect female births only, we set a
152 survival probability of stage one individuals of 0.45 to represent the slight male-biased sex ratio
153 at birth (van Noordwijk *et al.*, 2018). We derived subsequent survival probabilities from the most
154 recent orangutan Population and Habitat Viability Analysis report (Utami-Atmoko *et al.*, 2019;
155 Table 1). We added density dependence in both fecundity and development to the youngest
156 breeding stage (Table 1). The demographic model is described in detail in the Supplementary
157 Information SI 1. The strength of the density dependency (*l/b* parameters) for each habitat type
158 were informed by density estimates for 2016 from the most recent range wide density
159 distribution model (Voigt et al., 2018). These densities were summarised across discrete
160 landcover types and independently for each of the three subspecies. As we only modelled
161 females, we then halved density estimates (Table 2).

162 *Patch allocation*

163 On Borneo, orangutans predominantly occupy lowland forest areas and are generally absent
164 from, or found at very low densities at higher altitudes (Husson *et al.*, 2009). Thus, we focussed
165 our analysis on all suitable lowland habitat (≤ 500 m asl) having the potential to support
166 orangutans irrespective of whether they are currently present, thereby allowing for possible
167 future colonisation and range expansion.

168 Large rivers and multi-lane highways are likely to hinder orangutan movement (Utami-
169 Atmoko *et al.*, 2019). Large rivers and Major roads were derived from OpenStreetMap
170 (OpenStreetMap Contributors, 2022b, 2022a) using the identifiers “Primary”, “Primary_link”,
171 “Motorway”, “Motorway_link”, “Trunk” and “Trunk_link”. We thus divided all forest blocks
172 that were intersected by major roads and rivers to reflect potential movement constraints. The
173 current orangutan distribution crosses several large areas of forest, which would otherwise be
174 considered a continuous patch; in order to initialise the model with individuals within the current
175 range, we intersected forest areas with the IUCN orangutan range polygon (Ancrenaz *et al.*,
176 2016).

177 In RangeShifter, local populations are modelled within forest areas, which are called
178 patches, and each patch is assigned a unique identity. Orangutan nests have been observed in oil
179 palm plantations up to 50 m from natural forest areas and orangutans are regularly observed
180 making short-distance excursions into plantations (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022).

181 Therefore, small natural forest fragments close to larger forested areas are likely to be
182 incorporated into the home ranges of female orangutans. To represent this in the model
183 landscape, we placed a 50 m buffer around all forest areas and considered all fragments within
184 the buffer to be part of the same patch as the larger forest area. Patches were then assigned a
185 unique ID based on the spatial arrangement of forest fragments, whereby all fragments within
186 ≤ 100 m (if 50 m buffers overlapped) were assigned the same identity and considered a
187 discontinuous patch. If a patch was too small to support an orangutan based on the summarised
188 densities (Table 2), we removed these patches from the patch layers, but retained them for the
189 cost and landcover layer, as even small forest patches will provide resources and limit the cost of
190 moving across the landscape.

191 *Dispersal parameters*

192 RangeShifter simulates dispersal through three distinct processes: emigration, transfer, and
193 settlement (Travis *et al.*, 2012). Female orangutans display a high degree of philopatry, and it is
194 almost exclusively males that disperse over long distances (Nietlisbach *et al.*, 2012; Ashbury *et al.*,
195 2020). Therefore, range expansion is limited by short distance dispersal of females. We
196 further assumed that dispersal was limited to young adult females and characterised by a strong
197 density dependence in both emigration and settlement probabilities, replicating a high degree of
198 philopatry. We parametrised density dependence in emigration so that females would stay within
199 their natal patch until the patch reached its equilibrium density, above which there was a
200 maximum probability of 0.2 that a female would leave the patch.

201 To model the transfer (movement) process, we used the stochastic movement simulator,
202 an individual-based model which simulates step-based movements across a cost surface (Palmer,
203 Coulon and Travis, 2011), nested within RangeShifter 2.0. Here, movement trajectories during
204 transfer are governed by three parameters: perceptual range, directional persistence, and
205 memory. We based these parameters on previous expert judgement of visualised simulated
206 trajectories (Seaman *et al.*, 2021, described in Supplementary information). If a female
207 orangutan leaves her natal patch and is unable to find suitable habitat, we assumed it was likely
208 that she would return, and as a result, we modified the base version of RangeShifter 2.0 to allow
209 individuals to return and settle in their natal patch, even if it was at carrying capacity.

210 A female will usually settle close to or within the mother's home range (van Noordwijk
211 *et al.*, 2012; Ashbury *et al.*, 2020). This was approximated in the model by parameterising the
212 settlement probability at 100% with a steep density dependence. This parameterisation means a
213 female will almost certainly settle once reaching a patch, unless that patch is close to or above its
214 equilibrium density, at which point there is a rapid reduction in the settlement probability (Figure
215 SI 3). Through these two independent processes, emigration and settlement, females will only
216 leave their natal patch if the patch cannot support them, because it is at or above its carrying
217 capacity and will then settle at the first available opportunity. As there is limited information on

218 orangutan dispersal within human-modified landscapes, we undertook a sensitivity analysis to
219 determine how robust our model was to changes in dispersal parameters (Table 1).

220 *Cost surface*

221 We built a cost surface layer using a land-cover layer, a digital elevation model and observations
222 of terrestrial movement of orangutans and expert information. Although being predominantly
223 arboreal, terrestrial movement is a common behaviour for orangutans on Borneo. However, this
224 form of locomotion requires additional energetic expenditure, as well as risks from predation and
225 novel diseases (Ancrenaz *et al.*, 2014; Ashbury *et al.*, 2015). To capture this nuance, we created
226 a cost surface based on Tobler's hiking function using the Distance Accumulation tool in
227 ArcGIS Pro (v2.6.0; ESRI, 2020). We used three inputs, a 30 m digital elevation model (Farr *et*
228 *al.*, 2007), expert informed resistance surface values based on habitat type (Table SI 2), and
229 known barriers to movement (major roads and rivers, OpenStreetMap Contributors, 2022a,
230 2022b). To ensure rivers and major highways were represented in the simulated landscape and to
231 prevent diagonal movement between barrier pixels, we buffered all major roads and rivers by 50
232 m and pixels were assigned a no-data value. We included all suitable forest areas as starting
233 points, i.e. where cost was assigned the lowest value of 1. The resulting surface is a cost to
234 movement layer, where the cost increases when moving away from natural forest areas, mediated
235 by the resistance of the habitat type, degree of slope and barriers within the landscape (Figure SI
236 2).

237 *Landscape fragmentation and offtake scenarios*

238 We developed scenarios to explore the relative effects of both loss of fragments from the
239 landscape and offtake on orangutan population dynamics and connectivity. To investigate the
240 effects of fragment loss we established two landscape scenarios; the "Current landscape
241 configuration" scenario included all forest suitable for orangutans (≤ 500 m asl) across Borneo
242 and represented the landscape configuration in 2017. Small forest fragments are at much greater
243 risk of being deforested (Hansen *et al.*, 2020) and any fragment < 5000 ha is currently considered
244 unviable for supporting an orangutan population (Utami-Atmoko *et al.*, 2019; Sherman *et al.*,
245 2020), potentially increasing its risk for clearing as a consequence of perceived lower usefulness
246 to conservation. We therefore produced a scenario in which we removed all fragments $< 5,000$
247 ha, representing a worst-case scenario "Fragment removal". Patch and cost surfaces were
248 produced for the landscapes with and without fragments (Figures SI 1 and SI 2).

249 For both landscape scenarios, we modelled five potential yearly offtake rates from
250 hunting, retaliatory killing and/or live capture and translocation: 0%, 1%, 2%, 4% and 10% of
251 the population, estimated from published studies and extrapolations from crime data (Sherman *et*
252 *al.*, 2022). Individuals were removed from patches selected at random and individuals could be
253 removed from all age groups, as killing and translocation affect orangutans across age groups
254 (Sherman, Ancrenaz and Meijaard, 2020).

255 *Model initialisation and metrics*

256 Before applying the model to our landscape scenarios, we calibrated the strength of the density
257 dependency ($1/b$ parameter) on an artificial landscape to ensure the demographic model was
258 behaving correctly and the population reached the expected densities after reaching equilibrium.
259 After calibration, we initialised the model using the IUCN distribution (Ancrenaz *et al.*, 2016)
260 for each subspecies, populating all suitable patches within the range at equilibrium density. To
261 investigate the potential long-term effects of orangutan offtake and fragment removal, we ran
262 models for 250 years, i.e. approximately 10 generations. Each scenario was run with 50
263 iterations to allow for model stochasticity. We applied the five offtake rates to both landscape
264 scenarios, resulting in 10 model outcomes for each subspecies.

265 We recorded six metrics during the model runs: 1) the total population size at each time
266 step; 2) the percentage change in population compared to the starting population; 3) the
267 cumulative probability that the population becomes extinct across the 50 iterations at each 10-
268 year time interval; 4) the area occupied after 50 and 250 years (patch occupancy); 5) the
269 percentage of individuals settling in non-natal patches (dispersal success); 6) individual
270 dispersal distances.

271 *Sensitivity analysis*

272 The largest degree of uncertainty in our connectivity model comes from the dispersal parameters,
273 as relatively little is known about dispersal behaviour of female orangutans. Therefore, we
274 undertook a sensitivity analysis to determine the robustness of the model to these parameters,
275 mostly pertaining to orangutan movement (Table 1), by increasing and decreasing baseline
276 values by 5%. In particular, we varied perceptual range between 24 and 26, directional
277 persistence between 2.6 and 2.4 and memory between 11 and 8. In addition, we tested the
278 models sensitivity to 5% variations of other model parameters, specifically in the maximum
279 number of steps, maximum total number of steps, per step mortality, maximum emigration
280 probability (α_s), and the slope of the density dependency in settlement (d_0). For each permutation
281 we ran a baseline model (Current landscape configuration and no hunting pressure) for 250 years
282 and 50 iterations. We assessed the model sensitivity by comparing the proportion of patches
283 occupied at 250 years to the baseline model.

284 **Results**

285 Our demographic model revealed that in both landscape scenarios (Current landscape
286 configuration and Fragment removal) the populations of all three-orangutan subspecies increased
287 from their initial size and expanded their range over the duration of the model run when no
288 additional mortality was applied (Figures 1 & 2). All three subspecies increased in population
289 size over the first 50 years of the model run (80% – 82%), and continued to increase thereafter,
290 although at a slower rate until the final population size at 250 years (123% - 159% increase from

291 starting population). Although there was a similar percentage increase in population between
292 landscape scenarios, total abundance was on average 4% higher (1.8% - 5.4% or 724 individuals
293 for *P. p. pygmaeus* and 10,150 for *P. p. wurmbii*) under the Current landscape configuration and
294 when no offtake was applied. In both scenarios, the population growth had not reached an
295 asymptote, suggesting the population would continue to increase after 250 years (Figures 1 & 2).
296 When no offtake was applied, the extinction probability for all model outcomes among
297 subspecies and landscape scenarios over the modelled time frame was zero (Figure 2).

298 Even the lowest modelled offtake rate had a substantial effect on the projected population
299 size. When a 1% offtake rate was applied, the population increased, but substantially less at 50
300 years than under no offtake (16-19% from starting population) and after 250 years populations
301 had only increased by 60-71% (Fig. 1 & 2). This difference in population growth compared to no
302 offtake was most severe for *P. p. wurmbii*, which was projected to grow by 60% (from an initial
303 population of 128,000 to 205,000; ± 120 s.e. at 250 years) when the Current landscape
304 configuration was maintained and by 61% (from 124,000 to 199,000, ± 121) under the Fragment
305 removal scenario, a final abundance that was 28% lower than when no offtake was applied.

306 For both landscape scenarios, a 2% offtake rate led to marked declines in abundance
307 across subspecies of 76% on average after 250 years (73 – 79% Figure 1 and Table SI 2). When
308 we applied a 4% offtake rate, the population loss was substantial, with a >99% decrease in
309 abundance for all model outcomes after 250 years. Despite these large abundance declines,
310 offtake rates until 4% did not lead to an extinction of any subspecies within 250 years. However,
311 at an offtake rate of 4% and higher, overall numbers were reduced in a way that would likely
312 lead to a functional extinction of many of the populations (with 4 - 68 individuals of *P. p.*
313 *pygmaeus*, 28 - 106 individuals of *P. p. morio* and 183 - 284 individuals of *P. p. wurmbii* after
314 4% offtake was applied for 250 years for the entire landscape, in both landscape scenarios). The
315 highest offtake modelled of 10% resulted a 100% extinction probability for all subspecies under
316 both landscape configuration scenarios within before 250 years (Figure 2).

317 *Orangutan dispersal for different scenarios*

318 The percentage and number of dispersing individuals settling in non-natal patches was higher
319 under the current landscape configuration than under the fragment removal scenario. For
320 example, annually for *P. p. morio* 14% (± 0.10) of dispersing individuals or 28 (± 1.6) orangutans
321 successfully settled in a non-natal patch and 69% (± 0.15) or 133 individuals (± 3.8) settled in
322 their natal patch, when no offtake was applied. However, in the fragment removal scenario only
323 9% (± 0.11) of dispersers or 16 (± 1.2) individuals settled in a non-natal patch, and 73% (± 0.90) or
324 127 (± 3.8) individuals settled in their natal patch. In both the scenario a similar number of
325 individuals died during dispersal, 18% (± 0.15) or 31 when fragments were removed and 16%
326 (± 0.11) or 32 individuals under the current landscape configuration. Generally, a similar pattern
327 was observed when offtake was applied, but with a smaller majority settling in natal-patches and
328 a slightly higher percentage settling in non-natal patches (Figure 3), likely due to reduced

329 densities after offtake was applied allowing the settlement probability to increase. Despite these
330 differences, there was a consistent pattern among all scenarios, with a similar number of
331 individuals dying during dispersal but a higher percentage of individuals settling in non-natal
332 patches and fewer in natal patches under the Current landscape configuration, when fragments
333 were retained.

334 For all offtake scenarios, the median dispersal distance (from the natal patch to the non-
335 natal patch where individuals successfully settled) was generally greater when fragments had
336 been removed (Fragment removal scenario, Figure 3), although this difference was generally < 2
337 km. The greatest difference in dispersal distances between landscape scenarios was without
338 removal of orangutans. This difference was particularly true for *P. p. wurmbii*, which had a
339 median dispersal distance of 8.5 km under the current landscape configuration compared to 11
340 km in the fragment removal scenario. When offtake was applied this difference generally
341 decreased (Figure 3).

342 *Orangutan occupancy in different scenarios*

343 There was a substantial increase in the area occupied by the subspecies through dispersal after
344 the first 50 years of the model run, although with some variation among species (Figure 4). The
345 greatest increase was observed with *P. p. pygmaeus* which expanded from 21,858 km² at year
346 zero to 59,670 km² (± 305) in the Current landscape configuration scenario and from 21,486 km²
347 to 59,835 km² (± 610) in the Fragment removal scenario (or a 173% and 178% increase
348 respectively). *P. p. wurmbii* had a much smaller percentage increase after the first 50 years from
349 90,624 km² to 172,574 km² in the Current landscape configuration scenario and from 87,445 km²
350 to 167,560 km² (± 26) in the Fragment removal scenario (or a 90% and 92% increase
351 respectively), although occupying a much larger area.

352 Under the different rates of offtake, the area occupied was smaller than without offtake. When
353 the highest offtake of 10% was applied, the area occupied initially increased over the first 50
354 years, although at a much smaller rate than with no or less offtake (ranging from 24 – 45%
355 increase from starting area). After 80 years however, occupied areas had decreased from the
356 starting population under all landscape configuration scenarios with a 10% offtake rate.

357 *Sensitivity analysis*

358 Our sensitivity analysis on dispersal parameters led to only small variations in model outcomes
359 for both patch occupancy and final abundance, suggesting our model is relatively robust to
360 dispersal parameters (Figure SI 6). For all three subspecies, changing the maximum emigration
361 probability had the largest effect on patch occupancy, and although outside the standard error of
362 the baseline scenario (Current landscape configuration and no offtake), the proportion of
363 occupied patches differed by no more than 0.4% or an average of 4.3 patches, with this largest
364 deviation from *P. p. morio* (Figure SI 6).

365 Discussion

366 We modelled spatially explicit population dynamics for Bornean orangutans under landscape and
367 offtake scenarios, revealing that in the absence of additional killing, orangutan populations are
368 likely to increase in number and distribution. Although orangutan numbers increased regardless
369 of whether fragments were removed from the current landscape, the largest population size was
370 observed when the current forest cover, including all fragments under 5000 ha was maintained,
371 and no orangutan was lost due to additional mortality (Figure 2). Conversely, even a low offtake
372 rate of 1% led to markedly reduced population sizes compared to when no offtake was applied
373 (16-19% vs 80 – 82% growth after 50 years respectively). These results corroborate earlier
374 research using a non-spatially explicit approach (Marshall *et al.*, 2009). Given that estimates of
375 current annual offtake rates on Borneo are likely exceeding 5% (Sherman *et al.*, 2022), our
376 results suggest that a drastic reduction of orangutan killing or removal from the landscape is
377 necessary to allow orangutans to persist and recover from past losses. Here, we have assumed
378 spatially homogenous levels of offtake. Information on location of killings and translocations
379 within Kalimantan is likely to be spatially variable. Hunting, retaliatory killing and translocation
380 are driven by different variables, including human presence and other factors such as cultural
381 norms and belief systems (Meijaard *et al.*, 2011). Spatial data on translocation and orangutan
382 crime exist (Sherman *et al.*, 2022; Massingham *et al.*, 2023) but are likely underrepresenting
383 hunting in the interior and are absent for Sarawak and Sabah. Consequently, we have modelled
384 offtake rates found in Sherman *et al.* (2022) for Borneo uniformly in space and time to
385 understand general impacts across the subspecies. Future modelling work could examine the
386 implications of considering covariates of killing and translocations, and would refine
387 recommendations for local population management, and conservation actions.

388 We found that when no offtake was applied orangutan populations increased, regardless
389 of if fragments were removed from the landscape or not. Although the percentage increase in
390 population was often greater when fragments were removed, the total population size was always
391 greatest when fragments were maintained in the landscape, albeit these differences were only
392 marginal. While this result may suggest fragments are of limited importance, we would caution
393 against this view for several reasons. Although fragments under 5000 ha make up only 4.3% of
394 the total orangutan suitable forest cover, they may still support substantial numbers of
395 orangutans (e.g. >10,000 individuals for *P. p. wurmbii* when no offtake was applied in our
396 models). As well as supporting individual orangutans, fragments will also likely serve as
397 stepping-stones or corridors, aiding range expansion, as suggested by the larger number of
398 individuals settling in non-natal patches when fragments were present in the landscape. The use
399 of fragments connecting larger habitat fragments is also supported by direct observations from
400 the Kinabatangan region in Sabah, Borneo (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). Thus,
401 despite their limited impact on total orangutan numbers compared to offtake, maintaining
402 fragments in the landscape will likely then be crucial for allowing species recovery, maintaining

403 genetic connectivity, and may act as microrefugia and aid in facilitating range shifts in response
404 to climate change (Struebig *et al.*, 2015).

405 Under the Current landscape configuration scenario, a higher proportion of dispersing
406 individuals settled in non-natal patches and dispersed over shorter distances than under the
407 Fragment removal scenario, albeit this difference was relatively small (Figure 3). Shorter
408 dispersal distances are likely an important factor in facilitating natural movement in
409 anthropogenic landscapes for highly philopatric female orangutans (Goossens *et al.*, 2006; van
410 Noordwijk *et al.*, 2012). The longer dispersal distance predicted by the model when fragments
411 were removed, not only would result in increased energy expenditure during dispersal and likely
412 limit success, but also expose dispersing individuals to increased incidences of negative human-
413 orangutan interactions and heightened risk of contact with novel diseases (Russon, 2009;
414 Ancrenaz *et al.*, 2015). The difference in dispersal distances between landscape scenarios
415 became smaller as offtake rates increased (Figure 4). When individuals are removed from the
416 landscape, the resulting empty or low-density patches likely provide additional opportunities for
417 dispersing individuals to settle. There is a risk however, that under high levels of offtake,
418 fragments may become populations sinks if emigration and additional mortality exceeds birth or
419 immigration rates. Interestingly, for *P. p. pygmaeus* when no offtake was applied the area
420 occupied after 50 years was slightly larger when fragments were removed, although the opposite
421 was true for the other two subspecies or when offtake was applied. This is likely due to lack of
422 fragments meaning that, as well as having to travel longer distances, when orangutans find
423 suitable habitat to settle in, these areas are larger and may indicate *P. p. pygmaeus* habitat is less
424 isolated than for *P. p. wurmbii* and *P. p. morio*.

425 A growing body of literature is showing that even small or isolated terrestrial fragments
426 can support species occupancy (Lion *et al.*, 2016; Scriven *et al.*, 2019). Similarly, remnant forest
427 patches in anthropogenic landscapes have been shown to support a large proportion of forest
428 dependant species (Mitchell *et al.*, 2018; Deere *et al.*, 2019). Increasing zero-deforestation
429 commitments, uptake of certification schemes and growing levels of corporate environmental
430 and social responsibility, are providing opportunities for maintaining and restoring areas of forest
431 within agricultural landscapes (Morgans *et al.*, 2018). Orangutans are a flagship species, which
432 receive high public support and regularly bring in large amounts of conservation funding, e.g.
433 approximately USD 1 billion of conservation funding over 20 years from 2000 (Santika *et al.*,
434 2022). Investment in habitat protection, patrolling, and public outreach has already been shown
435 to be effective in conserving orangutan populations (Santika *et al.*, 2022). The research we
436 present here adds to the growing evidence base of the importance of maintaining forest in
437 anthropogenic landscape. By doing this it will likely have positive conservation outcomes for the
438 wider biodiversity.

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

442 have equal probability of receiving emigrants, but instead this is highly dependent not only on
443 their spatial arrangement and the cost of moving through the landscape, but also the stochastic
444 movement of individuals. This reflects the process of natural dispersal much better than more
445 correlative models (Coulon *et al.*, 2015). However, the approach relies heavily on the
446 assumptions used to parametrise the models. We based parameters on orangutan behavioural
447 ecology from available data drawn from relatively undisturbed areas, expert opinion and
448 observations from anthropogenic landscapes (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). To
449 capture the influence of those assumptions on model outcomes, we ran a sensitivity analysis that
450 asserted the robustness of the model. This analysis revealed the emigration probability, i.e. the
451 willingness of a female to leave her natal patch, had the greatest effect on the model outcome,
452 although overall effect on patch occupancy was small ($\leq 0.4\%$). This is unsurprising, as
453 emigration would directly affect the number of individuals moving across the landscape and
454 impact the probability of patches to be colonised. We know from field observations that females
455 exhibit a high degree of home range fidelity and generally settle close to their mother's home
456 range (Goossens *et al.*, 2006; Ashbury *et al.*, 2020). However, these observations are mostly
457 from areas with very low disturbance and high landscape connectivity. In highly modified (i.e.
458 non-forest dominated) landscapes where small fragments will contain finite resources,
459 individuals are likely to have greater incentive to leave and fewer opportunities to settle close to
460 their mother's home range, which may impact the emigration process, as is reflected in our
461 simulations. Similarly, we initiated our models with patches being at their assumed density
462 equilibrium. Although the starting density may not represent current abundances, which are also
463 driven by ongoing offtake (Marshall *et al.*, 2006) and can vary through time and space (Marshall
464 *et al.*, 2021), we aimed to address this by summarising densities across broad habitat types
465 (Table 2). However, starting at density equilibrium may lead to a higher level of emigration
466 earlier in the model run or, conversely, may extend the point at which the offtake initially
467 impacts the populations and this should be considered when interpreting our results.

468 The results from the RangeShifter model presented herein and in Seaman *et al.* (2021),
469 arise from individual behaviour based on assumptions in interaction with the landscape, where
470 verified by experts and seem to match broad orangutan dynamics observed in the landscapes
471 they work in (e.g. Ancrenaz *et al.*, 2015, 2021; Oram *et al.*, 2022). However, an intensification
472 of research efforts to collect more orangutan data from human-modified landscapes and on
473 orangutan movement and dispersal patterns in these landscapes, will allow us to refine models
474 further, improving their ability to predict local population responses to management and land-use
475 change.

476 **Conclusion**

477 There is growing recognition of the potential conservation value of forest fragments in human-
478 modified tropical landscapes for forest-dependent species (e.g. Lion *et al.*, 2016; Deere *et al.*,
479 2018). Our research demonstrates the potential importance of these fragments in facilitating

480 movement of a critically endangered vertebrate species across anthropogenic landscapes. This
481 movement is vital to allow dispersal, which is the basis to ensure populations remain genetically
482 connected, can recover in the event of a disturbance and facilitate range shifts in response to
483 future climate change (Årevall *et al.*, 2018; Lino *et al.*, 2019). However, removal of individuals
484 from the landscape via hunting, retaliatory killings and capture and translocation is likely to be a
485 more insidious threat for long lived, slow reproducing species such as orangutans even if
486 connectivity is maintained. For conservation initiatives aimed at retaining and restoring forest
487 areas within human-modified landscapes to be successful for species like the orangutan, they
488 will therefore also need to address offtake, through promoting tolerance and co-existence with
489 the species which share these landscapes.

References

- 490
491 Ancrenaz, M. *et al.* (2014) ‘Coming down from the trees: Is terrestrial activity in Bornean
492 orangutans natural or disturbance driven?’, *Scientific reports*, 4(Journal Article), p. 4024.
- 493 Ancrenaz, M. *et al.* (2015) ‘Of Pongo, palms and perceptions: a multidisciplinary assessment of
494 Bornean orang-utans *Pongo pygmaeus* in an oil palm context’, *Oryx*, 49(3), pp. 465–472.
- 495 Ancrenaz, M. *et al.* (2016) “‘Pongo pygmaeus”, The IUCN Red List of Threatened Species
496 2016: e.T17975A17966347.
497 <http://dx.doi.org/10.2305/IUCN.UK.20161.RLTS.T17975A17966347.en>. Downloaded on
498 23 October 2017.’, (Journal Article).
- 499 Ancrenaz, M. *et al.* (2021) ‘Importance of small forest fragments in agricultural landscapes for
500 maintaining orangutan metapopulations’, *Frontiers in Forests and Global Change*,
501 4(Journal Article), p. 5.
- 502 Årevall, J. *et al.* (2018) ‘Conditions for successful range shifts under climate change: The role of
503 species dispersal and landscape configuration’, *Diversity and Distributions*, 24(11), pp.
504 1598–1611.
- 505 Arora, N. *et al.* (2010) ‘Effects of Pleistocene glaciations and rivers on the population structure
506 of Bornean orangutans (*Pongo pygmaeus*)’, *Proceedings of the National Academy of
507 Sciences of the United States of America*, 107(50), pp. 21376–21381. Available at:
508 <https://doi.org/10.1073/pnas.1010169107>.
- 509 Ashbury, A.M. *et al.* (2015) ‘Why do orangutans leave the trees? Terrestrial behavior among
510 wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan’,
511 *American Journal of Primatology*, 77(11), pp. 1216–1229.
- 512 Ashbury, A.M. *et al.* (2020) ‘Home range establishment and the mechanisms of philopatry
513 among female Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan’, *Behavioral
514 Ecology and Sociobiology*, 74(4), pp. 1–21.
- 515 Bocedi, G. *et al.* (2014) ‘RangeShifter: a platform for modelling spatial eco-evolutionary
516 dynamics and species’ responses to environmental changes’, *Methods in Ecology and
517 Evolution*, 5(4), pp. 388–396.
- 518 Bocedi, G. *et al.* (2021) ‘RangeShifter 2.0: an extended and enhanced platform for modelling
519 spatial eco-evolutionary dynamics and species’ responses to environmental changes’,
520 *Ecography* [Preprint], (Journal Article).
- 521 Coulon, A. *et al.* (2015) ‘A stochastic movement simulator improves estimates of landscape
522 connectivity’, *Ecology*, 96(8), pp. 2203–2213.
- 523 Deere, N.J. *et al.* (2018) ‘High Carbon Stock forests provide co-benefits for tropical
524 biodiversity’, *Journal of Applied Ecology*, 55(2), pp. 997–1008.

525 Deere, N.J. *et al.* (2019) ‘Implications of zero-deforestation commitments: Forest quality and
526 hunting pressure limit mammal persistence in fragmented tropical landscapes’,
527 *Conservation Letters*, (Journal Article), p. e12701.

528 ESRI (2020) ‘ArcGIS Pro Release 2.6. 0’, *Environmental Systems Research Institute: Redlands,*
529 *CA, USA* [Preprint].

530 Farr, T.G. *et al.* (2007) ‘The Shuttle Radar Topography Mission’, *Reviews of Geophysics*, 45(2),
531 p. 2005RG000183. Available at: <https://doi.org/10.1029/2005RG000183>.

532 Gaveau, D.L. *et al.* (2014) ‘Four decades of forest persistence, clearance and logging on
533 Borneo’, *PloS one*, 9(7), p. e101654.

534 Gaveau, D.L.A. *et al.* (2016) ‘Rapid conversions and avoided deforestation: examining four
535 decades of industrial plantation expansion in Borneo’, *Scientific Reports*, 6(1), p. 32017.
536 Available at: <https://doi.org/10.1038/srep32017>.

537 Gilroy, J.J. and Edwards, D.P. (2017) ‘Source-sink dynamics: a neglected problem for
538 landscape-scale biodiversity conservation in the tropics’, *Current Landscape Ecology*
539 *Reports*, 2(1), pp. 51–60.

540 Goossens, B. *et al.* (2006) ‘Philopatry and reproductive success in Bornean orang-utans (*Pongo*
541 *pygmaeus*)’, *Molecular ecology*, 15(9), pp. 2577–2588.

542 Haddad, N.M. *et al.* (2015) ‘Habitat fragmentation and its lasting impact on Earth’s ecosystems’,
543 *Science Advances*, 1(2), p. e1500052.

544 Hansen, M.C. *et al.* (2013) ‘High-resolution global maps of 21st-century forest cover change’,
545 *science*, 342(6160), pp. 850–853.

546 Hansen, M.C. *et al.* (2020) ‘The fate of tropical forest fragments’, *Science Advances*, 6(11), p.
547 eaax8574.

548 Husson, S.J. *et al.* (2009) ‘Orangutan distribution, density, abundance and impacts of
549 disturbance’, *Orangutans: Geographic variation in behavioral ecology and conservation*,
550 (Journal Article), pp. 77–96.

551 Jalil, M. *et al.* (2008) ‘Riverine effects on mitochondrial structure of Bornean orang-utans
552 (*Pongo pygmaeus*) at two spatial scales’, *Molecular ecology*, 17(12), pp. 2898–2909.

553 Kool, J.T., Moilanen, A. and Treml, E.A. (2013) ‘Population connectivity: recent advances and
554 new perspectives’, *Landscape Ecology*, 28(2), pp. 165–185.

555 Laurance, S.G. (2004) ‘Landscape connectivity and biological corridors’, *Agroforestry and*
556 *biodiversity conservation in tropical landscapes*, 1, pp. 50–63.

557 Lino, A. *et al.* (2019) ‘A meta-analysis of the effects of habitat loss and fragmentation on genetic
558 diversity in mammals’, *Mammalian Biology*, 94(1), pp. 69–76.

- 559 Lion, M.B. *et al.* (2016) ‘The conservation value of small fragments for Atlantic Forest reptiles’,
560 *Biotropica*, 48(2), pp. 265–275.
- 561 Marshall, A.J. *et al.* (2006) ‘The blowgun is mightier than the chainsaw in determining
562 population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East
563 Kalimantan’, *Biological Conservation*, 129(4), pp. 566–578.
- 564 Marshall, A.J. *et al.* (2009) ‘Orangutan population biology, life history, and conservation’,
565 *Orangutans: Geographic variation in behavioral ecology and conservation*, (Journal
566 Article), pp. 311–326.
- 567 Marshall, A.J. *et al.* (2021) ‘Biotic and abiotic drivers of dispersion dynamics in a large-bodied
568 tropical vertebrate, the Western Bornean orangutan’, *Oecologia*, 196(3), pp. 707–721.
569 Available at: <https://doi.org/10.1007/s00442-021-04964-1>.
- 570 Massingham, E. *et al.* (2023) ‘Killing of orangutans in Kalimantan - Community perspectives on
571 incidence and drivers’, *Conservation Science and Practice*, 5(11), p. e13025. Available at:
572 <https://doi.org/10.1111/csp2.13025>.
- 573 Meijaard, E. *et al.* (2011) ‘Quantifying killing of orangutans and human-orangutan conflict in
574 Kalimantan, Indonesia’, *PLoS One*, 6(11), p. e27491.
- 575 Miettinen, J., Shi, C. and Liew, S.C. (2016) ‘2015 Land cover map of Southeast Asia at 250 m
576 spatial resolution’, *Remote Sensing Letters*, 7(7), pp. 701–710.
- 577 Mitchell, S.L. *et al.* (2018) ‘Riparian reserves help protect forest bird communities in oil palm
578 dominated landscapes’, *Journal of Applied Ecology*. Edited by C. Banks-Leite, 55(6), pp.
579 2744–2755. Available at: <https://doi.org/10.1111/1365-2664.13233>.
- 580 Morgans, C.L. *et al.* (2018) ‘Evaluating the effectiveness of palm oil certification in delivering
581 multiple sustainability objectives’, *Environmental Research Letters*, 13(6), p. 064032.
- 582 van Noordwijk, M.A. *et al.* (2012) ‘Female philopatry and its social benefits among Bornean
583 orangutans’, *Behavioral Ecology and Sociobiology*, 66(6), pp. 823–834.
- 584 van Noordwijk, M.A. *et al.* (2018) ‘The slow ape: High infant survival and long interbirth
585 intervals in wild orangutans’, *Journal of human evolution*, 125(Journal Article), pp. 38–49.
- 586 Nowak, M.G. *et al.* (2017) “‘Pongo tapanuliensis”, The IUCN Red List of Threatened Species
587 2017: e.T120588639A120588662.
588 <http://dx.doi.org/10.2305/IUCN.UK.20173.RLTS.T120588639A120588662.en>.
589 Downloaded on 23 October 2017.’, (Journal Article).
- 590 OpenStreetMap Contributors (2022a) ‘Indonesia (with East Timor). [online] OpenStreetMap.
591 Available at: <https://download.geofabrik.de/asia/indonesia.html> [Accessed 07 Feb 2022].’
- 592 OpenStreetMap Contributors (2022b) ‘Malaysia, Singapore, and Brunei. [online]
593 OpenStreetMap. Available at: [https://download.geofabrik.de/asia/malaysia-singapore-
594 brunei.html](https://download.geofabrik.de/asia/malaysia-singapore-brunei.html) [Accessed 07 Feb 2022].’

- 595 Oram, F. *et al.* (2022) “Engaging the Enemy”: Orangutan (*Pongo pygmaeus morio*)
596 conservation in human modified environments in the Kinabatangan floodplain of Sabah,
597 Malaysian Borneo’, *International Journal of Primatology*, pp. 1–28.
- 598 Pillay, R. *et al.* (2021) ‘Tropical forests are home to over half of the world’s vertebrate species’,
599 *Frontiers in Ecology and the Environment*, n/a(n/a). Available at:
600 <https://doi.org/10.1002/fee.2420>.
- 601 Rayadin, Y. and Spehar, S.N. (2015) ‘Body mass of wild Bornean orangutans living in human-
602 dominated landscapes: Implications for understanding their ecology and conservation’,
603 *American Journal of Physical Anthropology*, 157(2), pp. 339–346.
- 604 Russon, A.E. (2009) ‘Orangutan rehabilitation and reintroduction’, *Orangutans: Geographic*
605 *variation in behavioral ecology and conservation*, (Journal Article), pp. 327–350.
- 606 Santika, T. *et al.* (2022) ‘Effectiveness of 20 years of conservation investments in protecting
607 orangutans’, *Current Biology*, 32(8), pp. 1754–1763.
- 608 Scriven, S.A. *et al.* (2019) ‘Testing the benefits of conservation set-asides for improved habitat
609 connectivity in tropical agricultural landscapes’, *Journal of Applied Ecology*, 56(10), pp.
610 2274–2285.
- 611 Seaman, D.J. *et al.* (2019) ‘Densities of Bornean orang-utans (*Pongo pygmaeus morio*) in
612 heavily degraded forest and oil palm plantations in Sabah, Borneo’, *American Journal of*
613 *Primatology*, 81(8), p. e23030.
- 614 Seaman, D.J. *et al.* (2021) ‘Orangutan movement and population dynamics across human-
615 modified landscapes: implications of policy and management’, *Landscape Ecology*,
616 36(10), pp. 2957–2975.
- 617 Senior, R.A., Hill, J.K. and Edwards, D.P. (2019) ‘Global loss of climate connectivity in tropical
618 forests’, *Nature Climate Change*, 9(8), pp. 623–626. Available at:
619 <https://doi.org/10.1038/s41558-019-0529-2>.
- 620 Seymour, F. and Harris, N.L. (2019) ‘Reducing tropical deforestation’, *Science*, 365(6455), pp.
621 756–757.
- 622 Sherman, J. *et al.* (2020) ‘Envisioning a future for Bornean orangutans: Conservation impacts of
623 action plan implementation and recommendations for improved population outcomes’,
624 *Biodiversitas*, 21(2), pp. 465–477.
- 625 Sherman, J. *et al.* (2021) ‘Disease risk and conservation implications of orangutan
626 translocations’, *Frontiers in Veterinary Science*, p. 1290.
- 627 Sherman, J. *et al.* (2022) ‘Orangutan killing and trade in Indonesia: Wildlife crime, enforcement,
628 and deterrence patterns’, *Biological Conservation*, 276, p. 109744.

- 629 Sherman, J., Ancrenaz, M. and Meijaard, E. (2020) ‘Shifting apes: Conservation and welfare
630 outcomes of Bornean orangutan rescue and release in Kalimantan, Indonesia’, *Journal for*
631 *Nature Conservation*, (Journal Article), p. 125807.
- 632 Singleton, I. *et al.* (2017) “‘Pongo abelii”, The IUCN Red List of Threatened Species 2017:
633 e.T121097935A115575085. [http://dx.doi.org/10.2305/IUCN.UK.2017-](http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T121097935A115575085.en)
634 [3.RLTS.T121097935A115575085.en](http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T121097935A115575085.en). Downloaded on 23 October 2017.’, (Journal
635 Article).
- 636 Struebig, M.J. *et al.* (2015) ‘Anticipated climate and land-cover changes reveal refuge areas for
637 Borneo’s orang-utans’, *Global Change Biology*, 21(8), pp. 2891–2904. Available at:
638 <https://doi.org/10.1111/gcb.12814>.
- 639 Synes, N.W. *et al.* (2016) ‘Emerging opportunities for landscape ecological modelling’, *Current*
640 *Landscape Ecology Reports*, 1(4), pp. 146–167.
- 641 Travis, J.M. *et al.* (2012) ‘Modelling dispersal: an eco-evolutionary framework incorporating
642 emigration, movement, settlement behaviour and the multiple costs involved’, *Methods in*
643 *Ecology and Evolution*, 3(4), pp. 628–641.
- 644 Urban, M.C. *et al.* (2016) ‘Improving the forecast for biodiversity under climate change’,
645 *Science*, 353(6304).
- 646 Urban, M.C. *et al.* (2022) ‘Coding for life: Designing a platform for projecting and protecting
647 global biodiversity’, *BioScience*, 72(1), pp. 91–104.
- 648 Utami-Atmoko, S. *et al.* (2019) *Orangutan population and habitat viability assessment: final*
649 *report. Report of the IUCN/SSC Conservation Breeding Specialist Group* [Preprint],
650 (Journal Article).
- 651 Voigt, M. *et al.* (2018) ‘Global demand for natural resources eliminated more than 100,000
652 Bornean orangutans’, *Current Biology*, 28(5), pp. 761-769. e5.
- 653 Wich, S.A. *et al.* (2016) ‘Land-cover changes predict steep declines for the Sumatran orangutan
654 (Pongo abelii)’, *Science Advances*, 2(3), p. e1500789.
- 655 Zurell, D. *et al.* (2022) ‘Spatially explicit models for decision-making in animal conservation
656 and restoration’, *Ecography*, 2022(4).

657 **Data Accessibility Statement**

658 The data that support the findings of this study are openly available in Zenodo at
659 <https://doi.org/10.5281/zenodo.8386166>, reference number 10.5281/zenodo.8386166

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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 SII.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.

Parameter	Description	Value	Reference
Demographic			
Fecundity ϕ	Yearly probability of a reproductive female giving birth	0.167 ¹	(van Noordwijk, Atmoko, et al., 2018)
<i>Age-stages & Survival probabilities</i>			
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			
<i>Emigration</i>			
d_0 Max Emigration probability		0.2 [†]	Expert informed
α_0 (slope)		10	
β_0 (inflection point)		1	
<i>Transfer parameters</i>			
Directional persistence		2.5 [†]	Expert informed
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 [†]	
<i>Settlement</i>			
S_0 Max. Settlement probability		1	Expert informed
α_S (slope)		-50 [†]	
β_S (inflection point)		1	
Offtake rates			
	Mean percent 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%	

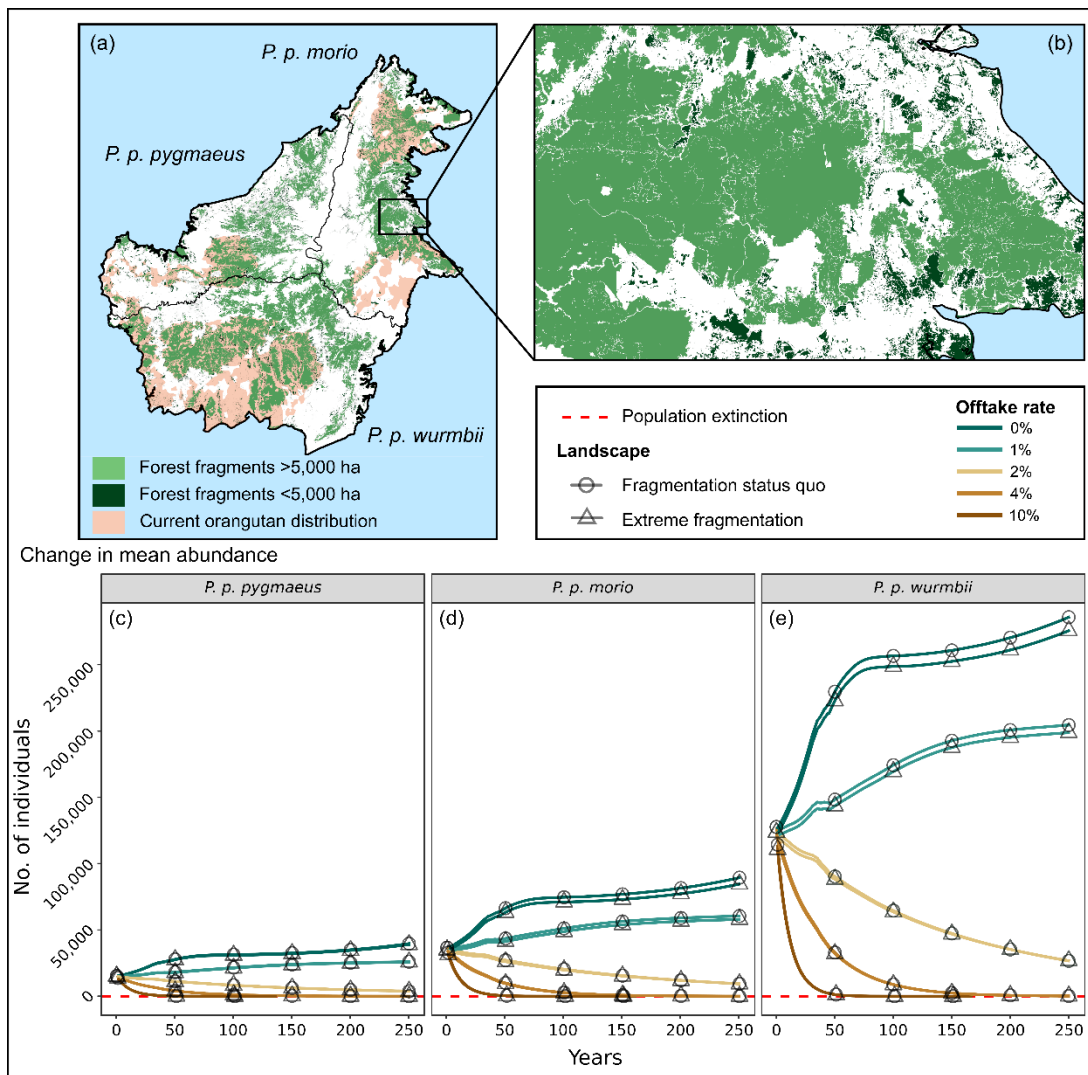
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Table 2: Habitat specific orangutan equilibrium density. Estimates derived by summarising a density distribution (sensu Voigt *et al.*, 2018) by landcover type (sensu Miettinen, Shi and Liew, 2016), and halved to represent the female only population.

Habitat type	Subspecies max. carrying capacity (females/km ²)		
	<i>P. p. morio</i>	<i>P. p. pygmaeus</i>	<i>P. p. wurmbii</i>
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

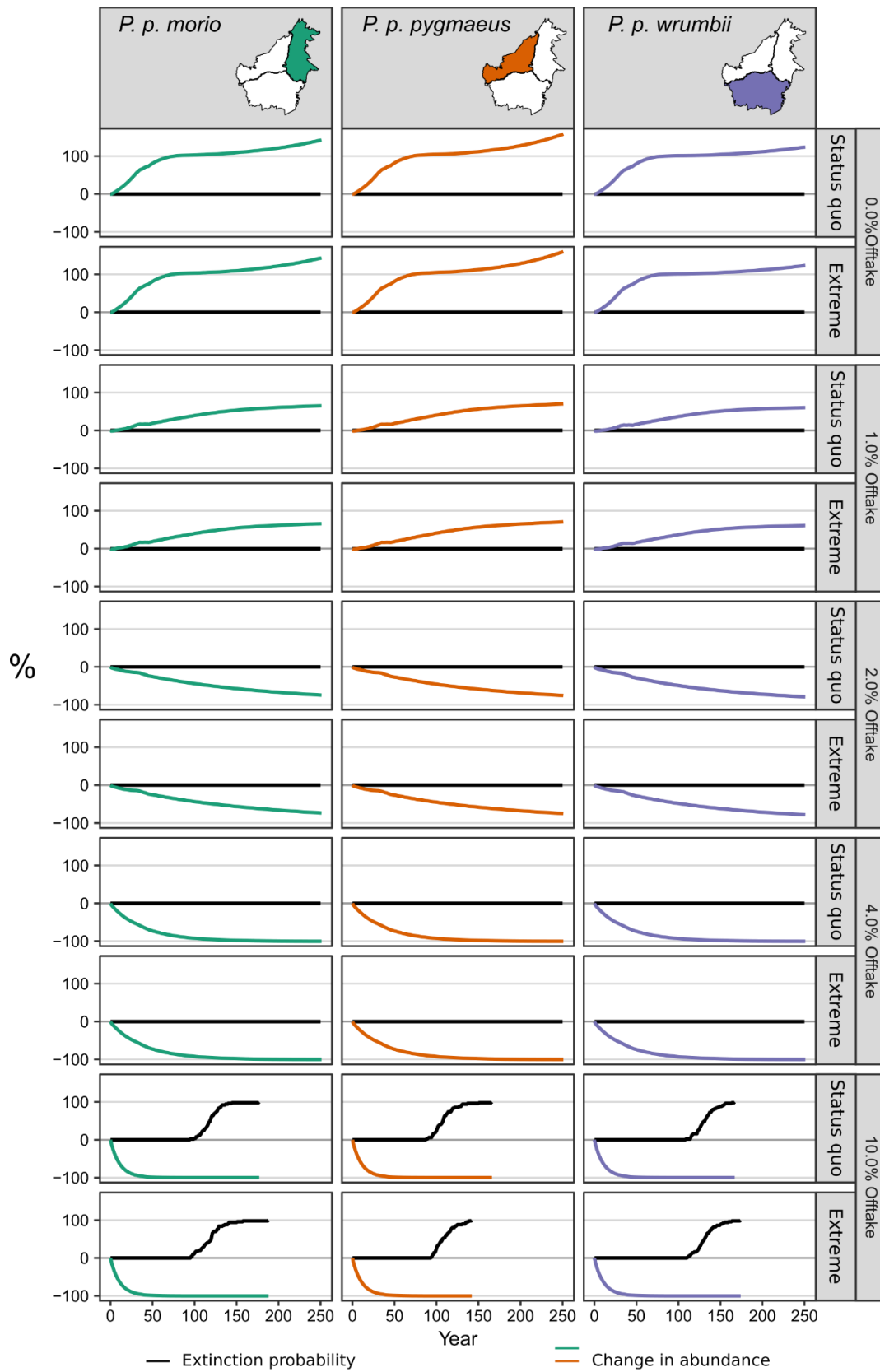
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671 **Figure 1** The impact of current forest fragmentation and different levels of orangutan off-take on
 672 the Bornean orangutan range-wide population size.

673 Population size over time for each orangutan subspecies. (a) Distribution of forest fragments across
 674 Borneo. (b) Example of landscape, with fragments $\le 5,000\text{ ha}$ shown in dark green. (c-e) Subspecies
 675 specific changes in abundance after offtake was applied, for the two fragmentation scenarios (circles:
 676 Fragmentation status quo; triangles: Extreme fragmentation).

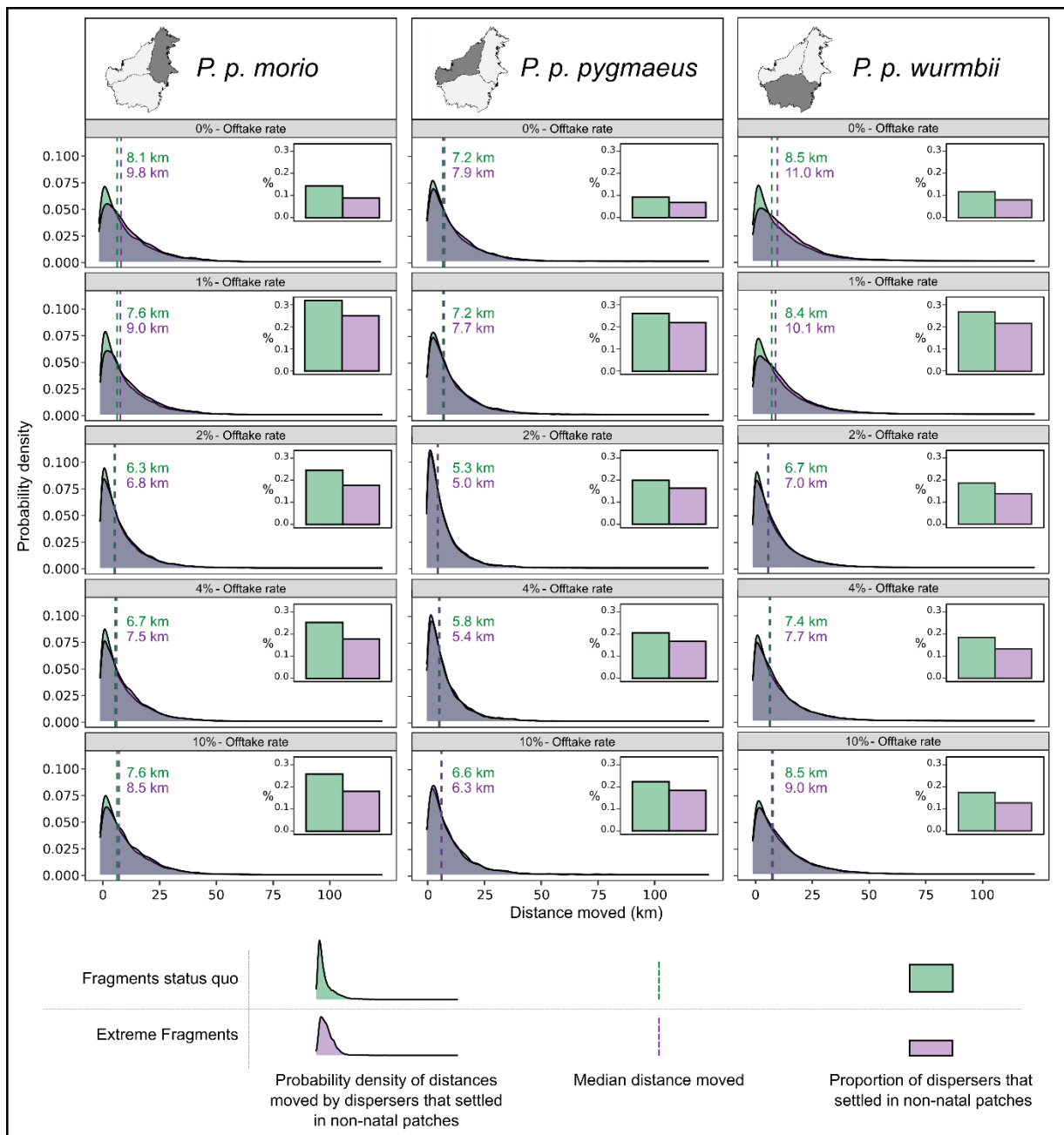


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Figure 2 Extinction probability and percentage change in abundance.

The black lines show the cumulative extinction probability averaged across the 50 iterations. for each subspecies, landscape, and offtake scenario. Percentage change in abundance is shown in solid colours lines. We do not show standard error, as it falls within the lines.



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Figure 3: Dispersal distance and success under different fragmentation and offtake scenarios.

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The probability density plots show the distribution of distances taken by successful dispersers (individuals

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that have settled in non-natal patches) for each subspecies, landscape, and offtake scenario, with dashed

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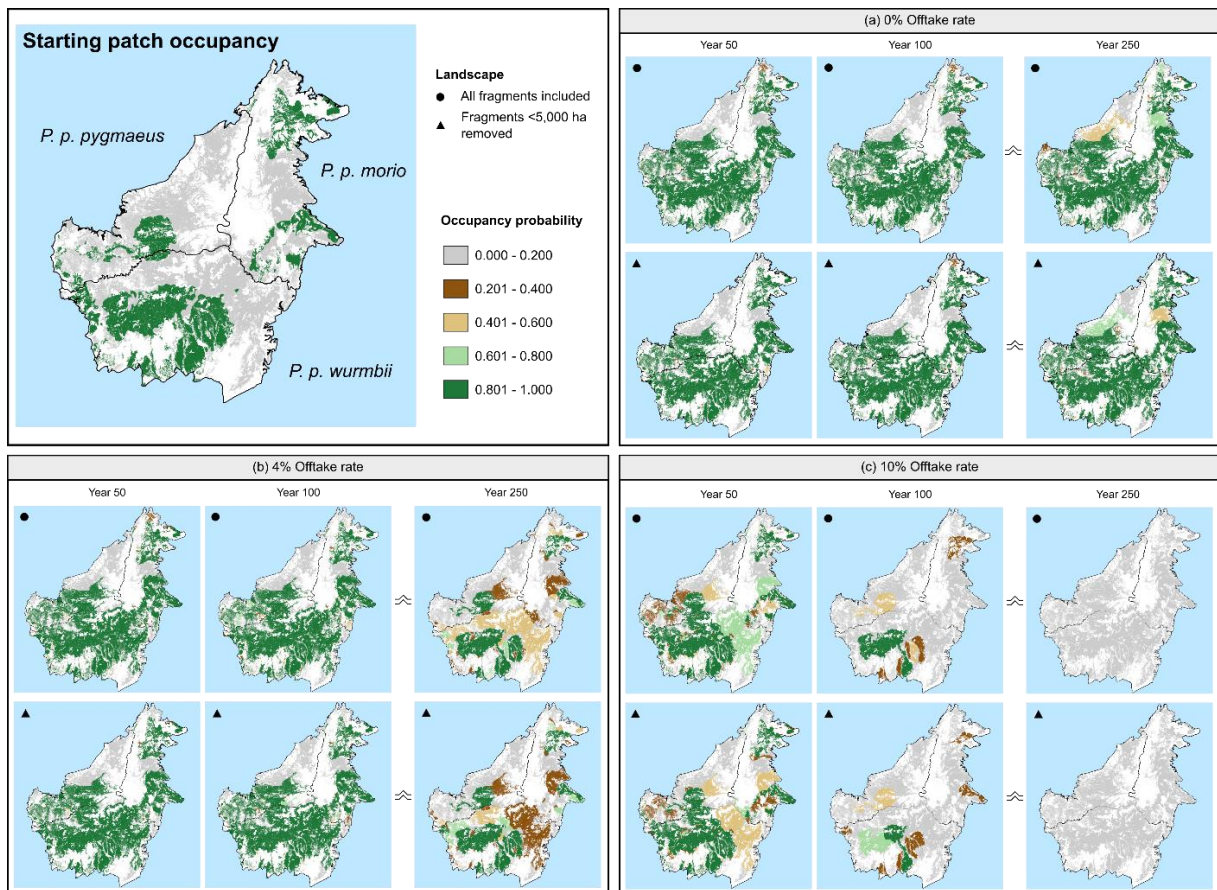
lines denoting the median distance travelled. Embedded bar charts show the proportion of dispersing

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individuals which settled in non-natal patches. We did not plot standard error as they were too fine to

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display.



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Figure 4. Occupancy probability different fragmentation and offtake scenarios. Cumulative patch occupancy (proportion of the simulations where each patch was occupied), under the Current Fragmentation and Extreme fragmentation scenario and three offtake (annual proportion of the population removed) rates, (a) no offtake, (b) 4% offtake and (c) 10% offtake.