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Title

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

Running title

Bornean Orangutan: Recovery Prospects

Abstract

Aim:

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

Location:

The 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 or individuals from 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 fragments in facilitating connectivity and species population viability in human-modified tropical landscapes is not well studied (Scriven *et al.*, 2019), particularly for large bodied primates (Ancrenaz *et al.*, 2021), undermining our ability to guide conservation planning.

Despite international commitments to halt biodiversity loss, species such as the orangutan (*Pongo* spp.) have been declining steeply over the past two decades (Wich *et al.*, 2016; Nowak *et al.*, 2017; Voigt *et al.*, 2018). Orangutan population losses in both Borneo and Sumatra have been driven by deforestation, as well as hunting and retaliatory killings (Ancrenaz *et al.*, 2016; Nowak *et al.*, 2017; Singleton *et al.*, 2017). Orangutans are also lost from populations through captures and translocations, where individuals are removed from areas following a real or perceived risk that the individual will otherwise be killed (Sherman *et al.*, 2021). Orangutans depend on forest for survival and large populations and highest densities are found in protected areas and other remaining forests with low anthropogenic pressure (Voigt *et al.*, 2018). However, orangutans can survive in human-modified landscapes in the absence of killing, where forest remnants offer sufficient food and nesting opportunities (Ancrenaz *et al.*, 2021). Although typically at low population densities (Seaman *et al.*, 2019), most individuals in human-modified landscapes appear to be in good health (Rayadin and Spehar, 2015) and are able to survive and reproduce in fragmented landscapes for extended periods of time (>20 years) (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). Forest fragments may therefore play an important role in connecting larger areas of orangutan habitat and preventing further population segregation and decline.

As there is currently a dearth of orangutan data from human-dominated landscapes, population viability analysis can be used to provide insights into the population dynamics and survival probability over longer periods of time. However, to date, these models have not accounted for spatially explicit habitat dynamics (Marshall et al 2009, Utami-Atmoko 2019) and offtake, or have assumed perfect knowledge of the landscape and no inter-individual variation in dispersal behaviour (Gregory et al 2014).

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

As a charismatic great ape species, orangutans attract a lot of public attention and are relatively well studied. We use the existing data on abundance, life history and population dynamics to showcase the analytical potential of the individual-based modelling approach for orangutans and predict the potential long-term consequences of loss of fragments from landscapes and offtake (hunting, retaliatory killings and capture and translocation) on orangutan populations across Borneo. The method and conclusions, however, could be equally applicable to other species that face challenges from habitat loss and offtake, and for which basic information on demography and dispersal behaviour is known.

Methods

Study system

Bornean orangutans are found across a third (227,000 km^2) of Borneo (IUCN, 2021: Figure 1a). The island is topographically complex, with the interior being predominantly mountainous, giving way to lowland forest (≤500 m asl) and peat swamps towards coastal areas. Borneo is governed among Indonesia (Kalimantan), Malaysia (Sabah and Sarawak) and Brunei Darussalam, although orangutans are absent from the latter.

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

Modelling framework

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

Landscape characterization

We used a fine-scale 30 m resolution gridded system (raster) to define our study landscape, to which we applied a patch-based model. Patches are aggregations of suitable habitat cells forming defined spatial clusters (specified below), where each patch is considered a discrete population. We developed a landcover layer based on high resolution forest maps for 2017 (v1.5, Hansen *et al.*, 2013) to coincide with orangutan density values from 2016 (Voigt et al 2018) that were used to populate patches. Forest was defined according to Margono et al (2014) as stands >5 ha with a natural composition and structure that had not been cleared in recent history (until 2017) and having >70% tree canopy cover. We acquired forest change data from the Global Forest Change repository (v1.5; Hansen et al 2013) and applied it to forest cover data from 2000. We further refined these maps by setting pixels that were prominently within areas of either water (including major rivers) or urban development to *no-data*, using habitat layers by Miettinen, Shi and Liew, (2016).

Demographic model

Male orangutans will range over large distances, often encompassing multiple female home ranges and are unlikely to be a limiting factor in reproduction (Nietlisbach et al., 2012). We, therefore implemented a female-only model, with stage-structured demographics, comprising nine stages (Table 1).

Rather than reduce the fecundity to reflect female births only, we set a survival probability of stage one individuals of 0.45 to represent the slight male-biased sex ratio at birth (van Noordwijk *et al.*, 2018). We derived subsequent survival probabilities from the most recent orangutan Population and Habitat Viability Analysis report (Utami-Atmoko *et al.*, 2019; Table 1). We added density dependence in both fecundity and development to the youngest breeding stage (Table 1). The demographic model is described in detail in the Supplementary Information SI 1. The strength of the density dependency ($1/b$ parameters) for each habitat type was informed by density estimates for 2016 from the most recent range wide density distribution model (Voigt et al., 2018). These densities were summarised across discrete landcover types and independently for each of the three subspecies. As we only modelled females, we then halved density estimates (Table 2).

Patch allocation

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

Large rivers and multi-lane highways are likely to hinder orangutan movement (Utami-Atmoko *et al.*, 2019). Large rivers were derived from Abram *et al.* (2015) and major roads were derived from OpenStreetMap (OpenStreetMap Contributors, 2022b, 2022a) using the identifiers “Primary”, “Primary_link”, “Motorway”, “Motorway_link”, “Trunk” and “Trunk_link”. We thus divided all forest blocks that were intersected by major roads and rivers to reflect potential movement constraints. The current orangutan distribution crosses several large areas of forest, which would otherwise be considered a continuous patch; in order to initialise the model with individuals within the current range, we intersected forest areas with the IUCN orangutan range polygon (Ancrenaz *et al.*, 2016).

In RangeShifter, local populations are modelled within forest areas, which are called patches, and each patch is assigned a unique identity. Orangutan nests have been observed in oil palm plantations up to 50 m from natural forest areas and orangutans are regularly observed making short-distance excursions into plantations (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). Therefore, small natural forest fragments close to larger forested areas are likely to be incorporated into the home ranges of female orangutans. To represent this in the model landscape, we placed a 50 m buffer around all forest areas and considered all fragments within the buffer to be part of the same patch as the larger forest area. Patches were then assigned a unique ID based on the spatial arrangement of forest fragments, whereby all fragments within ≤100 m (if 50 m buffers overlapped) were assigned the same identity and considered a discontinuous patch. If a patch was too small to support an orangutan based on the summarised densities (Table 2), we removed these patches from the patch layers, but retained them for the cost and landcover layer, as even small forest patches will provide resources and limit the cost of moving across the landscape.

Dispersal parameters

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

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

A female will usually settle close to or within the mother’s home range (van Noordwijk *et al.*, 2012; Ashbury *et al.*, 2020). This was approximated in the model by parameterising the settlement probability at 100% with a steep density dependence. This parameterisation means a female will almost certainly settle once reaching a patch, unless that patch is close to or above its equilibrium density, at which point there is a rapid reduction in the settlement probability (Figure SI 3). Through these two independent processes, emigration and settlement, females will only leave their natal patch if the patch cannot support them, because it is at or above its carrying capacity and will then settle at the first available opportunity. As there is limited information on orangutan dispersal within human-modified landscapes, we undertook a sensitivity analysis to determine how robust our model was to changes in dispersal parameters (Table 1).

Cost surface

We built a cost surface layer using a land-cover layer, a digital elevation model and observations of terrestrial movement of orangutans and expert information. Although being predominantly arboreal, terrestrial movement is a common behaviour for orangutans on Borneo. However, this form of locomotion requires additional energetic expenditure, as well as risks from predation and novel diseases (Ancrenaz *et al.*, 2014; Ashbury *et al.*, 2015). To capture this nuance, we created a cost surface based on Tobler’s hiking function using the Distance Accumulation tool in ArcGIS Pro (*v*2.6.0; ESRI, 2020). We used three inputs, a 30 m digital elevation model (Farr *et al.*, 2007), expert informed resistance surface values based on habitat type (Table SI 2), and known barriers to movement (major roads and rivers). To ensure rivers and major highways were represented in the simulated landscape and to prevent diagonal movement between barrier pixels, we buffered all major roads and rivers by

50 m and pixels were assigned a no-data value. We included all suitable forest areas as starting points, i.e. where cost was assigned the lowest value of 1. The resulting surface is a cost to movement layer, where the cost increases when moving away from natural forest areas, mediated by the resistance of the habitat type, degree of slope and barriers within the landscape (Figure SI 2).

Landscape fragmentation and offtake scenarios

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

For both landscape scenarios, we modelled five potential yearly offtake rates from hunting, retaliatory killing and/or live capture and translocation at: 0%, 1%, 2%, 4% and 10% of the population, estimated from published studies and extrapolations from crime data (Sherman *et al.*, 2022). These offtake rates were chosen as they represent plausible real-world values based on empirical data.

Individuals were removed from patches selected at random and individuals could be removed from all age groups, as killing and translocation affect orangutans across age groups (Sherman, Ancrenaz and Meijaard, 2020).

Model initialisation and metrics

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

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

Sensitivity analysis

The largest degree of uncertainty in our connectivity model came from the dispersal parameters, as relatively little is known about dispersal behaviour of female orangutans. Therefore, we undertook a sensitivity analysis to determine the robustness of the model to these parameters, mostly pertaining to orangutan movement (Table 1), by increasing and decreasing baseline values by 5%. In particular, we varied perceptual range between 24 and 26, directional persistence between 2.6 and 2.4 and memory between 11 and 8. In addition, we tested the model's sensitivity to 5% variations of other model parameters, specifically in the maximum number of steps, maximum total number of steps, per step mortality, maximum emigration probability (α_S), and the slope of the density dependency in settlement (d_0). For each permutation we ran a baseline model (Current Landscape Configuration and no offtake) for 250 years and 50 iterations. We assessed the model sensitivity by comparing the proportion of patches occupied at 250 years to the model parametrisation used in our main analysis, for the same landscape and no offtake.

Results

Our demographic model revealed that in both landscape scenarios (Current Landscape Configuration and Fragment Removal) the populations of all three-orangutan subspecies increased from their initial size and expanded their range over the duration of the model run when no additional mortality was applied (Figures 1 and 2). All three subspecies increased in population size over the first 50 years of the model run (80% – 82%), and continued to increase thereafter, although at a slower rate until the final population size at 250 years (123% - 159% increase from starting population). Although there was a similar percentage increase in population between landscape scenarios, total abundance was on average 4% higher (1.8-5.4% or 724 individuals for *P. p . pygmaeus* and 10,150 for *P. p. wurmbii*) under the Current Landscape Configuration and when no offtake was applied. In both scenarios, the population growth had not reached an asymptote, suggesting the population would continue to increase after 250 years (Figures 1 and 2). When no offtake was applied, the extinction probability was zero for all model outcomes among subspecies and landscape scenarios over the modelled time frame (Figure 2).

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

For both landscape scenarios, a 2% offtake rate led to marked declines in abundance across subspecies of 76% on average after 250 years (73 – 79% Figure 1 and Table SI 3 – 5). When we applied a 4% offtake rate, the population loss was substantial, with a >99% decrease in abundance for all model outcomes after 250 years.

Despite these large abundance declines, offtake rates until 4% did not lead to an extinction of any subspecies within 250 years. However, at an offtake rate of 4% and higher, overall numbers were reduced in a way that would likely lead to a functional extinction of many of the populations (with 4 - 68 individuals of *P. p. 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.

For all offtake scenarios, the median dispersal distance (from the natal patch to the non-natal patch where individuals successfully moved) was generally greater when fragments had been removed (i.e. the Fragment Removal scenario, Figure 3), although this difference was generally < 2 km. The greatest difference in dispersal distances between landscape scenarios was without removal of orangutans. This difference was particularly true for *P. p. wurmbii*, which had a median dispersal distance of 8.5 km under the Current Landscape Configuration compared to 11 km in the Fragment Removal scenario. When offtake was applied this difference generally decreased (Figure 3).

Orangutan occupancy in different scenarios

There was a substantial increase in the area occupied by the subspecies through dispersal after the first 50 years of the model run, although with some variation among species (Figure 4). The greatest increase was observed with *P. p. pygmaeus* which expanded from 21,858 km^2 at year zero to 59,670 km^2 (± 305) in the Current Landscape Configuration scenario and from 21,486 km^2 to 59,835 km^2 (± 610) in the Fragment Removal scenario (or a 173% and 178% increase respectively). *P. p. wurmbii* had a much smaller percentage increase after the first 50 years from 90,624 km^2 to 172,574 km^2 in the Current Landscape Configuration scenario and from 87,445 km^2 to 167,560 km^2 (± 26) in the Fragment Removal scenario (or a 90% and 92% increase respectively) (Table SI 6 – 8).

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

Sensitivity analysis

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

Discussion

We modelled spatially explicit population dynamics for Bornean orangutans under landscape and offtake scenarios, revealing that in the absence of non-natural offtake by killing, orangutan populations are likely to increase in number and distribution. Although orangutan numbers increased regardless of whether fragments were removed from the current landscape, the largest population size was observed when the current forest cover, including all fragments under 5,000 ha, was maintained, and no orangutan was lost due to additional mortality (Figure 2). Conversely, even a low offtake rate of 1% led to markedly reduced population sizes compared to when no offtake was applied (16-19% vs 80 – 82% growth after 50 years respectively). These results corroborate earlier research using a non-spatially explicit approach (Marshall *et al.*, 2009). Given that estimates of current annual offtake rates on Borneo likely exceed 5% (Sherman *et al.*, 2022), our results imply that a drastic reduction of orangutan killing or removal from the landscape is necessary to allow orangutans to persist and recover from past losses.

Here, we have assumed spatially homogenous levels of offtake. Information on killings and translocations are geographically dispersed and quite variable across the orangutan range (Sherman et al., 2022). Hunting, retaliatory killing and translocation are driven by different factors, including human presence, cultural norms and belief systems (Meijaard *et al.*, 2011). While spatial data on translocation and orangutan crime exist for Kalimantan (Sherman *et al.*, 2022; Massingham *et al.*, 2023), these likely underrepresent hunting in the interior, and there is no information from Sarawak and Sabah. Consequently, we have modelled offtake rates found in Sherman *et al.* (2022) for Borneo uniformly in space and time to understand general impacts across the subspecies. Future modelling work could examine the implications of considering covariates of killing and translocations, and would refine recommendations for local population management and conservation actions.

We found that when no offtake was applied orangutan populations increased, regardless of the landscape configuration scenario. Although the percentage increase in population was often greater when fragments were removed, the total population size was always greatest when fragments were maintained in the landscape, although these differences were marginal. While this may suggest habitat fragments are of limited importance, we caution against this view for several reasons. Although fragments under 5,000 ha make up only 4.3% of the total forest suitable for orangutans, these patches may still support considerable numbers of individuals (e.g. >10,000 individuals for *P. p. wurmbii* when no offtake was applied in our models). As well as supporting individual orangutans, fragments will also likely serve as stepping-stones or corridors, aiding range expansion, as suggested by the larger 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 instead this is highly dependent not only on their spatial arrangement and the cost of moving through the landscape, but also the stochastic movement of individuals. This reflects the process of natural dispersal much better than more correlative models (Coulon *et al.*, 2015). However, the approach relies heavily on the assumptions used to parametrise the models. We based parameters on orangutan behavioural ecology from available data drawn from relatively undisturbed areas, expert opinion and observations from anthropogenic landscapes (Ancrenaz *et al.*, 2021; Oram *et al.*, 2022). To capture the influence of those assumptions on model outcomes, we ran a sensitivity analysis that asserted the robustness of the model. This analysis revealed the emigration probability (i.e. the willingness of a female to leave her natal patch) had the greatest effect on the model outcome, although overall effect on patch occupancy was small (≤0.4 %). This is unsurprising, as emigration would directly affect the number of individuals moving across the landscape and impact the probability of patches to be colonised. We know from field observations that females exhibit a high degree of home range fidelity and generally settle close to their mother's home range (Goossens *et al.*, 2006; Ashbury *et al.*, 2020). However, these observations are mostly from areas with very low disturbance and high landscape connectivity. In highly modified (i.e. non-forest dominated) landscapes where small fragments will contain finite resources, individuals are likely to have greater incentive to leave and fewer opportunities to settle close to their mother's home range, which may impact the emigration process, as is reflected in our simulations. Similarly, we initiated our models with patches being at their assumed density equilibrium. Although the starting density may not represent current abundances, which are also driven by ongoing offtake (Marshall *et al.*, 2006) and can vary through time and space (Marshall *et al.*, 2021), we aimed to address this by summarising densities across broad habitat types (Table 2). However, starting at density equilibrium may lead to a higher level of emigration earlier in the model run or, conversely, may extend the point at which the offtake initially impacts the populations and this should be considered when interpreting our results.

The results from the RangeShifter model presented here arise from information on individual behaviour based on assumptions about the animal’s interaction with the landscape. The resulting patterns where verified by experts and seem to match broad orangutan dynamics observed in anthropogenic landscapes (e.g. Ancrenaz *et al.*, 2015, 2021; Oram *et al.*, 2022). However, an intensification of research efforts to collect more orangutan data from human-modified landscapes and on orangutan movement and dispersal patterns therein, will allow us to refine models further, improving their ability to predict local population responses to management and land-use change.

Conclusion

There is growing recognition of the potential conservation value of forest fragments in human-modified tropical landscapes for forest-dependent species (e.g. Lion *et al.*, 2016; Deere *et al.*, 2018). Our research demonstrates the potential importance of these fragments in facilitating movement of a critically endangered vertebrate species across anthropogenic landscapes. This movement is vital to allow dispersal, which is the basis to ensure populations remain genetically connected, can recover in the event of a disturbance and facilitate range shifts in response to future climate change (Årevall *et al.*, 2018; Lino *et al.*, 2019). However, removal of individuals from the landscape via hunting, retaliatory killings and capture and translocation is likely to be a more insidious threat for long-lived, slow reproducing species such as orangutans, even if connectivity is maintained. Conservation initiatives aimed at retaining and restoring forest areas for the benefit of species like the orangutan, should also address offtake. Broadly, this could be achieved by promoting tolerance of species amongst human populations and thus enhancing co-existence with the species that share these landscapes.

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Data Accessibility Statement

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

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

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Conflict of interest statement

The authors have no conflict of interest to declare.

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.

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		$0.2^\dagger$	
α_0 (slope)		10	
ß$_0$ (inflection point)		1	
Transfer parameters			Expert informed
Directional persistence		$2.5^\dagger$	
Perceptual range (cells)		$25^\dagger$	
Memory size (cells)		$10^\dagger$	
Max. steps per year		$3,000^\dagger$	(Singleton et al., 2009)
Total max. no. of steps		$12,000^\dagger$	
Per step mortality		$0.001^\dagger$	
Settlement			Expert informed
S_0 Max. Settlement probability		1	
α_S (slope)		$-50^\dagger$	
ß$_S$ (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%	

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

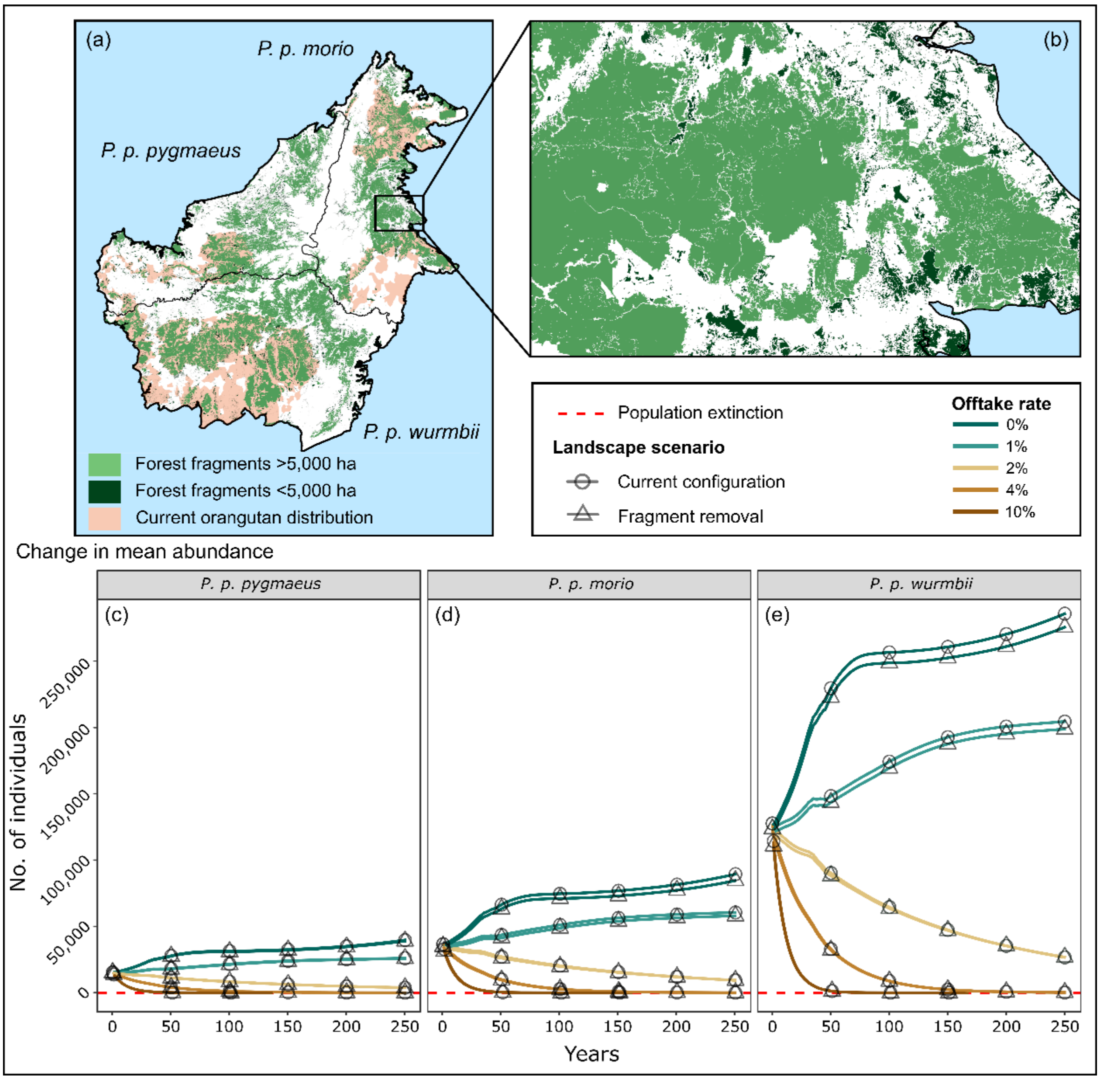

Figure 1 The impact of the Current Landscape Configuration and Fragment Removal scenarios on the Bornean orangutan population size, and under different levels of orangutan off-take.

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.

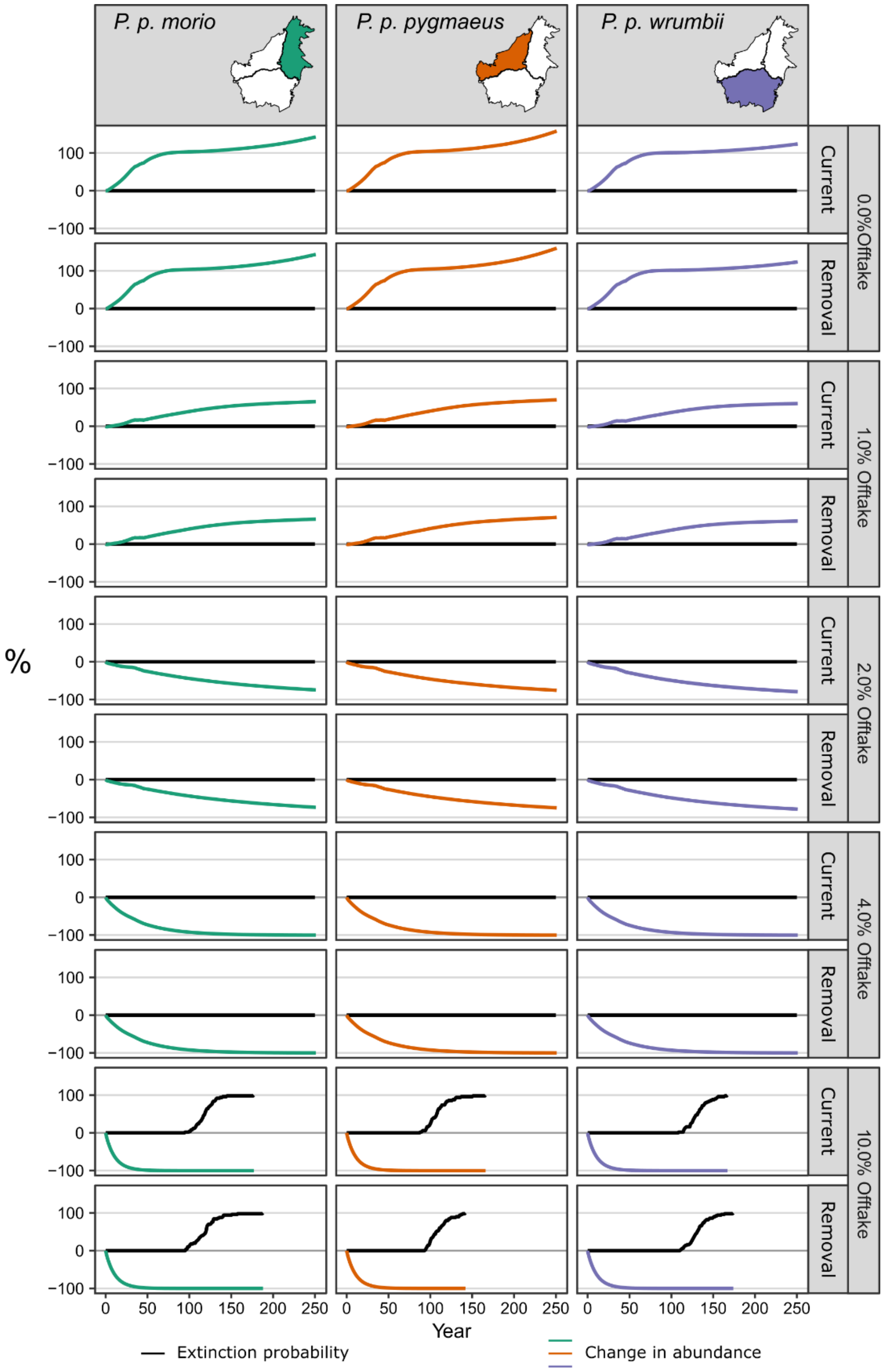

Figure 2 Extinction probability and percentage change in abundance over time from model initiation.

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.

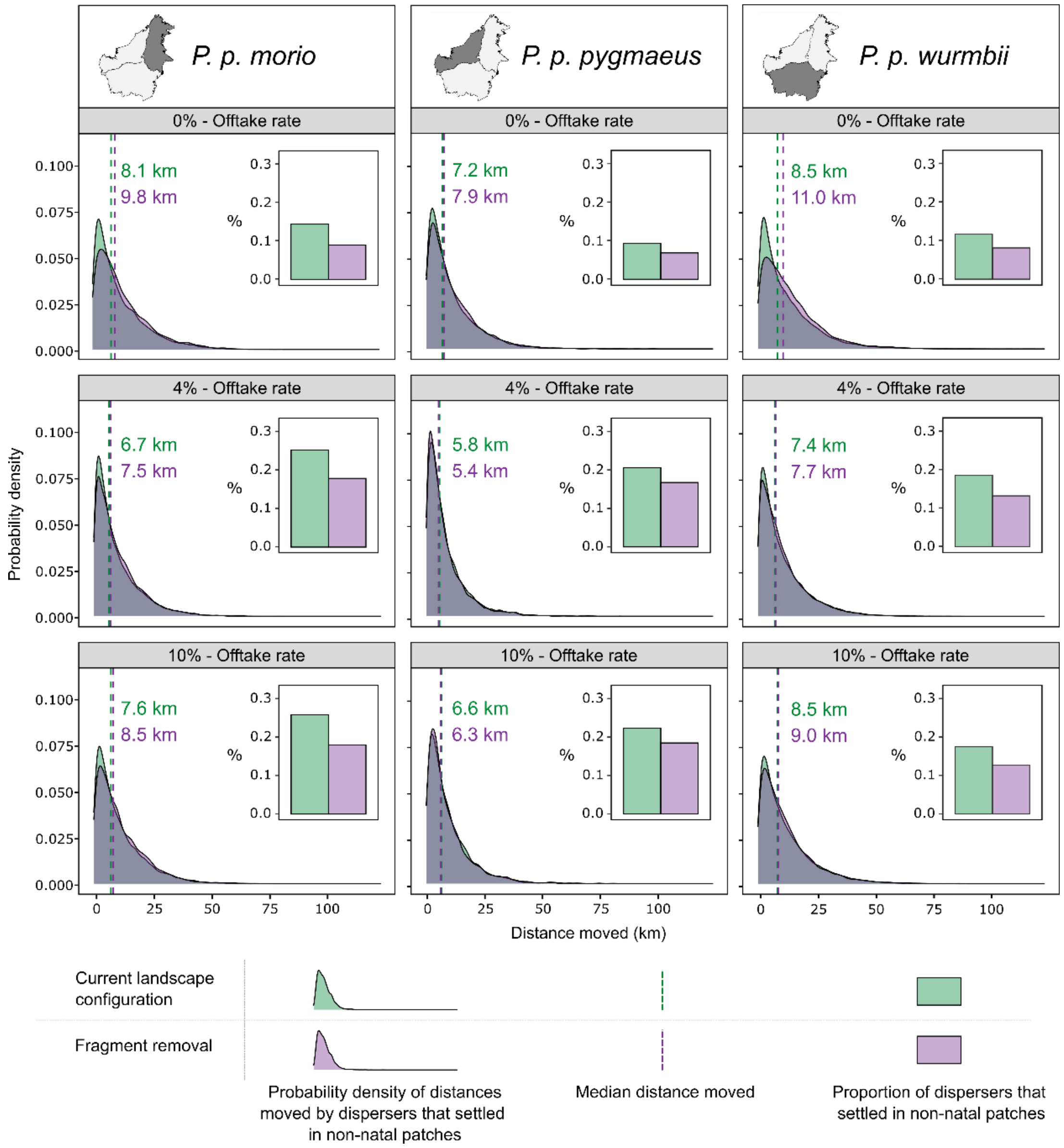

Figure 3: Dispersal distance and success under different landscape and offtake scenarios.

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.

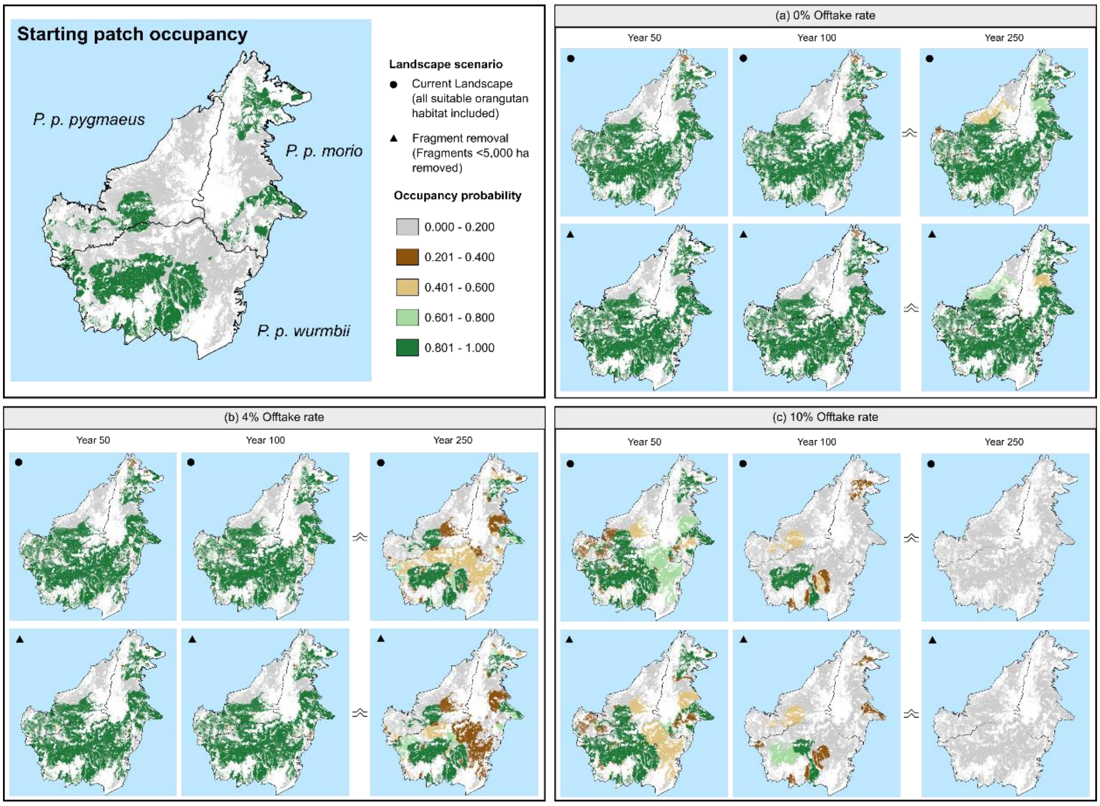

Figure 4. Occupancy probability different fragmentation and offtake scenarios. Cumulative patch occupancy (proportion of the simulations where each patch was occupied), under the Current Fragmentation and Extreme fragmentation scenario and three offtake (annual proportion of the population removed) rates,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