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Understanding orangutan habitat use and connectivity across human-modified landscapes

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Covid-19 Impact Statement

D. J. I. Seaman kindly requests his examiners to note how the COVID-19 pandemic impacted this thesis.

During the lockdown periods (March – June and October – December 2020) D.J.I. Seaman was forced to work from home without office space and a working environment conducive to focused work.

At the onset of the pandemic in 2020, a planned visit to external collaborators to further develop the methods used in **Chapters 3** and **5** could not go ahead. Between (March – October 2020) the collaborators were also not available for in-person and virtual meetings due to health and personal reasons. As a result, they were unable to provide necessary technical input, and the progress on model development was slower than it would have been without the pandemic.

He would like to take this opportunity to thank both the University of Kent for granting him a three-month extension period and his supervisors, who made working through this disruptive period much more manageable.

Author signature:

Date: 2nd December 2021

Main supervisor signature:

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Author declaration

All chapters were written by D. J. I. Seaman, with editorial suggestions provided by supervisors M. J. Struebig, T. Humle and M. Voigt. **Chapters 2-5** were undertaken in collaboration with researchers outside of the direct supervisory team, as outlined below.

Chapter 2 is a continuation of D. J. I. Seaman's Master's thesis, supervised by M. J. Struebig and T. Humle. Training for nest surveys was delivered by M. Ancrenaz and local support provided by H. Bernard. D. Coomes, T. Swinfield and D. T. Milodowski processed and provided LiDAR data. Work carried out during this PhD included adding the addition of a sensitivity analysis, to test the robustness of the density estimates. The manuscript also went through a substantial rewrite and reformatting in preparation for submission to the American Journal of Primatology. From suggestions provided by reviewers, D. J. I. Seaman updated and re-ran the analysis to improve the scientific rigour. The figures were improved for publication and additional supplementary material were added to increase clarity.

Chapter 3 originated from a workshop presented by G. Bocedi and J. M. J. Travis on the use of RangeShifter. Modifications to the model to better represent orangutan ecology were developed by G. Bocedi and D. J. I. Seaman, with additional technical support from J. M. J. Travis and S. C. F. Palmer. Input on orangutan ecology in human-modified landscapes was provided from M. Ancrenaz, S. Wich, E. Meijaard and H. Bernard. Advice on landscape management scenarios was given by N. J. Deere. The analysis was undertaken, and chapter written by D. J. I. Seaman, with editorial support from M. J. Struebig, T. Humle and M. Voigt.

Chapter 4 originated from a conversation with M. J. Sturebig, M. Voigt and D. J. I. Seaman. The modelling approach was developed by D. J. I. Seaman, D. E. Bowler, N. J. Deere and M. Voigt and analysis undertaken by D. J. I. Seaman. Of the two data sets used in the analysis, nest data were collected by D. J. I. Seaman during his Masters and camera trap data by N. J. Deere, E. L. Baking and J. K. Haysom. The chapter was written by D. J. I. Seaman, with editorial input from M. J. Struebig, T. Humle, N. J. Deere and M. Voigt.

Chapter 5 originated from discussions with D. J. I. Seaman, M. Ancrenaz, S. Wich, E. Meijaard M. J. Struebig, T. Humle and M. Voigt. This chapter used the same model as **Chapter 3** but with an extension developed by S. C. F. Palmer. Technical support was provided by G. Bocedi, J. M. J. Travis, S. C. F. Palmer and M. Voigt. Further details on orangutan ecological in human-modified landscapes, as well as offtake rates were supplied by F. Oram and J. Sherman respectively. The analysis was undertaken, and chapter written by D. J. I. Seaman, with editorial input from M. J. Struebig, T. Humle and M. Voigt.

Abstract

In this thesis I focus on the orangutan (*Pongo* spp), a charismatic mammal, that is critically endangered and thus emblematic of the biodiversity crisis in Southeast Asia. Although orangutans have received a large amount of conservation focus and funding in the past, the orangutan population status outside of key study areas in intact habitat remains poorly understood and overall their numbers continue to decline. This dearth of information in human-modified landscapes in particular, presents a challenge to the conservation of the species, as the majority of the orangutan range is found outside of strictly protected areas and land-use change continues to reduce and fragment these habitats.

Here, I employ both empirical and theoretical approaches to investigate orangutan populations in human-modified landscapes. First, I focus on the landscape scale and use orangutan nest data to estimate orangutan density in a multi-use human-modified landscape in Sabah, Malaysian Borneo. I then use these estimates to investigate orangutan abundance across a habitat disturbance gradient (from continuous logged forest to remnant forest in mature oil palm) and assess the relationship between abundance and environmental covariates. I show that orangutans are found across the landscape, although at substantially reduced densities in remnant forest patches in oil palm, corroborating that for orangutan abundance forest habitat quality appears more important than isolation of patches.

At the local scale I use these density estimates, as well as published and expert-elicited data on orangutan ecology, to adapt and parametrise an individual-based model for orangutan populations in the landscape. I generate four plausible landscape management scenarios founded on existing environmental policies,

sustainable certification standards and recommendations from published literature. By applying the individual-based model to these four management scenarios I was able to show that policies and certification standards maximising forest cover in human-modified landscapes may promote viable orangutan populations and facilitate movement among habitat patches, provided mortality during dispersal is minimised.

An impediment to understanding orangutans in human-modified landscapes, is a lack of targeted orangutan observational data. Data integration is a rapidly expanding field in ecology, which makes use of multiple different types of data sets to improve precision. I investigate if observations from surveys for mammal biodiversity, specifically orangutan bycatch on camera trapping images, can be used to augment targeted orangutan nest surveys through integration to improve precision whilst making use of existing data. Although I demonstrate the potential for data integration to be applied at the local scale for orangutans, ecological processes driving detection in different datasets, such as nesting behaviour and preference for terrestrial or arboreal movement need to be fully considered if this approach is to be successful.

Orangutan population viability assessments have been undertaken in the past, but crucially, these only consider dynamics in time and are not spatially-explicit. They are also limited to averaged parameters for vital demographic measures (e.g. emigration and immigration rates) across the species and do not take into account habitat outside large continuous areas of forest. With this in mind, in my last chapter, I scale up the individual-based model implemented at state level to the whole of Borneo and couple it with high resolution forest maps, to investigate the role small fragments play in maintaining orangutan populations and movement across the landscape. Using estimated offtake of orangutans from hunting, retaliatory killings and rescues, I also investigate how removing individuals from the landscape affects

population dynamics and movement. The results reveal the importance of small remnant forest fragments in facilitating individual orangutan movements, with high numbers of individuals dispersing out of their natal area when small fragments are present, thus demonstrating a greater ability to expand their range. However, even moderate levels of added mortality (>2%) lead to steep declines in populations, highlighting the disproportionate impact of removing orangutans (i.e. by killings or translocations on populations).

This thesis is an important step towards a better understanding of orangutan conservation in the Anthropocene, adding to the increasing recognition that orangutan research and conservation focus need to expand to also include human-modified landscapes and support efforts to promote peaceful co-existence between orangutans and humans. The evidence presented and our abilities to forecast the effects of potential conservation initiatives are vital to better inform orangutan management and ensure positive conservation outcomes for the species in the future.

Key words: *Pongo pygmaeus*; Landscape Connectivity; Individual-based model; Data integration; Survey and monitoring; Population viability; Corridor; Fragmentation; Borneo

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Chapter 1 Introduction

1.1 Anthropogenic drivers of species decline

Humans are having a profound influence on the natural world. Habitat modification, wildlife hunting and persecution, as well as the introduction of non-native species, have greatly influenced the distribution of biodiversity across the globe (Lewis and Maslin, 2015). Archaeological and subfossil records demonstrate that since early in our evolutionary history modern humans are, at least in part, responsible for the decline of many species (Sandom *et al.*, 2014). These early impacts are often most stark on islands, with numerous examples of extinctions coinciding with the arrival of humans. For example, on Madagascar, the arrival of humans from what is now Indonesia, led to the rapid decline and eventual extinction of the giant flightless elephant birds (family: Aepyornithidae) and several large lemur species (eg. *Megaladapis edwardsi* and *Palaeopropithecus maximus*) (Burney *et al.*, 2004; Hansford *et al.*, 2021). Similarly, the disappearance of the moa (family: Dinornithidae) from New Zealand can be attributed to the arrival of the Morai people from Polynesia (Turvey and Holdaway, 2005). However, the degree to which early humans played a role in the decline and extinction of many species is somewhat debated, with researchers pointing out that environmental change was already causing the decline of many populations (Sandom *et al.*, 2014; Stewart, Carleton and Groucutt, 2021).

The role of modern humans in shaping biodiversity is less ambiguous. With the increasing movement of humans around the planet, the decline of wildlife populations and extinctions have continued with notable examples such as the

Steller's sea cow (*Hydrodamalis gigas*) from the Commander Islands and the famous dodo (*Raphus cucullatus*) from Mauritius, both hunted to extinction just a few hundred years ago (Roberts and Solow, 2003; Turvey and Risley, 2006).

This trend of humans shaping the distribution of species continues today at an accelerated pace. Over the last 50 years, terrestrial vertebrate abundance has been reduced by >60% (Grooten and Almond, 2018). The number of species extinctions is currently more than 1,000 times higher than expected by background extinction rates, and this is estimated to increase 10-fold under current trajectories (De Vos *et al.*, 2015). Anthropogenic influence on the natural world is now so evident, that this has warranted the naming of a new geological epoch - the Anthropocene, which is marked by dramatic climate change and loss of biodiversity (Crutzen, 2006; Zalasiewicz *et al.*, 2011).

1.2 Conservation in the Anthropocene

Demands on the natural world for food and resources continue to grow rapidly, resulting in an ever-increasing anthropogenic influence on the natural world. Efforts in the mid to late twentieth century to curtail these losses in natural landscapes and biodiversity, led to a rapid growth in the number of protected areas (Watson *et al.*, 2014). This protection of large, predominantly intact areas of natural habitat has now formed the foundation of conserving global biodiversity (Cantú-Salazar and Gaston, 2010). Protected areas are generally seen as a conservation success story, cited as safeguarding areas of wilderness, maintaining functioning ecosystems and reducing human influence in these areas (Cantú-Salazar and Gaston, 2010). In spite of these successes, there remain key criticisms, both in terms of their effectiveness at conserving biodiversity and their social impacts. For instance, at their advent protected areas were often established with little regard for the rights of local communities and large-scale forced evictions were commonplace (Agrawal and Redford, 2009). Today, land ownership and the rights of local people are more fully considered with the establishment of new protected areas and poverty alleviation is often cited as a key goal (Ferraro and Hanauer, 2011; Watson *et al.*, 2014). Despite this, evidence for poverty-alleviation is mixed, and communities who heavily rely on natural resources for subsistence often receive little benefit from the creation of protected areas (Santika, Wilson, *et al.*, 2021).

Intonational commitments for conserving biodiversity, means the area of land under protection is continuing to expand. However, most of the world's protected areas are small (<100 ha), suffer from insufficient funding, lack of clear governance and competing stakeholder interests (Leverington et al., 2010; Jones et al., 2018; Sacre et al., 2019; Volenec and Dobson, 2020). Combined, these issues mean protected areas often fail to reduce the loss and degradation of habitats and biodiversity given their size (Andam *et al.*, 2008). Similarly, although protected areas continue to increase, there expansion does not keep pace with the rapidly expanding threats from human populations, with human encroachment and widespread hunting further degrading the ability of these areas to reduce habitat and biodiversity loss (Gardner *et al.*, 2018; Rija *et al.*, 2020). Although protected areas have clear short comings, on balance, to date the evidence indicates protected areas have a positive effect on biodiversity, and approximately 15% of terrestrial systems are formally protected for conservation (Maxwell et al., 2020). However, this is still 2.5% short of the 17.5% target set out by the Convention on Biodiversity (CBD) Aichi Biodiversity Target 11 for 2020 (Leadley et al., 2014).

Despite some conservation success within protected areas, recent estimates suggest that between 30 to 50% of the Earth's surface will need to be set aside for protection in order to maintain biodiversity and limit the negative effects of climate change (Pimm, Jenkins and Li, 2018; Dinerstein *et al.*, 2020). Although most protected areas are small, traditionally practitioners have attempted to focus the establishment of new protected areas to large and often remote areas of natural habitat, which have received limited anthropogenic pressure and hence disturbance (Venter *et al.*, 2014; Volenec and Dobson, 2020). Yet, with increasingly pervasive human influence across terrestrial systems, the opportunities to establish large, protected areas of natural habitat are diminishing. Therefore, although protected areas will remain a key conservation initiative, alone they are unlikely to safeguard current levels of biodiversity now and in the future (Allan *et al.*, 2021).

There is increasing recognition that protecting natural habitats within anthropogenic areas is crucial to overcome the limitations of the existing protected area networks (Ng, Payne and Oram, 2020). Mechanisms such as community forests can complement the network of traditional protected areas, in delivering on international biodiversity conservation commitments, whilst also providing food and resources for the growing human population (Santika, Meijaard, *et al.*, 2017). As a result, these mechanisms are increasingly incorporated in policy and spatial planning as 'other effective area-based conservation measures (OECMs). The less strict criteria and ability to include partially degraded habitats within OECMs, means these frameworks may be easier to establish for protecting natural habitats in anthropogenic landscapes, than more traditional forms of strict habitat protection (Jonas *et al.*, 2017).

1.3 Impacts of habitat loss and fragmentation on biodiversity

Anthropogenic land-cover change is the largest driver of global biodiversity decline (Song *et al.*, 2018; IUCN, 2020). Land conversion leads to the loss of natural habitats and the partitioning of remaining habitats into smaller and increasingly isolated fragments (Haddad *et al.*, 2015). This habitat loss and fragmentation directly affects wildlife populations through reducing population size, inhibiting movement, and impeding species range shifts in response to climate change (Chiarello, 2000; Dixo *et al.*, 2009; Krosby *et al.*, 2010). In addition to these direct effects, indirect consequences of habitat loss and fragmentation, such as decreased resource availability via a reduction in habitat extent and quality, and increased mortality linked to hunting or road collisions can also negatively affect wildlife populations (Peres, 2001; McCallum and Dobson, 2002).

Early ecological concepts of the effects of fragmentation were built on the Theory of Island Biogeography (Macarthur and Wilson, 1967). Viewing the problem through the lens of this theory assumes that habitat patches are isolated within an impermeable matrix and therefore mainly puts emphasis on two effects - area and isolation. The ensuing species-area relationship postulates that fragments of a greater area will support a greater number of species (Macarthur and Wilson, 1967). Whereas increased isolation reduces immigration and emigration rates and thus increases extinction risk from demographic and environmental stochasticity (Bowman, Cappuccino and Fahrig, 2002). In terrestrial systems, however, the matrix between fragments is rarely as inhospitable or homogenous as open water, and therefore the permeability of the matrix (i.e. the ease or difficulty for individual movements or dispersal) may have a large influence on how species respond to fragmentation (Kupfer, Malanson and Franklin, 2006). Characteristics of the matrix surrounding habitat patches will vary considerably based on land-use, disturbance regimes and ecological successional status and lead to further negative effects such as increased human presence, changes in microclimates and greater occurrence of invasive species (Cook *et al.*, 2002).

Area and isolation are not the only drivers which can influence biodiversity in fragmented landscapes. For instance, the edge of a fragment will often have very different biotic and abiotic conditions from its interior, leading to the creation of novel edge habitats (Laurance *et al.*, 2007). This is particularly true for forests, where edges are generally dryer and receive greater levels of solar radiation, fluctuations in temperature and exposure to adverse weather conditions (Hardwick *et al.*, 2015; Senior *et al.*, 2017). Edge effects may be experienced up to 1 km from the forest border but are dependent on several factors, such as size, shape and edge floral composition (Ewers, Thorpe and Didham, 2007; Laurance, 2008). The influence of forest edges is likely to be species-specific, with large mammals being less sensitive to edge influences than small to medium mammals, likely due to their ability to roam over larger areas and their increased abilities to disperse (Pfeifer *et al.*, 2017)

1.4 The concept of landscape connectivity

To mitigate these potential negative consequences of habitat loss and fragmentation, there is increasing emphasis in ensuring species are able to move across modified landscapes. As a result, landscape connectivity has become a cornerstone of modern conservation practice (Diniz *et al.*, 2020). Much of the current connectivity research has been biased towards North America and Europe and predominantly focuses on terrestrial landscapes (Carroll *et al*., 2015). Landscape connectivity analysis have been applied to a range of conservation issues, from identifying potential corridors for focal species to protected area conservation planning (Correa Ayram *et al.*, 2016). Although a comprehensive definition is currently lacking , landscape connectivity can be broadly defined as the ability of species to move between habitat patches, across a dissimilar matrix (Taylor, 2006a). Two levels of connectivity are generally considered:

1. ***Structural connectivity*** refers to the degree to which habitat patches are physically connected.
2. ***Functional connectivity*** considers both structural connectivity and species movement behaviour.

Assessing structural connectivity only requires data on landscape configuration and can be relatively simple to quantify. Through this approach, connectivity is defined by thresholds, such as the percentage of forest cover or patch contiguity (Groffman *et al.*, 2006). However, structural connectivity does not consider landscape features that may limit the ability of species to move through a given landscape (Frair *et al.*, 2008). For instance, if two habitat patches are physically connected by a narrow corridor, they may be considered structurally connected; but if the corridor is unsuitable for many species, this would result in the patches being functionally disconnected (Correa Ayram *et al*, 2016). Conversely, if a species is capable of moving through the matrix and regularly does, habitat patches may be structurally disconnected, yet remain functionally connected for that species (Correa Ayram *et al*., 2016). As a result, most recent landscape connectivity studies focus greater attention on species movement behaviour and functional connectivity.

1.5 Connecting habitats through corridors and Stepping-Stones

Corridors have traditionally been considered linear strips of primarily natural habitat, that aim to facilitate species movement between populations, otherwise disconnected by areas which are structurally and climatically different from the habitat they replaced (Chetkiewicz, St. Clair and Boyce, 2006). Increasingly, rather than viewing corridors as linear strips of habitat, corridors are being viewed as heterogeneous, pattern-based linkages or stepping-stones, which facilitate movement by providing patches of optimal habitat which species can ‘hop’ between (Figure 1.1) (Baum *et al.*, 2004). Although planning corridors may conceptually be relatively simple, evaluating the potential effectiveness of corridors before and after their establishment presents a greater challenge (Gilbert-Norton *et al.*, 2010).

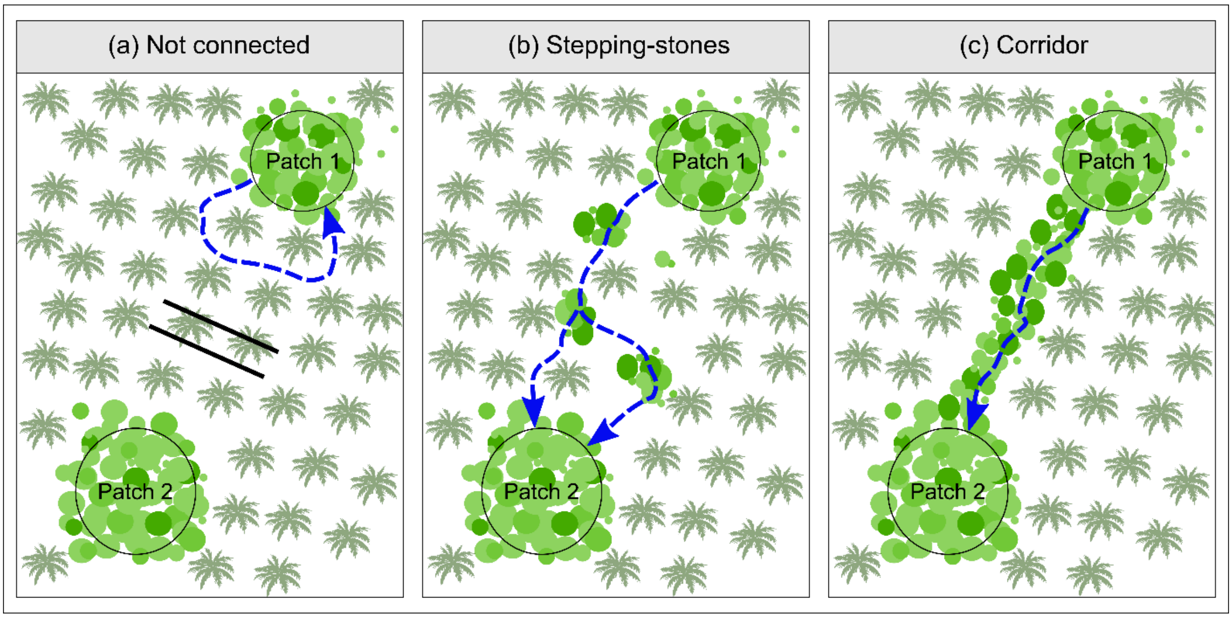

Figure 1.1: Conceptualisation of functional landscape connectivity.
When the matrix between areas of natural habitat is inhospitable, species may be unable to move between fragments (patches 1 and 2) which are functionally disconnected (a). Small patches of remnant natural habitat within the landscape can serve as 'stepping stones' (b) and linear strips of natural habitat act as corridors (c), providing functional connectivity and facilitating movement between patches.

The intrinsic properties of corridors and stepping-stones, such as floral composition, size, shape and spatial configuration, as well as the surrounding matrix, will highly influenced their conduciveness (Gregory and Beier, 2014). For instance, financial limitations or the willingness of landowners to set aside areas from production, will often constrain the width of a corridor (and by extension its area) (Andreassen, Halle and Ims, 1996). As a result, edge effects can have a considerable influence on a corridors suitability or quality (Harper *et al.*, 2007). Conversely, stepping-stones within a highly permeable matrix will promote higher rates of inter-patch dispersal and provide greater connectivity than those within an inhospitable matrix that differs greatly from the species optimal habitat (Ricketts, 2001).

Corridors are also often established to aid a narrow group of species, with limited species-specific information or any attempt at post monitoring validation (Vos, Baveco and Grashof-Bokdam, 2002; Caro, Jones and Davenport, 2009). For long-lived species, the success of a corridor may not become apparent for several generations, until individuals disperse from natal groups and reproduce in recipient populations (Riley *et al.*, 2006). In real world scenarios, corridors are often established retrospectively, in an attempt to reconnect previously linked populations, or in response to proposed development (Hilty, Lidicker Jr and Merenlender, 2012).

Despite this, a global meta-analysis by Gilbert-Norton *et al.*, (2010) found that corridors and stepping-stones generally have had a positive effect on species movement and are indeed an important conservation strategy for mitigating the negative effects of fragmentation. However, to maximise the effectiveness of corridors and/or stepping-stones at facilitating species movement, there needs to be a more proactive approach. This approach will involve designating corridors and/or stepping-stones before development or, to inform active restoration in areas that have already undergone land-use change. Prioritising these areas requires research in landscape connectivity which, for tropical regions, is still somewhat lacking.

1.6 Meta-population concept is also important for functional connectivity

Metapopulation theory was established by Hanski and Simberloff, (1997), and has become a foundational theory in ecology. Classical meta-population theory focused on the area and spatial configuration of habitat patches and ignored the effects of the surrounding matrix (Vandermeer and Carvajal, 2001). Contemporary approaches are more broad in scope, and simply define a metapopulation as a dynamic system containing linked populations and consider the effects of the landscape as a whole (Akçakaya, Mills and Doncaster, 2007).

Meta-population dynamics are substantially impacted by functional connectivity, through the regulation of dispersal (both emigration and immigration) but are often overlooked in studies (Karnatak and Wollrab, 2020). If metapopulation dynamics are not considered when evaluating connectivity, any resulting management recommendations may potentially have deleterious effects. For instance, small populations are at high risk of demographic and environmental stochasticity and are at threat of becoming population sinks, where the number of deaths exceeds births (Pulliam and Danielson, 1991). Metapopulation dynamics are therefore, of increasing importance to the conservation of species within human modified landscapes, where high levels of fragmentation mean populations often rely on the movement of individuals between subpopulations (Laurance, 2004). Thus, to protect natural habitat and manage human-modified landscapes, which both maintain biodiversity and provide food security for the human population, will require investigations of connectivity and how altering landscapes effects dynamic processes such as emigration and extinction (Fischer and Lindenmayer, 2006).

1.7 Deforestation in the tropics

Forest support more than 60% of terrestrial biodiversity, stabilize and regulate the global climate (Pillay *et al.*, 2021), support economies and livelihood and significantly contribute to human wellbeing (Foley *et al.*, 2005). As a consequence, the dramatic loss of forests is a major and growing global concern (Hoang and Kanemoto, 2021).

Forests in the tropics support exceptionally high levels of biodiversity (Gardner *et al.*, 2009), but have experienced among the highest deforestation rates worldwide (Curtis *et al.*, 2018). Although drivers of deforestation vary across regions, forest degradation following selective logging, and forest clearance for commodities, such as oil palm or paper pulp, are the leading cause for deforestation in Southeast Asia (Curtis *et al.*, 2018). On Borneo, deforestation has been among the highest worldwide and, starting in the early 1970s, large areas of lowland (≥ 500 m above sea level (masl)) dipterocarp forest were subject to industrial scale logging and clear cutting for industrial agriculture (Gaveau *et al.*, 2014). Selective harvest of large trees, forest degradation, clearance and draining of peat forests to facilitate timber harvest and plantations, has been attributed to extended periods of drought and increased fire prevalence and intensity, which, along with illegal logging, has further degraded much of Borneo’s lowland forest areas (Curran *et al.*, 2004; Sloan *et al.*, 2017; Santika *et al.*, 2020)

Conservation and corporate initiatives aimed at reducing deforestation and biodiversity loss, such as the Roundtable on Sustainable Palm Oil (RSPO; https://rspo.org/about), have gained increasing traction (Tey *et al.*, 2020). Additionally, companies are making voluntary zero-deforestation pledges, aimed at curbing deforestation in their supply chains and reducing their environmental and social impacts (Garrett *et al.*, 2019). Approaches such as the High Conservation Value and High Carbon Stock (HCV/HCS), used to delineate forest protection and development, have been established to facilitate agricultural expansion, while adhering to these zero-deforestation pledges (Rosoman *et al.*, 2017). The effectiveness of these policies, both at reducing deforestation and biodiversity loss, is now an active area of research (e.g. Deere *et al.*, 2019; Scriven *et al.*, 2019; Seaman *et al.*, 2021)

1.8 Orangutans as a flagship for conservation

The orangutans (*Pongo* spp.) are among the most emblematic species affected by deforestation in Southeast Asia. They are the only extant non-human great ape species found outside of Africa and have successfully been used as a conservation flagship, drawing funding and attention to biodiversity and habitat loss in the tropics (Walpole and Leader-Williams, 2002; Santika, Sherman, *et al.*, 2021). Similarly, orangutans rely on areas of natural forest for survival (Rijksen and Meijaard, 1999), and given their large home-range requirements (60 – 600 ha for females; Singleton *et al.*, 2009), many other species are likely to fall under the umbrella of conservation initiatives established for orangutans (Delgado and Van Schaik, 2000)

In addition to their role as a flagship or umbrella species, orangutans also play a key ecological role in facilitating long distance seed dispersal, a unique trait among primates in the region (McConkey, 2018). This is particularly true for Borneo, where the absence of other long distance seed dispersers (rhino *Dicerorhinus sumatrensis* and elephant *Elephas maximus*) across much of the island, means orangutans will be vital in ensuring the long-term health of forests (Corlett, 2017)

1.9 Orangutan, historic range and decline

Orangutans were once widespread throughout Southeast Asia. Fossil records indicate that at the end of the Miocene (5 to 6 million years ago), ancestral *Pongo* species ranged from Southern China through to Java (Rijksen and Meijaard, 1999; Harrison, Krigbaum and Manser, 2006). Natural shifts in climate caused tropical and subtropical forest cover to retreat to the south (Piper and Rabett, 2009). Along with hunting pressure by early humans, this likely led to a marked decline in the orangutan’s range and the extinction of several early orangutan species (Piper and Rabett, 2009; Reyes-Centeno, 2016; Westaway *et al.*, 2017; Spehar *et al.*, 2018).

From the start of the Holocene (ca. 12,000 years ago) to the present day, orangutans have been restricted to the islands of Borneo and Sumatra in the forest refugia that remained in these areas at the Last Glacial Maximum (Louys, Curnoe and Tong, 2007; Louys and Meijaard, 2010). Today the orangutan lineage comprises of one species on Borneo, the Bornean orangutan (*Pongo pygmaeus*) and two on Sumatra, the Sumatran orangutan (*Pongo abelii*) and the Tapanuli orangutan (*Pongo tapanuliensis*) (Figure 1.2).

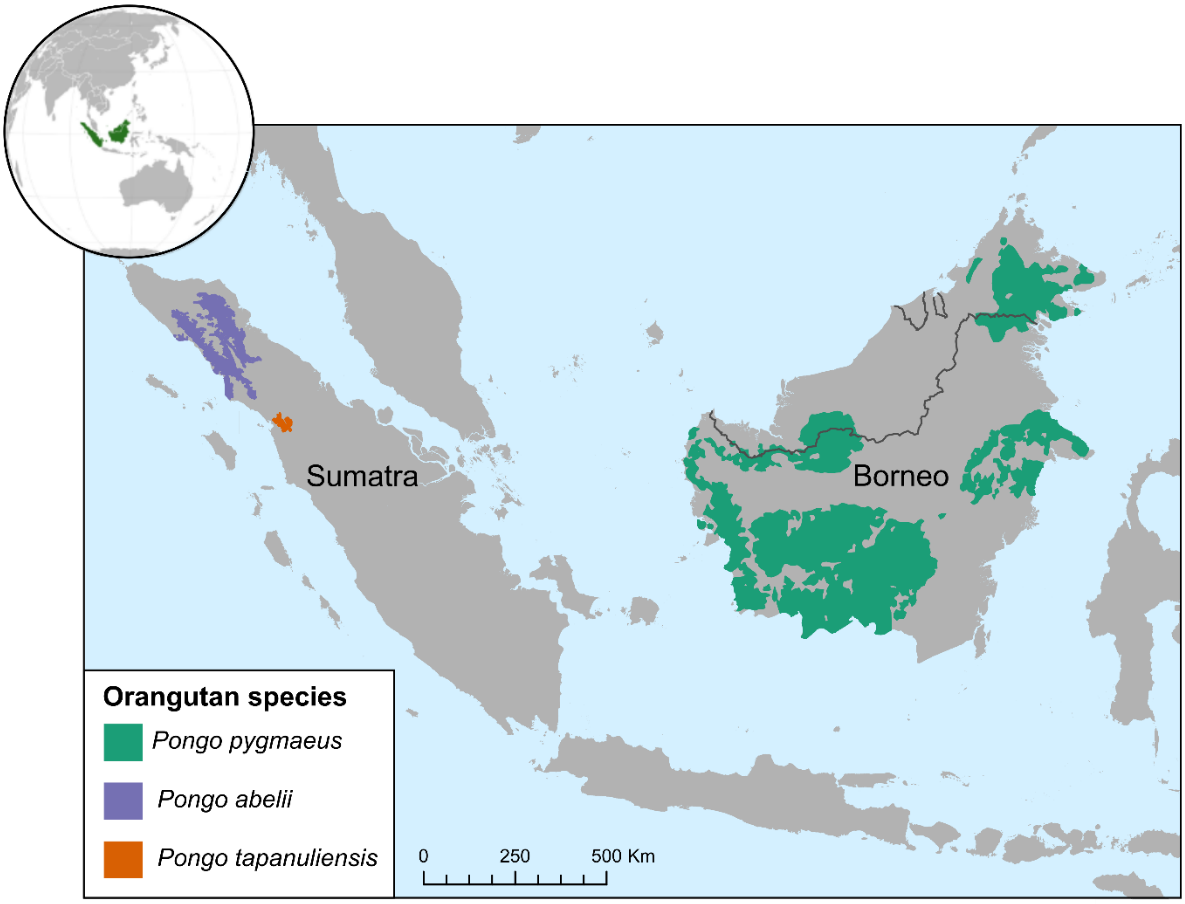

Figure 1.2: Current orangutan distribution.
The Bornean orangutan (*Pongo pygmaeus*) occurs on Borneo, while the the Sumatran orangutan (*Pongo abelii*) and the Tapanuli orangutan (*Pongo tapanuliensis*) are found in the North of Sumatra.

1.10 Drivers of orangutan declines

Bornean orangutans, like much of Borneo's biodiversity, are facing multiple threats, resulting in a marked and persistent trend in population decline. Over the past several decades, habitat loss has been attributed to much of the species decline (Meijaard and Wich, 2007). Approximately half of the orangutans existing habitat has already experienced some degree of human disturbance (e.g. logging, mining and fire) (Voigt *et al.*, 2018). Protected areas currently cover less than a quarter of the orangutan range (Wich *et al.*, 2012) and nearly half the population is found within degraded forest at high risk of conversion to commercial agriculture (Ancrenaz *et al.*, 2016).

While habitat loss remains a substantial threat (Ancrenaz *et al.*, 2016; Nowak *et al.*, 2017; Singleton *et al.*, 2017), with growing efforts to tackle deforestation, it is now illegal hunting and killing of orangutans that is the most significant threat to the species (Voigt *et al.*, 2018). Orangutans are killed for meat, out of fear and in response to negative interactions with humans, such as when foraging in gardens or when damaging young palms in plantations (Davis *et al.*, 2013). Although orangutans are protected by law across their range, a lack of awareness and enforcement of these laws is leading to high levels of killing (Meijaard *et al.*, 2011). Repeated surveys in villages within the orangutan range and subsequent modelling of these data have demonstrated an alarming rate of hunting (Davis *et al.*, 2013; Abram *et al.*, 2015). Several thousand orangutans are estimated to be hunted annually and hunting pressure appears most severe close to recently cleared forest (Meijaard *et al.*, 2011; Voigt *et al.*, 2018). Orangutans are likely to be particularly vulnerable to even small amounts of offtake from hunting due to their long-life histories, extended inter-birth period (6 – 9 years) and almost exclusively giving birth to a single offspring (Marshall *et al.*, 2009; van Noordwijk, Atmoko, *et al.*, 2018).

Orangutan populations have declined rapidly over the last few decades and now all three species are considered Critically Endangered on the IUCN Red List of Endangered Species (Ancrenaz *et al.*, 2016; Nowak *et al.*, 2017; Singleton *et al.*, 2017). Currently, there are an estimated 128,820 (98,800 – 182,500: Voigt *et al.*, 2018 unpublished data) Bornean orangutans and 13,900 (5,400 – 26,100: Wich *et al.*, 2016) Sumatran orangutans remaining, with both populations decreasing. The Tapanuli orangutan, which was only described as a distinct species in 2017, has an estimated population of >800 individuals, making it one of the rarest great ape species (Wich *et al.*, 2016; Nowak *et al.*, 2017).

1.11 Aims and objectives

Orangutans remain poorly understood in human-modified landscapes. Early observations and anecdotal evidence suggest orangutans may be able to persist and reproduce in remnant forest in these modified landscapes for extended periods of time (>20 years: Ancrenaz *et al.*, 2021). However, the current paucity of data means understanding how best to manage orangutan populations remains challenging (Spehar *et al.*, 2018). This presented a gap in our current knowledge base, which I aim to start exploring throughout this thesis.

Specifically, I aim to document orangutan populations in human-modified landscapes (**Chapter 2**) and from this information, forecast how landscape management scenarios are likely to affect the population dynamic and movement at the local scale (**Chapter 3**). Integrative modelling approaches are gaining traction in studying ecological systems, making use of multiple datasets to maximize the information that can be drawn from these data (Miller *et al.*, 2019). I seek to understand if these integrative approaches can be applied to modelling orangutan populations at the local scale, using existing datasets, as a method to rapidly increase our understanding of the species in these landscapes (**Chapter 4**).

The future of many orangutan populations are uncertain, with the majority of the current distribution outside of protected areas (Wich *et al.*, 2012), as well as hunting, retaliatory killings and rescues removing many individuals from the population (Meijaard *et al.*, 2011; Davis *et al.*, 2013; Sherman, Ancrenaz and Meijaard, 2020). I aim to understand the potential long-term viability of orangutan populations, given the current and possible future levels of fragmentation and offtake from hunting, retaliatory killings and rescues (**Chapter 5**).

1.12 Thesis outline

For **Chapter 2,** I generated orangutan density estimates within a heavily modified landscape in Sabah, Borneo. I examine how densities vary among heavily logged rainforest and forest remnants in oil palm plantations and how this might relate to forest structural metrics from LiDAR. The work was published in *American Journal of Primatology*, and served as the first published estimates of Bornean orangutan densities from an oil palm dominated landscape in Sabah.

In **Chapter 3,** I use the orangutan density information from chapter one with other ecological information for orangutans, to model the potential effects of various landscape management options on orangutan movement and population dynamics. I aided in modifying an individual-based model to explore how the potential landscape configurations could influence population connectivity in the case-study landscape in Sabah. The work was published in the journal *Landscape Ecology* and provides early evidence of the potential effectiveness of sustainability certification, at maintaining viable populations and increasing functional connectivity.

Chapter 4 also focuses on orangutan density estimates, but this time utilising data from camera trap surveys as well as traditional nest counts. I take an integrative modelling approach to combine information from these two data sources and investigate whether this approach provides an improved understanding of orangutan density and habitat use over the highly modified landscape. I find that the different ecological processes that the data result from (nesting vs terrestrial movement), can prove challenging for data integration and provide recommendations for future research.

In **Chapter 5,** I expand the individual-based model applied at the landscape-level in Chapter three, to estimate population dynamics and connectivity across the entire Bornean orangutan range. I find that small (<5,000 ha) remnant forest fragments in human-modified landscapes, may support viable orangutan populations and likely aid with movement across the landscape; however, orangutan populations appear highly vulnerable to even small levels of offtake (≥1% annually), greatly diminishing the positive effects of remnant forest fragments.

Chapter 6 is an overarching discussion, linking the individual chapters, considering their contribution to the field and highlighting remaining knowledge gaps and potential future research avenues.

Chapter 2 Densities of Bornean orangutan (*Pongo pygmaeus morio*) in heavily degraded forest and oil palm plantations in Sabah, Borneo

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2.1 Abstract

The conversion of forest to agriculture continues to contribute to the loss and fragmentation of remaining orangutan habitat. There are still few published estimates of orangutan densities in these heavily modified agricultural areas to inform range wide population assessments and conservation strategies. In addition, little is known about what landscape features promote orangutan habitat use. Using indirect nest count methods, we implemented surveys and estimated population densities of the Northeast Bornean orangutan (*Pongo pygmaeus morio*) across the continuous logged forest and forest remnants in a recently salvage-logged area and oil palm plantations in Sabah, Malaysian Borneo. We then assessed the influence of landscape features and forest structural metrics obtained from LiDAR data on estimates of orangutan density. Recent salvage logging appeared to have little short-term effect on orangutan density (2.35 ind/km^2), which remained similar to recovering logged forest nearby (2.32 ind/km^2). Orangutans were also present in remnant forest patches in oil palm plantations, but at significantly lower numbers (0.82 ind/km^2) than nearby logged forest and salvage-logged areas. Densities were strongly influenced by variation in canopy height but were not associated with other potential covariates. Our findings suggest that orangutans currently exist, at least in the short-term, within human-modified landscapes, providing that remnant forest patches remain. We urge greater recognition of the role that these degraded habitats can have in supporting orangutan populations, and that future range-wide analyses and conservation strategies better incorporate data from human-modified landscapes.

Keywords: habitat disturbance, human-modified tropical landscape, LIDAR, oil palm, orang-utan, *Pongo pygmaeus morio*

2.2 Introduction

Agriculture is a leading cause of deforestation globally and, with increasing demands for food and commodities, this trend is likely to continue (Sandker *et al.*, 2017). Inevitably, deforestation leads to losses of biodiversity and ecosystem services (Chapin Iii *et al.*, 2000), and nowhere are these losses felt more than in high biodiversity tropical regions (Pimm and Raven, 2000). Southeast Asia has experienced some of the highest deforestation rates in the world (Hansen *et al.*, 2013). Deforestation has been particularly severe in Borneo, Sumatra and Peninsular Malaysia, which, between 2000 and 2010 lost roughly 11% of their lowland forests and 20% of peat swamp forest (Miettinen, Shi and Liew, 2011). Forests in the region have been cleared for commercial plantations, such as rubber, timber, and fast-growing trees for the pulp and paper industry, but clearance for oil palm (*Elaeis guineensis*) has been particularly extensive over the last 20 years (Gaveau *et al.*, 2016). Mitigating the negative effects of further forest conversion presents a huge challenge for conservationists, balancing the needs of developing nations whilst protecting biodiversity and the valuable ecosystem services they provide.

Orangutans (*Pongo* spp.) are the only non-human great ape found outside Africa. Although heralded as conservation icons (Meijaard *et al.*, 2012) and under strict legal protection across all range states, all three species of orangutans are Critically Endangered on the IUCN Red List of Threatened Species (Ancrenaz *et al.*, 2016; Nowak *et al.*, 2017; Singleton *et al.*, 2017). Habitat loss, fragmentation, and hunting continue to be leading contributors of population decline (Meijaard *et al.*, 2011; Wich *et al.*, 2016; Voigt *et al.*, 2018), and could have particularly catastrophic consequences in combination with range contractions expected under climate change

(Struebig *et al.*, 2015). Currently, the highest densities of orangutans are in forests lower than 500 m above sea level (ASL; Voigt *et al.*, 2018). However, these low-lying areas are often the most suitable for agriculture, leading to high levels of deforestation and forest degradation within the orangutan range (Santika, Ancrenaz, *et al.*, 2017). Further forest conversion is expected and estimates of future orangutan habitat loss range from 23,000 km^2 to as much as 57,000 km^2 by the 2050s (9–20% reduction; Struebig *et al.*, 2015).

Orangutan dietary and behavioural ecology makes these species highly adapted to tropical forests (Marshall and Meijaard, 2009). Orangutans prefer moving through areas of uniform canopy height, avoid forest gaps (Felton *et al.*, 2003), and face energetic costs associated with their arboreal habits (Davies *et al.*, 2017). Although orangutans will readily move on the ground through areas of oil palm, most observations in oil palm (nests or signs of feeding) are within 50 m of forest areas (Ancrenaz *et al.*, 2015). The forest canopy buffers against extreme temperature changes and solar radiation (Hardwick *et al.*, 2015) and likely provide important refuge, resources, and nesting opportunities for orangutans in heavily modified landscapes. Therefore, three-dimensional structural features of the canopy are likely to be important determinants of orangutan presence.

On Borneo, an estimated 78% of the island's orangutan (*Pongo pygmaeus*) population is outside of protected areas (Wich *et al.*, 2012). Therefore, the inclusion of human-modified landscapes within orangutan conservation strategies will be vital to ensure the species' long-term persistence (Ancrenaz *et al.*, 2015). Recent efforts have yielded valuable information on distributions (Husson *et al.*, 2009; Wich *et al.*, 2012; Voigt *et al.*, 2018), population trends (Santika, Ancrenaz, *et al.*, 2017), responses to future human and climate-driven land cover changes (Struebig *et al.*, 2015; Wich *et al.*, 2016), as well as the effects of habitat disturbance (Ancrenaz *et al.*, 2015; Spehar and Rayadin, 2017). However, there is still a paucity of data on orangutan density, demographic responses, and dispersal within anthropogenic landscapes, which is vital to inform effective conservation initiatives.

Here we employ orangutan nest surveys to determine orangutan population densities in the continuous logged forest and forest remnants in a recently salvage-logged area and oil palm plantations in Sabah. We explore the role of forest structural data and landscape features in predicting orangutan density.

2.3 Materials and methods

2.3.1 Study site

Our study was conducted in and around the Stability of Altered Forest Ecosystems project (SAFE: https://www.safeproject.net), including the Kalabakan and Ulu Segama forest reserves and surrounding oil palm estates in the Malaysian state of Sabah, Borneo. The total study area comprises 13,000 ha, of which 7,200 ha is within the SAFE experimental area, which is being converted to oil palm plantation (Ewers *et al.*, 2011; Struebig *et al.*, 2013). Most of the forest has experienced several rounds of logging since 1978, yet still supports substantial primate biodiversity (Bernard *et al.*, 2016). The SAFE area was later salvage-logged (removal of all remaining commercially valuable trees) between 2013 and 2016, with some areas retained as forest fragments for scientific research (Figure 2.1). To the north, a block of continuous twice-logged forest in Ulu Segama connects to >1 million ha of forest habitat, including pristine conservation areas, such as Danum Valley and Maliau

Basin. Ulu Segama contains one of the largest unfragmented populations of orangutans in Malaysia (2,300 individuals), which is thought to have remained relatively stable since initial surveys in 2002 (Ancrenaz *et al.*, 2010). The wider landscape also contains a substantial block of old growth forest, the Brantian-Tatulit Virgin Jungle Reserve (VJR), which covers 2,200 ha, although logging encroachment has caused considerable degradation across much of the reserve (Deere *et al.*, 2018). The remainder of the site comprises oil palm estates, which were 8–12 years old at the time of this study. These estates contain remnant forest patches, many of which are within riparian reserves between 15 and 500 m wide (Mitchell *et al.*, 2018).

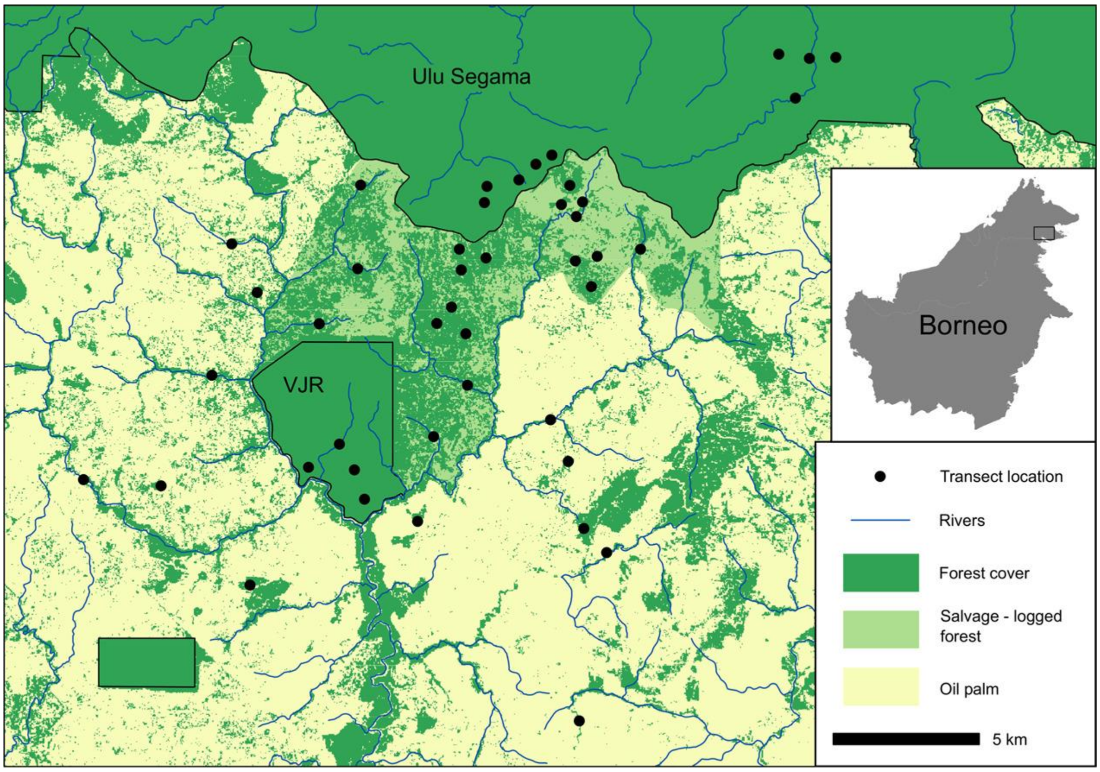

Figure 2.1: Placement of transects across the study landscape in Sabah, Borneo

2.3.2 Transect design

To investigate the effects of habitat modification on orangutan abundance, we placed transects and surveyed orangutan nests within three distinct habitat types representative of the wider landscape, as well as other parts of the oil palm producing regions of Borneo and Sumatra. These included:

- 13 transects in the logged forest of Ulu Segama Forest Reserve and Brantian-Tantulit VJR;
- 19 transects in newly isolated remnant forest patches and riparian reserves within the salvage-logged SAFE experimental area;
- 12 transects in forest remnants (hillside fragments and riparian reserves) within oil palm estates.

Transect length ranged between 0.6 km and 2 km, with an average of 1.6 km across the three habitats. We ensured >3 km of transect within each habitat, as this is the minimum length needed to produce density estimates in areas of low orangutan density (Singleton and van Schaik, 2001). To ensure spatial independence in sampling, transects were placed randomly at least 500 m apart, or were implemented on pre-existing routes established independently as part of the SAFE project experimental design. Transects in riparian remnants followed the river course to ensure the survey remained within the forest area and avoided oversampling the oil palm matrix. In total, 44 transects were surveyed once, with a combined survey effort of 51.3 km.

2.3.3 Orangutan nest surveys

Orangutans build nests daily to rest during the day and to sleep in overnight (van Casteren *et al.*, 2012). These nests are complex and have characteristics that make them easily distinguishable from those made by sympatric species, such as sun bear (*Helarctos malayanus*), giant squirrel (*Ratufa affinis*), or raptors (van Casteren *et al.*, 2012). Typically, a minimum of 60–80 nest observations is required to reliably estimate great ape densities using distance-based methods (Kühl, 2008).

We conducted nest surveys between April and August 2017, using the standing crop methods described by Spehar *et al.*, (2010). Transects were surveyed once by walking at a steady pace, stopping at regular intervals to scan every direction for nests. Upon nest encounter, we measured the perpendicular distance from directly under the nest to the transect line, using a tape measure. We assigned a decay category to each nest, ranging from A to E: where A = new nest, solid structure and leaves still green, B = leaves have started to dry out and discolor, C = nest structure still intact, leaves starting to disappear, D = most leaves gone, nest structure starting to disintegrate, and E = all leaves gone, structure visible but heavily degraded (Spehar *et al.*, 2010).

2.3.4 Parameters in the orangutan density model

Conversions of nest density to orangutan density requires three parameters: Proportion of nest builders within the population (p), nest production rate (r), and the nest decay rate (t). Because no measures were available for the site, we incorporated parameters from the published literature. We employed a conservative estimate of the proportion of nest producers (p) at 0.85 and used a nest production rate (r) value of 1.00, reported from a long-term study in the Lower Kinabatangan in Sabah

(Ancrenaz, Calaque and Lackman-Ancrenaz, 2004). As nest decay rate (*t*) shows the highest variation across sites, we calculated orangutan density using a rigorously estimated *t* value of 259 days, reported from Gunung Palung (Johnson *et al.*, 2005). We chose a decay rate from Gunung Palung as this is from a similar forest type and calculated from a large number of nests over an extended period. However, because changes in environmental conditions, altitude, and rainfall have been reported to influence decay rate (Mathewson *et al.*, 2008), comparing estimates from across a disturbance gradient using the same decay rate may not always be suitable. As we used parameters obtained from other sites, our results are best interpreted as relative measures of density between habitat types.

2.3.5 Sensitivity analysis

To test the robustness of our density estimates to uncertainties surrounding the three demographic and nest visibility parameters used in the orangutan density model, we performed a sensitivity analysis. We reproduced density estimates using high, medium (our original estimate), and low values, for each of the three input parameters *t*, *r*, and *p*. Parameter combinations resulted in 27 possible iterations, allowing us to examine variation in estimates via histograms. We produced three subsets of estimates, whereby one parameter was fixed at the medium value and the other two varied across all possible combinations of high, medium, and low values, allowing for the effect of each individual parameter on the density estimate to be examined. For *t*, we used the highest (602: Bruford *et al.*, 2010) and lowest values reported for Borneo (202: Ancrenaz, Calaque and Lackman-Ancrenaz, 2004), compared with the medium value (259: Johnson *et al.*, 2005). For *r*, we already incorporated the lowest value available in the literature of 1.00, therefore, we used the highest available value (1.16: Johnson *et al.*, 2005) and subtracted the difference between the high and medium values from the medium value, given a low r value of 0.84, which would be indicative of high levels of nest reuse. Similarly, for p, we already utilized a conservative value of 0.85 and, therefore, we used a high value of 0.88 (van Schaik *et al.*, 2005), resulting in a low value of 0.82.

2.3.6 calculating nest density

We calculated nest encounter rate by dividing the number of nests recorded along each transect by the total survey effort. As there was no significant difference in the distribution of perpendicular distances across the three habitat types ($X^2 = 1.080$, df = 2, $P = 0.583$), we were able to compare nest encounter rates between habitat types.

We obtained nest density using the formula:

$$D_{nest} = \frac{N}{(L * 2w)}$$

Where N is the number of nests observed along each transect, L is the length of each transect and w is the effective strip width, calculated using Distance software 7.1 (Thomas *et al.*, 2010). Examination of histograms of the data suggested density estimates were slightly spiked at zero, therefore, the data were aggregated into distance classes at 4 m intervals. Similarly, to avoid biases from outliers, we truncated data at 40 m. Six distance models were fitted to the data-uniform key with either cosine or simple polynomial adjustments, half-normal key with either cosine or hermite polynomial adjustments and hazard-rate key with cosine and simple polynomial adjustments. We then assessed model fit using the Chi-Square goodness of fit test (X^2) and obtained estimates of w from the best performing model, using

Akaike Information Criterion (AIC) values. As we observed sufficient numbers of nests within each habitat type, we fitted detection functions to pooled data from each habitat type separately.

We then converted nest densities to orangutan density using the formula:

$$D_{orang} = \frac{D_{nest}}{(p * r * t)}$$

Where *p* is the proportion of nest builders within the population, *r* is nest production rate and *t* is nest decay rate. To assess possible associations between orangutan density and environmental correlates, we calculated orangutan densities individually for each transect or fragment and produced estimates of error around the mean density of each habitat type.

2.3.7 Predictors of orangutan density

To identify potential predictors of orangutan density in the heavily modified landscape, we obtained vegetation structural metrics from airborne LiDAR data, collected by NERC's Airborne Research Facility between September and October 2014 (Jucker *et al.*, 2018). A detailed description of the data collection and processing is available in Jucker *et al*. (2018). Briefly, ground points from the georeferenced point cloud were classified into ground and non-ground returns, with a digital elevation model (DEM) produced from the ground data. A normalized canopy height model CHM was produced by subtracting the DEM from the non-ground returns. The CHM was then used to generate two derived raster products describing the three-dimensional vegetation structure: (a) a 50 cm resolution pit-free top of canopy height raster; and (b) a 20 m resolution stack of plant area index (PAI in m^2

m^{-2}; strictly plant area density) rasters, measuring the one-sided area of leaves and woody tissues per unit surface area, through 1 m deep vertical canopy profile slices. Total PAI was calculated as the sum of the vertical slices and PAI diversity was calculated using the Shannon index across all of the vertical slices (Table 2.1).

Table 2.1: Predictor variables for linear models.
LiDAR-based metrics were averaged within a 150 ha buffer of each transect

Predictor variables	**Description**
Local-level (LiDAR)	
Canopy height	Mean height of canopy within the buffer.
Canopy height variation	Standard deviation of canopy height. A measure of heterogeneity in the canopy.
No. layers	Number of contiguous layers within the vertical forest column.
Shannon index	Index of diversity in the distribution of material within the vertical column.
Landscape-level	
Habitat type	The habitat type in which the transect was embedded.
Forest cover	Percentage forest cover within a 150 ha buffer around each transect
Distance	Distance to the nearest continuous logged forest, measured from the midpoint of each transect to the closest border with either Ulu Segama Forest Reserve or the VJR.

In addition to the LiDAR-based information, we investigated landscape- level features as possible predictors of orangutan densities, because these measures influence densities elsewhere in Borneo. Spehar and Rayadin, (2017) found orangutan abundance to increase with proximity to natural forest. Therefore, we also included the distance from the nearest large forest area (Ulu Segama or the VJR) and the percentage of forest cover within a 150 ha buffer (typical home range of a female orangutan in a heavily disturbed forest; Ancrenaz Unpublished Data) around each transect, as possible predictors. We derived these covariates using layers produced by Hansen *et al*. (2013) to reflect forest cover at the time of our surveys (See Table 1). For pairwise comparison of predictor variables among habitat types see supporting information (Figure SI 2.1).

2.3.8 Statistical analysis

Both nest encounter rate and orangutan density estimates were normally distributed (Shapiro-Wilk test, $W = 0.958$, $P = .304$ and $W = 0.969$, $P = 0.553$, respectively) and had homogeneous variance between habitat types (Bartlett's test $K = 2.434$, $df = 2$, $P = 0.296$ and $K = 1.832$, $df = 2$, $P = 0.400$, respectively). We, therefore, employed a One-Way ANOVA to assess differences in nest encounter rate and orangutan density between habitat types. To assess relationships between nest encounter rate and orangutan density, relative to several landscape and forest structural predictor variables, we used multiple linear regression models (LM). We applied LMs with a Gaussian error structure and identity link function to the data. LMs were specified with an effects parameterisation, designating logged forest as the fixed intercept and reference habitat class from which to assess deviations in the response variable. Using methods delineated by (Grueber *et al.*, 2011), we fitted a global model to the data that included all predictor variables. Using the R package arm (Gelman and Su, 2018), we standardized variables to have a mean of 0 and a standard deviation of 0.5, to enable the direct comparison of the effect size of parameter estimates derived from model averages. The dredge function was then applied to the global model using the MuMIn package (Barton, 2009), which produces a set of all possible model outcomes, including an intercept-only model. Predictor variables were examined for collinearity using the Pearson product-moment correlation coefficient (*r*) and generalized variance inflation factors (GVIF), with variables considered highly collinear if $r \geq 0.7$ or GVIF ≥ 5 (Zuur, Ieno and Elphick, 2010). We observed a high degree of collinearity among variables and as a result, we coded models to exclude highly collinear variables from appearing in the same model.

We ranked models based on corrected AIC scores. Across all models, parameter estimates were averaged and parameters weighed on the basis of the proportion of models in which each was included (Grueber *et al.*, 2011). We inspected residual diagnostics to determine the influences of curvature and heteroscedasticity, considered indicative of poor model fit. Model validation identified a single outlier with high leverage (Cook's Distance > 1). Because subsequent removal and reanalysis found no significant effect on the parameter estimates, we present findings for models including the outlying data point. All analysis was performed using R version 3.4.2 statistical software (R Core Team, 2017). The data will be available from the NERC Environmental Information Data Centre following an embargo period (accessible from 18th March 2021, https://doi.org/10.5281/zenodo.3237506)

2.3.9 Ethical statement

The study was approved by the University of Kent's Animal Welfare Ethics Review Board and fully complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. Field research was authorized by Sabah Biodiversity Council under access license No. JKM/MBS.1000–2/2 JLD.4(104).

2.4 Results

We observed 678 nests along the 44 transects. After transects outside the LiDAR extent were excluded and the data were truncated, 594 nests on 35 transects remained for analyses.

2.4.1 Orangutan density

Over the whole landscape, we encountered an average of 13.31 nests/km, and generated an estimate of 2.01 orangutans per km^2 (Table 2.2). However, both nest encounter rate and resulting density estimates varied considerably across the landscape (nest encounter rate, 0.56-30.83 nests/km; density, 0.09-4.52 ind/km^2), with overall significant differences among habitats (ANOVA: nests, $F_{2, 12} = 15.49$, $P = < .001$; density $F_{2, 24} = 15.37$, $P = < 0.001$). Density estimates were similar between logged forest and forest remnants in the salvage-logged area (mean 2.32 and 2.35, respectively; Tukey post hoc test, $P = 0.601$), but were significantly lower in the forest remnants in the oil palm (mean 0.82, $P = < 0.001$; Figure 2.2).

Table 2.2: Summary of nest-count survey data.

Habitat Type	Site ID	No. of nests	Transect length (km)	Effective strip width[a] (m)	Nest encounter rate (nests/km)	Orangutan density (Ind/km^2)
Continuous logged forest						
	LF1	31	1.8	15.5	17.2	2.5
	LF2	23	2	15.5	11.5	1.7
	LF3	25	2	15.5	12.5	1.8
	LFR	15	1	15.5	15.0	2.2
	LFE1	17	2	15.5	8.5	1.3
	LFE2	24	1.5	15.5	15.7	2.3
	LFE3	24	1.2	15.5	20.0	2.9
	LFE4	17	1	15.5	17.0	2.5
	LFER	25	1.6	15.5	15.6	2.3
	VJR_R	25	1.6	15.5	15.6	2.3
	VJR_1	37	1.2	15.5	30.8	4.5
	VJR_2	10	1	15.5	10.0	1.5
Salvage-logged forest						
	RR0	30	1.6	14.3	19.1	3.0
	RR5	26	1.5	14.3	17.3	2.8
	RR15	28	1.6	14.3	17.5	2.8
	RR30	29	1.7	14.3	17.1	2.7
	RR60	11	1.5	14.3	7.3	1.2
	RR120	21	1.6	14.3	13.1	2.1
	Block_B	28	1.9	14.3	14.6	2.3
	Block_C	29	2.1	14.3	13.8	2.2
	Block_D	24	2.4	14.3	9.5	1.5
	Block_E	43	2.3	14.3	19.1	3.0
Forest remnants in oil palm plantations						
	OP02	13	1.6	14.7	8.1	1.3
	OP03	9	1.3	14.7	7.0	1.1
	OP07	1	1.8	14.7	0.6	0.1
	OP12	6	1.8	14.7	3.4	0.5
	OP14	16	1.8	14.7	8.9	1.4
	OP16	7	1.8	14.7	4.0	0.6

[a] Effective strip width was calculated in Distance 1.7 software (*Thomas et al.*, 2010).

2.4.2 Landscape determinants of orangutan density

Our information-theoretic statistical approach yielded 48 possible models (Tables SI 1.2 and SI 2.2) from which we produced full model-averaged estimates penalized for parameter redundancy. For habitat type, these models confirmed that nest encounter rate and orangutan densities were lower in remnant forest patches in oil palm (Coefficient $\beta = -16.44$, 95%CI $= -26.48, -6.39$ and $\beta = -2.33$, 95%CI $= -3.91, -0.75$, respectively, Figure 2.2). Variation in canopy height was also positively associated with nest encounters and densities ($\beta = 7.76$, 95%CI $= 2.62, 12.90$ and $\beta = 1.25$, 95%CI $= 0.45, 2.06$, respectively). The 95 % confidence intervals of all other variables crossed zero, indicating that they had little effect on orangutan abundance.

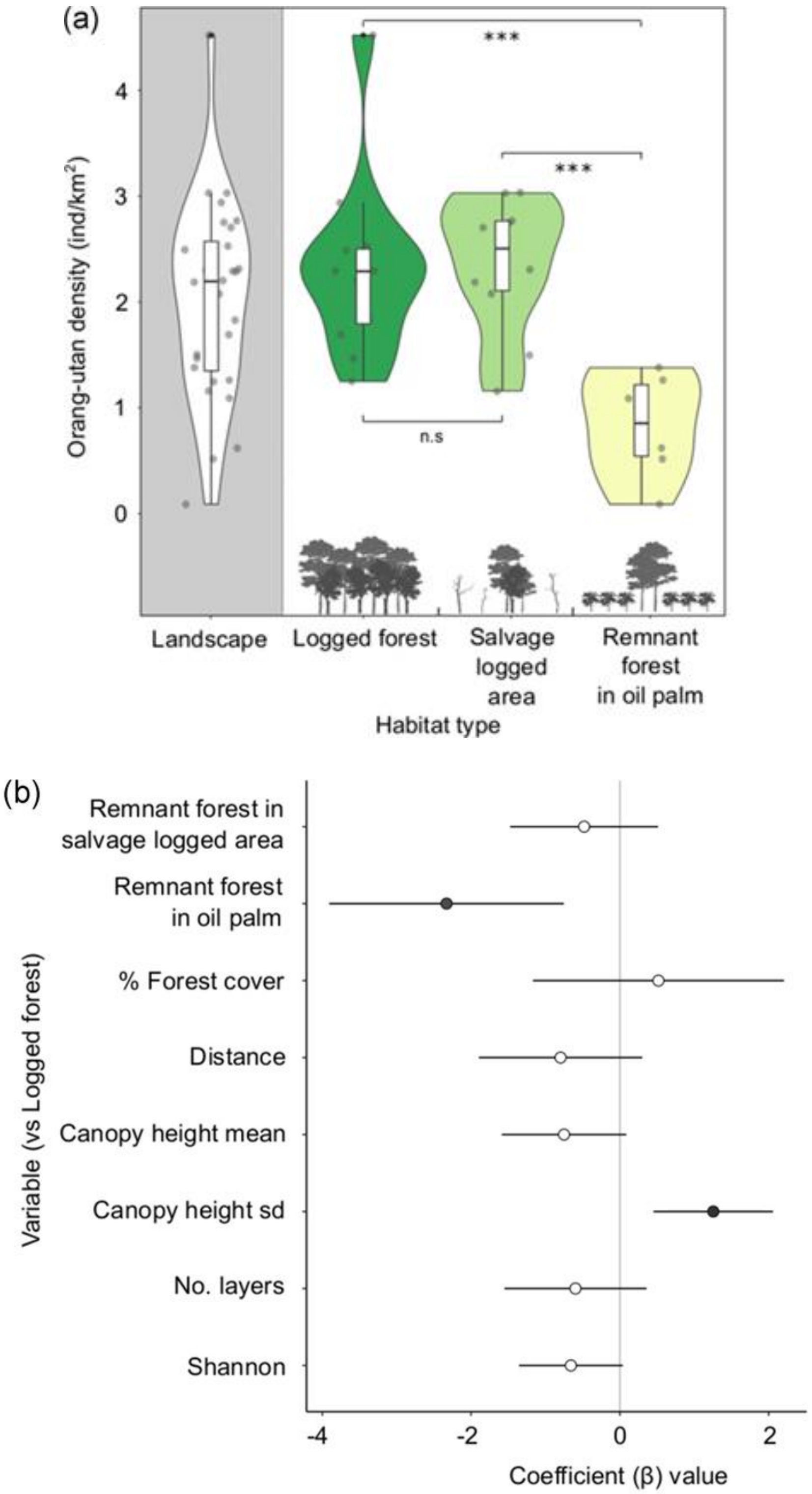

Figure 2.2: Orangutan density estimates and model averaged results.
(a) Violin plots of orangutan density (individuals/km^2), for the overall landscape and between habitat types. A significant difference of *P*<0.001 between habitat types is denoted by *** and no significance by n.s. Data points are jittered for visualization. (b) Coefficient

plot (β) from an averaged model of orangutan population density, showing 95% confidence intervals

2.4.3 Sensitivity analysis

Our sensitivity analysis resulted in a large range of possible density values, with several estimates substantially higher than our original estimate (Figure 2.3). For the logged forest, when *t* was fixed, density estimates ranged from 1.03 to 5.65. However, this range increased to between 0.51 and 6.09 when *r* was fixed and *t* and *p* were varied. We observed the largest variation in density estimates when p was fixed and both *t* and *r* varied, with estimates increasing to between 0.46 and 6.91. We observed a similar pattern across all habitat types (Table SI 2.3).

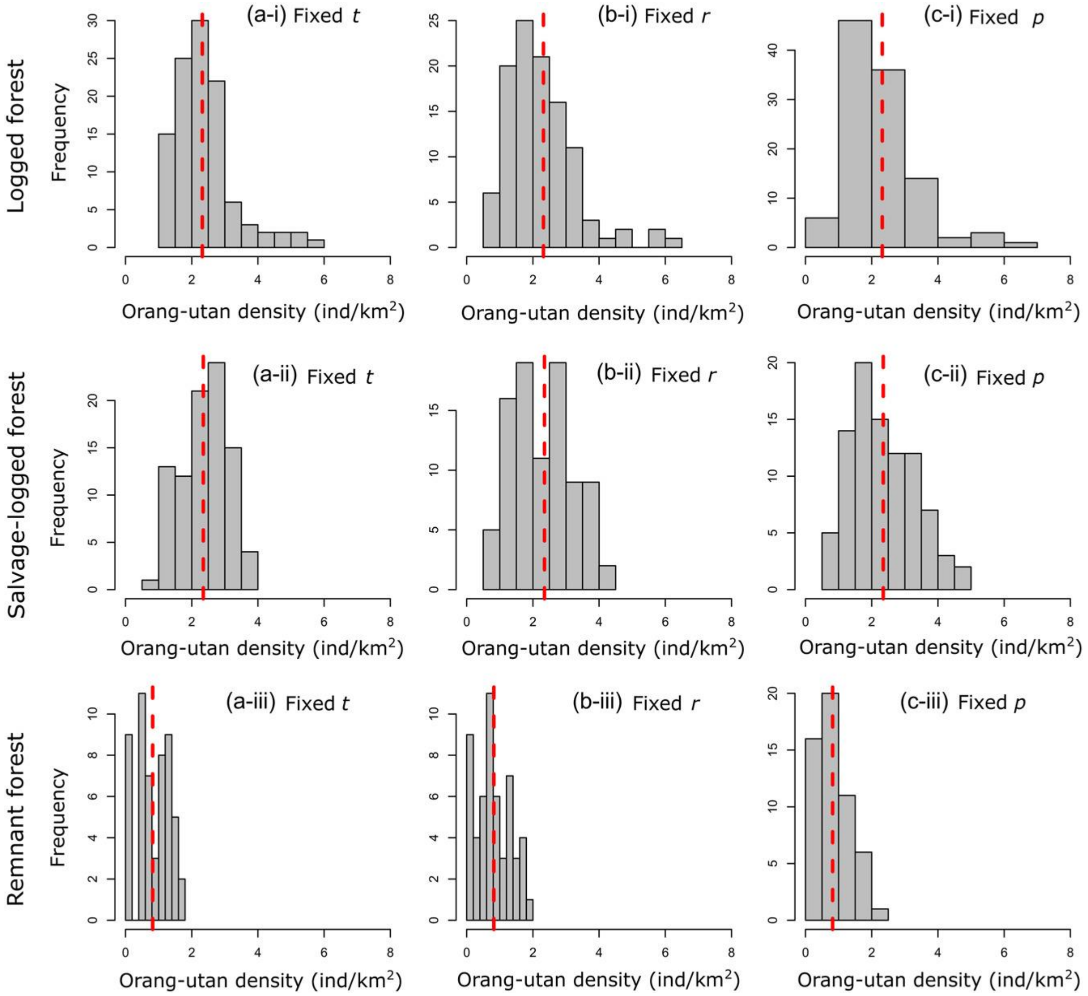

Figure 2.3: Sensitivity of density estimates to changes in parameter values. Sensitivity analysis, to demonstrate the effect of changing fixed parameters (nest decay rate *t*, nest production rate *r* and proportion of nest builders *p*), on orangutan density estimates. The density reported in the main text is labelled by a dashed line in each plot. Plots a, d, and g show results where *t* is fixed, b, e, and h where *r* is fixed and c, f, and i where *p* is fixed, across all three habitat types. For *t* we used the values: high 602 (Bruford *et al*., 2010), medium 259 (Johnson *et al*., 2005), and low 202 (Ancrenaz *et al*., 2004). For *r*: high 1.16 (Johnson *et al*., 2005), medium 1 (Ancrenaz *et al*., 2004), and low *r* value of 0.84. For *p* high 0.88 (Van Schail *at el*., 2005), medium 0.85 (Ancrenaz *et al*., 2004), and low value of 0.82

2.5 Discussion

We produced orangutan density estimates across a mosaic landscape in Malaysian Borneo and found orangutans were present in all forest habitats, although on average orangutan density was ≥65 % lower in remnant forest patches in oil palm. The average density across our landscape of 2.01 ind/km^2, is within the range of estimates produced by Ancrenaz *et al*. (2010) within the same area from aerial surveys (0.7-2.1 ind/km^2).

Recent salvage logging (2–5 years previous to this study) appeared to have little effect on orangutan density within remnant forest patches (2.35 ind/km^2), which was similar in this habitat to neighboring logged forest (Ulu Segama 2.17 ind/km^2 and the VJR 2.76 ind/km^2). This result is contrary to previous research that found densities across the orangutan range to be higher in areas surrounding recently logged forest (Husson *et al.*, 2009), perhaps because insufficient time had passed to capture the demographic response. At our study site, forest structural metrics revealed that remnant forest patches in the salvage-logged area are structurally more similar to remnant forest in oil palm, than to areas of logged forest. Although being structurally similar, the SAFE experimental area has been disturbed relatively recently 2–5 years before the study) compared to the remnant forest patches in the oil palm estates 8-12 years). Orangutans have the longest interbirth period of any mammal (ca. 9 years) and an extended period of adolescence before first birth (Knott and Wich, 2009). This long-life history may result in a large time lag before demographic responses to disturbance are truly observed, meaning that there may have been insufficient time for the full effects of the disturbance on orangutan populations to manifest in the SAFE experimental area.

The salvage-logged area at SAFE is due to be converted to oil palm. On the basis of the density of nests, the area still appears to support a relatively large number of orangutans. During the conversion process, any remaining vegetation will be felled and cleared before terracing and the planting of oil palm commences, forcing most wildlife, including orangutans, to move to the neighbouring forest areas or become isolated in remnant forest patches. In our study area, the nearby Ulu Segama and the VJR already support high densities of orangutans, and immigration of orangutans from surrounding areas would increase competition for resources. In addition, the VJR will be fragmented when the oil palm is planted. Unless a wildlife corridor is maintained to link the VJR to Ulu Segama, orangutans in this forest will be isolated and overcrowded unless they are able to disperse across several kilometers of oil palm plantation. A recent integrative trend analysis found orangutan survivorship was lowest in areas of fragmented forest or near to areas of recent forest conversion to agriculture (Santika, Ancrenaz, *et al.*, 2017). With increasing areas of orangutan habitat likely to be converted to oil palm, practical matters need to be considered to ensure resident animals can disperse successfully.

Both indices of orangutan abundance in remnant forest patches within oil palm estates were lower than those in the logged forest and remnant forest in the salvage-logged area. As expected, conversion to oil palm has a negative effect on local orangutan populations. Despite these negative effects, we encountered nests on all transects within remnant forest patches and riparian reserves in oil palm estates. We also directly observed three adult females with dependent young within several riparian reserves, suggesting reproductive orangutans use these areas. Additionally, as nests were observed at large distances (≥6 km) from the nearest large forest area, it is likely at least some of these individuals are resident within the estates. Equally, because densities were similar in salvage-logged and logged forest, it is doubtful that orangutans within oil palm estates are those displaced during the salvage logging process. The above observations suggest that the oil palm plantation still hosts an orangutan population, albeit at a lower density than in the logged forest.

The linear models revealed certain nuances in the data that may be important in explaining orangutan persistence within oil palm estates. Although we expected distance from continuous logged forests to have a negative effect on orangutan presence, we found no evidence in our survey that distance from this forest affects orangutan density. Davies *et al.* (2017) found the number of contiguous layers in the canopy did not determine orangutan movement through disturbed forests in the Kinabatangan region. Similarly, we found little evidence that vertical layering had an effect on orangutan densities across our study landscape. However, contrary to Davies *at el.* (2017), we found that large variation in canopy height was positively associated with orangutan density. Across our study site, the most heavily degraded areas tended to be dominated by pioneer species, such as Macaranga spp (Struebig *et al.*, 2013), giving the canopy a highly uniform structure. Orangutans also appear averse to nesting within Macaranga spp., and therefore these areas may be ecologically unsuitable to support orangutans (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004). Variation in canopy height is strongly associated with successional status (Deere *et al*., 2018) and thus indicates greater environmental heterogeneity and breadth of resources. Further research is needed to quantify resource availability in remnant forest patches under various levels of degradation and gain an improved understanding of the long-term carrying capacity of agricultural landscapes. However, at least in our study site, it appears orangutans have been able to persist in oil palm estates for several years.

Our sensitivity analysis revealed two important points. First, across all possible iterations of parameter values, the upper limit of our density estimates for remnant forest sites in oil palm were lower than half the upper limits for the logged forest, and density estimates were on average close to a third that of logged forest. These results provide strong evidence that, despite using parameters acquired from other sites in our density calculations, oil palm estates support <50 % of the orangutan density of the logged forest. Second, our sensitivity analysis corroborates previous research, that density estimates are highly sensitive to changes in nest decay rate (Marshall and Meijaard, 2009). However, our analysis also revealed that nest production rate could have a large influence on density estimates. High levels of disturbance may limit nesting opportunities or alter the abundance of tree species orangutans preferentially use for nesting and increase nest reuse (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004). If unaccounted for, high levels of nest reuse may potentially lead to an underestimation of orangutan density. Therefore, to improve future density estimates in highly modified landscapes, further research is needed to assess orangutan nesting behaviour within remnant forest patches in oil palm.

Previous research on orangutan behavioural ecology in modified landscapes suggests young subordinate males are dispersing from optimal habitat from where they have been displaced by dominant flanged males (Ancrenaz *et al.*, 2015). However, the three orangutans we observed directly during our surveys of remnant forest in oil palm were all adult females with dependent offspring. Spehar and Rayadin (2017) also recorded adult females with dependent offspring in timber plantations in East Kalimantan. Orangutans exhibit female philopatry and are less likely to disperse over large distances than males (van Noordwijk *et al.*, 2012). Female range fidelity may, therefore, explain the number of females we encountered. Equally, this may indicate female orangutans are becoming effectively stranded in heavily degraded landscapes. In any case, our results suggest remnant forest patches in modified landscapes are likely to hold a significant number of reproductive females, which are important to the population and largely overlooked within conservation strategies. Further research is needed to fully understand how these areas affect reproduction and survival rates and the role they play in connecting meta-populations.

Integrating modified landscapes into orangutan conservation strategies poses a significant challenge. Leaving 1,000 ha of land unconverted can entail annual losses to oil palm producers of over US$ 0.5 million (Nantha and Tisdell, 2009). Despite these potential losses, the oil palm industry is increasingly moving towards business models based on corporate environmental and social responsibility (Morgan *et al.*, 2016; Morgans *et al.*, 2018). As a result, certification schemes, such as the RSPO, have considerable potential to help conserve orangutans within oil palm estates (Nantha and Tisdell, 2009). Across Indonesia, RSPO certification has reduced deforestation by 33% on land managed by certified companies (Carlson *et al.,* 2018). Currently, however, there may be greater numbers of orangutans within non-RSPO certified estates than in certified estates (Morgans *et al.*, 2018). Therefore, increasing the uptake of RSPO certification among oil palm producers will likely reduce deforestation further and aid orangutan conservation.

If orangutan populations are maintained in human-modified landscapes, individuals face additional risks which conservationists and policymakers should consider. An increase in orangutan proximity to humans is likely to result in a greater risk of zoonotic disease transmission (Russon, 2009). Persecution of orangutans is common throughout their range in Borneo (Meijaard *et al.*, 2011). Without adequate law enforcement to eradicate persecution, simply retaining forest fragments is likely to be insufficient to allow orangutans to persist in modified landscapes.

The ability of orangutans to use modified landscapes is, to some degree, likely to be species-specific. Bornean orangutans display higher dietary flexibility than their Sumatran counterparts (Russon, 2009). Therefore, their ability to cope with reduced food availability is likely to be greater. Furthermore, our study was conducted with the Northeast Bornean orangutan (*P. p. morio*), which may be particularly adapted to persist on tough, fall-back foods, as northeast Borneo is subject to more severe droughts and resource fluctuation as a result of the El Nino Southern Oscillation (Taylor, 2006b).

2.6 Conclusion

Despite pledges by the Indonesian and Malaysian government to stabilize orangutan populations, they have continued to decline by 25 % over the past 10 years (Santika, Ancrenaz, *et al.*, 2017). Our results show forest conversion to oil palm negatively affects orangutan populations, leading to reduced densities. Nevertheless, we found orangutans still persist in remnant forest patches within oil palm estates. The presence of orangutans within oil palm estates demonstrates that these great apes may have greater ecological resilience to disturbance than previously assumed. Although forest patches alone cannot maintain viable populations, if managed appropriately, they may act as important corridors or stepping-stones, connecting isolated populations, and facilitate migration in response to climate change. As orangutan habitats are the most suitable areas for oil palm production in Borneo and Sumatra, these modified landscapes should be taken more seriously in orangutan conservation and monitoring efforts.

2.7 Acknowledgements

This research was funded by the UK Natural Environment Research Council via the Human-Modified Tropical Forests research program (NE/K016407/1; http://lombok.nerc-hmtf.info/), as well as the Primate Society of Great Britain. We would like to thank the Sabah Biodiversity Council, Sabah Forest Department, Benta Wawasan, and Sabah Softwoods for permitting access. We are grateful to Arnold James, Mohd. Shah Nizam Mustamin, Ampat Siliwong, Sabidee, and Mohd. Rizan for their assistance in the field. We would also like to thank field staff at HUTAN for their training in survey methods and Nicolas J. Deere for statistical advice.

2.8 Supplementary information

Densities of Bornean orangutans (*Pongo pygmaeus morio*) in heavily degraded forest and oil palm plantations in Sabah, Borneo

Dave J. I. Seaman, Henry Bernard, Marc Ancrenaz, David Coomes, Thomas Swinfield, David T. Milodowski, Tatyana Humle, Matthew J. Struebig

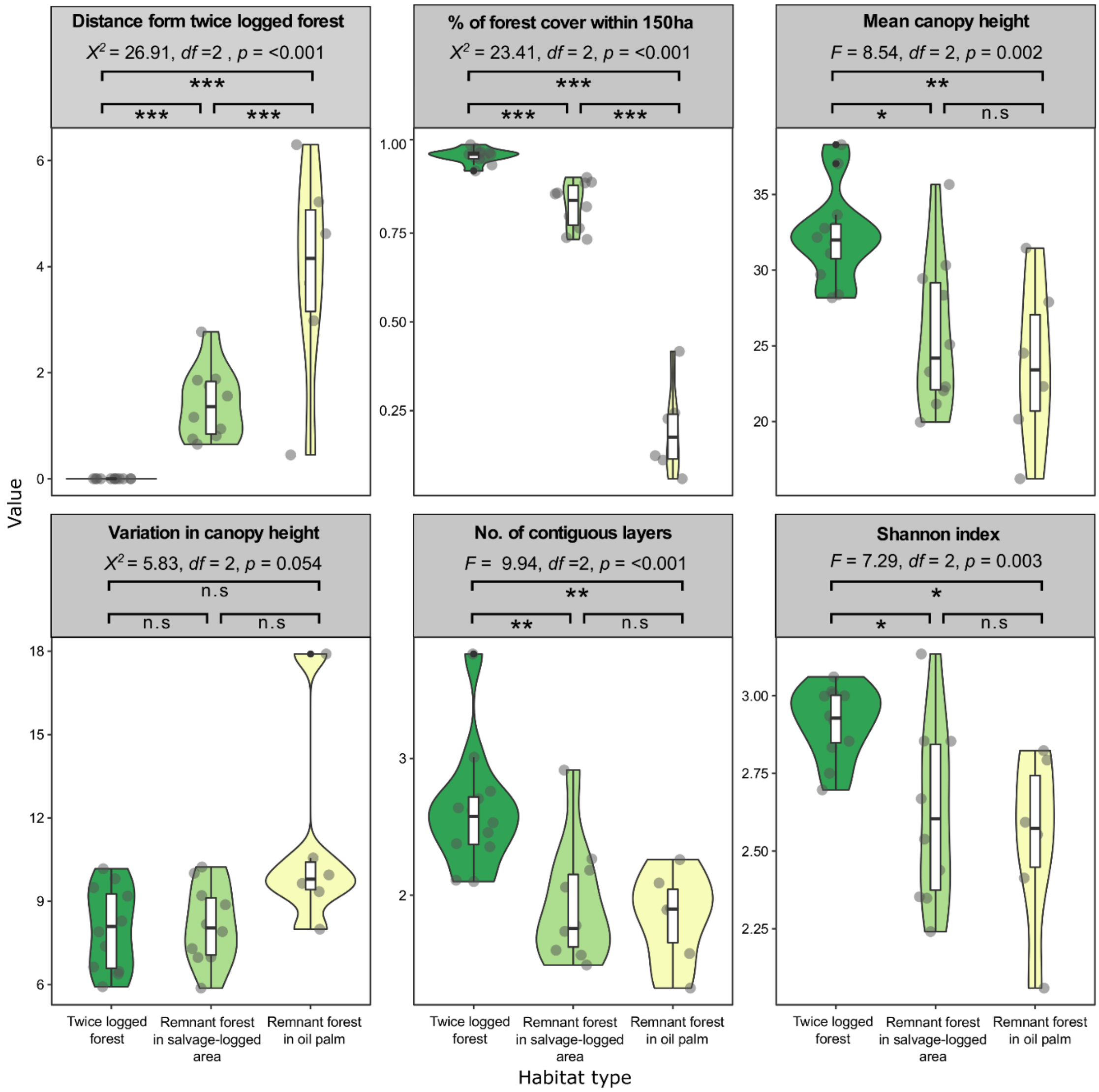

Figure SI 2.1: Violin plots showing pairwise comparison of each predictor variable among habitat types.

Variables were compared using One way ANOVA (*F*) with post hoc Tukey test or Kruskal–Wallis tests (X^2) with post hoc Wilcoxon signed-rank tests. A significance of <0.05 is denoted by *, <0.01 by **, <0.001 by *** and no significance by n.s. Results suggest that remnant forest patches in both the salvage-logged area and oil palm are structurally more similar to each other than to the continuous logged forest.

Densities of Bornean orangutans (*Pongo pygmaeus morio*) in heavily degraded forest and oil palm plantations in Sabah, Borneo

Dave J. I. Seaman, Henry Bernard, Marc Ancrenaz, David Coomes, Thomas Swinfield, David T. Milodowski, Tatyana Humle, Matthew J. Struebig

Table SI 2-1. Candidate models used to characterize nest encounter rate

Model	k†	logLik‡	AICc§	ΔAICc¶	wt¥
Encounter rate ~					
Habitat type + Canopy sd + Distance + Shannon	7	140.52	295.04	0.00	0.22
Habitat type + Canopy mean + Canopy sd + Distance	7	140.62	295.23	0.19	0.20
Habitat type + Canopy sd + Shannon	6	141.95	295.90	0.85	0.14
Habitat type + Canopy mean + Canopy sd	6	142.32	296.64	1.60	0.10
Habitat type + Canopy sd + Distance + No layers	7	141.76	297.51	2.47	0.06
Habitat type + Canopy sd + Forest Cover + Shannon	7	141.81	297.63	2.58	0.06
Habitat type + Canopy sd + Distance	6	143.05	298.10	3.05	0.05
Habitat type + Canopy mean + Canopy sd + Forest Cover	7	142.05	298.11	3.06	0.05
Habitat type + Canopy sd	5	144.24	298.49	3.45	0.04
Habitat type + Canopy sd + No layers	6	143.32	298.64	3.60	0.04
Habitat type + Canopy sd + Forest Cover	6	143.96	299.93	4.88	0.02
Habitat type + Canopy sd + Forest Cover + No layers	7	143.00	299.99	4.95	0.02
Canopy sd + Forest Cover + Shannon	5	146.97	303.93	8.89	0.00
Canopy sd + Forest Cover + No layers	5	147.08	304.17	9.12	0.00
Canopy mean + Canopy sd + Forest Cover	5	147.23	304.45	9.41	0.00
Canopy sd + Forest Cover	4	148.70	305.39	10.35	0.00
Habitat type	4	148.93	305.86	10.82	0.00
Habitat type + Shannon	5	147.94	305.87	10.83	0.00
Forest Cover + Shannon	4	149.25	306.50	11.46	0.00
Canopy sd + Distance	4	149.30	306.61	11.56	0.00
Canopy sd + Distance + Shannon	5	148.42	306.84	11.80	0.00
Forest Cover	3	150.48	306.96	11.92	0.00
Habitat type + Forest Cover	5	148.48	306.96	11.92	0.00
Habitat type + Forest Cover + Shannon	6	147.61	307.22	12.17	0.00
Habitat type + Distance + Shannon	6	147.81	307.63	12.59	0.00
Canopy sd + Distance + No layers	5	148.83	307.65	12.61	0.00
Habitat type + Distance	5	148.85	307.71	12.67	0.00
Canopy mean + Canopy sd + Distance	5	148.87	307.73	12.69	0.00
Forest Cover + No layers	4	149.89	307.77	12.73	0.00
Habitat type + Canopy mean	5	148.91	307.81	12.77	0.00
Habitat type + No layers	5	148.91	307.83	12.79	0.00

Canopy mean + Forest Cover	4	150.15	308.30	13.26	0.00
Habitat type + Canopy mean + Forest Cover	6	148.46	308.91	13.87	0.00
Habitat type + Forest Cover + No layers	6	148.46	308.91	13.87	0.00
Habitat type + Canopy mean + Distance	6	148.81	309.63	14.59	0.00
Habitat type + Distance + No layers	6	148.83	309.67	14.62	0.00
Distance	3	153.02	312.04	17.00	0.00
Distance + Shannon	4	152.80	313.61	18.57	0.00
Canopy mean + Distance	4	152.96	313.92	18.88	0.00
Distance + No layers	4	153.01	314.03	18.98	0.00
Null	2	156.41	316.82	21.78	0.00
Canopy mean	3	155.58	317.16	22.11	0.00
No layers	3	155.68	317.37	22.33	0.00
Shannon	3	156.31	318.63	23.58	0.00
Canopy sd	3	156.41	318.82	23.78	0.00
Canopy mean + Canopy sd	4	155.58	319.16	24.11	0.00
Canopy sd + No layers	4	155.68	319.36	24.32	0.00
Canopy sd + Shannon	4	156.31	320.62	25.58	0.00

† K indicates the number of parameters used by the model. ‡ The log-likelihood value, an alternative measure of model performance and denotes the plausibility of the model. § Akaike’s Information Criterion AICc. ¶ Delta AICc score, the difference between the AICc score of each model against the best preforming model. ¥ Akaike weight.

Table SI 2-2: Candidate models used to characterize orangutan density.

Model	*k*[†]	logLik[‡]	AICc[§]	ΔAICc[¶]	wt[¥]
Oran-utan density ~					
Habitat type + Canopy sd + Distance + Shannon	7	-16.45	46.90	0.00	0.22
Habitat type + Canopy mean + Canopy sd + Distance	7	-16.54	47.08	0.18	0.20
Habitat type + Canopy sd + Shannon	6	-17.87	47.74	0.83	0.14
Habitat type + Canopy mean + Canopy sd	6	-18.24	48.47	1.57	0.10
Habitat type + Canopy sd + Distance + No. layers	7	-17.67	49.35	2.44	0.06
Habitat type + Canopy sd + Forest cover + Shannon	7	-17.73	49.47	2.56	0.06
Habitat type + Canopy mean + Canopy sd + Forest cover	7	-17.97	49.93	3.03	0.05
Habitat type + Canopy sd + Distance	6	-18.97	49.94	3.03	0.05
Habitat type + Canopy sd	5	-20.16	50.31	3.41	0.04
Habitat type + Canopy sd + No. layers	6	-19.23	50.46	3.56	0.04
Habitat type + Canopy sd + Forest cover	6	-19.87	51.75	4.85	0.02
Habitat type + Canopy sd + Forest cover + No. layers	7	-18.90	51.81	4.91	0.02
Canopy sd + Forest cover + Shannon	5	-22.88	55.77	8.86	0.00
Canopy sd + Forest cover + No. layers	5	-22.99	55.98	9.08	0.00
Canopy mean + Forest cover	5	-23.14	56.28	9.38	0.00
Canopy sd + Forest cover	4	-24.61	57.23	10.32	0.00
Habitat type	4	-24.85	57.71	10.80	0.00
Habitat type + Shannon	5	-23.87	57.73	10.83	0.00
Forest cover + Shannon	4	-25.17	58.35	11.45	0.00
Canopy sd + Distance	4	-25.23	58.46	11.55	0.00
Canopy sd + Distance + Shannon	5	-24.35	58.70	11.79	0.00
Forest cover	3	-26.40	58.80	11.90	0.00
Habitat type + Forest cover	5	-24.41	58.81	11.91	0.00
Habitat type + Forest cover + Shannon	6	-23.54	59.07	12.17	0.00
Habitat type + Distance + Shannon	6	-23.74	59.48	12.58	0.00
Canopy sd + Distance + No. layers	5	-24.75	59.50	12.60	0.00
Habitat type + Distance	5	-24.78	59.55	12.65	0.00
Canopy mean + Canopy sd + Distance	5	-24.79	59.59	12.68	0.00
Forest cover + No. layers	4	-25.81	59.61	12.71	0.00
Habitat type + Canopy mean	5	-24.83	59.66	12.76	0.00
Habitat type	5	-24.84	59.68	12.77	0.00
Canopy mean + Forest cover	4	-26.07	60.15	13.24	0.00
Habitat type + Canopy mean + Forest cover	6	-24.38	60.76	13.85	0.00
Habitat type + Forest cover	6	-24.38	60.76	13.85	0.00
Habitat type + Canopy mean + Distance	6	-24.74	61.47	14.57	0.00
Habitat type + Distance	6	-24.76	61.51	14.61	0.00
Distance	3	-28.95	63.89	16.99	0.00
Distance + Shannon	4	-28.73	65.46	18.56	0.00

Canopy mean + Distance	4	-28.88	65.77	18.86	0.00
Distance + No. layers	4	-28.94	65.88	18.97	0.00
Null	2	-32.32	68.64	21.74	0.00
Canopy mean	3	-31.49	68.98	22.08	0.00
No. layers	3	-31.60	69.20	22.29	0.00
Shannon	3	-32.22	70.45	23.54	0.00
Canopy sd	3	-32.32	70.64	23.74	0.00
Canopy mean + Canopy sd	4	-31.49	70.98	24.08	0.00
Canopy sd + No. layers	4	-31.59	71.19	24.28	0.00
Canopy sd + Shannon	4	-32.22	72.44	25.53	0.00

† *k* indicates the number of parameters used by the model. ‡ The log-likelihood value, an alternative measure of model performance and denotes the plausibility of the model. § Akaike’s Information Criterion AICc. ¶ Delta AICc score, the difference between the AICc score of each model against the best preforming model. ¥ Akaike weight.

Densities of Bornean orangutans (*Pongo pygmaeus morio*) in heavily degraded forest and oil palm plantations in Sabah, Borneo

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Sensitivity analysis

Table SI 2-3: Results of sensitivity analysis.

		Orangutan density			
Habitat type	Fixed parameter	Mean	Max	Min	SD
Logged forest					
	Reported†	2.32	4.52	1.25	0.81
	t fixed	2.36	5.58	1.04	0.89
	r fixed	2.10	6.01	0.52	1.14
	p fixed	2.13	6.91	0.46	1.20
Salvage-logged forest					
	Reported†	2.35	3.03	1.16	0.60
	t fixed	2.39	3.74	0.97	0.70
	r fixed	2.13	4.02	0.48	1.02
	p fixed	2.16	4.62	0.43	1.08
Remnant forest in oil palm					
	Reported†	0.82	1.38	0.09	0.45
	t fixed	0.84	1.70	0.07	0.48
	r fixed	0.75	1.83	0.04	0.53
	p fixed	0.76	2.10	0.03	0.55

†Figures reported in this study

Chapter 3 Orangutan movement and population dynamics across human-modified landscapes: implications of policy and management

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3.1 Abstract

Context

Agricultural expansion is a leading cause of deforestation and habitat fragmentation globally. Policies that support biodiversity and facilitate species movement across farmland are therefore central to sustainability efforts and wildlife conservation in these human-modified landscapes.

Objectives

We investigated the conservation impact of several potential management scenarios on animal populations and movement in a human-modified tropical landscape, focusing on the critically endangered Bornean orangutan, *Pongo pygmeus*.

Methods

We used an individual-based modelling platform to simulate population dynamics and movements across four possible landscape management scenarios for a highly modified oil palm-dominated landscape in Sabah, Malaysian Borneo.

Results

Scenarios that maximised the retention of natural forest remnants in agricultural areas through sustainability certification standards supported stable orangutan populations. These populations were up to 45% larger than those supported under development-focused scenarios, where forest retention was not prioritised. The forest remnants served as corridors or stepping-stones, increasing annual emigration rates across the landscape, and reducing orangutan mortality by up to 11%. Sensitivity analyses demonstrated that this outcome was highly contingent on minimising mortality during dispersal.

Conclusions

Management that promotes maximising natural forest cover through certification, such as that promoted by the Roundtable on Sustainable Palm Oil, can maintain viable orangutan populations over the lifespan of an oil palm plantation and facilitate movement among otherwise isolated populations. However, minimising hunting and negative human-orangutan interactions, while promoting peaceful co-existence between apes and people, will be imperative to insure positive conservation outcomes.

Keywords: Connectivity; High Carbon Stock approach; Oil palm; RangeShifter; Wildlife corridors

3.2 Introduction

Agricultural expansion is the leading cause of deforestation and biodiversity loss across the tropics (P. G. Curtis *et al.*, 2018). The demand for commodities and the need to sustain an increasing human population means further agricultural expansion will be unavoidable (Laurance, Sayer and Cassman, 2014). Oil palm (*Elaeis guineensis*) is a prominent driver of tropical deforestation, with 21.5-23.4 million ha already under production globally (Descals *et al.*, 2020). Biodiversity is heavily impoverished in intensively managed oil palm plantations, which typically support <15% of the species found in native forests (Fitzherbert *et al.*, 2008; Meijaard *et al.*, 2018). However, there is growing evidence that by retaining forest remnants within plantations and managing them effectively, some wildlife species can survive in these human-modified landscapes (Deere *et al.*, 2018, 2019; Mitchell *et al.*, 2018). There is thus an increasing emphasis on including human-modified landscapes into the broader agenda of wildlife conservation in tropical countries (Ng, Payne and Oram, 2020).

Agricultural expansion contributes to the partitioning of remaining habitats into smaller, more isolated patches (Haddad *et al.*, 2015). This fragmentation can limit individual movements over a landscape, thereby restricting the exchange of genetic information within and among populations, and inhibiting range shifts in response to environmental change (Årevall *et al.*, 2018; Lino *et al.*, 2019). Enhancing the connectivity value of human-modified landscapes is therefore a central theme in conservation by, for example, facilitating species movement between forest patches, which increases the population viability. Linear corridors and 'stepping-stone' patches of natural habitat are keyways by which such connectivity can be achieved (Keitt, Urban and Milne, 1997; Baum *et al.*, 2004; Saura, Bodin and Fortin, 2014; Carroll *et al.*, 2015).

Emerging environmental sustainability standards are beginning to recognise the importance of maintaining functional connectivity in agricultural landscapes. The Roundtable on Sustainable Palm Oil (RSPO), for example, is an international sustainable certification standard, which aims to alleviate both environment degradation and social impacts associated with oil palm production (https://rspo.org/). Recent uptake of zero-deforestation commitments by the RSPO seeks to align environmental sustainability and development goals by decoupling deforestation and agricultural expansion to ensure ecologically functional forest mosaics are retained during the development of new plantations (Deere *et al.*, 2019;

Meijaard *et al*., 2018). The High Conservation Value (HCV) concept has emerged as the principal methodology for palm oil producers to honour these commitments, and the High Carbon Stock (HCS) approach is integrated into the RSPO standard to assist in the quantification of HCV (http://highcarbonstock.org/leading-palm-oil-certification-system-adopts-no-deforestation-requirements/). HCS is a transparent land-use planning tool that aims to direct agricultural development towards degraded land of limited conservation value, while prioritising conservation set-asides based on ecological conditions, such as forest quality, fragment size and connectivity. While previous research on certification standards has emphasised the importance of forest fragments and riparian margins for biodiversity (Deere *et al*., 2018; 2019), the extent to which these habitat remnants promote functional connectivity at local scales remains poorly understood (Scriven *et al.*, 2019).

Acquiring sufficient empirical data to assess connectivity is often prohibitively expensive, time consuming, and may raise welfare concerns if animals have to be habituated to the presence of observers or captured and restrained for individual identification or for tracking devices to be fitted (Gutema, 2015). Therefore, ecological modelling remains an important tool for investigating landscape connectivity and the potential for animal movements across landscapes (Kool, Moilanen and Treml, 2013). Advances in spatially-explicit population modelling and the incorporation of stochastic environmental and biological processes may provide more realistic model outcomes than correlative approaches, particularly when applied to highly complex landscapes (Urban *et al.*, 2016). Mechanistic dispersal models incorporate stochastic movement, whereby simulated individuals make probabilistic decisions governed by movement rules and, as a result, are likely to more closely align with reality (Palmer, Coulon and Travis, 2011; Aben *et al.*, 2016). If coupled with spatially explicit demographic models, the long-term effects of management options on population viability and species movement can be assessed concurrently (Bocedi *et al.*, 2014; Cabral, Valente and Hartig, 2017). This allows detailed investigations into management scenarios, which can provide a powerful tool to inform effective land-use planning and to direct research.

Here, we apply a spatially explicit individual-based model to test the conservation impact of several potential management scenarios for a highly degraded landscape in Sabah, Malaysian Borneo – a major palm oil producing region (Meijaard *et al.*, 2018). Retaining forest fragments in the landscape is particularly important when new development takes place: i.e. through informed land-use planning such as the HCV and HCS approaches. Around 25% of the land in Sabah is planted with oil palm, with only a small proportion of the previous forest cover remaining in these plantations. However, every 25-30 years palms need to be removed and replanted, providing an opportunity to incorporate and restore additional forest fragments within existing farmland. Thus, the effectiveness of sustainable certification standards will be critical to ensuring positive conservation outcomes under future development. Our appraisal focuses on the Bornean orangutan (*Pongo pygmaeus*), a large-bodied flagship species characterised by a slow life-history and low population densities, attributes that make the species particularly vulnerable to the effects of habitat fragmentation (Marshall *et al.*, 2009). On Borneo, orangutans have already lost substantial habitat, and research suggests further reduction of up to 57,000 km^2, equal to a 20 % decline (Struebig *et al.*, 2015; Voigt *et al.*, 2018) is possible by 2050 under a business-as-usual scenario. Recent surveys provide evidence that orangutans can persist at low densities in fragmented landscapes and oil palm estates where forest remnants are retained (Ancrenaz *et al.*, 2015; Spehar and Rayadin, 2017; Seaman *et al.*, 2019). Initial estimates suggest as many as 10,000 orangutans, or between 10 and 15% of the remaining Bornean population, may already occur in oil palm plantations (Morgans *et al.*, 2018). As most of the remaining orangutan range is found outside of protected areas in Indonesia, this number will almost certainly increase with future forest conversion (Wich *et al.*, 2012). It is therefore essential to understand how the processes of habitat modification affect orangutan population dynamics and connectivity across disturbed landscapes to provide some conservation options for the species. Hence, our study aimed to investigate the potential of prospective management scenarios to create agricultural landscapes that can also support orangutan populations and promote functional connectivity between large protected forests.

3.3 Materials and methods

3.3.1 Study system

We modelled orangutan movement across the southern district of Tawau, an area of ca. 208,000 ha (51.8 km x 40.3 km) encompassing the Stability of Altered Forest Ecosystems project (SAFE; www.safeproject.net) and surrounding oil palm estates. The landscape is a heterogeneous mosaic of degraded forest remnants embedded within oil palm plantations, and to a lesser extent, non-native softwoods (Figure 3.1 panel I). Palms range in age from newly established plantations to mature stands of >15 years (Mitchell *et al.*, 2018). The landscape also harbours several large areas of intensively logged lowland or hill dipterocarp forest, including protected forest in

Mt. Louisa Forest Reserve (contiguous with ca. 1 million ha of forest, of which 18,160 ha is situated in the study system), Tawau Hills (28,000 ha; of which 3,890 ha is situated in the study system), and four smaller Virgin Jungle Reserves (525-2,000 ha). The study area contains multiple settlements and an extensive network of permanent roads since much of the landscape is actively managed as plantation. Orangutans have been documented in all forest types across the landscape (Ancrenaz *et al.*, 2004; Bernard *et al.*, 2016; Seaman *et al.*, 2019).

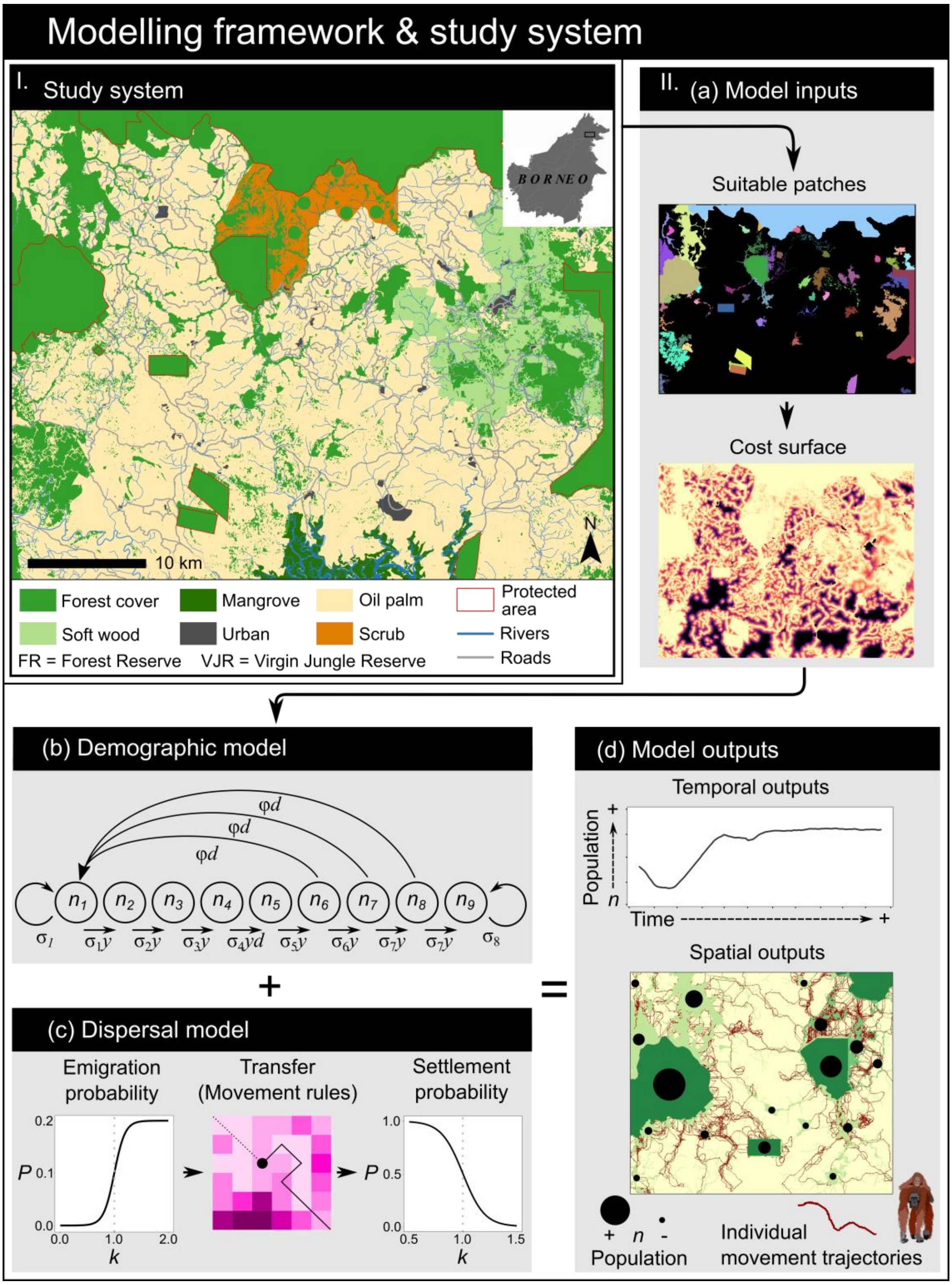


Figure 3.1: Model framework and study system.

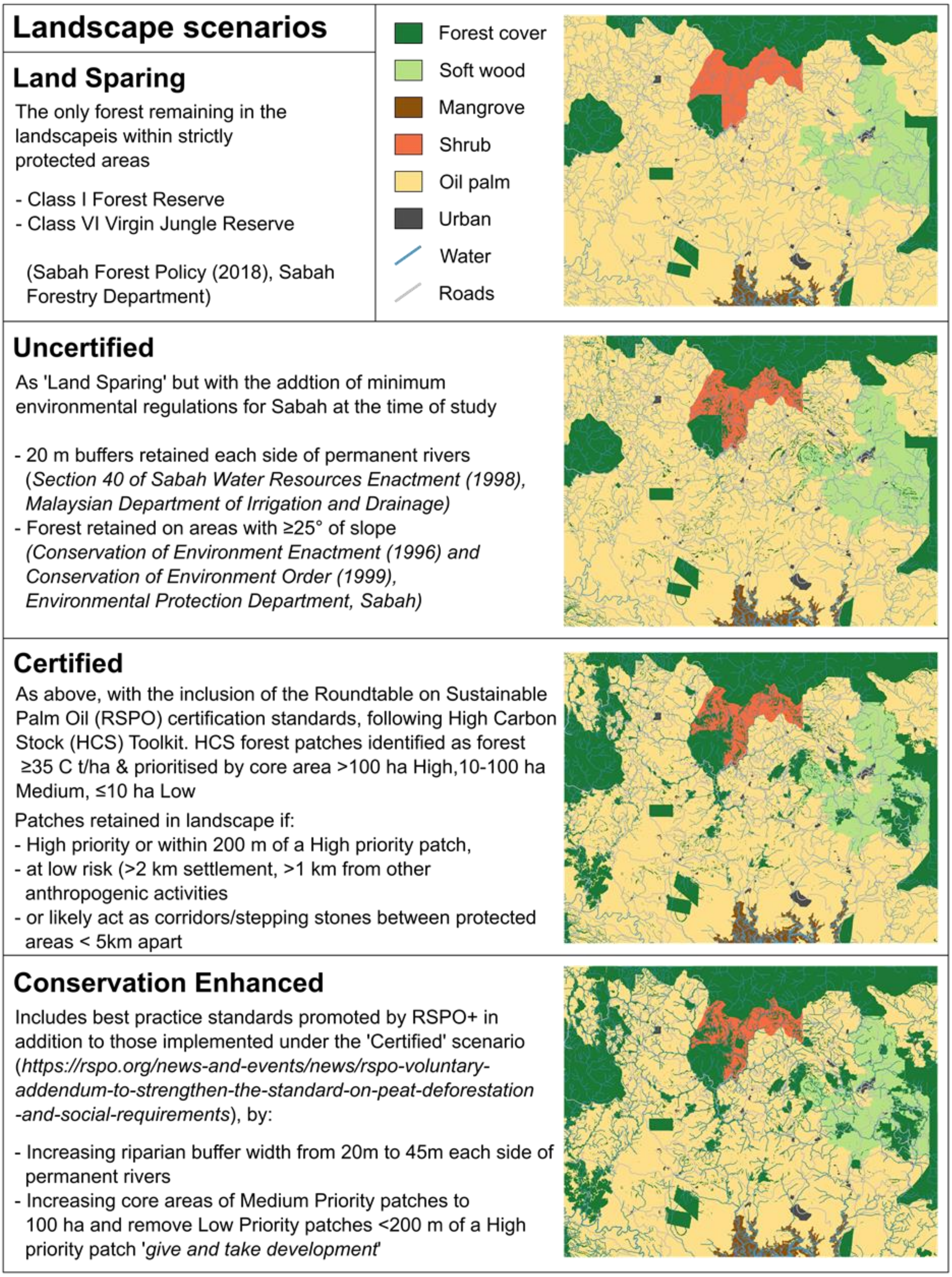
I The study system is a highly fragmented landscape in the north of Borneo (location in inset). II. Modelling framework: (a) Model inputs used by RangeShifter 2.0. (b) The stage-structured demographic model of nine stages *n*, where σ signifies survival probability of each stage, y denotes the probability of an individual developing to the next stage, φ signifies individual fecundity and d indicates where density dependence in development is applied (Modified from Neubert and Caswell, 2000). (c) The dispersal model, both emigration and settlement probabilities (*P*) are dependent on the density relative to the carrying capacity of the habitat patch (*K*). The transfer process uses a stochastic movement simulation implemented in RangeShifter 2.0. (d) Model outputs are both temporally and spatially explicit.

3.3.2 landscape scenarios

We modelled four land-use scenarios that could be reasonably expected given current environmental policy and conservation approaches in Sabah and typical to other human-modified tropical landscapes: ‘Land Sparing’, ‘Uncertified’, ‘Certified’, and ‘Conservation Enhanced’. ‘Land Sparing’ assumes the conversion to agriculture of all land except that which is strictly protected (Class I Forest Reserve & Class IV Virgin Jungle Reserve), thus representing a worst-case scenario (Figure 3.2). We simulated an ‘Uncertified’ Landscape, by using the minimum environmental policy currently in place for Sabah, whereby all areas were converted except the protected areas, riparian buffers 20m each side of permanent rivers and areas above 25^{o} slope. A ‘Certified’ Landscape was modelled by following the High Carbon Stock (HCS) approach decision tree to prioritise land for conservation (Rosoman *et al.*, 2017), through which forests were classified into strata defined by thresholds of carbon density, and forest patches prioritised based on their core area after applying a 100 m internal buffer into High (>100 ha), Medium (10 – 100 ha), of Low priority (<10 ha). Forest patches were further prioritised for conservation or development by patch proximity, forest quality and risk from anthropogenic activities. Lastly, we constructed a ‘Conservation Enhanced’ landscape, using recommendations from published literature. Here, we increased the riparian buffer width to 45m each side of the river, as this is recently recommended to improve biodiversity outcomes (Gray *et al.*, 2014; Mitchell *et al.*, 2018), and increased the core area of the HCS medium priority patches to 100 ha but removed low priority patches in the ‘give and take’ process defined by the HCS protocol.

3.3.3 Modelling framework

We applied a modified version of RangeShifter 2.0 (Bocedi *et al.*, 2021), a freely available individual-based modelling platform, to model orangutan population persistence and connectivity across our study landscape (Figure 3.1 panel II) and landscape scenarios. RangeShifter simultaneously models population dynamics and landscape connectivity, by integrating spatially explicit demographic and dispersal models (Bocedi *et al.*, 2014).



Landscape scenarios

Land Sparing

The only forest remaining in the landscapeis within strictly protected areas

- Class I Forest Reserve
- Class VI Virgin Jungle Reserve

(Sabah Forest Policy (2018), Sabah Forestry Department)

Uncertified

As 'Land Sparing' but with the addtion of minimum environmental regulations for Sabah at the time of study

- 20 m buffers retained each side of permanent rivers (*Section 40 of Sabah Water Resources Enactment (1998), Malaysian Department of Irrigation and Drainage)*
- Forest retained on areas with ≥25° of slope *(Conservation of Environment Enactment (1996) and Conservation of Environment Order (1999), Environmental Protection Department, Sabah)*

Certified

As above, with the inclusion of the Roundtable on Sustainable Palm Oil (RSPO) certification standards, following High Carbon Stock (HCS) Toolkit. HCS forest patches identified as forest ≥35 C t/ha & prioritised by core area >100 ha High,10-100 ha Medium, ≤10 ha Low

Patches retained in landscape if:
- High priority or within 200 m of a High priority patch,
- at low risk (>2 km settlement, >1 km from other anthropogenic activities
- or likely act as corridors/stepping stones between protected areas < 5km apart

Conservation Enhanced

Includes best practice standards promoted by RSPO+ in addition to those implemented under the 'Certified' scenario (*https://rspo.org/news-and-events/news/rspo-voluntary-addendum-to-strengthen-the-standard-on-peat-deforestation-and-social-requirements*), by:

- Increasing riparian buffer width from 20m to 45m each side of permanent rivers
- Increasing core areas of Medium Priority patches to 100 ha and remove Low Priority patches <200 m of a High priority patch '*give and take development*'

Figure 3.2: Landscape scenarios based on plausible management options in southern Tawau district, Sabah.

3.3.4 Patch allocation and orangutan demography

The landscape was defined on a gridded system at a resolution of 30 m x 30 m. We used a patch-based approach to model population demography; whereby adjacent cells of suitable habitat were aggregated into discrete patches. The equilibrium density of each patch was based on habitat type, using existing orangutan density estimates from the same site (Table 1) (Seaman *et al.*, 2019). In large forest areas we reduced density estimates by half to represent the female density. However, for small remnant forest patches that are likely to be occupied by resident females (Ancrenaz *et al.*, 2021) we maintained density estimates to reflect this. Female orangutan home ranges are difficult to determine, and on Borneo estimates vary from 40 to 600 ha (Singleton *et al.*, 2009). Although density estimates varied widely across the landscape, the mean density in remnant forest in oil palm was 0.82 individuals/km^2, equating to a minimum of 122 ha to support a single orangutan. We therefore considered 122 ha of suitable habitat to be the minimum patch size (which would therefore sustain a single adult female) (Seaman *et al.*, 2019). We considered suitable habitat to be any area of natural forest defined following HCS protocols as cells with 35 t C ha^{-1}, produced using LiDAR data from the Carnegie Airborne Observatory (Asner *et al.*, 2018). Mean carbon values extracted from transects in remnant forest in oil palm estates where orangutan nests have been observed range from 3.04 to 106.03 t C ha^{-1}, and therefore, forest delineated by this carbon threshold is known to be capable of supporting orangutans. Habitat patches large enough to support one or more orangutan (i.e. > 122 ha) were numbered with a unique numeric identifier (detailed in Supplementary Information SI 3.2).

We developed an overlapping stage-structured demographic model limited to females, and comprising nine age-related stages (Table 3.1). There is a slight male-bias sex ratio in orangutans of 55%, so we set survival probability of 0.45 at the neonate stage. Subsequent stage survival probabilities were derived from the 2019 Bornean Orangutan Population and Habitat Viability Analysis (PHVA; Utami-Atmoko *et al.*, 2019). We added density dependence in development between the young adult and adult stages, so that females becoming reproductive would be delayed if their resident patch was at, or close to, population equilibrium density. We modelled a yearly reproductive season. However, as orangutans have a long interbirth interval ranging from 6-9 years (van Noordwijk, Utami Atmoko, *et al.*, 2018), we set the annual fecundity at 0.167 (equating to a 6-year inter-birth period). Density dependence was also incorporated in fecundity (with a bespoke function added to match Utami-Atmoko, *et al*., 2019), with the interbirth period increasing as patches became close to equilibrium density (Supplementary Information SI.1)

3.3.5 Dispersal

Females are highly philopatric (van Noordwijk *et al.*, 2012); however, little is known about how female orangutans disperse in oil palm landscapes. Since females have been observed in forest patches in human-modified landscapes many years after conversion (Ancrenaz *et al*., 2015; Spehar and Rayadin, 2017; Seaman *et al.*, 2019), it is likely these animals continue to display a high level of home range fidelity even within these highly disturbed habitats. To account for this, we used a strongly density-dependent emigration probability, meaning orangutans remained within their natal patch until the patch reached its equilibrium density, at which point there was a conservative 0.2 maximum emigration probability (Figure SI 3.2a). Settlement probability was also density-dependent. As female orangutans tend to stay close to their mothers’ home range (Goossens *et al.*, 2006), we set a probability of 1 of an orangutan immediately settling in a new patch, unless that patch was near equilibrium, at which point there was a shallow decline in settlement probability (Figure SI 3.2b). The emigration and settlement values we selected resulted in a pattern where females only emigrate if absolutely necessary (i.e. when there is no possibility of reproducing in the natal patch) and would likely settle at the first available opportunity, which is supported by our current understanding of orangutan behaviour (Ashbury *et al.*, 2020).

We modelled dispersal movement with the stochastic movement simulator (SMS), which simulates stepwise nearest-neighbour movements informed by a cost surface (Palmer, Coulon and Travis, 2011). Additionally, individual movements depend on three parameters: perceptual range (the distance at which the individual can evaluate its surroundings), directional persistence (DP, the tendency of an individual to move in a straight line) and memory size (the number of previous movement steps used to calculate the directional persistence).

As orangutans are arboreal, they are likely to have a large perceptual range. We therefore set the parameter to 25 cells (750 m). Simulated trajectories resulting from a range of values were visualised and plausible combinations were selected by expert judgement (the approach is consistent with that used for determining the cost values). We found plausible paths for intermediate values of directional persistence (between 2.0 and 3.0 when memory was set to 10: detailed in Supplementary Information SI.4). We thus used directional persistence = 2.5 and memory = 10 as our baseline values but also undertook a sensitivity analysis to investigate the impact of changing these parameters.

The study area is characterised by little hunting or conflict killings of orangutans and has a large number of small patches that orangutans can potentially utilize for resources. We therefore assumed mortality rates in the landscape to be low (per step mortality 0.001) and set the maximum number of steps per year to 3,000 (equating to a path length of approx. 108 km), which seems reasonable based on daily path length from wild orangutans multiplied over the same period (Singleton *et al*., 2009) and visual inspection of dispersal trajectories. We also set the total maximum number of steps an individual may make during dispersal to 12,000 (approx. 435 km), and any individual exceeding that limit would die. Since the area is part of a much larger multi-use landscape and as a result, dispersing animals are not constrained to the area, we applied a reflective study boundary as orangutans may also enter the landscape from outside the study system.

3.3.6 Cost surface

Orangutans are primarily arboreal but will also travel terrestrially where necessary (Ancrenaz *et al.*, 2014a). However, this form of terrestrial locomotion incorporates additional energetic costs (Thorpe, Crompton and Alexander, 2007). To capture this cost, we produced a composite cost surface layer informed by both expert-derived landscape resistance and a time cost model (Frakes, Flowe and Sherrill, 2015) (detailed in Supplementary information SI.2). The resulting cost surface is time travel distance in seconds, weighted by the resistance of the landcover type.

Table 3.1: Parameter values included within the model.

Model parameter	Description	Value	Reference
1/b	Number of females per km^2		(Seaman *et al.*, 2019)
Continuous logged forest / VJR		1.12	
Salvage logged forest		1.18	
Remnant forest		0.82	
Mean fecundity	Yearly probability of a reproductive female giving birth	0.167	(Utami-Atmoko et al., 2017)
Survival probabilities	Yearly survival probability of each age stage		(Utami-Atmoko *et al.*, 2019)
First year		0.45*	
Infant	1-2 years	0.97	
Juvenile	3-9 years	0.99	
Adolescent	10-11 years	0.98	
Young adult	12+ years; subject to density-dependent development to adult	0.99	
Adult	13-41 years	0.99	
Mature adult	42-45 years	0.95	
Senior adult	46-51 years	0.85	
Senescent	52-55 years	0.75	
Emigration probability			
D_0	Maximum probability of emigrating at stage 'young adult'	0.2[†]	
α	Slope of emigration function	10[†]	
ß	Inflection point of emigration function	1	
Settlement probability			Estimates based on (Nietlisbach *et al.*, 2012)
α_S	Slope of settlement function	-10[†]	
ß$_S$	Inflection point of settlement function	1	

Movement parameters		Expert informed
Directional persistence	2.5[†]	
Perceptual range (cells)	25[†]	
Memory size	10	
Per step mortality	0.001[†]	
Cost to movement		Expert informed

* 0.45 survival probability accounts for slight male sex bias in births. [†] Tested for model sensitivity.

3.3.7 Model initialisation and metrics

We initialised the model on each landscape scenario so that all suitable patches were occupied at female carrying capacity (based on habitat type), with the population distributed with a right-skew towards older ages classes (20% of the population among Adolescent or below and 80% among Young adult and above (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004). For each scenario, we modelled population dynamics over 100 years for 100 iterations. To evaluate the effects of each scenario, we derived several metrics, with respect to population dynamics and movement, recorded after the population had reached equilibrium (see Figure SI 3.3). Mean Population size was calculated for the whole landscape and agricultural areas only (i.e. excluding all protected areas and VJRs) at 100 years. Dispersal Distance was derived from the centre of the cell from which the individual initially dispersed to the centre of the cell at which it settled in a non-natal patch. We determined Dispersal Success as the proportion of dispersing individuals that either settled in a non-natal patch, returned and settled in their natal patch, or died during transfer. Relative Dispersal Success was derived by comparing the annual number of individuals that either returned and settled in their natal patch, settled in a non-natal patch or died during transfer, compared to the ‘Uncertified’ scenario. We also created network maps, by plotting links between patches where individuals had successfully dispersed and settled.

3.3.8 Sensitivity analysis

As our movement parameters were largely based on anecdotal evidence and expert opinion, we undertook a sensitivity analysis to evaluate the robustness of our model to permutations in parameter values (detailed in Supplementary information SI.5). To assess the model sensitivity to permutation in parameter values, we compared Mean Population size at 100 years between landscape scenarios and percentage change in Dispersal Success relative to the baseline scenarios, under the range of parameter values.

3.4 Results

3.4.1 Population size in each landscape configuration

We modelled orangutan population dynamics over 100 years in four different landscape scenarios. At a mean of 645 individuals in year 100 (± standard error (SE) 2.27 individuals), the 'Conservation Enhanced' configuration supported the largest simulated orangutan population across the whole landscape. The 'Certified' Landscape supported a comparable Mean Population of 612 individuals (±2.12). The smallest population sizes were predicted for the 'Uncertified' Landscape (450 ±1.70 individuals) and the 'Land Sparing' scenario (445 ±1.62 individuals). When we excluded protected areas and assessed the population in the agricultural landscape only, the largest population was again predicted for the 'Conservation Enhanced' scenario (214 ±1.23 individuals), with only a slight reduction estimated for the 'Certified' landscape (181 ±1.18 individuals). The 'Uncertified' landscape had a final estimated Mean Population of 20 individuals (±0.33), and with no suitable habitat within the production landscape the 'Land Sparing' scenario had an estimated Mean Population of < 1 individual (±0.04; Figure 3.3).

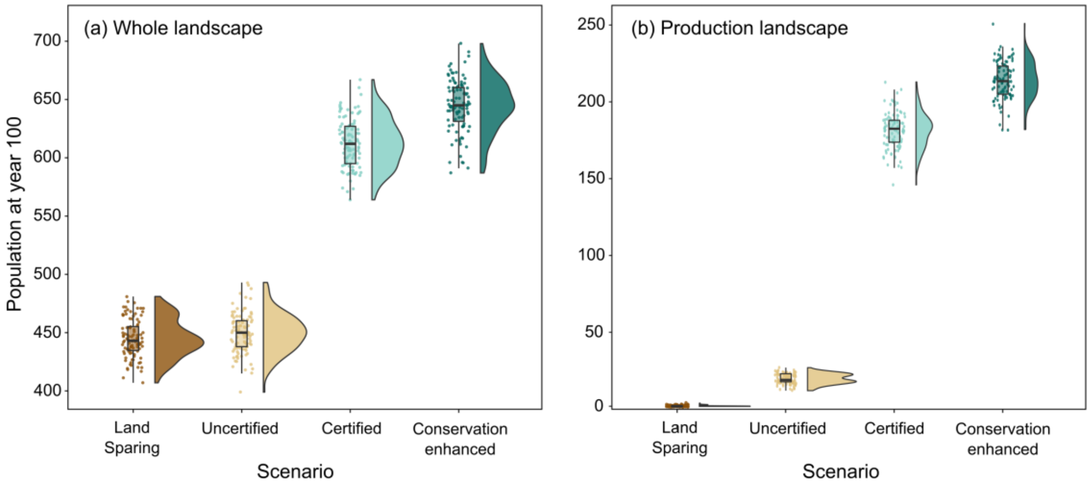


Figure 3.3: Raincloud plot showing Population size at 100 years over 100 iterations for each of the four management scenarios.
Right side of each plot shows the probability density, with the left showing the raw data and boxes denoting the median, first and third quartiles, and whiskers indicating 95% confidence intervals. (a) Population for the whole landscape including the protected areas and remnant forest patches in the production landscape, (b) population size for patches in the production landscape only.

3.4.2 Dispersal distance and success

In terms of absolute numbers, when considering all patches in the landscape the mean number of annual successful dispersers settling into non-natal patches averaged 2.83 (±0.02, Figure 3.4) in the 'Certified' scenario and 3.16 (±0.03) in the 'Conservation Enhanced' scenario, which was an increase relative to the 'Uncertified' landscape (1.08 and 1.33 individuals respectively). If limited to only individuals dispersing from one of the eight protected areas, annually an average of 2.03 (±0.02) individuals settled in non-natal patches in the 'Certified' scenario and 2.16 (±0.02) in the 'Conservation Enhanced' scenario. The mean number of dispersing orangutans that went back and settled in natal patches annually was comparable across the ‘Certified’ (2.07 ±0.02), ‘Conservation Enhanced’ (2.00 ±0.02) and ‘Uncertified’ (1.93 ±0.02) landscape scenarios when considering all patches. When constricted to the protected areas only, fewer individuals settled in their natal patches in the ‘Certified’ (1.68 ±0.02) and ‘Conservation Enhanced’ (1.54 ±0.01) scenarios, compared to the ‘Uncertified’ (1.89 ±0.02) landscape. The ‘Land Sparing’ scenario which only included the eight protected areas, experienced the lowest annual number of individuals settling into non-natal patches (1.05 ±0.01) and the highest number of individuals returning and settling in their natal patches annually (2.28 ±0.02).

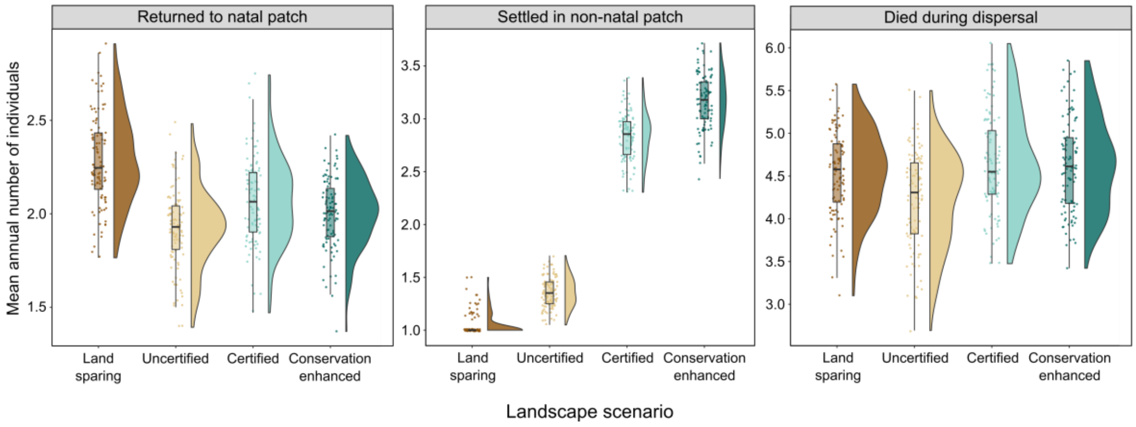


Figure 3.4: Raincloud plot showing of mean annual *Dispersal Success*
We define successful dispersers as individuals that either settled in a non-natal patch or returned emigrated but then returned to their natal patch. Unsuccessful dispersers were individuals that died during dispersal.

Dispersal mortality rate was 46 % in the ‘Land Sparing’ scenario, with a similar rate recorded in the ‘Uncertified’ landscape (44 %, Figure 3.5). Mortality rate during dispersal was lower in the ‘Certified’ and ‘Conservation Enhanced’ landscapes (36 % and 35 % respectively). In the ‘Land Sparing’ scenario, only 13 % of dispersing individuals settled in non-natal patches. This increased slightly in the ‘Uncertified’ landscape to 18%, and again increased further to 30 % in the ‘Certified’ and 32 % in the ‘Conservation Enhanced’ scenarios. In the ‘Land Sparing’ and ‘Uncertified’ scenarios a slightly larger proportion of dispersing individuals returned and settled in their natal patches (29 % and 25 % respectively), compared to the ‘Certified’ (22 %) and ‘Uncertified’ (21 %) landscapes (see Figure 3.5). When only considering successful dispersers (those that either returned to their natal patch or settled in a non-natal patch), the difference between scenarios was greater, with most individuals in the ‘Land Sparing’ and ‘Uncertified’ scenarios returning to their natal patches (68 % and 57 % respectively). In the ‘Certified’ and ‘Conservation Enhanced’ scenarios over half the successful dispersers settled in non-natal patches (58 % and 61 % respectively) compared to 41 % in the ‘Uncertified’ landscape, and just 32 % in the ‘Land Sparing’ scenario.

Across all four scenarios, *Dispersal Distance* ranged between 0.03 km and 58 km, with the distribution heavily skewed towards shorter distances (Figure 3.5). Under the ‘Certified’ and ‘Conservation Enhanced’ scenarios median *Dispersal Distances* were 5.96 km and 5.82 km respectively. The largest median *Dispersal Distance* was estimated for the ‘Uncertified’ scenario (7.35 km), with the shortest median distance modelled in the ‘Land Sparing’ landscape (4.15 km). Across scenarios, there were successful emigration events from all habitat patches, with the exception of 3 patches embedded in the plantation matrix in the Uncertified landscape, indicating possible population sinks (Figure 3.5).

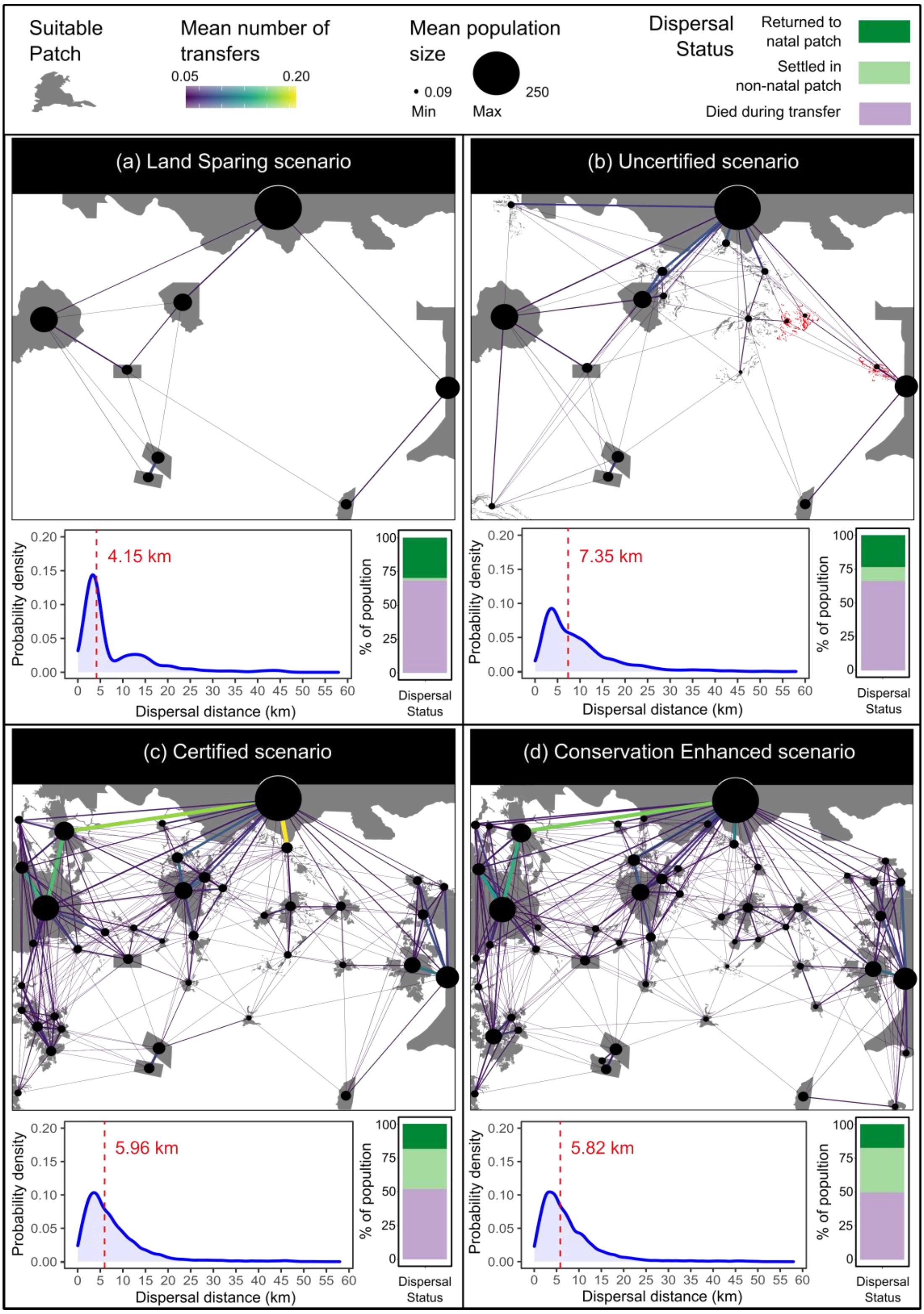


Figure 3.5: Dispersal network maps for the four management scenarios. Lines on maps indicate where successful dispersal events between suitable habitat patches occurred, scaled in size and colour for mean number of individuals per year over a 40-year period. Each point denotes the Mean Population size for individual patches at the end of each simulation (n = 100). The probability density plots show

the distribution of Dispersal Distances for each management scenario, with dotted red lines denoting the median distance travelled during dispersal. Dispersing individuals are characterized into three dispersal statuses, settled in their natal patch, settled in a non-natal patch, or died during transfer. The proportion of dispersing individuals within each dispersal status is represented by stacked bar charts. Red patches indicate patches which produced no successful emigrants.

The higher number of suitable patches in the ‘Certified’ and ‘Conservation Enhanced’ landscapes (Figure 3.2) provided many more potential connections, with multiple linkages between patches (mean number of connections across all model iterations 37.6 ±0.42 and 49.2 ±0.52 respectively), compared to the ‘Uncertified’ and ‘Land Sparing’ scenarios (11.3 ±0.19 and 1.62 ±0.65 respectively). Across all scenarios the largest number of potential connections summed over all 100 iterations were for the ‘Conservation Enhanced’ scenario with 348 and the ‘Certified’ Landscape with a total of 248 connections (Figure 3.5). The development focused scenarios again had substantially fewer connections: 62 for the ‘Uncertified’ landscape and just 13 in the ‘Land Sparing’ scenario (Figure 3.5). The mean number of connections per patch also differed between scenarios, with 1.77 (±0.02) for the ‘Conservation Enhanced’ scenario, 2.21 (±0.02) in the ‘Certified’ Landscape, 1.15 (±0.02) in the ‘Uncertified’ landscape and with the fewest 0.44 (±0.02) in the ‘Land Sparing’ scenario.

3.4.3 Sensitivity analysis

With the exception of the ‘Land Sparing’ and ‘Uncertified’ scenarios, the model outcomes did not change the ranking of the scenarios for most parameter combinations. Variations (± 99 individuals) in population size did change the ranking of ‘Land Sparing’ and ‘Uncertified’ scenarios; however, their baseline population size did not differ substantially (‘Land Sparing’ 445 ind. and ‘Uncertified’ 450 ind.: See Figure 3.6). The model was sensitive to Per Step Mortality (the probability of an individual dying at each step taken during dispersal) with final population estimates changing the ranking of several of the scenarios. When Per Step Mortality was reduced to 0.0001, the *Mean Population* estimate for the ‘Uncertified’ landscape increased by 99 individuals (18 %), increasing its ranking above the ‘Certified’ landscape (Figure 3.6). Similarly, reducing Per Step Mortality increased the population estimate of the ‘Certified’ landscape by 100 individuals (14 %) elevating it above the baseline estimate for the ‘Conservation Enhanced’ scenario by 67 individuals (Figure 3.5). When Per Step Mortality was increased to 0.01, the final population estimates for the ‘Conservation Enhanced’ landscape reduced by 12 %, which was 37 fewer individuals than the baseline scenario for the ‘Certified’ scenario (Supplementary information Table SI.5.1).

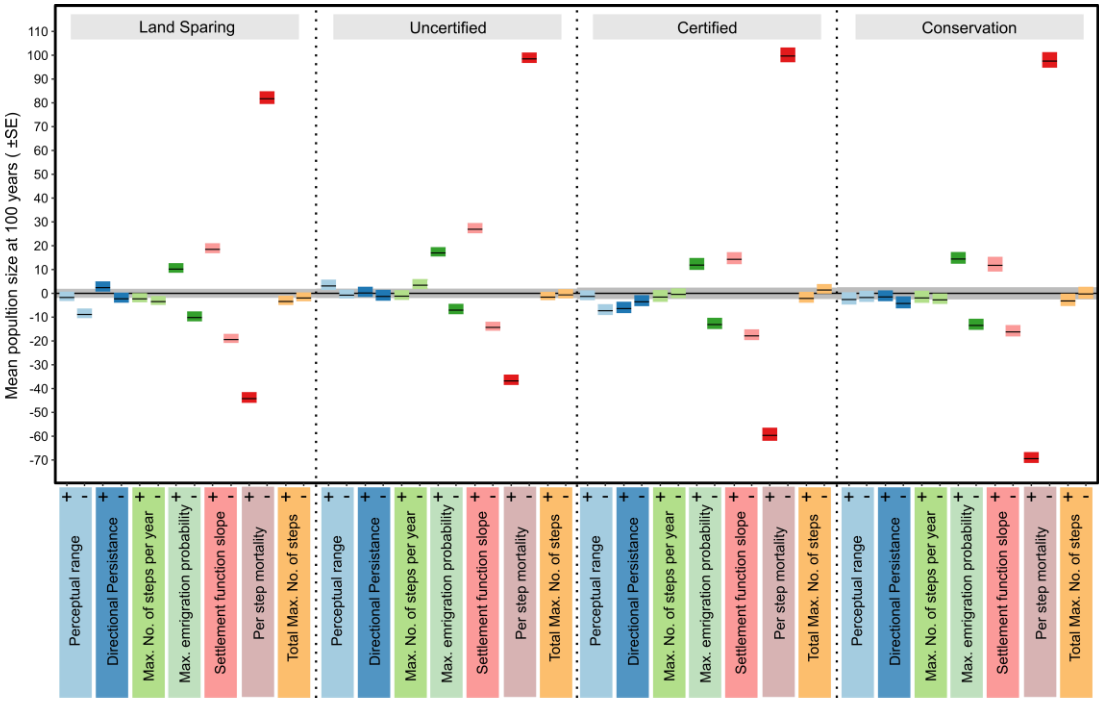


Figure 3.6: Outcomes of sensitivity analyses showing the *Mean Population* size at 100 years across 100 iterations of each model parametrisation.
Model parameters on the x axis, including pairs of extreme higher (+) and lower (-) parameter values. Solid black lines show the *Mean Population* size for each scenario, with the shaded area indicating the standard error.

Dispersal Success also appeared sensitive to a reduction in per step mortality, with >100% increase in individuals settling in non-natal patches in all scenarios with the exception of the ‘Land sparing’ scenario which saw a large increase (186 %) in individuals returning to their natal patches (Figure 3.7). A similar pattern was seen when per step mortality was increased but to the lesser degree of change <50 % change in the number of individuals (Supplementary information Table SI.5.2).

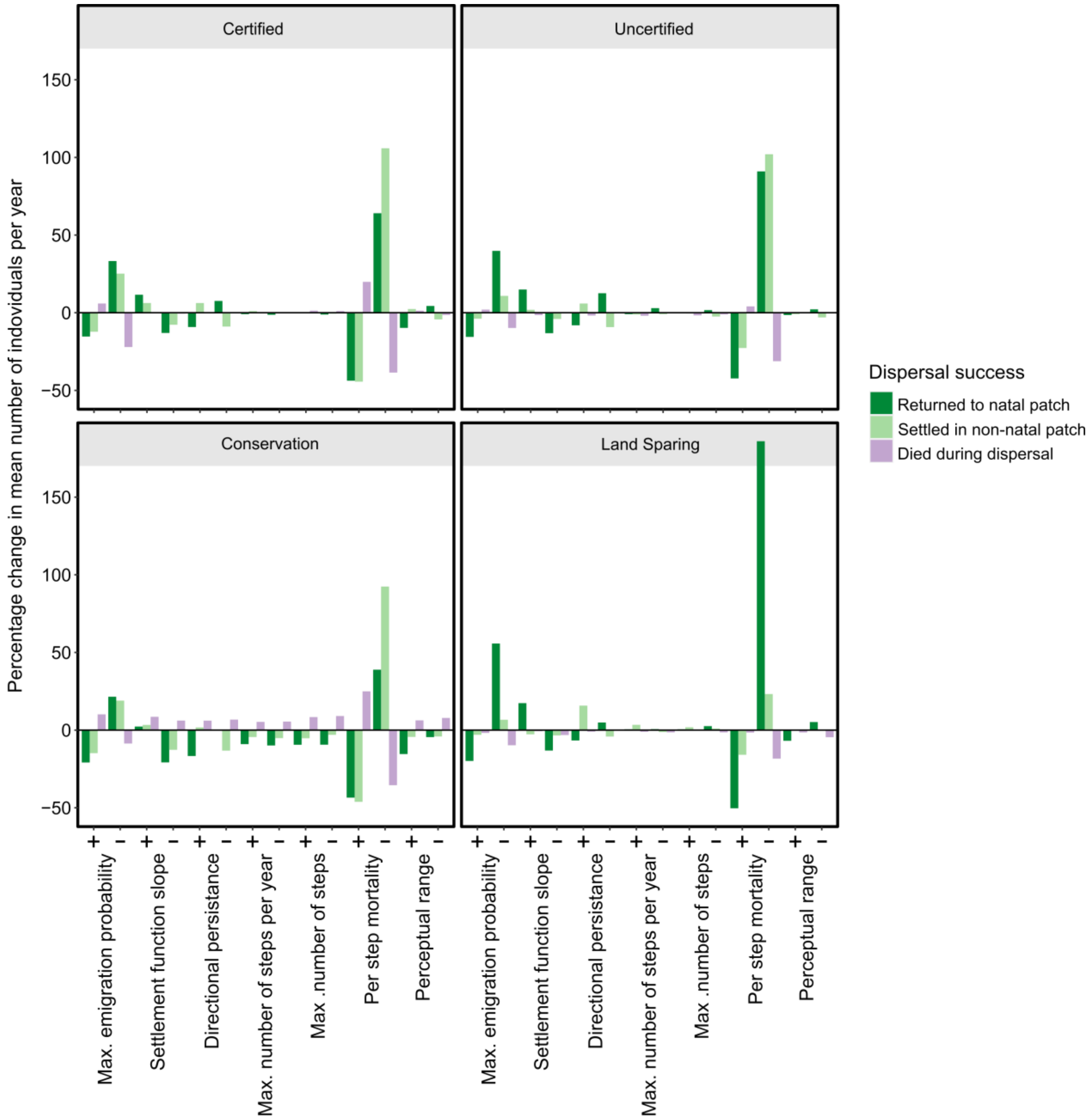


Figure 3.7: Sensitivity analysis results, showing percentage change *Dispersal Success* mean number of individuals per year, compared to baseline models.
Model parameters on the x axis, including pairs of extreme higher (+) and lower (-) parameter values.

3.5 Discussion

Our models pertaining to animal movement and population ecology in a highly fragmented landscape demonstrate that management options to maximise forest cover (‘i.e. the Certified’ and ‘Conservation Enhanced’ scenarios) can sustain substantial orangutan populations in areas under agricultural production for a period of at least 40 years. Oil palm plantations are productive for 25-30 years before replanting (Ng *et al.*, 2013), and therefore, these landscapes are likely able to support stable populations of orangutans over the lifespan of a plantation. This is in line with several field observations that orangutans have survived in similar human-modified landscapes for long periods (>20 years: Ancrenaz *et al.*, 2021). To date, orangutan research has focused almost exclusively on intact landscapes, and no long-term empirical data are available from human-modified landscapes to investigate population dynamics (Voigt *et al.*, 2018). Our models provide longitudinal insights into the increasingly recognised potential of human-modified landscapes to support orangutan populations. These results require validation from field observation and highlight the need for increased research focus in these highly modified landscapes.

A striking difference between the outcomes of the landscape scenarios was the proportion of dispersing individuals that either settled back in their original natal patch or transferred to a non-natal patch. Our simulations demonstrated that in the ‘Land Sparing’ scenario, where there is limited structural connectivity (e.g. the absence of riparian buffers and other remnant forest patches), individuals are largely confined to protected areas, with the majority of successfully dispersing females settling within their natal patches, and hence unable to disperse elsewhere. In the ‘Land Sparing’ scenario there was also a limited number of connections among patches (a mean of 1.9 connections over 100 iterations) and dispersing individuals moved over the shortest distances before settling (median 4.1km). This short-distance dispersal is supported by observations of females from areas of continuous forest, that are generally philopatric and will move and settle close to their mothers’ home range (Goossens *et al.*, 2006; Ashbury *et al.*, 2020). The inclusion of Malaysia's current minimum ecological requirements in the 'Uncertified' scenario (retention of 20 m riparian buffers on permanent rivers and forest on slopes above 25°) increased the connectedness of the landscape, with an average of 12.7 connections and 30% of successfully dispersing individuals settling in non-natal patches. However, this rise in animal movement across the landscape did not greatly increase the total population size (a population increase of 0.2% compared to the 'Land Sparing' scenario) and produced the largest median *Dispersal Distance* at 7.4km, compared to just over 6km in the 'Certified' and 'Conservation Enhanced' scenarios. The retention of additional natural forest through conservation set-asides in the 'Certified' and 'Conservation Enhanced' scenarios resulted in higher proportions of individuals settling in non-natal patches (58% and 63% of all successful dispersers respectively) and a substantial number of connections amongst patches (an average of 40.3 connections in 'Certified' and 52.4 in 'Conservation Enhanced'). The retention of natural forest also led to a considerable increase in the final population size (by 20% in the 'Certified' scenario, and 24% in the 'Conservation Enhanced' compared to the 'Land Sparing' scenario).

In fragmented landscapes, facilitating orangutan movement between isolated populations will be a key conservation strategy to ensure the long-term genetic health of populations (Templeton *et al.*, 1990; Bruford *et al.*, 2010) and to facilitate range shifts in response to climate change (Struebig *et al.*, 2015; McGuire *et al.*, 2016). Our simulations suggest orangutans are more likely to move short distances across agricultural matrixes when connected by smaller fragments or riparian remnants, rather than undertaking long excursions into plantations (see Figure SI

3.4). Similar behaviour has been observed with wild female orangutans in oil palm landscapes, where individuals have been reported to move between areas of natural forest to cross plantations (Ancrenaz *et al*., 2015). Thus, small patches can function as stepping-stones and are likely to be of high importance in facilitating orangutan movement across human-modified landscapes, whilst not necessarily supporting high levels of biodiversity on their own (Deere *et al.*, 2019). A phenomenon we captured in our simulations were female orangutans occupying and reproducing in remnant forest patches in oil palm. This is consistent with field observations, where practitioners have identified female orangutans residing in remnant forest in oil palm dominated landscapes for a sufficient amount of time for an offspring to reach maturity and leave to establish its own home range (Ancrenaz *et al*., 2021).

These individuals born in remnant forest patches will have limited opportunities to establish their own home range and this will be contingent on the amount of remaining natural forest. However, the highly philopatric nature of female orangutans means movements over long distances for this sex are likely to be extremely rare. Our simulations suggest that orangutans in heavily modified landscapes may have to change their behaviour, moving over larger distances to find suitable areas to settle, particularly when there is minimal remaining natural forest cover. In the ‘Uncertified’ scenario, three of the remnant forest patches were occupied by dispersing individuals but failed to produce successful emigrants, representing potential population sinks. Thus, we highlight the need for not only providing linear forest corridors (such as riparian buffers) and/or stepping stones to increase the permeability of the landscape, but also to increase the potential for females to establish their own home ranges, reducing the need for long distance dispersal and maximising the population size.

Ensuring sufficient habitat remains or is restored in agricultural landscapes will be vital to promote functional connectivity, but this is only half the battle. Connectivity may be overestimated if negative human-wildlife interactions (such as crop foraging or hunting) are not considered (Day *et al.*, 2020; Ghoddousi *et al.*, 2020; Bleyhl *et al.*, 2021). Our sensitivity analysis suggests changes in mortality risk during dispersal are likely to have a large effect on the ability of the agricultural landscape to support orangutan and allow movement between patches. As part of the certification process itself, the High Carbon Stock methodology includes a risk assessment to prioritise patches for conservation based on proximity to anthropogenic features (such as roads and settlements), aiming to limit the impact of human-wildlife interactions. Despite this, human accessibility to forest patches is high in oil palm estates and hunting can be common (Azhar *et al.*, 2013; Deere *et al.*, 2019). Here, we assumed all HCS forest areas to be suitable for orangutans, however, other factor such as hunting may limit the ability of these areas to support orangutans. In Kalimantan, hunting of orangutans for meat and persecutory killings following negative orangutan-human interactions is widespread (Meijaard *et al.*, 2011). Although hunting of orangutans in Sabah appears to be relatively low (Ancrenaz, Dabek and O’Neil, 2007), further research is needed to fully establish the extent to which human-wildlife interactions will inhibit the ability of oil palm certification to facilitate movement for orangutans.

A conservation strategy routinely employed in anthropogenic landscapes is the translocation of orangutans from forest fragments to areas of continuous forest or rescue centres (Sherman, Ancrenaz and Meijaard, 2020). However, most orangutans translocated from agricultural landscapes appear to be in good health (Sherman *et al.*, 2020), indicating that these individuals have been surviving in these landscapes. In addition, our models demonstrate the potential importance of these individuals in maintaining movement and connectivity across the landscape (Ancrenaz *et al.*, 2021). Although orangutan translocation can be justified when the life of an individual is threatened, such as during fire events or direct conflict with people, the blanket deployment of translocation may in fact be detrimental to the species (Sherman *et al*., 2020). Indeed, we showed that maintaining orangutan numbers within remnant forest in plantations will increase the overall population size and increase movement across the landscape, potentially providing vital transfer of genetic information between isolated individuals or groups of individuals.

There is mounting evidence that orangutans can survive and reproduce within plantation-dominated landscapes (Ancrenaz *et al.*, 2015; Spehar and Rayadin, 2017; Seaman *et al.*, 2019) and our models show these animals are likely to play an important role in maintaining movement between otherwise isolated populations. However, there remains little known regarding orangutan movement behaviour in human-modified landscapes. Therefore, we used our current understanding of orangutan dispersal and expert judgment to parametrise the model and create an approximation to the same pattern as observed in the field. Our use of an individual based model allowed the incorporation of individual variability in both movement and demography, providing a more realistic processes than other modelling approaches. There is unavoidably a level of subjectivity to this approach and to address this, we performed an extensive sensitivity analysis. Encouragingly, the model projections, especially in how the alternative plausible scenarios ranked, seem robust to permutations in almost all emigration, movement, and settlement parameter values, giving us confidence in the conclusions we draw here. The orangutan’s slow life history and low reproductive rate makes the species highly vulnerable to even small rises in mortality rates above natural levels (~1 %: Leighton *et al.*, 1995). This sensitivity highlights the critical need to ensure mortality in human-modified landscapes is kept to a minimum though reducing hunting and conflict killings, raise the level of acceptance of people sharing the same habitat for peaceful co-existence via targeted awareness campaigns and capacity building, as well as increasing conservation focus towards these areas.

3.6 Conclusions

With increasing environmental degradation, protected areas alone will be insufficient to secure conservation goals for much of the earth’s biodiversity (Dinerstein *et al.*, 2020). Maintaining wildlife populations and ensuring connectivity in agricultural landscapes is therefore now essential, particularly to sustain viable populations of large-bodied and wide-roaming terrestrial mammals (Carroll *et al.*, 2015). The extent to which this can be achieved will depend on the overall design of the landscape and how land-use practices meet the ecological needs of species, as well as the acceptance of people to coexist in proximity with wildlife. We need a paradigm shift about how we conserve wide-ranging species such as orangutans – to embrace landscape-level management in human-modified habitats as well as staunch protection in intact forest areas (Kremen and Merenlender, 2018). There is currently a paucity of research from these landscapes and additional research will be vital to better inform land-use policy and focus conservation efforts. As further agricultural expansion is unavoidable, our modelling suggests that maximising natural forest cover in farmland landscapes through conservation set-asides, will lead to improved long-term conservation outcomes for critically endangered species such as orangutan.

3.7 Supplementary information 1: Demography and dispersal parameters

3.7.1 Demography

To account for the long life history, varying survival probability and development phases of orangutans, we developed an overlapping stage-structured demographic model of females only A (i.e. which models only the female part of the population and assumes that fertilization by males is always available):

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & \phi_1 & \phi_2 & \phi_3 & 0 \\ \sigma_1 y_1 & \sigma_2(1-y_2) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2 y_2 & \sigma_3(1-y_3) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 y_3 & \sigma_4(1-y_4) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 y_4 & \sigma_5(1-y_5) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma_5 y_5 & \sigma_6(1-y_6) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_6 y_6 & \sigma_7(1-y_7) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \sigma_7 y_7 & \sigma_8(1-y_8) & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_8 y_8 & \sigma_9 \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0.167 & 0.167 & 0.167 & 0 \\ 0.45 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.97 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.99 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.98 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.99 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.99 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.85 & 0.75 \end{pmatrix}$$

where σ is the survival probability, y is the probability of developing to the next stage and ϕ is fecundity.

We modelled density dependence in development between the young adult and adult stages by changing the default exponential function implemented in RangeShifter to the following function:

$$\gamma_i = \gamma_{0,i} - \ b * \sum_{j=1}^{S} \omega_{ij}\, N_{j,t}$$

where γ_i is the development probability of stage *i*, $\gamma_{0,i}$ is its development probability at low densities (habitat dependant) and *b* is the strength of density dependence (where 1/*b* is a proxy of carrying capacity; see Table 1). *S* indicates the number of stages and ω_{ij} is the contribution of stage *j* to the density dependence in the development of stage *i*. Hence, the total number of individuals N_t becomes a weighted sum of the number of individuals in each stage *j* ($\omega_{ij}N_{j,t}$). We assume only the density of adult stages (Adult, Mature adult, Senior adult and Senescent) to impact on the development of young adults.

Density dependence was also incorporated in fecundity, with the interbirth period increasing as patches became close to carrying capacity (See Figure SI 3.1). For this, we modified the default density-dependence function implemented in RangeShifter to the following function (Adapted from Marshall *et al.*, 2009):

$$\phi_i = \phi_{0,i} * \left(1 - \left(\frac{\sum_{j=1}^{S} \omega_{ij}\, N_{j,t}}{1/b}\right)^{10}\right) + 0.118 * \left(\frac{\sum_{j=1}^{S} \omega_{ij}\, N_{j,t}}{1/b}\right)^{10}$$

where ϕ_i is the fecundity of stage *i*, $\phi_{0,i}$ is its maximum fecundity at low densities (0.167), *b* is the strength of density dependence (where 1/*b* is a proxy of female carrying capacity; see Table 1). *S* indicates the number of stages and ω_{ij} is the contribution of stage *j* to the density dependence in the fecundity of stage *i*. Hence, the total number of individuals N_t becomes a weighted sum of the number of individuals in each stage *j* ($\omega_{ij}N_{j,t}$). We assume only the density of adult stages (Adult, Mature adult, Senior adult and Senescent) to impact on the fecundity of the reproductive stages. Generally, orangutans will give birth to a single offspring, and on the rare occurrence of twin births, it is likely one of the offspring will die (Goossens *et al.*, 2012). In RangeShifter, the number of infants is drawn from a

Poisson distribution having a given mean (ϕ_i); however, this was constrained to be no greater than one offspring per birth in our model.

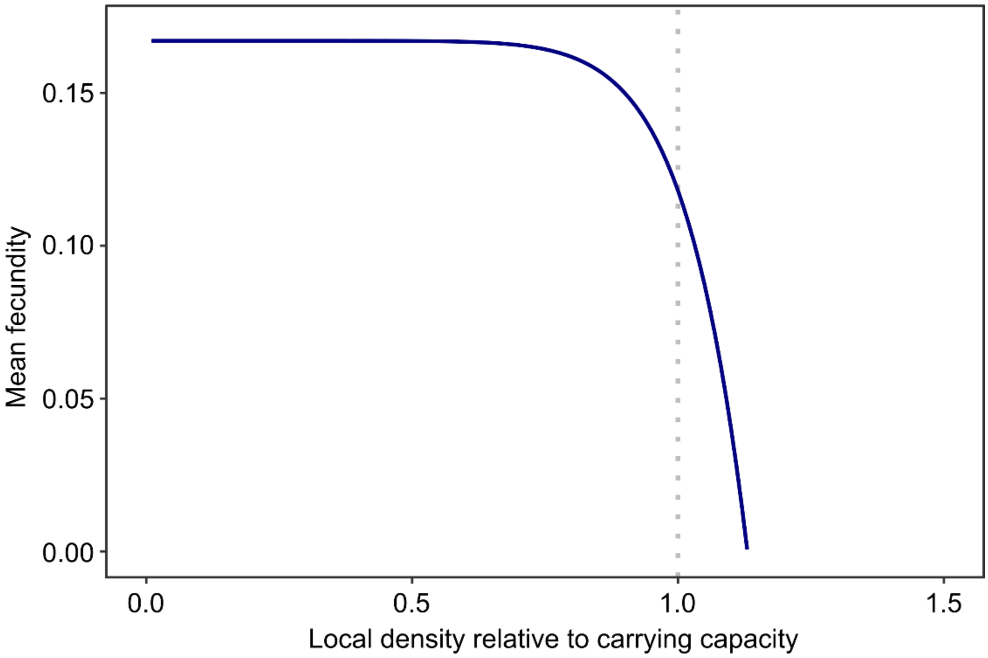


Figure SI 3.1: Annual fecundity in relation to the local density within the patch.

3.7.2 Dispersal

By default, RangeShifter does not allow a dispersing individual to ever return to its natal patch. However, the home range fidelity of female orangutans means individuals are likely to return to their natal patch if they are not able to locate suitable habitat close to their natal patch (Ashbury *et al.*, 2020). We therefore modified RangeShifter such that dispersing females may go back to their natal patch once they have moved out beyond their perceptual range and have not found any new suitable habitat. This does not mean that females will automatically go back to the natal patch but that they do have this option. Once a female has settled in a patch, she may not disperse again.

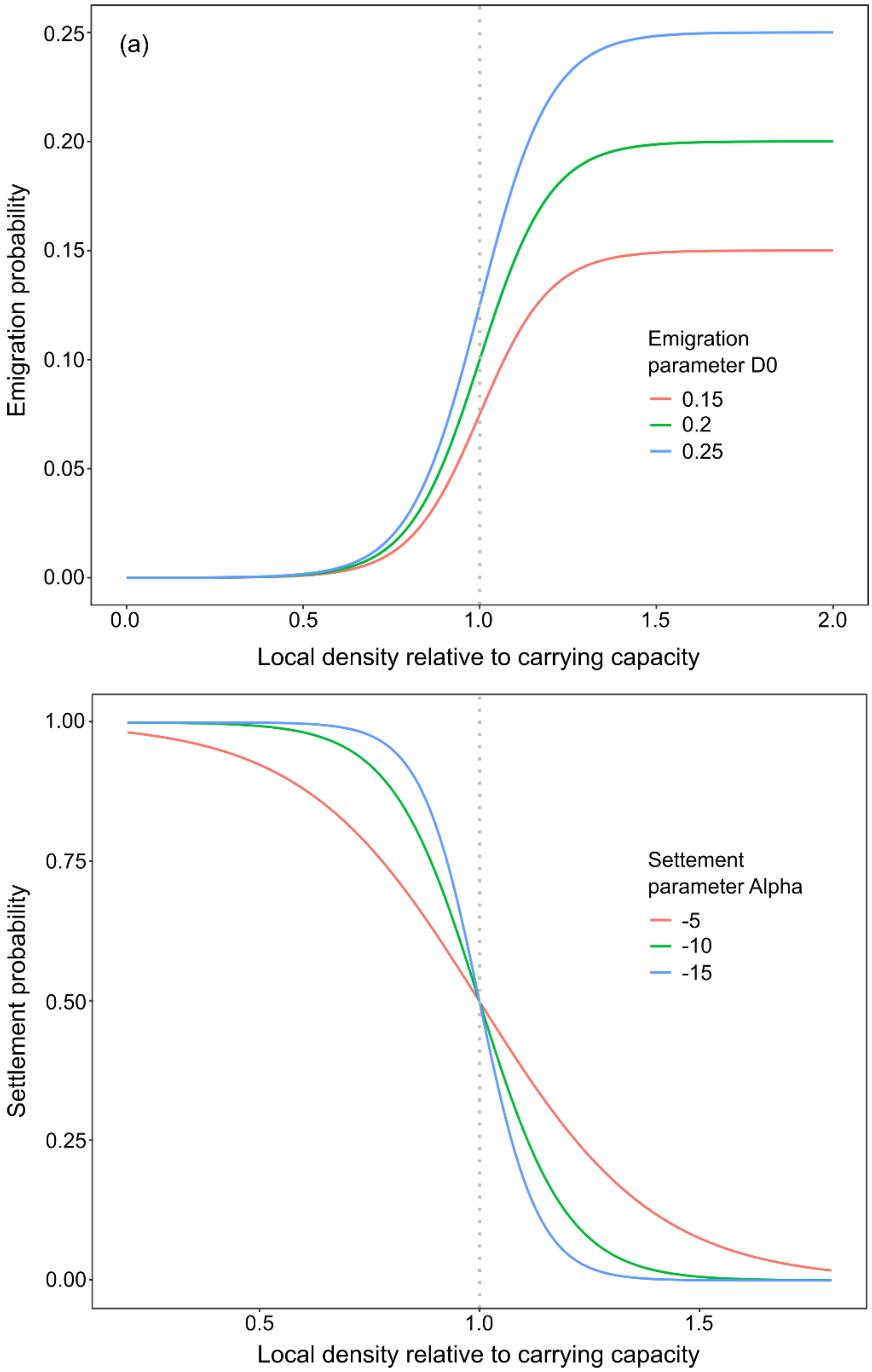


Figure SI 3.2: Density-dependent functions applied during dispersal.
Green lines indicate the functions used in our main model, red and blue lines were used to test model sensitivity. The dotted lines signify local equilibrium density ($1/b$). (a) Emigration (b) Settlement function.

3.8 Supplementary information 2: Landscape scenarios, patch allocation, and cost surfaces

3.8.1 Patch allocation

Habitat patches were numbered with a unique numeric identifier (Figure SI 3.3), as follows. Any habitat patch with an area large enough to support one or more orangutan (i.e. > 122ha) was given a unique patch ID. As orangutans with home ranges adjacent to agricultural areas will incorporate areas of remnant forest within their home range (Ancrenaz *et al*., 2015), any patch too small to support a single animal but within 100 m of a large patch was included within the larger patch. Groups of small (< 122ha) patches that were <100m apart from one another and cumulatively had >= 122 ha of suitable habitat were considered to be a single discontinuous patch, and each group was assigned a unique patch ID. The remaining patches of natural forest that were < 122 ha and >100 m apart from any other suitable area were given an ID of zero (as unsuitable habitat), which indicates areas in which an individual could not settle or reproduce. This patch allocation process resulted in 8 patches of suitable habitat in the Land Sparing scenario. This increased to 19 the in the Uncertified scenario, 39 in the Certified scenario and 53 in the Conservation Enhanced scenario.

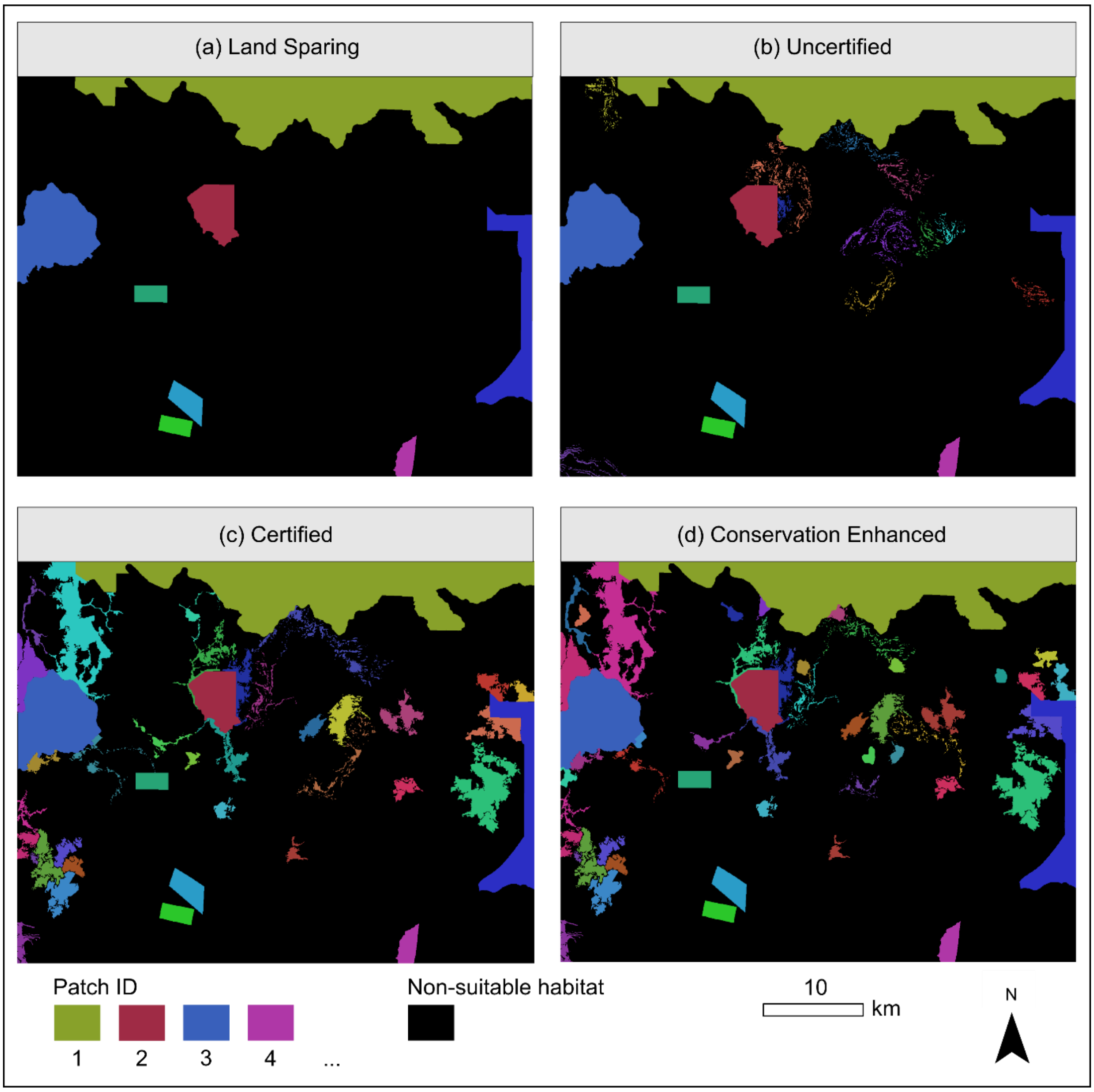


Figure SI 3.3: Patch allocation under each scenario.

3.8.2 Cost surface

Orangutans are reported to build temporary night-time refuges (nests) within oil palms, so far, this has primarily been observed within 50 m of a forest edge (Ancrenaz *et al*., 2015), indicating a reliance on forest remnants within these landscapes. This, along with the additional energetic costs associated with terrestrial locomotion (Thorpe *et al*., 2007), means the cost of moving across the landscape will increase with distance from natural forest areas. Expert-derived resistance values are generally constant for individual land cover types, but this does not take into account the additional energetic cost an orangutan would face when moving large distances terrestrially away from natural forest areas. To account for this, we produced a composite cost surface layer informed by both expert-derived landscape resistance and a time cost surface model (Frakes, Flowe and Sherrill, 2015). This cost surface model estimates the time in seconds required to reach each pixel within a landscape from multiple starting points, based on an average moving speed. Through following wild habituated orangutans, the average speed when actively moving across disturbed forest is estimated at 2.5 km/hour (Range: 1 – 4 km/hour: Ancrenaz, et al., unpublished data). Our expert-informed resistance values ranged between 5 and 100 and these were subtracted from 100 to provide a relative speed for the time cost surface model. We used all forest areas within the landscape as starting points and the resulting cost surface is a time travel distance in seconds, weighted by the resistance of the landcover type (Figure SI 3.4).

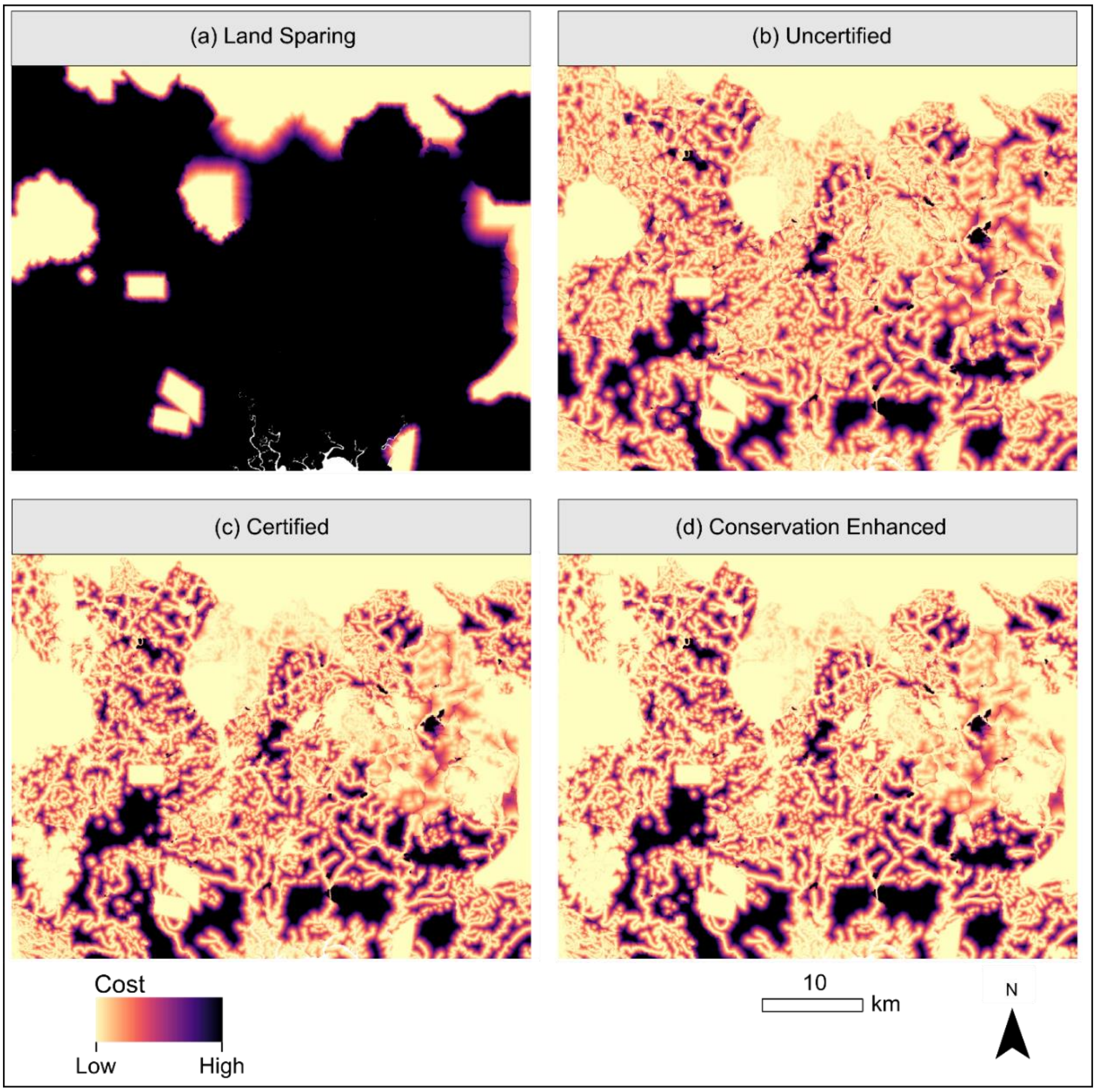


Figure SI 3.4: Cost surface for each scenario.

3.9 Supplementary information 3: Model initialization

Each model was initialised with all patches ‘at female carrying capacity’ and the population distributed 20% among Adolescent or below and 80% among Young adult and above, which is in keeping with demographic observation from a disturbed landscape in Sabah (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004). For all scenarios, the model reached equilibrium after approximately 60 years, at which point metrics (e.g. populations size and patch occupancy) were recorded for each year until completion after 100 years (Figure SI 3.5).

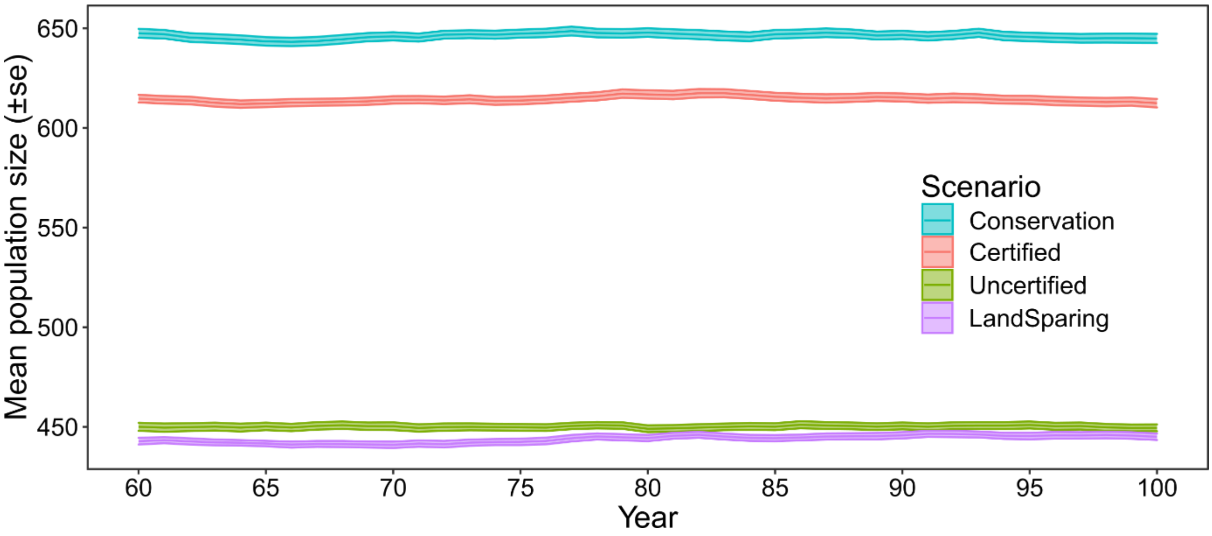


Figure SI 3.5: Mean population size (±se) over the 40 year period the model had reach equilibrium.

3.10 Suplimentary information 4: Example of movement trajectories and effects of parameter variation

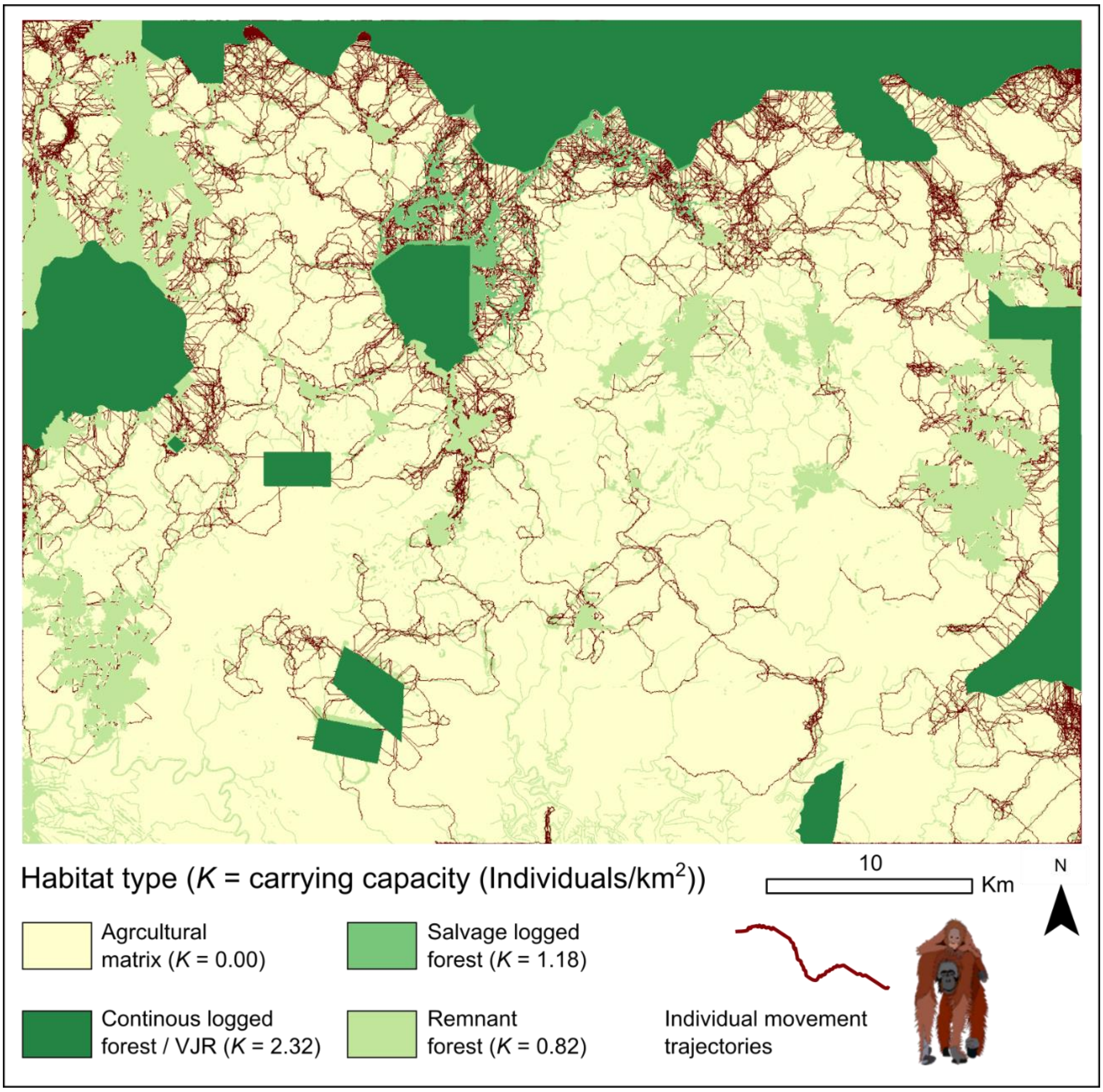


Figure SI 3.6: Example of individual movement trajectories produced by RangeShifter's stochastic movement simulator.

We modelled individual movement trajectories using RangeShifter's stochastic movement simulator (SMS), which uses stepwise nearest-neighbour calculations based on a cost surface (Palmer, Coulon and Travis, 2011). Telemetry data on orangutan movements were not available to us from which to estimate the SMS parameters Directional Persistence and Memory Size. Instead, combinations were selected by expert appraisal, based on visual inspections of plotted individual trajectories under various parameter value combinations (Figure SI 3.6). As this is open to a level of subjectivity, we also performed a sensitivity analysis to assess the effects of varying parameter values on the ranking of management scenarios based on final population size, and here provide visualisations of simulated individual movement trajectories when varying values Directional Persistence (between 2.0, 2.5 and 3.0: Figure SI 3.7) and Perceptual Range (between 15, 25 and 35: Figure SI 3.8)

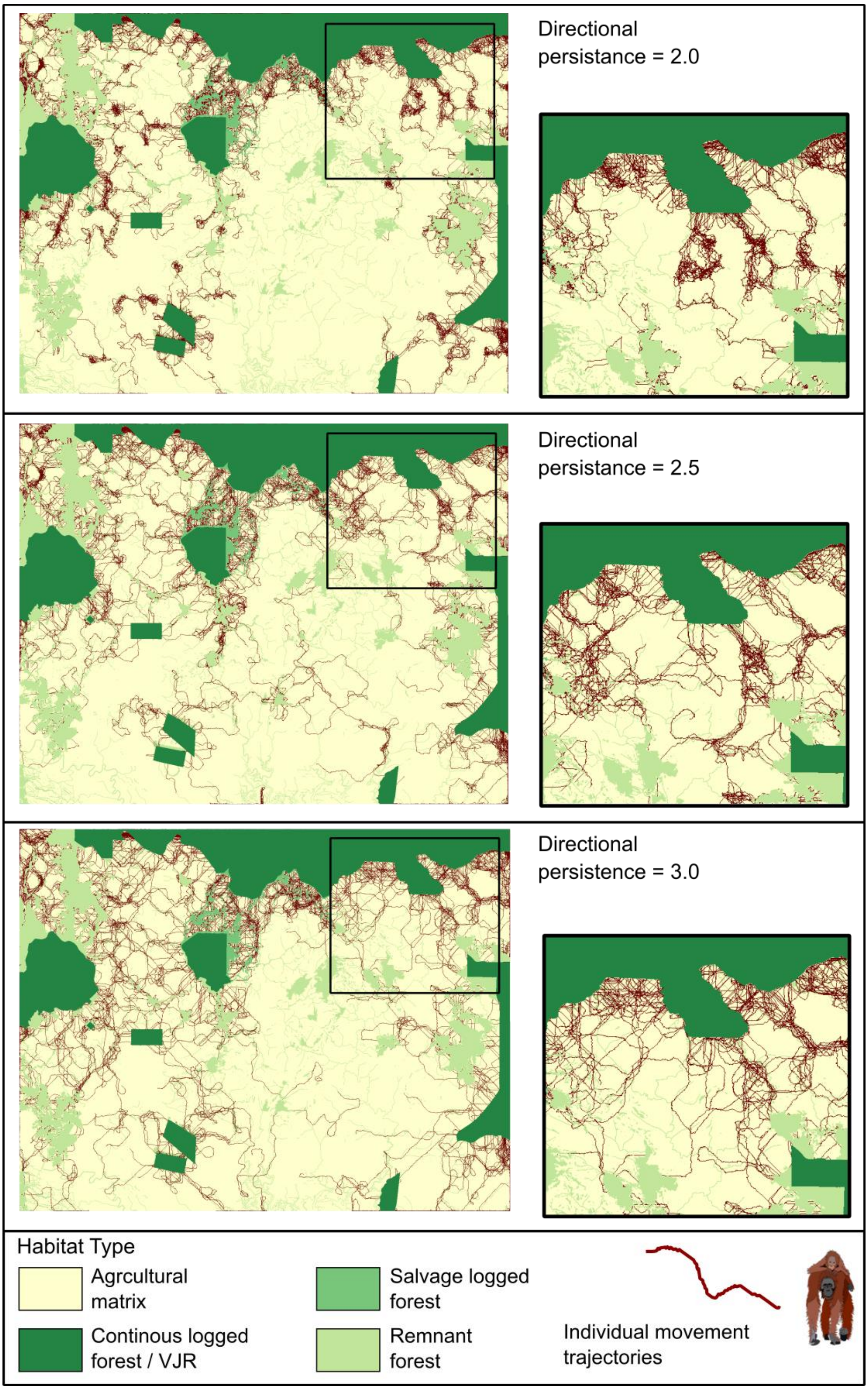


Figure SI 3.7: Plotted individual movement trajectories produced by RangeShifter's stochastic movement simulator (SMS) from our sensitivity analysis.

Here showing variation in Directional Persistence between 2.0, 2.5 and 3.0.

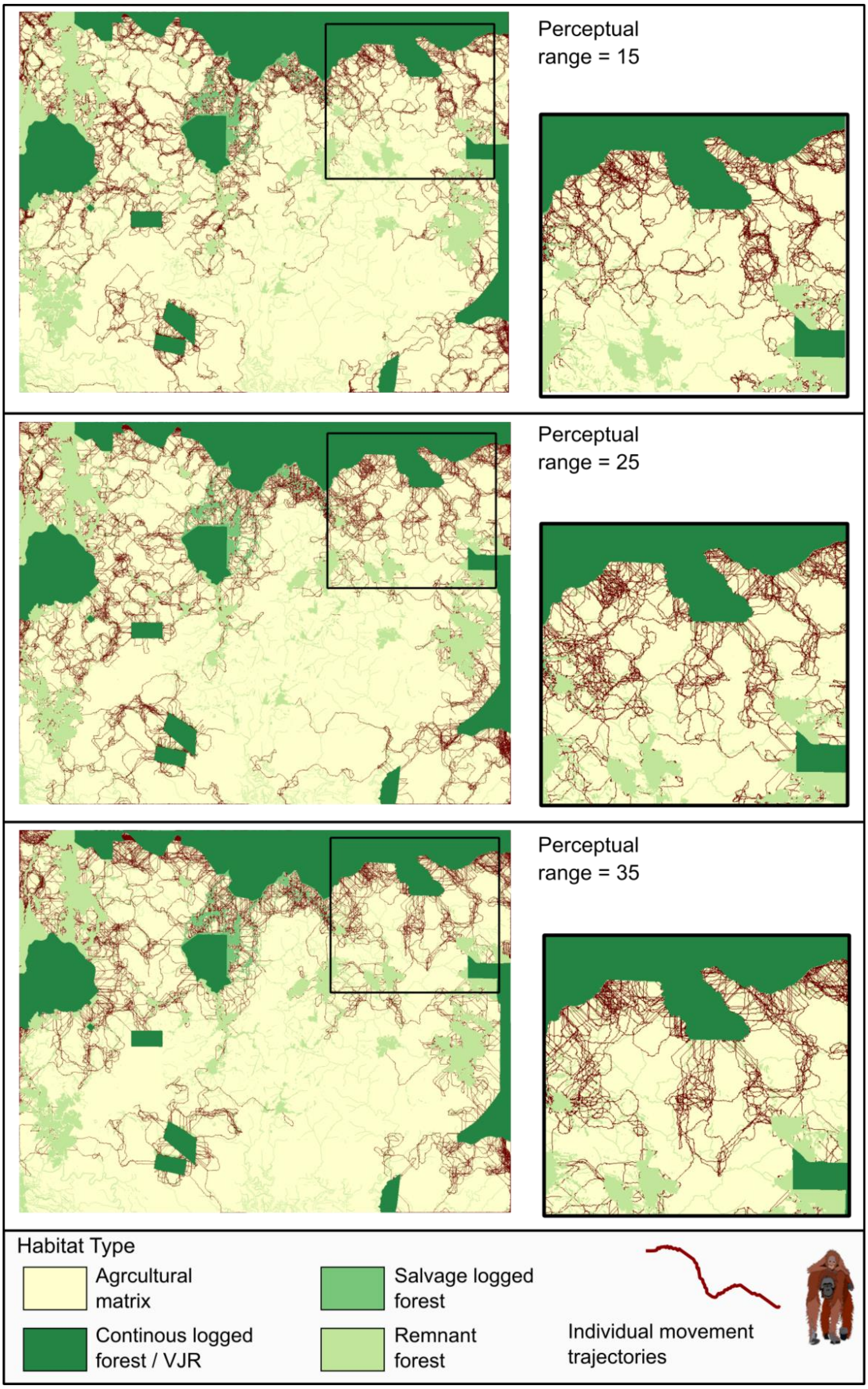


Figure SI 3.8: Plotted individual movement trajectories produced by RangeShifter's stochastic movement simulator (SMS) showing variation in Perceptual Range (between 15, 25 and 35 cells) from our sensitivity analysis.

The SMS calculates the effective cost of moving to each neighbouring cell at each step over the Perceptual Range.

3.11 Supplementary information 5: Sensitivity analysis

We undertook a sensitivity analysis to evaluate the robustness of our model to permutations in movement parameter values, as these were largely based on anecdotal evidence and expert opinion. To test the effect of perceptual range, we ran models set at 15 and 35 cells, equating to 450 m and 1,050 m (± 300 m on our original value). Our standard model includes a directional persistence of 2.5 and we ran models with directional persistence values of 2.0 and 3.0. The Maximum number of steps per year was altered to 2,500 and 3,500, and we varied the maximum number of total steps an orangutan could take before settling or dying to 9000 and 15,000 cells. For emigration, we varied the maximum emigration probability (D_0) to 0.15 and 0.25, a change of 0.05 on our standard model (See Figure SI 3.1). We varied the slope of the settlement function (α_S) to -5 and -15 (See Figure SI 3.2). Each parameter value was tested by running each model over 100 replicates and over a 100-year period, keeping all other parameters constant. Model sensitivity was investigated through comparing both mean population size at 100 years and dispersal success relative to the baseline scenarios, under the range of parameter values (Table SI.5).

Table SI 3-1: Sensitivity analysis results.
Showing results of RangeShifter models with parameters at extreme lower (-) and higher (+) values. Results show variations in both demographic (final population size at 100 years) and dispersal success, (mean number of individual annually either returning and settling in natal patches, settling in none-natal patches, or dying during dispersal) as well as percentage change compared to the baseline results reported in this study.

			Population at 100 year		Returned to natal patch		Settled in non-natal patch		Died during dispersal	
Certified landscape	Parameter		Mean (±se)	% change	Mean (±se)	% change	Mean (±se)	% change	Mean (±se)	% change
	Baseline		612 (2.12)		3.46 (0.14)		4.75 (0.19)		4.65 (0.03)	
	Perceptual range	-	611 (1.77)	0%	3.61 (0.15)	4%	4.55 (0.18)	-4%	4.59 (0.03)	-1%
		+	605 (1.98)	-1%	3.12 (0.13)	-10%	4.86 (0.20)	2%	4.71 (0.04)	1%
	Directional persistence	-	606 (2.10)	-1%	3.72 (0.15)	8%	4.33 (0.17)	-9%	4.66 (0.04)	0%
		+	609 (1.03)	-1%	3.14 (0.13)	-9%	5.05 (0.20)	6%	4.65 (0.04)	0%
	Max. No. steps per year	-	611 (2.20)	0%	3.41 (0.14)	-1%	4.76 (0.19)	0%	4.65 (0.04)	0%
		+	612 (1.77)	0%	3.43 (0.14)	-1%	4.8 (0.20)	1%	4.65 (0.04)	0%
	Max. emigration probability	-	624 (2.22)	2%	3.01 (0.12)	-13%	4.38 (0.17)	-8%	4.62 (0.03)	-1%
		+	599 (2.08)	-2%	3.86 (0.16)	12%	5.05 (0.21)	6%	4.65 (0.04)	0%
	Settlement function slope	-	627 (2.24)	2%	4.61 (0.19)	33%	5.95 (0.25)	25%	3.63 (0.03)	-22%
		+	595 (1.98)	-3%	2.93 (0.12)	-15%	4.17 (0.17)	-12%	4.93 (0.04)	6%
	Per step mortality	-	553 (2.47)	-10%	5.67 (0.23)	64%	9.78 (0.38)	106%	2.86 (0.03)	-39%
		+	712 (2.81)	16%	1.96 (0.08)	-44%	2.64 (0.10)	-44%	5.58 (0.04)	20%
	Total Max. No. of steps	-	611 (2.00)	0%	3.42 (0.14)	-1%	4.73 (0.19)	-1%	4.70 (0.03)	1%
		+	614 (1.74)	0%	3.46 (0.14)	0%	4.76 (0.19)	0%	4.71 (0.03)	1%
Uncertified landscape										
	Baseline		450 (1.70)		3.17 (0.13)		2.29 (0.09)		4.23 (0.03)	
	Perceptual range	-	453 (1.88)	1%	3.24 (0.13)	2%	2.22 (0.09)	-3%	4.23 (0.03)	0%
		+	449 (1.57)	0%	3.12 (0.13)	-1%	2.27 (0.09)	-1%	4.23 (0.03)	0%
	Directional persistence	-	450 (1.85)	0%	3.56 (0.15)	13%	2.07 (0.08)	-9%	4.23 (0.03)	0%
		+	449 (2.00)	0%	2.19 (0.12)	-8%	2.42 (0.10)	6%	4.15 (0.03)	-2%
	Max. No. steps per year	-	449 (1.75)	0%	3.26 (0.14)	3%	2.26 (0.09)	-1%	4.22 (0.03)	0%
		+	453 (1.79)	1%	3.14 (0.12)	-1%	2.26 (0.09)	-1%	4.15 (0.03)	-2%
	Max. emigration probability	-	467 (1.67)	4%	2.75 (0.11)	-13%	2.19 (0.09)	-4%	4.21 (0.03)	0%

	+	443 (1.89)	-1%	3.64 (0.15)	15%	2.33 (0.10)	2%	4.17 (0.03)	-1%
Settlement function slope	-	477 (1.86)	6%	4.43 (0.18)	40%	2.53 (0.11)	11%	3.38 (0.03)	-10%
	+	436 (1.58)	-3%	2.67 (0.11)	-16%	2.20 (0.09)	-4%	4.32 (0.03)	2%
Per step mortality	-	413 (1.89)	-8%	6.05 (0.23)	91%	4.62 (0.17)	102%	2.91 (0.03)	-31%
	+	549 (1.91)	22%	1.83 (0.07)	-42%	1.77 (0.06)	-23%	4.40 (0.03)	4%
Total Max. No. of steps	-	448 (1.43)	0%	3.22 (0.13)	2%	2.23 (0.09)	-2%	4.19 (0.03)	-1%
	+	449 (1.64)	0%	3.16 (0.13)	0%	2.27 (0.09)	0%	4.16 (0.03)	-2%
Conservation landscape									
Baseline		645 (2.27)		3.35 (0.14)		5.39 (0.22)		4.63 (0.04)	
Perceptual range	-	643 (2.30)	0%	3.20 (0.13)	-4%	5.17 (0.21)	-4%	4.99 (0.04)	8%
	+	644 (2.04)	0%	2.83 (0.12)	-15%	5.15 (0.21)	-4%	4.91 (0.04)	6%
Directional persistence	-	644 (1.99)	0%	3.33 (0.13)	0%	4.68 (0.19)	-13%	4.94 (0.04)	7%
	+	641 (2.25)	-1%	2.79 (0.11)	-17%	5.48 (0.23)	2%	4.91 (0.04)	6%
Max. No. steps per year	-	644 (2.26)	0%	3.02 (0.12)	-10%	5.11 (0.21)	-5%	4.88 (0.04)	5%
	+	643 (1.91)	0%	3.05 (0.12)	-9%	5.15 (0.21)	-4%	4.87 (0.04)	5%
Max. emigration probability	-	659 (2.18)	2%	2.65 (0.11)	-21%	4.71 (0.19)	-13%	4.91 (0.04)	6%
	+	632 (2.05)	-2%	3.34 (0.14)	2%	5.57 (0.23)	3%	5.02 (0.04)	9%
Settlement function slope	-	657 (2.81)	2%	4.07 (0.16)	21%	6.41 (0.27)	19%	4.23 (0.03)	-9%
	+	629 (2.11)	-2%	2.65 (0.11)	-21%	4.59 (0.19)	-15%	5.09 (0.04)	10%
Per step mortality	-	576 (2.01)	-11%	4.56 (0.19)	39%	10.37 (0.41)	92%	2.99 (0.03)	-35%
	+	743 (2.99)	15%	1.86 (0.08)	-43%	2.90 (0.12)	-46%	5.78 (0.04)	25%
Total Max. No. of steps	-	645 (2.34)	0%	3.03 (0.12)	-9%	5.23 (0.21)	-3%	5.04 (0.04)	9%
	+	645 (2.25)	0%	3.03 (0.12)	-9%	5.11 (0.21)	-5%	5.01 (0.04)	8%
Land Sparing landscape									
Baseline		445 (1.62)		3.78 (0.15)		1.50 (0.05)		4.53 (0.03)	
Perceptual range	-	445 (1.67)	0%	3.98 (0.16)	5%	1.51 (0.05)	0%	4.32 (0.03)	-5%
	+	436 (1.72)	-2%	3.52 (0.14)	-7%	1.50 (0.05)	0%	4.46 (0.03)	-1%
Directional persistence	-	448(1.85)	1%	3.97 (0.16)	5%	1.44 (0.05)	-4%	4.54 (0.03)	0%
	+	445 (1.84)	0%	3.53 (0.14)	-7%	1.74 (0.07)	16%	4.49 (0.03)	-1%
Max. No. steps per year	-	445 (1.64)	0%	3.81 (0.15)	1%	1.49 (0.05)	-1%	4.46 (0.03)	-1%
	+	442 (1.57)	-1%	3.80 (0.15)	1%	1.56 (0.06)	3%	4.48 (0.03)	-1%

Max. emigration probability	-	456 (1.73)	2%	3.28 (0.13)	-13%	1.45 (0.05)	-3%	4.39 (0.03)	-3%
	+	435 (1.79)	-2%	4.44 (0.18)	17%	1.46 (0.05)	-3%	4.50 (0.03)	-1%
Settlement function slope	-	464 (1.80)	4%	5.89 (0.23)	56%	1.61 (0.06)	7%	4.09 (0.03)	-10%
	+	426 (1.61)	-4%	3.03 (0.12)	-20%	1.46 (0.05)	-3%	4.45 (0.03)	-2%
Per step mortality	-	401 (1.96)	-10%	10.82 (0.40)	186%	1.85 (0.07)	23%	3.70 (0.03)	-18%
	+	527 (2.38)	18%	1.88 (0.07)	-50%	1.27 (0.06)	-16%	4.46 (0.03)	-2%
Total Max. No. of steps	-	442 (1.67)	-1%	3.88 (0.16)	3%	1.52 (0.05)	1%	4.46 (0.03)	-1%
	+	445 (1.56)	0%	3.8 (0.15)	1%	1.53 (0.05)	2%	4.51 (0.03)	0%

Chapter 4 Lessons learnt from integrating orangutan data in a heterogeneous landscape

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4.1 Abstract

In an age of global change, effective management of human-modified landscapes and the wildlife that utilise them will be vital to prevent further biodiversity loss. Successful management will depend on robust survey and monitoring data to inform and assess management initiatives. Increasingly, conservation practitioners integrate available monitoring data, often from multiple sources and structures, to maximise the information that can be drawn, but this approach is often applied at large scales and coarse resolutions. Here, we apply data integration methodology to investigate its potential to monitor orangutans in human-modified habitats at the landscape scale where conservation initiatives are generally undertaken. We integrate survey data from two sources: nest data undertaken on transects and targeted for orangutans, and a second non-targeted dataset on orangutan ‘bycatch’ from camera traps surveys. We found moderate support among forest structural metrics on both density and occurrence. However, there was an inverse relationship between each state variable and forest structural metrics (e.g. tree canopy height had a positive effect on orangutan density but negative effect on occurrence), making common integration approaches challenging here. We therefore show that competing ecological processes need to be considered to effectively integrate information from these data sources. Advances in integrative models are expanding our abilities to understand the natural world. We demonstrate the potential for integrated modelling of survey data to be applied in understanding fine-scale drivers in patterns of orangutan abundance across heavily modified landscapes using existing data. However, we highlight the need to better understand the ecological processes from which the data result and provide recommendations for future applications.

Keywords: Data integration; Human-modified landscape; *Pongo pygmaeus*; Hierarchical modelling; Distance sampling; Occupancy

4.2 Introduction

Anthropogenic pressure on landscapes directly threatens species and creates novel habitats, leads to dramatic changes in wildlife populations, community composition, and species interactions (Foley *et al.*, 2005; Wiegand, Revilla and Moloney, 2005; Tilman *et al.*, 2017). To effectively understand the ecological impacts of land-use change and inform conservation management for threatened wildlife populations, robust survey and monitoring of biodiversity both in design and data collection, is crucial (Pereira and Cooper, 2006).

Government led monitoring schemes, citizen science projects and the increasing culture of making data openly accessible are providing a wealth of biodiversity data available to researchers (Schmeller *et al.*, 2009). Whilst widely accessible data opens new research opportunities, disparate datasets are often underpinned by differing methodologies, resulting in non-standardised data (Miller *et al.*, 2019). This lack of standardisation creates challenges for researchers analysing data and reduces the ability to identify trends and make accurate predictions needed to inform management recommendations (Miller *et al.*, 2019).

Increasingly, researchers are addressing the challenges of non-standardised data with the utilisation of integrated modelling approaches (Zipkin, Inouye and Beissinger, 2019). Integrating data from multiple sources and structures (e.g. presence/absence or counts), allows a greater amount of information to be obtained than from a single data type alone, and can help expand the scope of analyses beyond the original purpose of the data collection (Bowler *et al.*, 2019; Miller *et al.*, 2019). Such integration not only addresses the challenges of modelling non-standardised data but allows researchers to optimise the explanatory power extracted from existing information, thus enhancing our understanding of highly complex ecological systems.

Hierarchical modelling is a popular method to integrate datasets in ecological research. Hierarchical approaches combine two or more mechanistic stages, describing both observational and ecological processes to estimate latent state-variables of interest (variables not directly observed but rather inferred from the data. e.g. occupancy, abundance and survival), quantify the effects of spatial and/or temporal parameters and provide both conceptual and computational benefits (Cressie *et al.*, 2009). An extension of this modelling framework is data integration, where information can be shared between different data structures through shared parameters with a joint likelihood (Kery and Royle, 2020). At their core, spatially-explicit ecological models are realisations of an underlying point pattern process (Kéry and Royle, 2016). While describing this common process, data integration accounts for differences in various data structures or ecological processes (Miller *et al.*, 2019). A major advantage of combining data sets from different sources in this way allows information to be shared, increasing the precision of estimates and the power to detect trends in latent state variables (Bowler *et al.*, 2019).

Orangutans (*Pongo* spp.) are a good example of where integrative models can be utilised, as they are of high conservation concern, relatively well studied compared to many other taxa and thus, there is an extensive catalogue of existing data available (e.g IUCN SSC Ape Populations, Environments and Surveys (A.P.E.S.) database: http://www.primate-sg.org/apes/). Despite this, there are still multiple methods available to researchers (e.g. transect surveys, camera trapping, drone surveys and interviews with local human populations), with each being best suited for a particular situation, site or research objective (Kühl, 2008). Integrative modelling thus provides an opportunity to analyse these data under a unified framework. Integrative models have already been used to assess orangutan population trends and distributions at national or multi-national scales across the entire Bornean orangutan's (*Pongo pygmaeus*) range (Santika, Ancrenaz, *et al.*, 2017; Santika *et al.*, 2019). These studies investigated trends in population over time, but data integration has not yet been applied at a finer scale, where conservation interventions are typically implemented.

There is increasing recognition that human-modified landscapes are central to orangutan conservation efforts (Spehar *et al.*, 2018; Ancrenaz *et al.*, 2021). However, there is currently a paucity of orangutan monitoring data within degraded landscapes, as research has typically focussed on intact habitats (Voigt *et al.*, 2018). Successful conservation initiatives will rely on our understanding of fine-scale determinants of orangutan populations within human-modified landscapes. Capitalising on non-targeted biodiversity data (e.g. camera trap bycatch) provides an opportunity to augment existing datasets and better understand patterns of abundance and habitat use in heavily-degraded areas.

Here we use a hierarchical integrative modelling approach to accommodate monitoring data from transect surveys and camera traps within a unified analytical framework and quantify orangutan abundance across a heavily modified landscape in Sabah, Malaysian Borneo. On Borneo, orangutans of all sex and age classes will regularly move terrestrially (Ancrenaz *et al.*, 2014a) and as a result, images of orangutans are frequently captured on camera traps. We investigate the potential to complement targeted orangutan transect survey data with camera trap bycatch of orangutans, aiming to improve precision of model estimates and better understand effects of anthropogenic and environmental factors.

4.3 Methods

4.3.1 Study site

Our study was conducted in and around the Stability of Altered Forest Ecosystems project (SAFE: https://www.safeproject.net), Sabah, Malaysian Borneo (Figure 4.1a). The heterogeneous landscape includes a large, protected area of continuous logged forest and two small Virgin Jungle Reserves (525 and 2000 ha). The core of the site is a 6,000 ha area of forest which was salvage logged between 2013 and 2016. With the exception of several fragments (size range: 1 – 100 ha) and riparian reserves set aside for scientific research, all commercially valuable trees have been removed. The remainder of the site is made up of actively managed mature oil palm plantations (0 – 12 years at the time of this study) (Mitchell *et al.*, 2018), with remnant forest patches (0.3 – 508 ha) and riparian reserves distributed throughout. Here, we classify the site into three broad forest types:

1. "*Continuous logged forest"* protected areas, which have received limited recent disturbance
2. *"Remnant forest in salvage-logged area"* fragments and riparian reserves set aside for scientific research in the core SAFE area and
3. *"Remnant forest in oil palm"* fragments and riparian reserves remaining in surrounding mature oil palm plantations

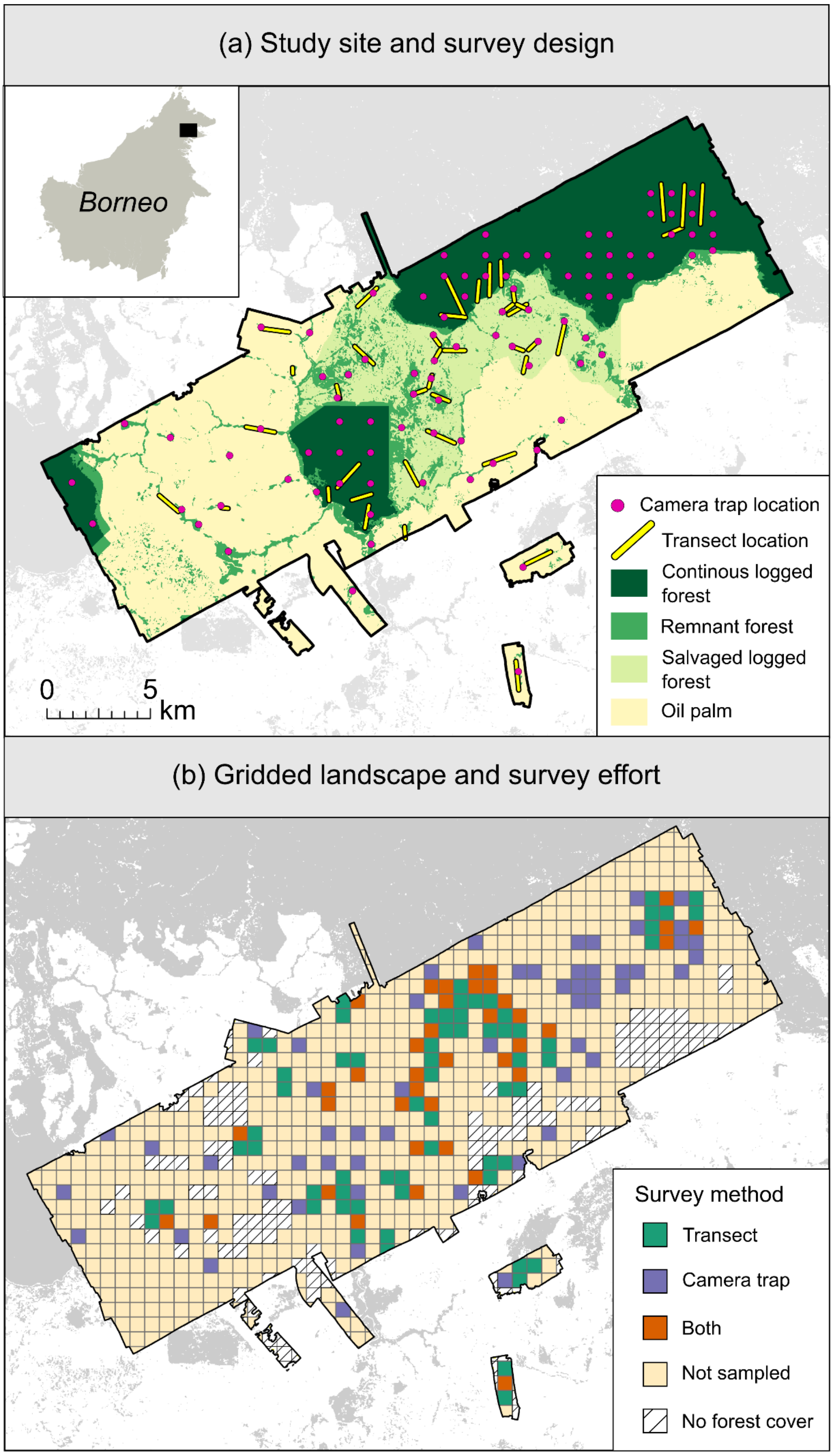


Figure 4.1: Study system.
(a) Study site in Sabah, Borneo and survey placement for both of the datasets within the LiDAR extent from which covariates were derived. (b) 50 ha gridded system used to integrate both line

transects and camera trap data, the colours show if each cell was sample by transect, camera, both or was not sampled. Grid cells without forest were not included within the analysis.

4.3.2 Transect design and nest surveys

We established 44 line transects (mean length: 1.6 km; range: 0.6– 2 km), positioned to ensure spatial randomisation and independence while capturing a representative sample of the disturbance gradient (Seaman *et al.,* 2019). Teams of observers, comprising two to four trained individuals, used a standard distance sampling approach (Buckland *et al.,* 2005) combined with the standing crop method (Spehar *et al.*, 2010) to survey each transect for orangutan nests between April and August 2017, yielding a total survey effort of 53.1 km. Orangutans build recognisable nests daily for resting and sleeping, by interweaving branches of mature trees (Prasetyo *et al.*, 2009). For confirmed orangutan nests, we recorded the perpendicular distance from the transect line to directly under the nest using a measuring tape and the location with a handheld GPS.

4.3.3 Camera trap design and surveys

We deployed camera traps (Reconyx HC500) at 74 sites, to collect detection/non-detection data of mammals between June 2015 and December 2017 (Deere *et al.*, 2018, 2019, 2020). Sites were positioned across the study landscape using stratified random sampling and provided a comparable representative sample of the same disturbance gradient. Camera traps were deployed using a paired design, where two units were placed at each site up to 250 m apart (mean = 207 m) to target different habitat features and maximise species detections. Target species were medium-large mammals; therefore, cameras were placed approximately 30 cm above the ground.

Units were deployed for a minimum of 42 consecutive nights, providing a total survey effort of 10,097 camera-trap nights.

4.3.4 Modelling framework

We modelled abundance and occupancy as ecological state variables of interest, using orangutan nest survey data to estimate abundance and camera trap data for occupancy. We employed a Bayesian hierarchical modelling framework and treated data as a thinned point pattern process, that simultaneously accounted for spatial variation in abundance or occupancy and imperfect detection (Miller *et al.*, 2019). We modelled heterogeneity in both abundance and occupancy by dividing the landscape into a 50 ha gridded system. We selected a grid size of 50 ha (707 m by 707 m) to detect fine-scale drivers of orangutan abundance and occurrence at a biologically appropriate scale for the species (orangutan home range: 40 – 600 ha; Singleton and van Schaik, 2001).

4.3.5 Covariates

Forest structure has been shown to influence orangutan nest site selection and movement in degraded forests in Sabah (Davies *et al.*, 2017, 2019). We quantified forest structural metrics from high resolution LiDAR data collected by NERC’s Airborne Research Facility between September and October 2014 (Jucker *et al.*, 2018; Table 4.1). However, given that orangutan abundance and occurrence are likely to be driven by a combination of environmental and anthropogenic factors (Santika, Ancrenaz, *et al.*, 2017; Voigt *et al.*, 2018), we also included a human accessibility metric developed by Deere *et al*. (2019) and Euclidean distance from the edge of continuous logged forest (Table 4.1).

Table 4.1: Description and justification of covariates used to model state variables. Description and justification of covariates used within the modelling framework, for both transect and camera trap datasets. Light Detection and Ranging (LiDAR) metrics, were derived from point-cloud data by either a canopy height model (CHM) or plant area density (PAD) and additional covariates produced in GIS. Each covariate was summarised across each 50 ha grid cell, representing the minimum home range for a female orangutan,

Covariate	Description	Derived	Justification
Above ground carbon	Measure of carbon store the living plant tissue above ground level	LiDAR - PAD	Orangutan nest density and above ground carbon have been shown to be correlated in a multi-use landscape in Sabah (Milne *et al.*, 2021)
No. of layers	Number of contiguous layers within the vertical forest strata	LiDAR - PAD	Forest structural metrics have been shown to influence orangutan movement and nesting behaviour in disturbed forest in Borneo (Davies *et al.*, 2017, 2019)
Plant area index	Vegetation density across the vertical column	LiDAR - PAD	
Gap fraction	Measure of canopy opening, % of tree cover below 5 m within a focal region	LiDAR -CHM	
Shannon	Measure of forest structural diversity among vertical strata	LiDAR - PAD	
Skew	Measure of the vertical distribution of vegetation	LiDAR - PAD	
Shape	Measure of the vertical distribution of vegetation	LiDAR - PAD	
Tree canopy height	Mean canopy height	LiDAR - CHM	
Variation in Tree canopy height	Standard deviation in canopy height	LiDAR - CHM	
Forest cover	% of canopy >5m	LiDAR - CHM	
Distance from forest edge	Euclidean distance from the edge to protected continuous logged forest (positive with increasing distance from forest area and negative with increasing distance towards forest interior).	GIS	Orangutan density has been shown to decrease with distance from natural forest areas at other disturbed sites (Spehar and Rayadin 2017)
Human accessibility	Combining a time travel model, distance from roads, villages and population density	GIS	Orangutan density has been shown to decrease in areas with high human pressure (Santika *et al.*, 2017; Voigt *et al.*, 2018)

4.3.6 Abundance ecological and detection processes

We analysed nest data using a modified three-stage multinomial/binomial/Poisson mixture model described in Kéry and Royle (2016), where data were binned into h = 1,2,...,H distance classes from 0 m to 40 m. The model describes spatial variation in estimated abundance N_s within grid cell s, conditional on the observed number of orangutan nests n_s.

The first stage models the detection function of binned distance data:

$$\gamma_s | n_s \sim Multinomial(n_s, \pi_s^c)$$

where $\pi_s^c = \pi_k / (1 - \pi_0)$, k denotes the index for each element of the vector π_s^c and π_0 is the detection probability of the last distance class or $\pi_0 = 1 - \Sigma \pi_h$.

The second stage describes the imperfect detection of all available nests from the number of nests that were physically observed:

$$n_s | N_s \sim Binomial(N_s, 1 - \pi_0)$$

Where n_s is the total number of observed nests and N_s is the estimated total number of nests.

The third stage models spatial heterogeneity in abundance:

$$N_s \sim Poisson(\lambda_s)$$

where N_s is local estimated abundance and λ_s is the expected abundance in grid cell s.

Data were truncated at 40 m to avoid bias from extreme outliers and were binned at 4 m intervals for analysis. We used a hazard-rate detection process adapted from

Schmidt *et al.* (2012), as this outperformed other functions with previous analysis of the data (Seaman, Bernard et al. 2019):

$$1 - exp\left(-\left(\frac{h}{\sigma}\right)^{-b}\right)$$

where *h* is the distance class and the detection processed is governed by both a scale parameter σ and shape parameter *b*. Overdispersion in the Poisson observation model, common with count data, was addressed using an observation-level random effect (Moore and Barlow, 2011) (*Obs*; full model specification presented in Supporting Information SI 4.7). Transects were segmented by grid cell, with the effective surveyed area considered as the proportion of the transect which fell within each cell plus twice the truncation distance. To account for non-independence between transect which crossed two of more grid cells, we included a spatial random effect for transect (*Transect*). As there was a slight disparity in transect length, we included an offset term (*Offset*), as the log of each transects length divided by the mean transect length (Marshall *et al.*, 2021).

To assess orangutan population status relative to forest structure and anthropogenic influences, we described abundance and detection using models of the form:

Abundance:

$$log(\lambda_i) = \beta(Habitat\ type_s) + \beta_1 Covariate_s + \varepsilon_1(Transect_{\ s}) \\ + \log(Offset_s) + Obs_s$$

Detection probability:

$$log(\sigma_i) = \alpha(Habitat\ type_s) + \alpha_1 Canopy\ height_s \\ + \alpha_2 No.observers_s$$

4.3.7 Occupancy and habitat use ecological and detection processes

Detection histories were derived by pooling camera trap data into six-day temporal sampling periods, with a 1 assigned if an orangutan was detected during each sampling period and zero if no orangutan was detected. To account for the nested survey design, we employed a three-level multiscale occupancy model:

The first stage models occupancy at the large grid scale 50 ha:

$$z_i \sim Bernoulli(\psi)$$

where z_i describes the presence/absence state as the outcome of a Bernoulli process at site i, where ψ denotes the occupancy probability.

The second stage describes the probability of habitat use at the 1 ha level:

$$a_{ij}|z_i \sim Bernoulli(z_i * \theta)$$

where a_{ij} is the presence/absence of each site i sampled small-scale cell j drawn as a realisation of a second Bernoulli trial, describing the probability of habitat use θ, which is conditionally dependent on z_i (i.e. a small-scale cell can only be in use, when the large-scale grid is occupied).

The third stage describes the detection process:

$$y_{ijk}|a_{ij} \sim Bernoulli(a_{ij} * P)$$

where y_{ijk} represent the detection/nondetection at sampling occasion k within the 1 ha cell j and 50 ha cell i (site), specified as a Bernoulli process described using probability of detection P, which was conditionally dependent on a_{ij}. As data were collected over multiple years, we fitted a temporal random effect representing sampling year (*Year*). The resulting models were:

$$logit(\psi_i) = \beta(Habitat\ type_i) + \beta_1 Covariate_i$$

$$logit(\theta ij) = \beta_0 + \beta_1 Tree\ canopy\ height + \beta_1 Shape_{ij} + \varepsilon\left(Year_{ij}\right)$$

$$logit\left(P_{ijk}\right) = \alpha\left(Habitat\ type_{ij}\right) + \alpha_1 Camera\ trap\ nights_{ij} + \alpha_2 Tree\ canopy\ height_{ij}$$

We assessed for collinearity among covariates using Pearson product-moment correlation (*r*) and Generalized Variance Inflation Factors (GVIF), which was revealed to be high among covariates (|*r*| <-0.7 or >0.7 and GVIF ≥ 7: Figure SI 4.1). We therefore fitted univariate models with habitat type specific intercepts, where each covariate was fitted individually whilst keeping the rest of the model constant. To improve model convergence and place covariates on a comparable scale, we centred all covariates around their mean values and scaled to one-unit standard deviation. Models were ranked based on Deviance Information Criterion (DIC) for abundance estimates or Watanabe Akaike-Information-Criterion (WAIC) for occupancy. We also calculated delta DIC (ΔDIC) and WAIC (ΔWAIC), being the difference between each model and the best preforming model.

For the detection process on each dataset, we included habitat type specific intercepts and two covariates. In the abundance model based on nest data we included number of observers and tree canopy height. In the occurrence model (camera trap data) we included number of camera trap nights and tree canopy height.

4.3.8 Data integration

A common approach to data integration is to assume a shared latent process (Kery, Royle 2020), whereby the underlaying pattern in state variables are assumed to be common among datasets and parameters can be shared, resulting in a joint likelihood. Here, as we are using orangutan bycatch on cameras targeting terrestrial mammals, we cannot assume a shared latent process between data sets, meaning a joint likelihood is not an appropriate approach. Instead, we fit a hurdle style model, whereby both data sets are modelled independently and the outputs are then integrated by multiplying occupancy in grid *k* by abundance grid *k*.

$$Realised\ abundance_k = (Occurrence_k * Orangutan\ abundance_k)$$

We considered covariate effects to be highly influential if their 95% Bayesian Credible Intervals (BCI) did not overlap zero. We considered a more liberal 75% BCI threshold for moderate support, to account for the heterogeneity of the landscape (Tilker *et al.*, 2020). We ran Markov chain Monte Carlo (MCMC) algorithms using JAGS (*v*4.3.0: Plummer, 2003) with the package JagsUI (*v*1.5.1: Kellner, 2019) in R (v3.5.3: R Core Team, 2019). For each modelled parameter we applied vague uniform or normal priors, initiated three chains for 50,000 iterations each, discarding the first 25,000 as a burn-in period. For each parameter, we assessed model convergence visually by inspecting trace plots to ensure sufficient mixing and numerically by checking that the Gelman-Rubin statistics were close to 1 (±0.1). To assess model fit, we performed visual posterior predictive checks and estimated Bayesian *p*-values (*bpv*), considering models a good fit if *bpv* were close to 0.5 (±0.3).

4.3.9 Abundance estimation and model prediction

To estimate orangutan abundance from nest data, first nest density is estimated and then converted to orangutan density as follows:

Nest density was estimated by:

$$Nest\ density = \frac{N}{(2L * B)}$$

Where N is the estimated number of nests from the abundance model, L is the transect length and B is the truncation distance.

Nest density was then converted to orangutan density by:

$$Orangutan\ density = \frac{Nest\ density}{(p * r * t)}$$

Where p is the proportion of nest builders within the population, r is the nest production rate and t is the nest decay rate. Here, we specified these constants using values: p 0.85 and r 1.0, taken from long-term studies of the same orangutan subspecies as our focal species (*P. p. morio*) (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004) and t 259, reported from similar lowland forest (Johnson *et al.*, 2005) and consistent with previous analysis of these data (Seaman *et al.,* 2019).

Predictions were made using habitat specific intercepts and coefficient values for predictor variables for each grid cell. We then excluded grid cells whose values were outside the ranges used within our model. To calculate the total population size, we predicted the number of individuals per grid cell by multiplying density by grid area and summing across all grid cells. We derive predictions from the mean, 2.5th and 97.5th percentiles of the posterior distribution of the best performing model based on

DIC for abundance and WAIC for occupancy. We examined correlation between orangutan abundance and occurrence using Pearson correlation (*r*) on predicted spatial layers.

4.4 Results

4.4.1 Abundance /Density model from transect data

When considering only transect data, 104 of the 774 grid cells were sampled, giving a coverage of 13% of our study site (Figure 4.1b). With the abundance model we estimated mean orangutan density across the landscape at 2.0 individuals per km^2 (95%BCI 1.7 – 2.3), and a total orangutan population of 578 (441 – 751). When broken down into habitat specific estimates, continuous logged forest had the highest mean density of 2.29 (1.46 – 3.45) individuals. Remnant forest in the salvage-logged area had a density of 1.90 (1.16 - 2.91) and remnant forest in oil palm had the lowest density with 0.71 (0.36 - 1.25) individuals.

Our models suggest orangutans are sensitive to forest architecture. The best performing model demonstrates that orangutan abundance is higher in areas characterised by tall canopies (30, 75%BIC: 0.14 - 0.45; Figure 4.2 and Table 4.2). There is equivalent statistical support (ΔDIC of <4 ; Burnham and Anderson, 2004) for an influence of gap fraction (-23, 75%BIC: -0.37 - -0.08) and plant area index (19, 75%BIC: 0.05 - 0.32), with abundance appearing to be higher in closed canopy forest with dense vegetation, albeit with only moderate support. We also found a moderate positive influence for skew (20, 75%BIC: 0.10 - 0.30), above ground carbon density (29, 75%BIC: 0.15 - 0.44) and canopy height variability (15, 75%BIC: 0.08 - 0.22), and a substantial positive influence of shape (-0.69, 95%BIC:

-1.30 - -0.02); however, these received considerably less statistical support when compared to the top-ranking model (ΔDIC >4).

Table 4.2: Abundance model outputs.
Outputs from univariate hierarchical Bayesian distance sampling models fitted to orangutan nest data, including the post-posterior mean (β coefficients) and associated errors of 95% and 75% Bayesian credible intervals (BCI). Models were ranked based on Deviance information criterion (DIC), an indicator of model fit with, low values suggesting a better fit. ΔDIC provides a measure of relative fit compared to the best performing model. For additional quantitative support, we used DIC*w*, which provides the probability each model is the best preforming model. Bayesian *p*-value(BPV) is a measure of model fit with a value of 0.5 indicating a perfect model fit, values between 0.05 and 0.95 are generally considered an indication of adequate model fit. We fit two BPVs, one for the observation (BPV^{obs}) and for the abundance process (BPV^{N}). * Bold indicates were the 95% BCI of a covariate did not cross zero, suggesting a substantial effect on nest site selection.

Univariate model with Predictor	BPV^{N}	DIC	ΔDIC	DIC*w*	β	95%BCI*	75%BIC*
Tree canopy height	0.48	2891.37	0.00	0.55	0.30	-0.18 - 0.81	**0.14 - 0.45**
Gap fraction	0.47	2893.96	2.59	0.15	-0.23	-0.68 - 0.19	**-0.37 - -0.08**
Plant area index	0.46	2894.76	3.38	0.10	0.19	-0.18 - 0.58	**0.05 - 0.32**
Edge	0.47	2895.30	3.93	0.08	0.29	-0.11 - 0.70	**0.15 - 0.42**
Skew	0.48	2896.84	5.47	0.04	0.20	-0.09 - 0.48	**0.10 - 0.30**
Number of layers. layers	0.47	2897.61	6.24	0.02	0.05	-0.53 - 0.66	-0.16 - 0.25
Above ground carbon density	0.47	2898.70	7.33	0.01	0.29	-0.14 - 0.74	**0.15 - 0.44**
Variation in tree canopy height	0.46	2898.72	7.35	0.01	0.15	-0.06 - 0.36	**0.08 - 0.22**
Shannon	0.46	2899.07	7.70	0.01	0.08	-0.35 - 0.53	-0.07 - 0.23
Human accessibility	0.47	2899.49	8.12	0.01	0.07	-0.21 - 0.35	-0.03 - 0.16
Shape	0.46	2900.25	8.88	0.01	-0.69	**-1.30 - -0.02**	**-0.91 - -0.48**

4.4.2 Occupancy model and camera trap data

With the camera trap data, the number of cells sampled was 94 or 12 % of grid cells (Figure 4.1b). There was a relatively high probability of orangutan occupancy across the entire landscape (0.63, 95%BCI: 0.54 – 0.72), with no substantial difference between habitat types, suggesting orangutans are common across the landscape (Figure 4.3).

The highest orangutan occurrence probabilities where in areas characterised by low above ground carbon density (Figure 4.2), which received moderate support (-0.58 75%BIC: -0.91 - -0.24) Above ground carbon density also had substantially more support than any other model, having a conditional probability (WAIC*w*) of 0.98 and the next best preforming model having a ΔWAIC of 7.98 and (Table 4.3). We also found moderate support for several forest structural metrics, with a positive influence of skew (0.52 75%BIC: 0.17 - 0.84), gap Fraction (0.46 75%BIC: 0.15 - 0.75), variation in tree canopy height (0.43 75%BIC: 0.16 - 0.69), as well as a negative influence of the number of layers in the vertical column (-0.59 75%BIC: -0.99 - -0.17), tree canopy height (-0.43 75%BIC: -0.77 - -0.08) and plant area index (-0.52 75%BIC: -0.79 - -0.23). These metrics suggest orangutan occurrence increases in areas of low canopy height, reduced structural complexity and low vegetation density.

Table 4.3: Occupancy model outputs.

Outputs from univariate hierarchical Bayesian multi-scale occupancy models fitted to orangutan by-catch data from camera traps, including the post-posterior mean (β coefficients) and associated errors of 95% and 75% BCI. The models were ranked based on Watanabe–Akaike information criterion (WAIC), an indicator of model fit with low values suggesting a better fit. ΔWAIC provides a measure of relative fit compared to the best performing model, with lower values indicating increased support. For additional quantitative support, we used WAIC*w*, analogous to a conditional probability of the model being the best preforming among all candidate models. Bayesian *p*-value (BPV) is a measure of model fit with a value of 0.5 indicating a perfect model fit, values between 0.2 and 0.8 are generally considered an indication of adequate model fit when using an occupancy modelling framework. 95%BIC which do not cross zero demonstrate substantial support for covariate effect and 75%BCI which do not cross zero indicating moderate support.

Univariate model with Predictor	**BPV**	**WAIC**	**ΔWAIC**	**WAIC*w***	**β**	**95%BCI**	**75%BCI**
Above ground carbon density	0.64	538.85	0.00	0.98	-0.58	-1.6 - 0.47	**-0.91 - -0.24**
Skew	0.65	546.83	7.98	0.02	0.52	-0.44 - 1.61	**0.17 - 0.84**
No. of layers	0.64	552.08	13.23	0.00	-0.59	-1.86 - 0.5	**-0.99 - -0.17**
Shannon	0.64	553.08	14.23	0.00	-0.24	-1.42 - 0.74	-0.6 - 0.15
Tree canopy height	0.64	553.25	14.40	0.00	-0.43	-1.51 - 0.56	**-0.77 - -0.08**
Gap Fraction	0.64	554.84	15.99	0.00	0.46	-0.38 - 1.38	**0.15 - 0.75**
Shape	0.64	555.62	16.77	0.00	-0.14	-0.82 - 0.57	-0.37 - 0.08
Variation in tree canopy height	0.65	558.92	20.07	0.00	0.43	-0.32 - 1.26	**0.16 - 0.69**
Plant area index	0.63	561.34	22.49	0.00	-0.52	-1.34 - 0.25	**-0.79 - -0.23**
Edge	0.64	568.11	29.26	0.00	-0.17	-0.99 - 0.86	-0.48 - 0.1
Human accessibility	0.63	580.85	42.00	0.00	0.17	-0.87 - 1.11	-0.16 - 0.52

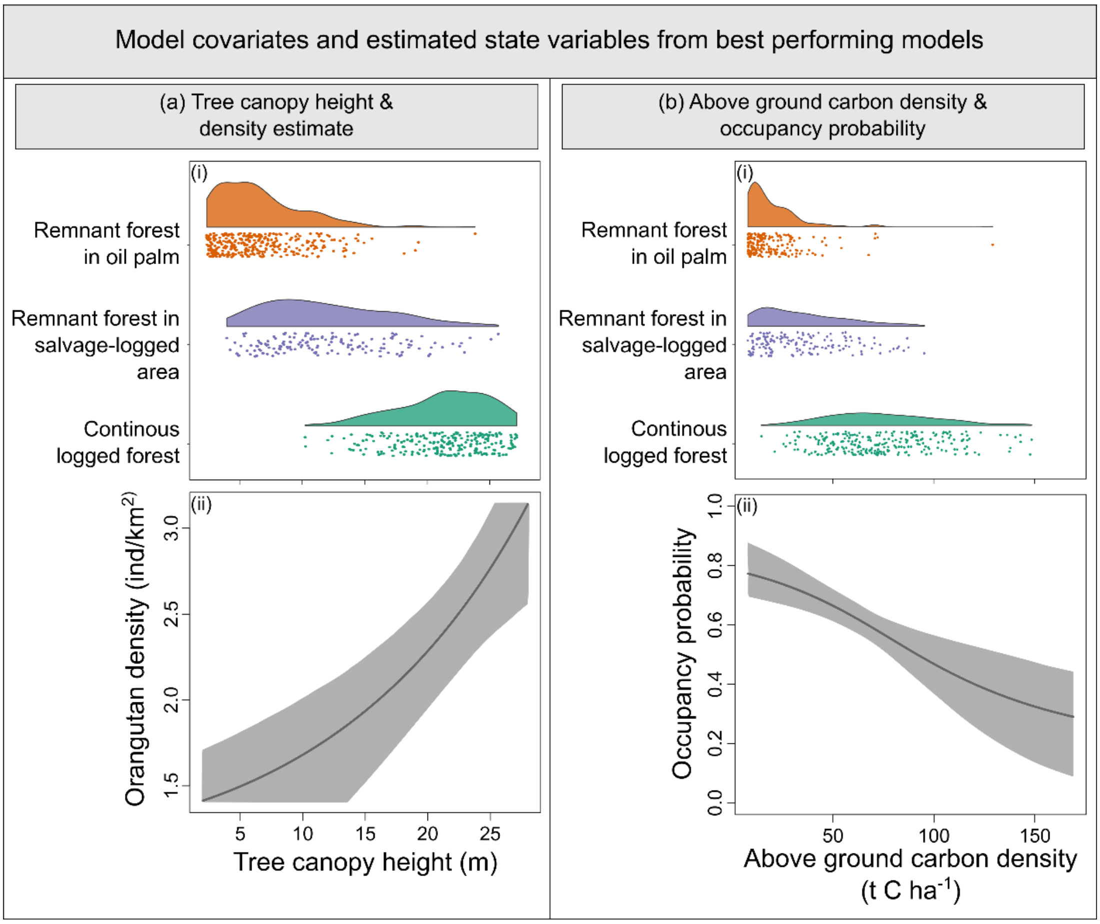


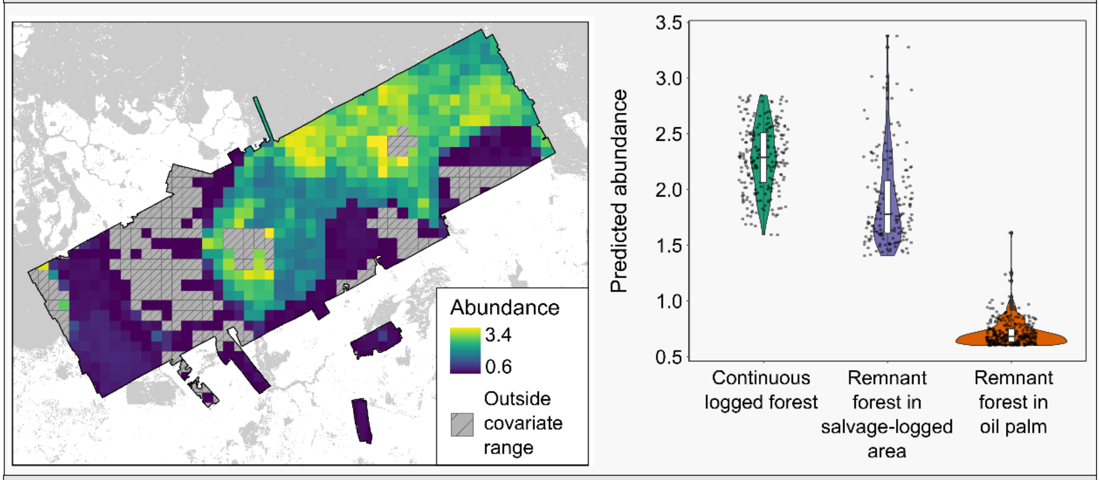
Figure 4.2: Distribution of covariates with habitat types and state variable response. (i) Density plot and jittered points for covariate data associated with the best preforming model for each data set (Orangutan nest data = Tree canopy hight and orangutan by-catch on camera = Above ground carbon), among the three broad habitat types. (ii) Response curve for the relationship between the covariate effect and each state variable (orangutan density per km^2 for nest data and occupancy probability for camera trap data), with shaded area showing the 75% Bayesian confidence intervals, which demonstrated moderate support.

4.4.3 Data integration

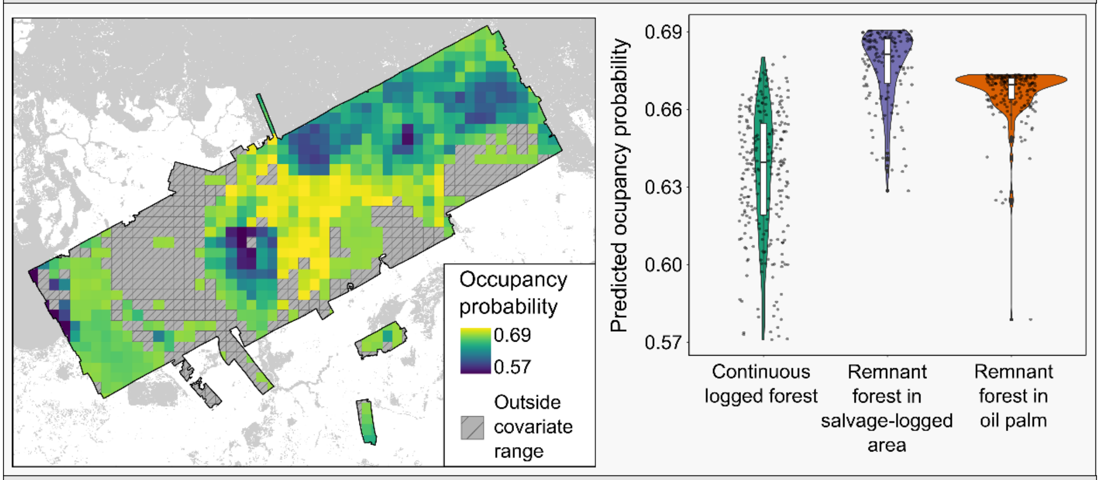
The integration of transect and camera trap data increased the number of sampled cells to 158 cells or 20% of the study site (in comparison to 13% and 12% for transects and camera trap data alone). The combination of abundance and occurrence data through integration led to a greatly reduced total population estimate of 290 (185 – 443) orangutans. The precision also increased, with the range between

Bayesian credible interval, reducing to 258, compared to 310 when the nest data was modelled alone.

(a) Predicted abundance



(b) Predicted occurrence



(c) Predicted intergrated abundance

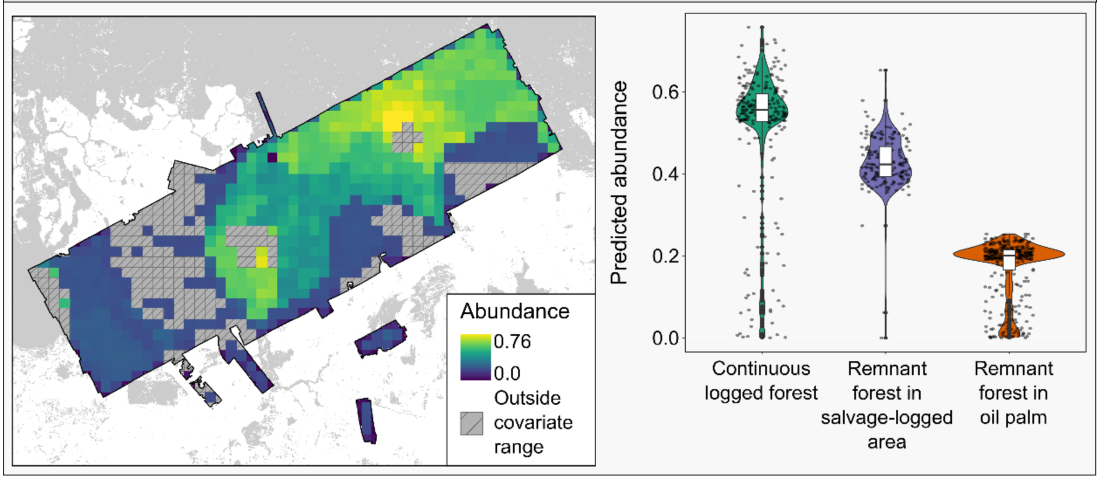


Figure 4.3 Model predictions using abundance, occurrence and integrated modelling. Maps show the predicted state variable (a and c = orangutan density, b = orangutan occupancy) for each grid cell and Violin plots display the predicted state variable for each 50 ha grad cell, summarised across the three broad habitat types. (a) Is orangutan density when

using only the nest count data, (b) is occupancy from only the camera trap data and (c) is density when integrating both the nest and camera trap data. Grey cells are those which included no forest cover or had values outside the covariate range used within the model, and therefore excluded from predictions.

There was a significant negative correlation between predicted occurrence and abundance in all three habitat types (Continuous logged forest = -0.89, *p* = <0.001, remnant forest in salvage-logged area = -0.98, *p* = <0.001, and remnant forest in oil palm = -0.80, *p* = <0.001; Figure 4.4).

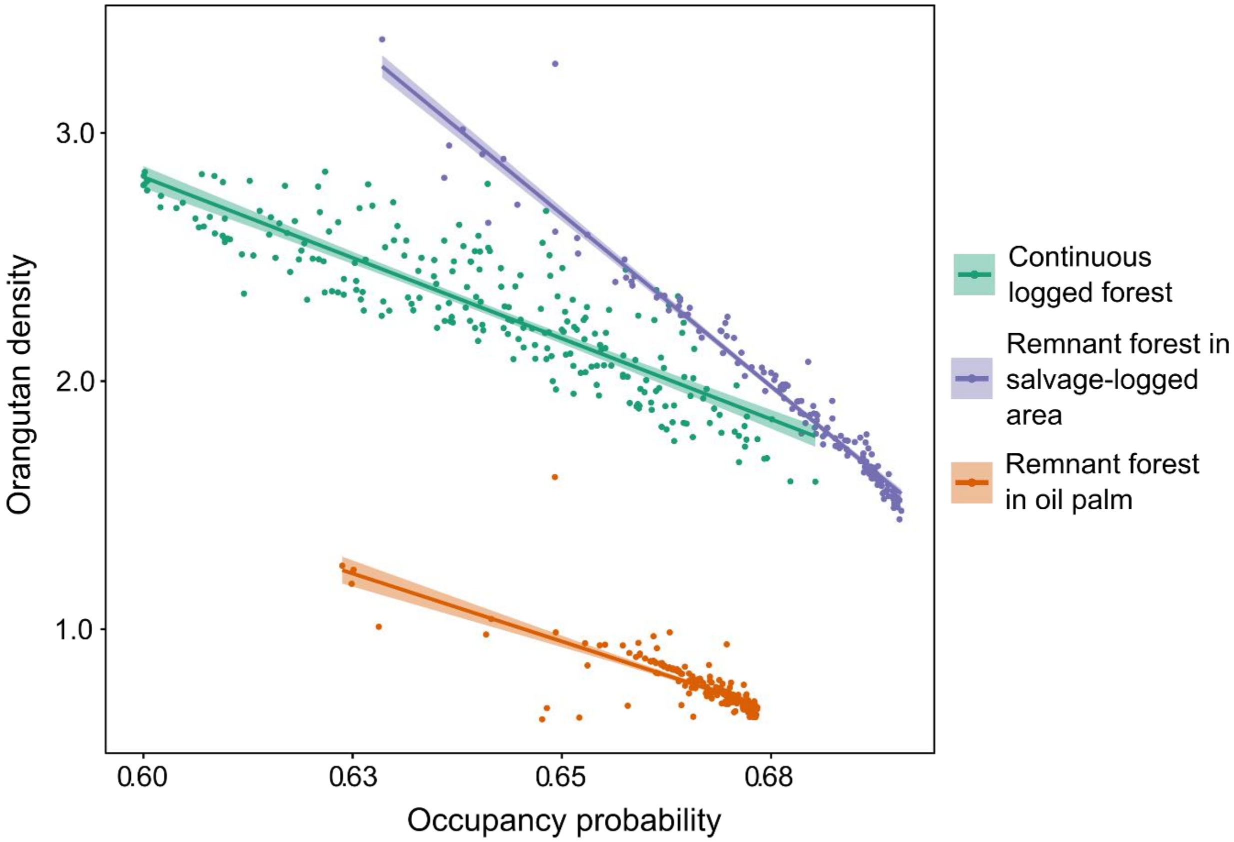


Figure 4.4 Correlation between predicted abundance and occupancy probability for each habitat type.
Points show density or occurrence predictions for each 50 ha grid cell, from the orangutan nest and camera trap by-catch data modelled separately. Regression lines indicate the relationship between orangutan density and occupancy for each of the three broad habitat types from Pearson correlations, with 95% confidence intervals shown as shaded areas.

4.5 Discussion

We estimated fine-scale orangutan abundance through integrating nest survey and camera trap datasets, collected in a human-modified landscape in Malaysian Borneo. The integration almost doubled our effective survey area and expanded the sampling effort to include orangutan signs in different forest strata, representing different aspects of orangutan ecology.

In Sabah, forest cover has reduced by ca. 40% since 1973 (Gaveau *et al.*, 2016). Our results practically demonstrate that remnant forest in converted areas may facilitate orangutan persistence, with orangutans appearing to be common across our study landscape. However, our covariates did not significantly describe patterns of abundance as the 95% Bayesian credible interval crossed zero or received very little quantitative support (Table 4.2). This lack of support may be related to the proximity of the study site to a large continuous area of protected forest (Ulu Segama), which has a large and stable orangutan population (Ancrenaz *et al.*, 2010), which may spill over into the study site irrespective of habitat quality.

Likely due to the different ecological processes underling the data (discussed below), predicted occurrence and abundance patterns across the area diverge spatially and areas estimated to have high orangutan abundance receive the lowest occurrence probability. Integrating occurrence probability into the abundance model thus, lowered the overall abundance estimate by almost half from 578 to 290 orangutans. These results corroborate findings that although orangutan nest density varies with habitat type (Spehar and Rayadin, 2017; Seaman *et al.*, 2019; Milne *et al.*, 2021), they have a high resilience to disturbance and, in the absence of hunting, can utilize heavily degraded habitats as part of their home range (Ancrenaz *et al.*, 2021).

A degree of terrestrial activity is a natural behaviour for orangutans in Borneo, but there is evidence that terrestrial locomotion increases in areas of high disturbance (Ancrenaz *et al.*, 2014a). As the camera traps used for the occurrence model were targeting medium-large mammals at the ground-level, cameras would only capture orangutans when they were moving terrestrially. Conversely, orangutans are more likely to nest, as detected by the transects used in the abundance, in high, uniform canopies, more indicative of areas with lower disturbance. By using data that represent both terrestrial locomotion, and nesting, we brought together different, but complementary aspects of the ecology of the species leading to a more informed estimate with increased precision. As nests accumulate over time and are thus more likely to overinflate the estimate, the occurrence data serve as a bias reduction factor for the abundance dataset.

By combining data from different ecological processes at a high spatial resolution, this study also expands on previous orangutan data integration work. Santika *et al.* (2019) integrated orangutan nest data from ground and aerial surveys with coarse orangutan presence records from interview surveys to estimate orangutan population trends. In future, expanding the spatial overlap between datasets and incorporating monitoring data from additional sites may allow further applications of model integration. For instance, hierarchical models with spatially correlated random effects allow information to be shared between data sets through correlated spatial patterns, regardless whether these are positively or negatively associated (Pacifici *et al.*, 2017). However, these models require large datasets and a high degree of spatial overlap (Pacifici *et al.*, 2017), limiting their applicability for ecological data, which are often sparse and collected over relatively small areas with limited resources (Ovaskainen and Soininen, 2011). This is particularly true for tropical regions where large monitoring programs and citizen science projects are unfeasible or still in their infancy (Chandler *et al.*, 2017). Our research thus highlights potential methodological challenges when applying data integration methods on heterogenic and fine-scale datasets derived from different ecological processes, especially when data are sparse.

Monitoring methods commonly utilised to survey orangutans (e.g. transects or drone surveys) were originally developed for use in intact habitats. With increasing focus being directed towards conserving great apes within human-modified landscapes, the ability to effectively estimate and monitor populations within these areas is paramount. Despite this, knowledge about the accuracy and feasibility of survey and monitoring techniques in these landscapes is still lacking (Voigt *et al.*, 2018). Surveying great apes in highly modified landscapes poses several additional challenges for researchers. Habitat fragmentation can create heterogeneity in detection and influence abundance or occupancy estimates (Duarte, Adams and Peterson, 2018). For instance, vegetation structure, fragment shape and disturbance histories or proximity to features such as roads and villages or large intact forest areas, are likely to impact abundance and habitat use. The resulting spatial heterogeneity in abundance and detection is particularly difficult with long linear transects which may traverse multiple landscape features or environmental gradients, diminishing the ability to capture more local or patchy drivers of abundance (Guillera-Arroita *et al.*, 2012). Therefore, conventional sampling and modelling approaches which have typically been applied to more homogenous, large areas of intact forest, may not be appropriate when applied to highly complex modified landscapes.

A major benefit to integrative modelling is the ability to draw information from large, low resolution, inexpensive datasets, such as citizen science or surveys of farmers and plantation workers. These data are likely to be more readily available in human-modified landscapes, in combination with high resolution, intensive and thus more expensive data sets such as systematic nest surveys on transects (Kühl *et al.*, 2020). Although this study identified methodological challenges when integrating fine scale datasets with small spatial overlap in highly heterogeneous landscapes, it also demonstrated the potential for expanding datasets and improving precision. Integrative models should be further explored as a flexible approach to integrate more traditional and systematic data with less structured observations, and improve representation in landscapes with high heterogeneity, typical for anthropogenic landscapes. For instance, there is a substantial number of camera trap data surveys across gradients of disturbance available from across the orangutan range, where traditional nest counts are lacking (Spencer et al., unpublished data). Such observations are more likely in human-modified landscapes such as plantations with a greater human presence and programmes to collect these could have the dual aim of raising awareness about orangutan presence and increase tolerance towards coexistence.

4.6 Conclusions

The drastic expansion of degraded and human-modified landscapes in combination with insufficient data on species trends, call for a significant increase in species monitoring both spatially and temporally. Given finite conservation resources, data integration has been shown to be effective in expanding information content of existing but underutilized data (Miller *et al.*, 2019; Zipkin, Inouye and Beissinger, 2019). While being mindful of data requirements and potential limitations of methodologies, it is of utmost urgency to improve our evidence base about species abundance patterns, trends and drivers in the age of the Biodiversity Crisis and especially in rapidly expanding anthropogenic landscapes. The knowledge we create about changes in such a way is, however, only useful when it goes hand-in-hand with the implementation of conservation tools to address the drivers of change. Then, monitoring and data integration can be used to target and evaluate those tools effectively, instead of merely describing species declines (Nichols and Williams, 2006).

4.7 Supplementary information: BUGS model code

```
#==========================================================
#
#        BUGS model specification for integrating data from for line-transect nest
#        and camera trap data
#
#==========================================================
model{
##############################################################
   #Dataset 1: Model to predict orangutan density from nest data
 # Priors
   for(r in 1:nRegion){
   int.hab.det[r] ~ dunif(-10,10)        # Habitat specific intercept on detection
   int.hab.lam[r] ~ dunif(-10,10)        # Habitat specific intercept on abundance
   }
   alpha.1.dis ~ dunif(-10,10)           # Detection covariate prior 1
   alpha.2.dis ~ dunif(-10,10)           # Detection covariate prior 2
   beta.1.lam ~ dunif(-10,10)            # Abundance covariate prior
# Overdispersion term
   for(s in 1:nsites){
   obs[s] ~ dnorm(0,obs.tau)
   }
   obs.tau <- 1/(obs.sd * obs.sd)
   obs.sd ~ dunif(0,10)
# Transect random effect
   for(k in 1:nTran){
   TranEffect[k] ~ dnorm(0, tau.lam)
   }
```

```
   tau.lam <- pow(sd.lam, -2)
   sd.lam ~ dunif(0, 2)                  # Site heterogeneity in lambda
# For hazard-rate
   #b ~ dnorm(0,0.01)                    # Option 1
   b ~ dgamma(0.1, 0.1)                  # Option 2
#==========================================================
# Code modified from (Kéry and Royle, 2016 p. 454)
   for(i in 1:nind){
   dclass[i] ~ dcat(fc[site[i],]) # Part 1 of hierarchical model
#Generate new observations and calculate residuals for Bayesian p-value on the
# detection component
   dclassnew[i] ~ dcat(fc[site[i],1:nD])
   Tobsp[i]<- pow(1- sqrt(fc[site[i],dclass[i]]),2)
   Tobspnew[i]<- pow(1- sqrt(fc[site[i],dclassnew[i]]),2)
   }


 #==========================================================
   for(s in 1:nsites){
   # Construct cell probabilities for nD multinomial cells
   for(g in 1:nD){                       # midpt = mid-point of each cell
## Half-norm detection function
 #log(p.1[s,g]) <- -midpt[g] * midpt[g] / (2*sigma[s]*sigma[s])
## Hazard-rate detection function
   cloglog(p.1[s,g]) <- b*log(sigma[s]) - b*log(midpt[g])
   pi[s,g] <- delta / B                  # Probability per interval
   f[s,g] <- p.1[s,g] * pi[s,g]
   fc[s,g] <- f[s,g] / pcap[s]
  }
#==========================================================
   pcap[s] <- sum(f[s,])            # Pr(capture): sum of rectangular areas
   ncap[s] ~ dbin(pcap[s], N[s])         # Part 2 of hierarchical model
```

```
   N[s] ~ dpois(lambda[s])                # Part 3 of hierarchical model
   }

#=========================================================
## Linear models
   for(s in 1:nsites){
# Abundance
   log(lambda[s]) <-   int.hab.lam[Region.1[s]] +
                        beta.1.lam * cov.1.lam[s] +
                        TranEffect[Tran[s]] +
                        log(offset[s]) +
                        obs[s]


# Detection
   log(sigma[s]) <-     int.hab.det[Region.1[s]] +
                        alpha.1.dis * cov.1.sig[s] +
                        alpha.2.dis * cov.2.sig[s]
      }

#=========================================================
## Create replicate abundances for Bayesian p-value on abundance component (Kéry
## and Royle, 2016 p. 193)
   for(s in 1:nsites){
   Nnew[s]~dpois(lambda[s])


   ## Residuals for 'observed' and new abundances
   FT1[s]<-pow((N[s]-lambda[s]),2)/(sqrt(lambda[s])+0.0001)
   FT1new[s]<-pow((Nnew[s]-lambda[s]),2)/(sqrt(lambda[s])+0.0001)
   T1p[s]<-sum(FT1[1:nsites])
   T1newp[s]<-sum(FT1new[1:nsites])
   }
```

```
#=================================================================
    # Derived parameters
    Bp.Obs<-sum(Tobspnew[1:nind])>sum(Tobsp[1:nind])   # Only works in jags
    Bp.N<- sum(T1newp[1:nsites])>sum(T1p[1:nsites])        # Only works in jags
    fit.n <- sum(FT1[])
    fit.new.n <- sum(FT1new[])
    fit.obs <- sum(Tobsp[])
    fit.new.obs <- sum(Tobspnew[])
    Ntotal <- sum(N[])
    MeanN <- Ntotal / 642
    D <- Ntotal/(A)
    OU <- D / (0.85 * 1 * 249)                                      # Convert nest density to
                                                                    # orangutan density
    #mean.sig  <- mean(sigma[])
    #mean.esw  <- mean(esw[])
    #mean.f0   <- mean(f0[])
 # Continous forest vs. salvage logged
    lam.hab.effect.1 <- int.hab.lam[1] - int.hab.lam[2] #
# Continous forest vs. oil palm remnant
    lam.hab.effect.2 <- int.hab.lam[1] - int.hab.lam[3]
# Salvage logged vs. oil palm remnant
    lam.hab.effect.3 <- int.hab.lam[2] - int.hab.lam[3]
# Transect level density
    #for(r in 1:nsites){
    #NestD[r]  <- N[r]/(TranLengthkm[r]*2*Bkm)
    #OUDens[r] <- NestD[r]/(0.85 * 1 * 249)
    #}

#=================================================================
# Predict abundance across landscape
    for(k in 1:nGridX){
```

```
    lam.pred[k] <- exp(int.hab.lam[habX[k]] + beta.1.lam  *  X.lam.1[k])
    NestDens[k] <- lam.pred[k]/(TranLengthkmX*2*Bkm)
    Do_X[k] <- NestDens[k]/(0.85 * 1 * 249)
    N_OU[k] <- Do_X[k]*Grid_area[k]
    }
    OU_Population <- sum(N_OU[]) # Total estimated population

#===========================================================

###############################################################
    #Dataset 2: Model to predict orangutan occupancy from camera trap data
    # Priors and model for params
    for(r in 1:nRegion){
    int.p[r] ~ dunif(0,1)              # Habitat specific intercept on detection
    int.psi[r]~ dunif(0,1)             # Habitat specific intercept on occupancy
    }
    for(t in 1:n.CT){
    int.theta[t] ~ dunif(0,1)          # Intercepts of availability probability
    }
    beta.lpsi.1 ~ dunif(-10,10)        # Occupancy covariate prior
    beta.ltheta.1 ~ dunif(-10,10)      # Habitat covariate prior 1
    beta.ltheta.2 ~ dunif(-10,10)      # Habitat covariate prior 2
    alpha.lp.1 ~ dunif(-10,10)         # Detection covariate prior 1
    alpha.lp.2 ~ dunif(-10,10)         # Detection covariate prior 2
# Year random effect
   for(i in 1:nYear){
    YearEffect[i] ~ dnorm(0,Year.tau)
    }
    Year.tau <- pow(Year.sd,-2)
    Year.sd ~ dunif(0,2)
```

```
#=========================================================
   for (i in 1:n.site){
   # Occurrence
   z[i] ~ dbern(psi[i])
#=========================================================
   for (j in 1:n.CT){ # Habitat use
   a[i,j] ~ dbern(mu.a[i,j])
   mu.a[i,j] <- z[i] * theta[i,j]
#=========================================================
   for (k in 1:n.Reps){ # Detection error process in sample k
   y[i,j,k] ~ dbern(mu.y[i,j,k])
   mu.y[i,j,k] <- a[i,j] * p.2[i,j,k]
#=========================================================
## Linear models
# Occupancy
   logit(psi[i]) <-        int.psi[Region.2[i]] +
                           beta.lpsi.1 * Broad_cov.1[i]
# Habitat use
   logit(theta[i,j]) <-    int.theta[j] + beta.ltheta.1 *
                           Fine_cov.1[i,j] + beta.ltheta.2 *
                           Fine_cov.2[i,j] +
                           YearEffect[Year[i,j]]
# Detection
   logit(p.2[i,j,k]) <-    int.p[Region.det[i,j]] +
                           alpha.lp.1 * CTN[i,j] +
                           alpha.lp.2 * chm[i,j]

#=========================================================


   # Computation of fit statistic to calculate Bayesian p-value
```

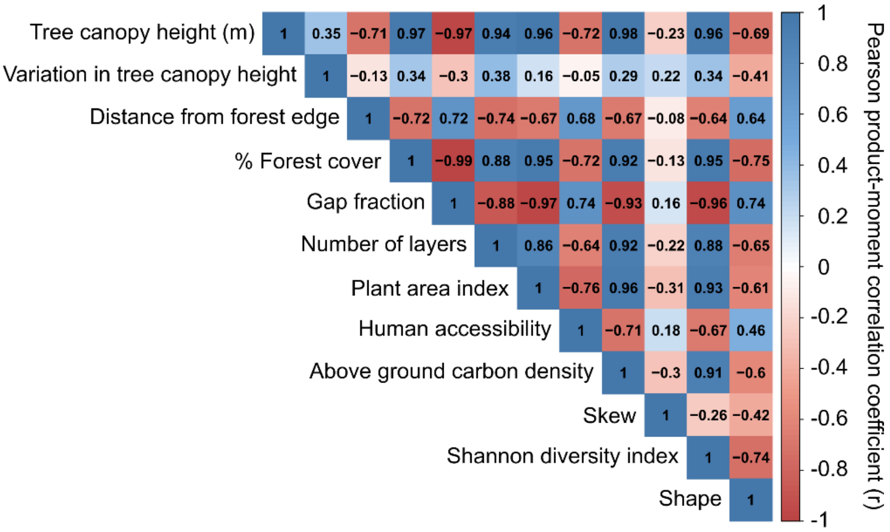
```
   Presi[i,j,k] <- abs(y[i,j,k]-p.2[i,j,k])                    # Absolute residual
   y.new[i,j,k]~dbern(mu.y[i,j,k])
   Presi.new[i,j,k] <- abs(y.new[i,j,k]-p.2[i,j,k])
   }
   } tmp[i] <- step(sum(a[i,])-0.1)
   }
#===========================================================
# Derived quantities
   fit <- sum(Presi[,,])                          # Discrepancy for actual data set
   fit.new <- sum(Presi.new[,,])                  # Discrepancy for replicate data set
   sum.z <- sum(z[])                              # Total No. of occupied Sites
   psi.fs <- sum.z/n.site

   psi.hab.effect.1 <- int.psi[1] - int.psi[2] # Continous forest vs. salvage logged
   psi.hab.effect.2 <- int.psi[1] - int.psi[3] # Continous forest vs. oil palm remnant
   psi.hab.effect.3 <- int.psi[2] - int.psi[3] # Salvage logged vs. oil palm remnant
#===========================================================
# predict occupancy across landscape
  for(k in 1:nGridX){
   logit(occ.pred[k]) <-  int.psi[habX[k]] + beta.lpsi.1 * X.pis.1[k]
   }
#===========================================================
###############################################################
   # 3: Integrate results from each model of both datasets
   # Realised abundance = Occupancy(presence/absence) * abundance
   # Predict across landscape
   for(k in 1:nGridX){
   realAbund[k] <- (occ.pred[k] * N_OU[k])
   }
   OU_Population_inter <- sum(realAbund[]) # Total estimated realised population
```

```
} # end model
```

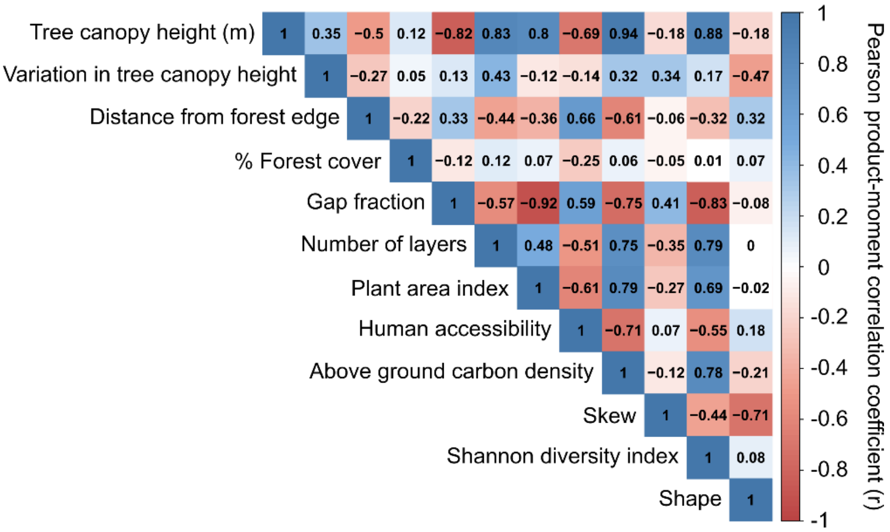
4.8 Supplementary information: Collinearity among predictors

(a) Covariates used on abundance



Tree canopy height (m)	1	0.35	−0.71	0.97	−0.97	0.94	0.96	−0.72	0.98	−0.23	0.96	−0.69
Variation in tree canopy height		1	−0.13	0.34	−0.3	0.38	0.16	−0.05	0.29	0.22	0.34	−0.41
Distance from forest edge			1	−0.72	0.72	−0.74	−0.67	0.68	−0.67	−0.08	−0.64	0.64
% Forest cover				1	−0.99	0.88	0.95	−0.72	0.92	−0.13	0.95	−0.75
Gap fraction					1	−0.88	−0.97	0.74	−0.93	0.16	−0.96	0.74
Number of layers						1	0.86	−0.64	0.92	−0.22	0.88	−0.65
Plant area index							1	−0.76	0.96	−0.31	0.93	−0.61
Human accessibility								1	−0.71	0.18	−0.67	0.46
Above ground carbon density									1	−0.3	0.91	−0.6
Skew										1	−0.26	−0.42
Shannon diversity index											1	−0.74
Shape												1

(b) Covariates used on occupancy



Tree canopy height (m)	1	0.35	−0.5	0.12	−0.82	0.83	0.8	−0.69	0.94	−0.18	0.88	−0.18
Variation in tree canopy height		1	−0.27	0.05	0.13	0.43	−0.12	−0.14	0.32	0.34	0.17	−0.47
Distance from forest edge			1	−0.22	0.33	−0.44	−0.36	0.66	−0.61	−0.06	−0.32	0.32
% Forest cover				1	−0.12	0.12	0.07	−0.25	0.06	−0.05	0.01	0.07
Gap fraction					1	−0.57	−0.92	0.59	−0.75	0.41	−0.83	−0.08
Number of layers						1	0.48	−0.51	0.75	−0.35	0.79	0
Plant area index							1	−0.61	0.79	−0.27	0.69	−0.02
Human accessibility								1	−0.71	0.07	−0.55	0.18
Above ground carbon density									1	−0.12	0.78	−0.21
Skew										1	−0.44	−0.71
Shannon diversity index											1	0.08
Shape												1

Figure SI 4.1 Collinearity among covariates.

We assessed collinearity among covariates using Pearson product-moment correlation coefficient (*r*), considering covariates to be highly correlated if *r* was equal to or greater than 7 or equal to or less than -7. (a) covariates for dataset one the abundance model and (b) for dataset two the occupancy model

Chapter 5 Forest patches enhance the population viability of Bornean orangutans if offtake is limited

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5.1 Abstract

Deforestation and logging have degraded and fragmented much of Borneo’s lowland forest (>500 m above sea level). Small fragments in human dominated landscapes appear to support orangutan populations, but it is unclear how viable these are in the long term or if fragments can promote movement across heavily modified landscapes. In the absence of longitudinal data, we applied a spatially-explicit individual-based model to investigate the long term viability of orangutan populations across Borneo. Specifically, we address how the loss of fragments from the landscape and removal of individuals through hunting, retaliatory killings and rescues, effect population dynamics and dispersal. Small remnant forest fragments facilitated movement, increasing the number of individuals settling in non-natal patches. These small fragments are also likely to support a substantial number of orangutans, which currently receive limited conservation focus. However, major rivers remain a substantial barrier to movement and limit the ability of orangutan populations to recover from recent declines. Moreover, orangutan populations are highly vulnerable to even small amounts of offtake, with annual removal of >2% individuals leading to large declines in population and diminish the positive role that small fragments play in sustaining connectivity and long-term viability. Our modelling implies that orangutan populations could increase and potentially expand in extent if further habitat loss in human-modified landscapes can be limited. However, this will only be possible if efforts are focused to reduce the removal of orangutans from the system by curbing rescues and translocations to only the most appropriate cases, and promoting co-existence between these flagship animals and people across the orangutan range.

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

5.2 Introduction

The levels of deforestation, forest degradation and fragmentation in tropical regions are a major concern for conservation and environmental decision makers (Seymour and Harris, 2019). Tropical forests support more than half of the world's terrestrial vertebrates, but many of these are highly threatened with extinction (Pillay *et al.*, 2021). Deforestation has been particularly high in Southeast Asia, with some of the highest rates concentrated on the island of Borneo. For example, between 1973 and 2016, 19.5 million ha of old growth forest was lost, reducing Borneo's forest cover from 76% to 50% (Gaveau *et al.*, 2014). Widespread loss and fragmentation of forest habitats, particularly in lowland areas, has created extensive human-modified landscapes (Gaveau *et al.*, 2016). These areas are characterised by large areas of mono-culture crops, mainly oil palm and softwoods, with scattered remnant natural forest fragments (Gaveau *et al.*, 2016).

Much of the worlds remaining forest areas are highly fragmented and roughly 70% of this remaining forest is within 1 km of its edge with dissimilar landcovers (Haddad *et al.*, 2015). This proximity to the edge exposes species in these areas to changes in biotic and abiotic conditions, with 85% of vertebrate species affected in some way (Pfeifer *et al.*, 2017). Habitat loss leads to a reduction in biodiversity, yet remnant forest fragments can act as important refuges for many forest dependent species (Lion *et al.*, 2016; Mitchell *et al.*, 2018; Deere *et al.*, 2019). Remnant forest patches are also likely to be crucial for maintaining connectivity across landscapes, allowing species movement among meta-populations and facilitating range shifts in response to climate change (Laurance, 2004; Senior, Hill and Edwards, 2019). Despite these benefits, populations in remnant forest patches are also at greater risk of environmental and demographic stochasticity (such as drought, fire, disease or fluctuations in population size) and 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 concerning habitat fragmentation, there is a current paucity of research regarding the role of fragments in human-modified tropical landscapes in facilitating connectivity and population viability, undermining our ability to provide practical solutions.

Advances in computational power have allowed the development of increasingly complex models which can simulate dynamic environmental systems (Kool, Moilanen and Treml, 2013). Individual-based models epitomise this progress and are increasingly popular in ecological studies (Synes *et al.*, 2016). Using individual-based modelling approaches to investigate species responses to environmental change or management options, has several advantages over other commonly used methods. For instance, species distribution and environmental niche models assume populations are at equilibrium and species presence data is correlated with environmental covariates, but this is rarely likely to be the case (Urban *et al.*, 2016). With individual-based models, the incorporation of population dynamics and species movement as well as inter-individual variation in these processes, addresses several of these limitations (Bocedi *et al.*, 2014). Developments in these dynamic models, both computationally and statistically, means they are likely to become increasingly important tools in managing biodiversity and landscapes (Synes *et al.*, 2016). These models are most effective for species which are relatively well studied, in terms of ecology and population dynamics.

Despite international commitments to halt biodiversity loss, species such as the orangutan have been declining steeply over the past two decades (Wich *et al.*, 2016; Santika, Ancrenaz, *et al.*, 2017; Voigt *et al.*, 2018). This loss is primarily 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 rescues, where individuals are removed from fragments when at real or perceived risk from hunting, fire or further habitat loss (Sherman, Ancrenaz and Meijaard, 2020). 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, recent work has highlighted the potential importance of remnant natural forest in human-modified landscapes for orangutan populations. For instance, in Borneo, orangutans and their nests have been observed in forest fragments within human-modified landscapes (Meijaard *et al.*, 2010; Ancrenaz *et al.*, 2021). Although found at reduced densities (Seaman *et al.*, 2019), most orangutan individuals found in these landscapes are in good health based on measures of body mass (Sherman, Ancrenaz and Meijaard, 2020) and appear to be able to survive and reproduce in remnant forest areas for extended periods of time (>20 years) (Ancrenaz *et al.*, 2021). Forest fragments may therefore play an important role in connecting larger areas of orangutan habitat and preventing further population fragmentation and decline.

Orangutan population viability analyses have been performed in the past. For instance Marshall *et al.* (2009), used a non-spatially explicit approach to investigate the effects of logging, hunting and initial population size on simulated orangutan populations. Likewise, Gregory *et al.*, (2014) applied a spatially-explicit individual-based model to investigate the effectiveness of corridors under future climate-change in Sabah; however, they modelled dispersal through least-cost path analysis and maximum dispersal distance. Here, we employ a spatially explicit individual-based model and stochastic movement simulator, to examine the potential long-term consequences of widespread deforestation and forest degradation, on orangutan populations across Borneo. Further, we investigate the additional effects of offtake from hunting, retaliatory killings and rescues on population viability and movement. We based our assessment on the orangutan, as they are a relatively well study species in the region, making them an ideal candidate for the application of an individual-based model. Orangutans are also a high-profile species, bringing large amounts of conservation funding annually (Morgans *et al.*, 2018; Santika, Sherman, *et al.*, 2021). Additionally, they are a large bodied species, requiring relatively large amounts of forest cover; therefore, focusing long-term conservation initiatives on orangutans will likely have positive outcomes for the wider biodiversity across Borneo.

5.3 Methods

5.3.1 Study system

Our study focuses on Borneo, the third largest island in the world covering an area of over 740,000 km^2 (Figure 5.1a). Borneo's governance is shared among Indonesia (Kalimantan), Malaysia (Sabah and Sarawak) and Brunei. Orangutans are found across much of Borneo's lowland areas, with the exception of Brunei where the species is absent. 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. There is a large network of rivers across the island, which pose a substantial barrier to movement for orangutans (Jalil *et al.*, 2008; Arora *et al.*, 2010).

5.3.2 Modelling framework

We modelled orangutan population dynamics and dispersal using a modified version of RangeShifter 2.0 Contain (Bocedi *et al.*, 2021). RangeShifter is an individual-based population viability and connectivity modelling platform which combines both demographic and dispersal models, allowing the spatially-explicit concurrent simulation of population dynamics and dispersal, including inter-individual stochasticity (Bocedi *et al.*, 2021). The Contain extension has been developed to model potential management options for controlling invasive non-native species through culling. Our study applies RangeShifter 2.0 Contain to investigate the long-term effects of habitat loss, fragmentation and offtake on orangutan population viability and connectivity. Here, rather than managed culling, we used the Contain extension to model offtake of individuals from the population through hunting retaliatory killings and rescues, using offtake rates estimated by Sherman *et al.*, (in review) from crime and social media data.

5.3.3 Meta-population delineation and dynamics

We used a fine-scale 30 m resolution gridded system to define our study landscape, to which we applied a patch-based model. Patches are then aggregations of suitable habitat cells within defined spatial clustering (specified below section 5.3.4), with each patch considered a separate population. Male orangutans will range over very large distances, often encompassing multiple female home ranges and are unlikely to be a limiting factor in reproduction (Nietlisbach *et al.*, 2012). Similarly, there does not appear to be a bias in offtake rates between sexes (Sherman *et al.*, in review). We therefore, implemented a female only stage-structured demographic model comprised of nine overlapping age stages (Table 5.1).

Genetic data suggests major rivers and mountain ranges have been a significant barrier to movement across evolutionary time scales for orangutans (Jalil *et al.*, 2008; Arora *et al.*, 2010). This separation has resulted in sufficient genetic divergence for the Bornean orangutan population to be divided into three subspecies, the largest population being the Southwest Bornean (*Pongo pygmaeus wurmbii*) found across southern west and central Kalimantan. The Northeast Bornean (*P. p. morio*) ranging from Sabah in the North down to East Kalimantan and the smallest population the Northwest Bornean (*P. p. pygmaeus*) in the Malaysian state of Sarawak and Northwestern Kalimantan. Although orangutan demography (e.g birth rate and survival) is broadly consistent across Borneo (van Noordwijk, Atmoko, *et al.*, 2018), environmental variation means orangutan densities vary considerably across the island (Santika, Ancrenaz, *et al.*, 2017; Voigt *et al.*, 2018). To capture this variation in abundance, we treated each subspecies as a discrete meta-population and modelled movement and population dynamic separately among subspecies. Realised patch densities (the interaction between the demographic model and carrying capacities), were based on the most recent range wide density distribution model (Voigt *et al.*, 2018). These densities were summarised across discrete landcover types independently for each of the three subspecies, using 250 m resolution landcover maps (Miettinen, Shi and Liew, 2016). As we only modelled females, we then halved density estimates to represent the female only population (Table 5.2). Orangutans tend to have a slight male bias sex ratio at birth (van Noordwijk, Atmoko, *et al.*, 2018), and so we set a survival probability of stage one individuals at 0.45 to represent this trend. We derived subsequent survival probabilities from the most recent orangutan Population and Habitat Viability Analysis report (Utami-Atmoko *et al.*, 2019; Table 5.1).

Table 5.1: Demographic and dispersal parameters of Bornean orangutan populations used in the population viability and connectivity model. RangeShifter is comprised of two models, a stage-structured demographic model (here a female only model with overlapping age stages) used to investigate population viability, and a dispersal model to simulate movement. Dispersal is modelled through three distinct processes, emigration, transfer and settlement, each parametrised separately. We modelled offtake (individuals removed from the landscape by hunting or translocations) using rates estimated from crime data, which resulted in either orangutans being killed or translocated to avoid negative interactions with humans.

Parameter	Description		Value	Reference
Demographic				
Fecundity ϕi		The yearly probability of a reproductive female giving birth	0.167¶	(van Noordwijk, Atm al., 2018)
Age-stages & Survival probabilities		Age range (years) and annual survival probability of each age stage		
At birth			0.45§	(van Noordwijk, et a
Infant	1-2 years		0.97	(Utami-Atmoko et a
Juvenile	3-9 years		0.99	
Adolescent	10-11 years		0.98	
Young adult	12+ years		0.99‡	
Adult	13-41 years		0.99‡	
Mature adult	42-45 years		0.95	
Senior adult	46-51 years		0.85	
Senescent	52-55+ years		0.75	
Max. age (years)			55	
Dispersal				
Emigration				Expert informed
D_0 Max Emigration probability			0.2†	
α_0 (slope)			10	
ß$_0$ (inflection point)			1	
Transfer parameters				Expert informed
Direction persistence			2.5†	
Perceptual range (cells)			25†	
Memory size			10†	
Max. steps per year			3,000†	(Singleton et al., 200
Total max. no. of steps			12,000†	
Per step mortality			0.001†	
Settlement				Expert informed
S_0 Max. Settlement probability			1	
α_S (slope)			-50†	
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., in re
At 10.0% detection rate			1%	
At 6.2% detection rate			2%	
At 3.2% detection rate			4%	
At 1.2% detection rate			10%	

¶ Uses a modified function than the default RangeShifter, described in SI1.1 § Represents male bias in birth ratio. † Tested for sensitivity. ‡ Density dependency applied.

We added density dependence in both development and fecundity population parameters. Female age at first reproduction in orangutans has been estimated at roughly 15 years but there is some variability (Kuze *et al.*, 2012). As a result, we applied density dependence between stages four and five (Young adult and Adult: table 5.1), resulting in a female's reproductive development being slightly delayed as their resident patch approaches or reaches its population equilibrium density. Orangutans have one of the longest interbirth periods of any mammal, ranging between six to nine years (van Noordwijk, Atmoko, *et al.*, 2018). As we modelled a yearly reproductive season, we used an annual fecundity probability of 0.167 (equating to a 6-year inter-birth interval) and included a density dependence function matching Utami-Atmoko *et al.*, (2019), reducing the fecundity probability (and therefore extending the inter-birth interval) as patches approach or achieve their population equilibrium density (Detailed in Supporting Information SI5.7.1).

Table 5.2: Habitat specific orangutan carrying capacities.
Estimates derived by summarising a density distribution (sensu Voigt *et al.*, (2018), by landcover types (sensu Miettinen, Shi and Liew, (2016) and halved to represent the female only population. Habitat specific carrying capacities are used to informed density dependencies within the RangeShifter modelling framework.

Habitat type	**Subspecies max. carrying capacity (females/km2)**		
	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

5.3.4 Patch allocation

Orangutans are forest-dependent, requiring natural forest for both food and nesting resources for their long-term survival (Rijksen and Meijaard, 1999). We delineated habitat suitable for orangutans to settle and reproduce in forests using high resolution (30 m) Borneo-wide forest maps (Gaveau *et al.*, 2016). On Borneo, orangutans predominantly occupy lowland areas and are generally absent from or at extremely low densities in areas <500 m asl (Husson *et al.*, 2009). Thus, we focussed analyses in areas >500 m asl, retaining all suitable lowland habitat which has the potential to support orangutans irrespective of the current orangutan occurrence status, to allow possible future colonisation and range expansion.

In addition to large rivers, major multi-lane highways are also likely to be a barrier to orangutan movement. As RangeShifter models population dynamics at the patch level, it is therefore unrealistic to model large forest blocks intersected by major rivers and multi-lane highways as a single population. To account for this, we divided all forest blocks that were intersected by major rivers (Wells *et al.*, 2016) and multi-lane highways with layers produced by (https://nusantara-atlas.org/). The current IUCN orangutan distribution crosses several large areas of forest, in order to initialise the model with the current range, we divided forest areas by the orangutan distribution (Ancrenaz *et al.*, 2016). Although roads and rivers are impermeable to movement, orangutans could freely move between patches divided by the IUCN orangutan distribution during dispersal.

In RangeShifter, each patch, and thus population, is given a unique identity. Orangutan nests have been observed in oil palms up to 50 m from natural forest areas in plantations and individuals are regularly observed making short distance excursions into plantations (Ancrenaz *et al.*, 2015, 2021). Therefore, small natural forest fragments close to large forested areas are likely to be incorporated into female home ranges. To integrate this dynamic, we placed a 50 m buffer around all forest areas, dividing the buffer by major rivers, roads and the orangutan range. Patches were then assigned unique IDs based on their spatial arrangement, whereby all patches within an unbroken buffer (therefore ≤100 m apart) were assigned the same identity and considered a discontinuous patch. Using zonal statistics in ArcGIS Pro (*v*2.6.0; ESRI, 2020), we calculated the mean orangutan density per patch, based on the same landcover-specific population densities from a Borneo wide population assessment (Voigt *et al.*, 2018). The number of individuals a patch could contain was then calculated. We then removed patches too small to support a single orangutan from the patch layer and retained patches which could support more than one individual. Patches to small to support a single orangutan were retained within the cost surface (Section 5.3.6).

5.3.5 Dispersal parameters

RangeShifter models dispersal through three distinct processes: emigration, transfer, and settlement. Female orangutans display a high degree of philopatry, with long-distance dispersal being almost exclusively male based (Nietlisbach *et al.*, 2012; Ashbury *et al.*, 2020), and therefore, range expansion is determined by short distance female dispersal. To simulate this process, we modelled stage dependent young adult female dispersal, including a strong density-dependency in both emigration and settlement probabilities. We parametrised emigration, so that females would stay within their natal patches until the patch reached its density equilibrium, after which there was a maximum probability a female would emigrate of 20%.

To model the transfer process, we used a stochastic movement simulator. The stochastic movement simulator is an individual-based model which simulates step-based movements across a cost surface (Palmer, Coulon and Travis, 2011). This provides an advantage over other least cost path algorithms, as it assumes an individual is naive to both the surrounding landscape and their destination. Movement trajectories during transfer are governed by three parameters, perceptual range, directional persistence, and memory. We set perceptual range at 25 cells (750m) as, being arboreal by nature, orangutans are likely to have a relatively large perceptual range (Table 5.1). The two additional parameters, directional persistence, and memory, were set to 2.5 and 10 respectively, based on previous expert judgement of visualised simulated trajectories (Seaman *et al.*, 2021). In the base version of RangeShifter 2.0, once an individual has dispersed from there natal patch they cannot return to the same patch. If a female orangutan leaves their natal patch and is unable to find suitable habitat, we assumed it was likely that they would return and as a result, we modified RangeShifter to allow individuals to return and settle in their natal patch. The length of movement trajectories is constrained by two parameters, yearly maximum number of steps and a total maximum number of steps. We set a yearly maximum number of steps at 3,000, based on multiplying the average daily path length of followed habituated orangutans (Singleton *et al.*, 2009) by 365. The total maximum number of steps an individual could take while dispersing was set at 12,000, after which if the individual failed to settle, they would die. Mortality during dispersal is likely to be low, and we therefore set a per step mortality probability of 0.001. As we are modelling the entire potential range for each subspecies, we included reflective boundaries, preventing individuals from leaving the landscape.

Females will generally settle close to or within their mothers' home range (van Noordwijk *et al.*, 2012; Ashbury *et al.*, 2020) and to approximate this, we set a 100% settlement probability with a shallow density-dependence, meaning females would settle at the first patch encountered during transfer, unless the patch was near or had reached its density equilibrium. Parametising the model in this way means females will only leave their natal patch if the patch cannot support them (i.e. at or above its carrying capacity) and will settle at the first available opportunity, replicating the high degree of philopatry. As there is limited information on orangutan dispersal within human-modified landscapes, we undertook an extensive sensitivity analysis to determine how robust our model was to changes in dispersal parameters (Table 5.1 and Section 5.3.9).

5.3.6 Cost surface

We built a cost surface layer using both expert informed opinion and the increased cost an orangutan would face when moving terrestrially. Albeit being predominantly arboreal, terrestrial movement is a common behaviour for orangutans on Borneo; however, this form of locomotion presents additional energetic costs, as well as risks from predation and novel diseases (Ancrenaz *et al.*, 2014b; Ashbury *et al.*, 2015). To capture this nuance, we created a cost surface using the Distance Accumulation tool in ArcGIS Pro (*v*2.6.0; ESRI, 2020) based on Tobler's hiking function. We used three inputs, a 30 m digital elevation model, expert informed resistance surface values based on habitat type (Table SI 5.1), and barriers to movement (major roads and rivers). To ensure rivers and major highways were represented in the landscape and prevent diagonal movement between barrier pixels, we buffered all major roads and rivers by 50 m. We included all suitable forest areas as starting points, regardless of whether they were identified as being large enough to support an orangutan, as these small forest patches will provide resources and limit the cost of moving across the landscape. The resulting surface is a cost to movement layer, where the cost increases when moving away from natural forest areas, mediated by the expert informed resistance of the habitat type, degree of slope and barriers within the landscape. Here rather than time travelled, values represent the cost to an orangutan of moving across the landscape (Figure SI 5.2).

5.3.7 Landscape and offtake scenarios

We developed scenarios to explore the relative effect of both fragmentation and offtake on orangutan population dynamics and connectivity. To investigate the effects of fragmentation we established two landscape scenarios, one "Fragmentation status quo” included all forest suitable for orangutans (<500 masl) across Borneo and represents the current levels of fragmentation. Small forest fragments are at much greater risk of being deforested (Hansen *et al.*, 2020) and previous population viability analyses have considered any fragment <5000 ha to be unviable for supporting orangutan populations (Utami-Atmoko *et al.*, 2019), limiting evidence for protection of these fragments. We therefore, produced a second fragmentation scenario “Extreme fragmentation”, by removing any fragment which was <5,000 ha, representing a worst-case scenario. Patch and cost surfaces were produced for both landscapes (Figures SI 5.1 and SI 5.2).

We modelled five different yearly offtake rates from hunting, retaliatory killing and/or rescues: 0%, 1%, 2%, 4% and 10%, estimated from social media and crime data (Sherman *et al*., In review). Individuals were removed from patches selected at random and individuals could be removed from all age groups. As single orangutans are often removed from fragments in oil palm landscapes by rescues and hunting is likely to be opportunistic or in response to perceived conflict (Meijaard *et al.*, 2011; Sherman, Ancrenaz and Meijaard, 2020), offtake is unlikely to be related to density and therefore, we did not include a density threshold, meaning there was no relationship between density and offtake. We ran models for 100 years (ca. 8 generations) to allow the population to reach equilibrium before starting the offtake.

5.3.8 Model initialisation and metrics

We initialised the model using the IUCN distribution for each subspecies, populating all suitable patches within the range at carrying capacity. The population was distributed among age classes based on model test runs where the population had reached equilibrium. To investigate the potential long-term effects of hunting, fragmentation, and habitat loss, we ran models for ca. 40 generations (500 years) and for 100 iterations. We applied the five offtake rates to both landscape scenarios, resulting in 10 model outcomes for each subspecies.

We considered eight metrics.

- *Total population,* the population at each time step.
- *Percentage change in population,* the percentage change in population compared to the starting population
- *Extinction probability,* the cumulative probability that the population becomes extinct across the 100 iterations at each 10-year time interval
- *Patch occupancy,* the proportion of patches occupied after 500 years
- *Area occupied,* the summed areas of all occupied patches
- *Percentage change in area occupied,* the percentage change in summed areas of all occupied patches compared to the starting area
- *Dispersal success,* the percentage of individuals settling in non-natal patches
- *Dispersal distance,* the linear distance moved from the cell an individual took the decision to emigrate to the cell they took the settlement decision

5.3.9 Sensitivity analysis

The largest degree of uncertainty regarding our model surrounds dispersal. We consequently undertook a sensitivity analysis to determine the robustness of the model to these parameters. Parameters were both increased and decreased by 5% and the model run for 500 years and 100 iterations. As the parameters tested were mainly pertaining to orangutan movement (Table 5.1), we assessed the model sensitivity by comparing the proportion of patches occupied at 500 years, to the baseline model of current fragmentation levels and with no hunting pressure.

5.4 Results

Our demographic model revealed that when no offtake was applied, in both fragmentation scenarios the populations of all three orangutan subspecies increased from their initial size and expanded their range over the duration of the model run. Despite this, the final abundance and area occupied were lower in the Extreme fragmentation scenario compared to the status quo. For instance, the population for *P. p. morio* in the Fragmentation status quo scenario increased by an average of 56% (from 39,773; ± 24 standard error, SE to 62,139; ±424 females), compared to a 49% increase (36,619; ±22 to 54,606; ±463) in the "Extreme fragmentation" scenario (Figures 5.1, 5.2 and Table SI 5.2). Similarly, the total area occupied increased by 64% (from 24,874 km^2 to 40,761 km^2, ±57) compared to 60% (from 22,261 km^2 to 35,524 km^2, ±99) in the Fragmentation status quo and Extreme fragmentation scenarios respectively. When no offtake was applied, there was also a zero extinction probability for all model outcomes among subspecies and fragmentation scenarios (Figure 5.3).

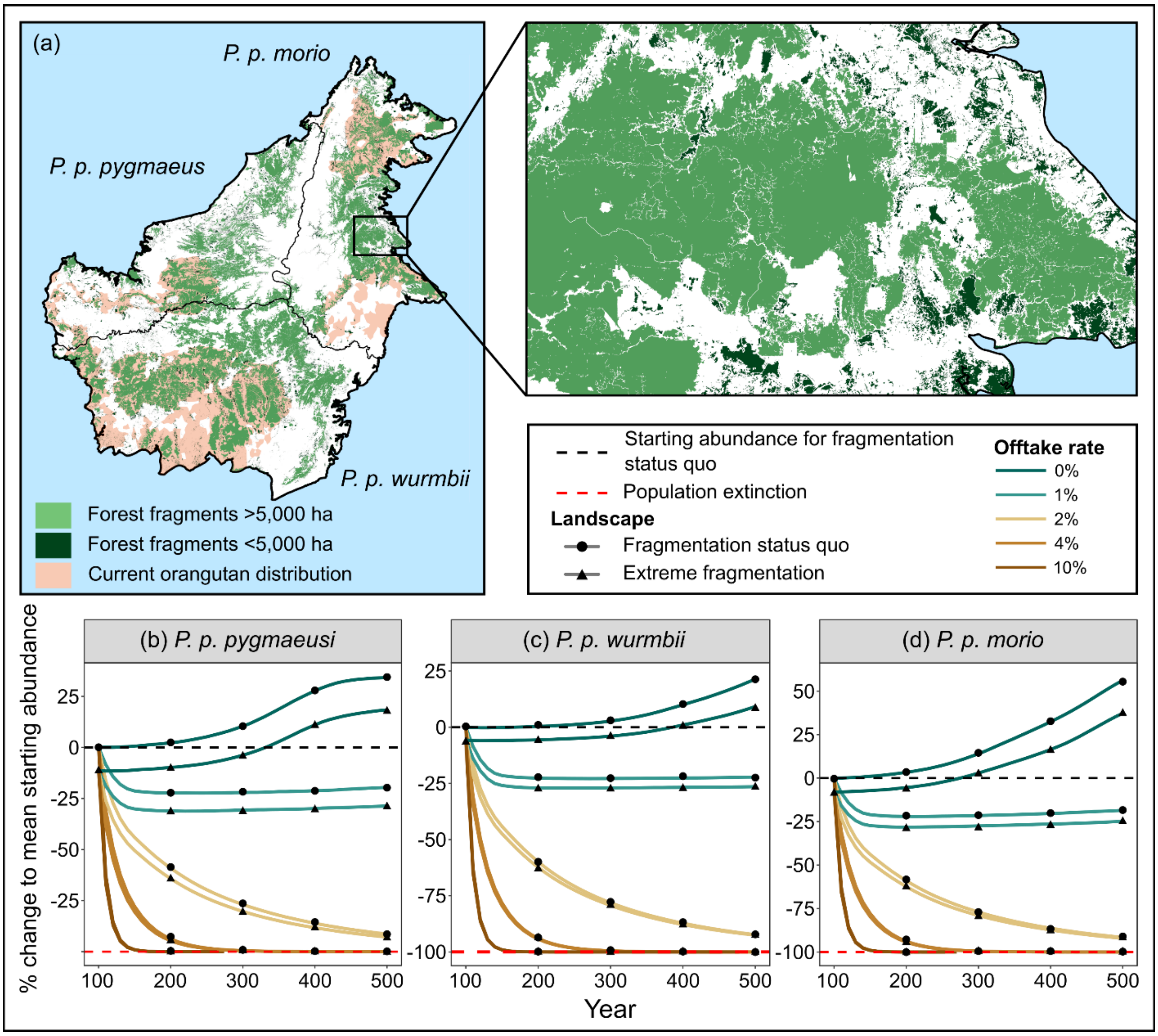

Figure 5-1 The impact of forest fragmentation on orangutan range-wide population size.

Percentage change in population size over time for each orangutan subspecies, when forest fragments <5000 ha were included or excluded from connectivity assessments. Models were run for 100 years until the population had reached equilibrium, after which point the offtake was applied and the models run for an additional 400 years. (a) Distribution of forest fragments suitable for orangutans (<500 masl) across Borneo. (b-d) Subspecies specific percentage changes in abundance after offtake was applied, compared to the starting abundance under Fragmentation status quo (current situation).

Orangutan populations appear to be highly sensitive to offtake, with even small amounts having a substantial effect on the final population size. In both fragmentation scenarios, when the lowest offtake rate of 1% was applied there was on average a 20% (18% - 22%) decline in the final population size for all subspecies (Figure 5-1 and Table SI 5.1). This population decline was most severe for *P. p. wurmbii*, which fell by 22% (from 155,478; ±38 to 120,973; ±76) when the status quo was maintained and by 21.9% (from 146,501, ± 41 to 114,332, ± 59) under Extreme fragmentation. For both fragmentation scenarios moderate levels of offtake (2% and 4%) led to extreme declines in the final abundance across subspecies of <90% (Figure 5-1 and Table SI 5.2). This was particularly true for the 4% offtake rate, which led to almost total extinction with a 99.9% population decline for all model outcomes.

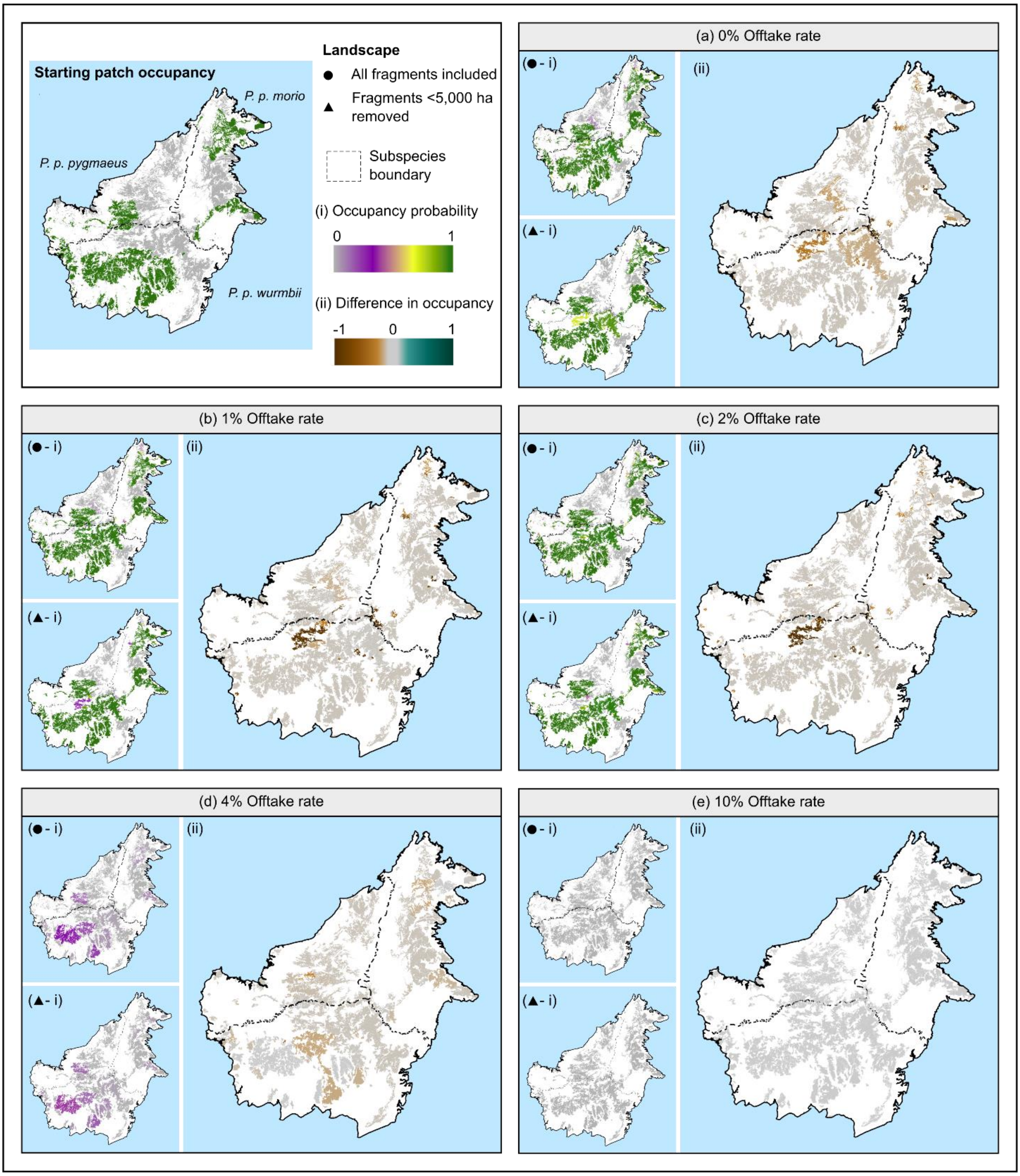

Figure 5.2: Difference in orangutan occupancy across Borneo

(i) Indicates the orangutan occupancy probability under both fragmentation scenarios, when all fragments are included (Fragmentation status quo) and when fragments <5000 ha were removed (Extreme fragmentation) at increasing levels of offtake from the population (a-e, from 0% to 10%). (ii) The relative difference in occupancy between fragmentation scenarios and when differing offtake rates were applied. Low numbers indicate a higher occupancy probability under the Fragments status quo scenario and high values indicating higher occupancy probability under Extreme fragmentation.

Despite these marked population declines, there was a zero-extinction probability when off rate was relatively low (1% – 2%). Extinction probabilities varied among subspecies when a moderate offtake of 4% was applied, with the highest probability for *P. p. pygmaeus*, with a 72% (±5) probability of extinction with the Fragmentation status quo and 74.0% (±4) in the Extreme fragmentation scenario. An extreme off take of 10% resulted in a 100% extinction probability for all subspecies under both fragmentation scenarios (Figure 5.3).

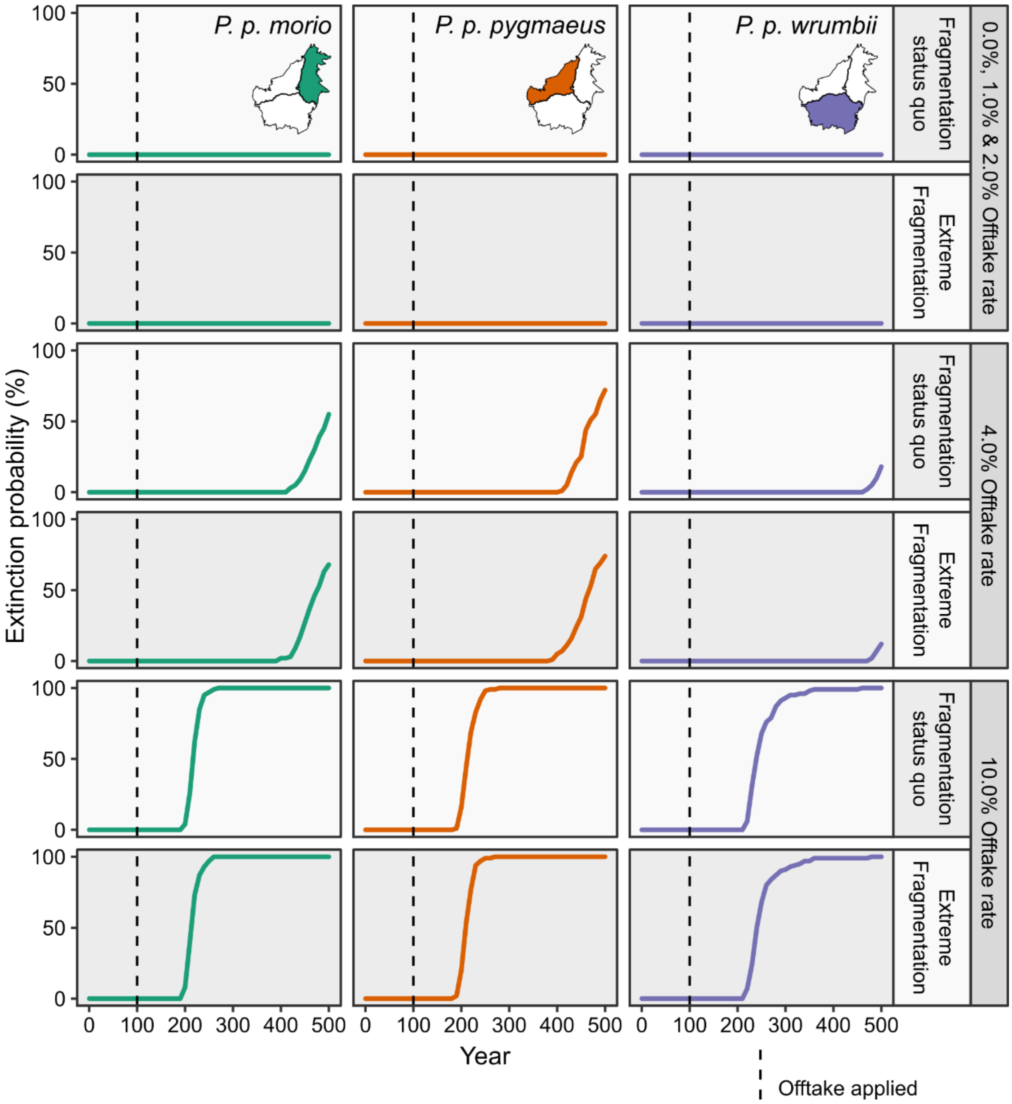

Figure 5-3 Extinction probability.
The cumulative extinction probability averaged across 100 iterations for each subspecies. Extinction probabilities are shown for both fragmentation scenarios, when all fragments are included (Fragmentation status quo) and when fragments <5000 ha were removed (Extreme fragmentation) and offtake scenarios, ranging from 0% to 10% of the population being removed annually. Offtake rates were applied after the first 100 years when the population had reached equilibrium, shown by the vertical dashed lines. We do not show standard errors, as they fall within the lines.

For all offtake scenarios, of the dispersing individuals which successfully settled in non-natal patches, the median dispersal distance (the linear distance from taking the decision to emigrate to the decision to settle) was greater when fragmentation levels were extreme (Figure 5.4). The greatest difference between fragmentation scenarios was when no offtake was applied. This difference was particularly true for *P. p. pygmaeus*, with a median distance of 4.34 km compared to 21.92 km in the Fragmentation status quo and Extreme fragmentation scenarios respectively. This difference in dispersal distance between fragmentation scenarios decreased as the offtake rate increased, but nevertheless the distances were always greater under Extreme fragmentation. The percentage of dispersing individuals settling in non-natal patches was substantially higher under the Fragmentation status quo. With increasing levels of offtake, the percentage of successful dispersers settling in non-natal patches also increased among all subspecies and fragmentation scenarios, yet remained substantially lower under extreme fragmentation (Figure 5.4).

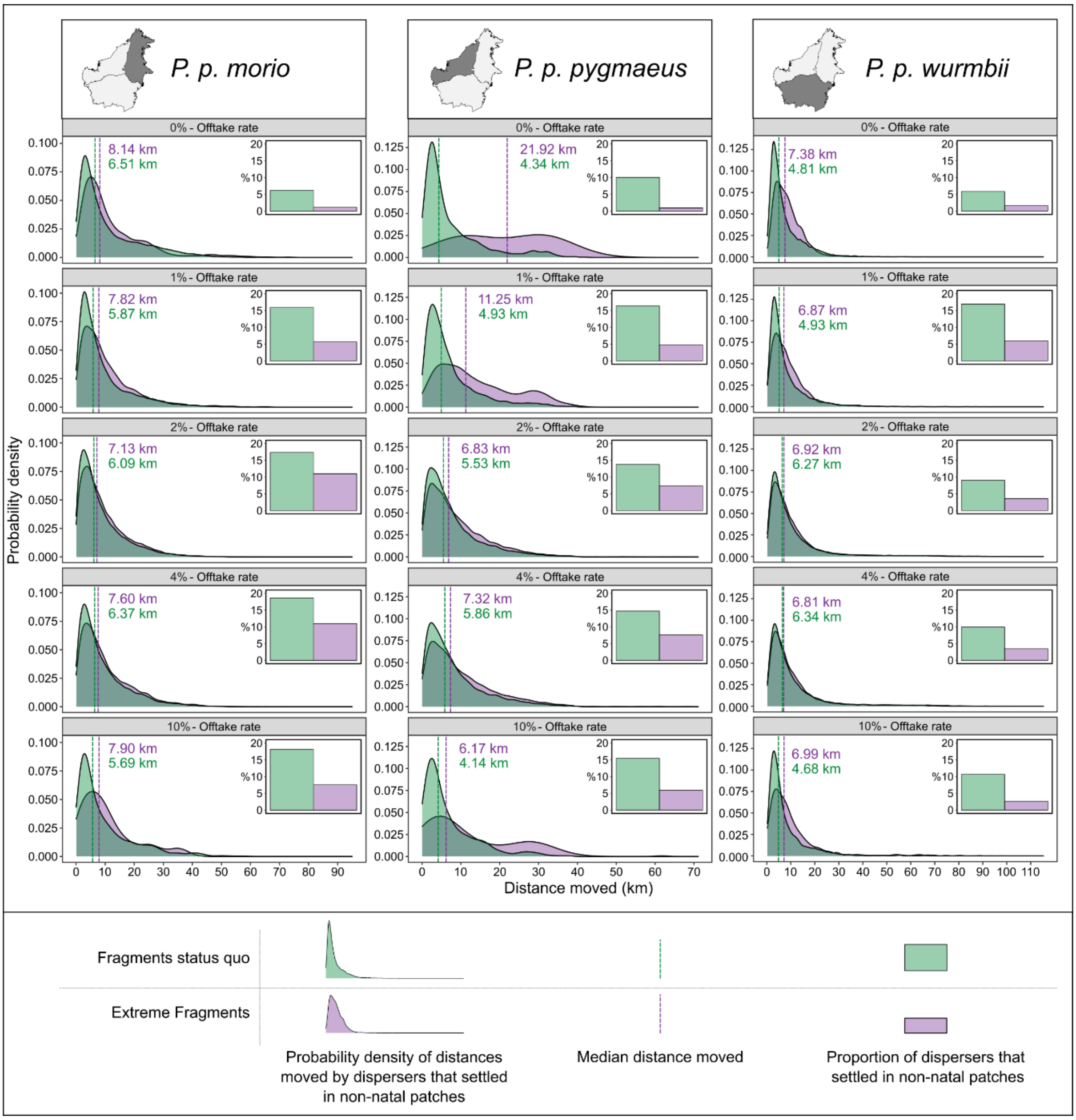

Figure 5-4: Dispersal distance and success.
The probability density plots show the distribution of distances taken by successful dispersers (individuals that have settled in non-natal patches) for each subspecies. Distances are summarised for both landscape scenarios (Fragmentation status quo and Extreme fragmentation) and among offtake rate scenarios ranging from 0% to 10%. The dashed lines denote the median distance travelled. Embedded bar charts show the proportion of dispersing individuals which settled in non-natal patches for the same fragmentation and offtake rate scenarios. We did not plot standard errors as they were to fine to display.

Our sensitivity analysis led to only slight variations in model outcomes for both patch occupancy and final abundance, suggesting our model is relatively robust to permutations in parameter values. 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, the proportion of occupied sites differed by no more than 0.4% or an average of 4.3 patches, with this largest deviation from *P. p. morio* (Figure SI 5.3).

5.5 Discussion

By using high resolution forest maps, density distribution data and an individual based model, we were able to simulate potential outcomes of fragment removal and offtake on orangutan population dynamics and movement. We show that offtake rates of ≤1% are likely to be sustainable in the long term but would lead to a markedly reduced population size. However, our models suggest that offtake rates ≥2%, is likely to be unsustainable over the long term. These results corroborate earlier research by Marshall *et al.*, (2009) who, using a non-spatially explicit modelling approach, similarly showed an offtake rate of 1% was sustainable but that ≥2% would lead to the extinction of orangutan populations.

Our models suggest that in the absence of offtake, orangutan populations are likely to increase in number and expand their range if forest cover is maintained at present-day levels. Although populations grew whether or not fragments were removed from the modelling landscape, the greatest increase in orangutan numbers was experienced when the status quo was maintained (Figure 5.2). Under forest fragmentation status quo, orangutan occupancy was highest in patches outside the initial population distribution than in the extreme fragmentation scenario. This implies that small patches are important at facilitating movement across landscapes, by serving as stepping-stones or corridors, aiding range expansion. This is particularly true for *P. p. wurmbii,* under extreme fragmentation and when there was moderate offtake applied (2% - 4%), a large area remained unoccupied in the Northwest of the distribution, isolating a small population to the Northwest of the range (Figure 5.2). This dependence on small patches is supported by a growing body of literature that suggests in terrestrial systems, area and isolation are weak predictors of patch occupancy, and highlights the importance of small fragments to act as "stepping-stones" in maintaining connectivity across populations (Laurance, 2004; Kool, Moilanen and Treml, 2013; Scriven *et al.*, 2019).

Our results suggest substantial numbers of orangutans are likely to be present in remnant forest patches within human-modified landscapes. Crucially, under the status quo, a higher proportion of dispersing individuals settled in non-natal patches and dispersed over shorter distances. Due to the orangutan's high degree of philopatry (Goossens *et al.*, 2006; van Noordwijk *et al.*, 2012), these shorter dispersal distances allow for more natural behaviours whilst also facilitating movement across the landscape. The longer dispersal distance needed when smaller fragments are removed, would also likely expose dispersing individuals to increased incidences of negative human-orangutan interactions and heightened risk of contact with novel diseases (Russon, 2009).

The difference in dispersal distances between fragment scenarios diminished as offtake rates increased (Figure 5.4). The removal of individuals from the landscape through hunting or rescue, will provide additional opportunities for dispersing individuals to settle in empty or low-density patches, resulting in decreased dispersal distances. If individuals are being lost from the population faster than recruitment from births or emigration, these patches will become populations skins.

Although males can disperse across rivers, they appear to pose a substantial, near total barrier to females (Nietlisbach *et al.*, 2012). This impediment to dispersal may also explain the current distribution of orangutans across Borneo - if extirpated from certain areas, orangutans may be unable to recolonise if rivers pose a substantial barrier to movement. We included rivers as a impermeable barriers within our cost matrix, and similar patterns in distributions emerged from our simulations. For instance, our models imply for *P. p. pygmaeus* rivers will greatly limit the ability for the population to expand outside the current range, agreeing with empirical research (Santika *et al.*, 2017; Voigt *et al.*, 2018). The situation could be more problematic for the *P. p. morio* population, which is highly fragmented and separated into northern and southern units by several large rivers. Without additional management interventions, rivers are likely to impose a substantial barrier the species recovery.

There are currently a large number of orangutans in captive centres in Borneo, and future release sites may be considered for assisted colonisation of new breeding population on opposite sides of major rivers to existing orangutan populations, where female dispersal is unlikely, but populations would remain connected through long distance male dispersal. We note however, that there is limited evidence for the effectiveness of orangutan translocations (Sherman, Ancrenaz and Meijaard, 2020).

Alternatively, rivers may be strategically bridged to allow for wildlife crossings, as has been successfully done in the Kinabatangan flood plain (Ancrenaz *et al.*, 2018). Climate change will be an important consideration in the future of tropical wildlife, and when combined with the effects of expected land-cover change, may lead to a

74% decline in suitable orangutan habitat by 2080 (Struebig *et al.*, 2015). Although we did not model climate change scenarios, our simulations demonstrated that orangutans are able to expand their range and, under current fragmentation levels there is a high proportion of females settling in non-natal patches. Forest to the western side of Sabah is likely to be important orangutan habitat with future climate change (Gregory *et al.*, 2012), small forest fragments will likely then act as microrefugia and aid in facilitating range shifts to these important areas.

A major benefit of our approach compared to other orangutan population viability analysis, is the incorporation of stochastic movement, inter-individual variability and naivety of the landscape within the dispersal process. This approach means not all forest patches have equal probability of receiving emigrants, but instead this is highly influenced by not only their spatial arrangement and the cost of moving through the matrix, but also the stochastic movement of individuals, giving a more realistic reflection of this dynamic process (Palmer, Coulon and Travis, 2011). However, this approach relies heavily on the assumptions used to parametrise the models, which here we based on orangutan behavioural ecology from available data drawn from relatively undisturbed areas. As data becomes available from human-modified landscapes, these models can be refined further, improving their ability to predict population responses to management and land-use change.

Our sensitivity analysis revealed the emigration probability had the largest effect on the model outcome, albeit resulting in only a slight variation. 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 display a high degree of home range fidelity and generally settle close to their mothers home range (Goossens *et al.*, 2006; Ashbury *et al.*, 2020). However, these observations are mostly from areas with very low disturbance. In highly modified 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 and this may impact the emigration process. This sensitivity highlights the importance of increasing our understanding of orangutan behaviour in human-modified landscapes. Increased research focus is thus needed to monitor orangutan movements in human-modified landscapes to improve future models and aid in planning effective management.

Future models could be further improved, through including variation in patterns of spatiotemporal habitat use, driven by seasonal changes in resource use and masting events. A recent longitudinal study of orangutan density in continuous but differing forest types in West Kalimantan, showed orangutans will shift their movement in response to local resource availability (Marshall *et al.*, 2021). Similarly, our assessment does not include other biotic or abiotic factors which may affect orangutan movements, our model could further be advanced with the use of a dynamic landscape which model spatiotemporal changes in environmental conditions, such as temperature or rain fall, which may affect survival and habitat use.

5.6 Conclusion

There is growing recognition in the conservation value of remnant forest in human-modified tropical landscapes for supporting biodiversity (e.g. Lion *et al.*, 2016; Deere *et al.*, 2018). Our research demonstrates the potential importance of small remnant forest fragments in facilitating movement across these areas. This movement will be vital to allow dispersal, ensuring populations remain genetically connected, aid in species recovery and facilitate range shifts in response to future climate change (Årevall *et al.*, 2018; Lino *et al.*, 2019). These positive effects will likely be diminished if removal of individuals from the landscape from hunting, retaliatory killings and rescues are not limited. This will be particularly true for large bodied species with slow life histories, such as the orangutan. For conservation initiatives aimed at retaining and restoring forest areas within human-modified landscapes to be successful, they will therefore also need to address offtake, through promoting tolerance and co-existence with the biodiversity which share these landscapes.

5.7 Supplementary information

5.7.1 Demography and dispersal parameters modifications

Orangutans have a long-life history with several periods of development and varying survival probabilities. To represent this, our meta-population model comprised nine overlapping stages of females only A, which assumes males are always present to fertilize females.

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & \phi_1 & \phi_2 & \phi_3 & 0 \\ \sigma_1 y_1 & \sigma_2(1-y_2) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2 y_2 & \sigma_3(1-y_3) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 y_3 & \sigma_4(1-y_4) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 y_4 & \sigma_5(1-y_5) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma_5 y_5 & \sigma_6(1-y_6) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_6 y_6 & \sigma_7(1-y_7) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \sigma_7 y_7 & \sigma_8(1-y_8) & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_8 y_8 & \sigma_9 \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0.167 & 0.167 & 0.167 & 0 \\ 0.45 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.97 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.99 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.98 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.99 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.99 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.85 & 0.75 \end{pmatrix}$$

here, ϕ is the annual fecundity, y is the probability of developing to the subsequent development stage and σ is the annual survival probability.

We modified two of the default density dependence functions implemented in RangeShifter to better represent orangutan ecology. First, to incorporate a density dependency between young adult and adult stages, we included the exponential function:

$$\gamma_i = \gamma_{0,i} - \, b * \sum_{j=1}^{S} \omega_{ij} \, N_{j,t}$$

where γ_i is the realised development probability of individual *i* developing from stage Young Adult to stage Adult, $\gamma_{0,i}$ is the probability of development when the individuals patch density is low (below the habitat dependent carrying capacity *1/b*), with the strength of density dependence is controlled by *b*. Stages Mature adult, Senior adult and Senescent *S* contribute to the density dependence in development, with ω_{ij} being each individual stages *j* influence. Thus, the cumulative effect of individuals in stages *S* is a weighted sum of all individuals N_t in each stage *j* ($\omega_{ij}N_{j,t}$).

The second modified density dependence function effects fecundity and extends the interbirth period when an individual's patch is close to its density equilibrium, by applying the following function taken from Marshall *et al.*, (2009):

$$\phi_i = \phi_{0,i} * \left(1 - \left(\frac{\sum_{j=1}^{S} \omega_{ij} N_{j,t}}{1/b}\right)^{10}\right) + 0.118 * \left(\frac{\sum_{j=1}^{S} \omega_{ij} N_{j,t}}{1/b}\right)^{10}$$

here ϕ_i denotes the annual fecundity probability of stage *i* and $\phi_{0,i}$ is its maximum fecundity (0.167) when the individual is below carrying capacity, with the strength of the density dependency regulated by *b* (carrying capacity is approximated by *1/b* and is habitat specific: Table 1). The density determined by only individuals in *S* stages Adult, Mature adult, Senior adult and Senescent, where ω_{ij} is the contribution of stage *j*. Again, N_t becomes a weighted sum of the number of individuals *S* in each stage *j* ($\omega_{ij}N_{j,t}$). Lastly, in RangeShifter the number of infants is drawn from a Poisson distribution with mean (ϕ_i); however, for orangutans having >1 infants is rare and in most cases of twin births one offspring will usual die (Goossens *et al.*, 2012). We therefore constrained the number of infants per birth to be no greater than one.

5.7.2 Patch allocation

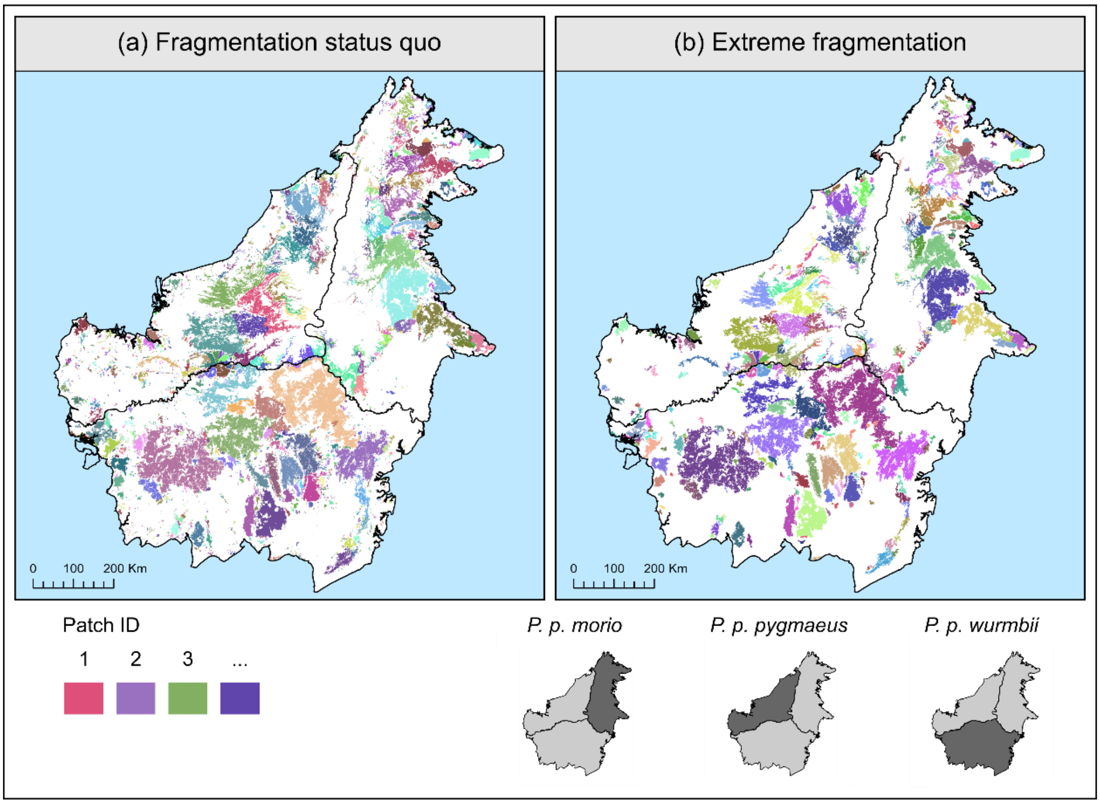

Figure SI 5-1: Suitable patches for each of the three subspecies for both fragmentation scenarios. a) Fragmentation status quo, using the current forest cover and b) extreme fragmentation, when forest fragments <5,000 ha were removed.

We considered any area of natural forest below 500 m above sea level as potential orangutan habitat. This habitat was further delineated and assigned a unique numeric identifier (equating to a unique population within each broader subspecies meta-population; Figure SI 5.1), with the following process. As orangutans regularly move short distances between forest areas in human-modified landscapes and have been observed nesting in oil palms ≤50 m from natural forest (Ancrenaz et al., 2015), we considered patches ≤100 m apart to be part of the same discontinuous patch. Using density estimates averaged across discrete habitat types for each of the three subspecies, we calculated the cumulative maximum number of orangutans each discontinuous patch could support (Miettinen, Shi and Liew, 2016; Voigt et al., 2018). If a patch could support ≥1 orangutan, we assigned it a unique numeric identifier and removed patches which supported <1 orangutan from the patch layer. This process was carried out for each of the three orangutan subspecies and for both fragmentation scenarios. For the Fragmentation status quo scenario, the patch allocation process resulted in a large number of suitable habitat patches (1,077 for *P. p. moro*, 783 *P. p. pygmaeus* and 1,597 for *P. p. wurmbii*). However, the number of suitable patches was greatly reduced for all subspecies in the Extreme fragmentation scenario (129 for *P. p. moro*, 112 for *P. p. pygmaeus* and 123 for *P. p. wurmbii*).

5.7.3 Cost surface

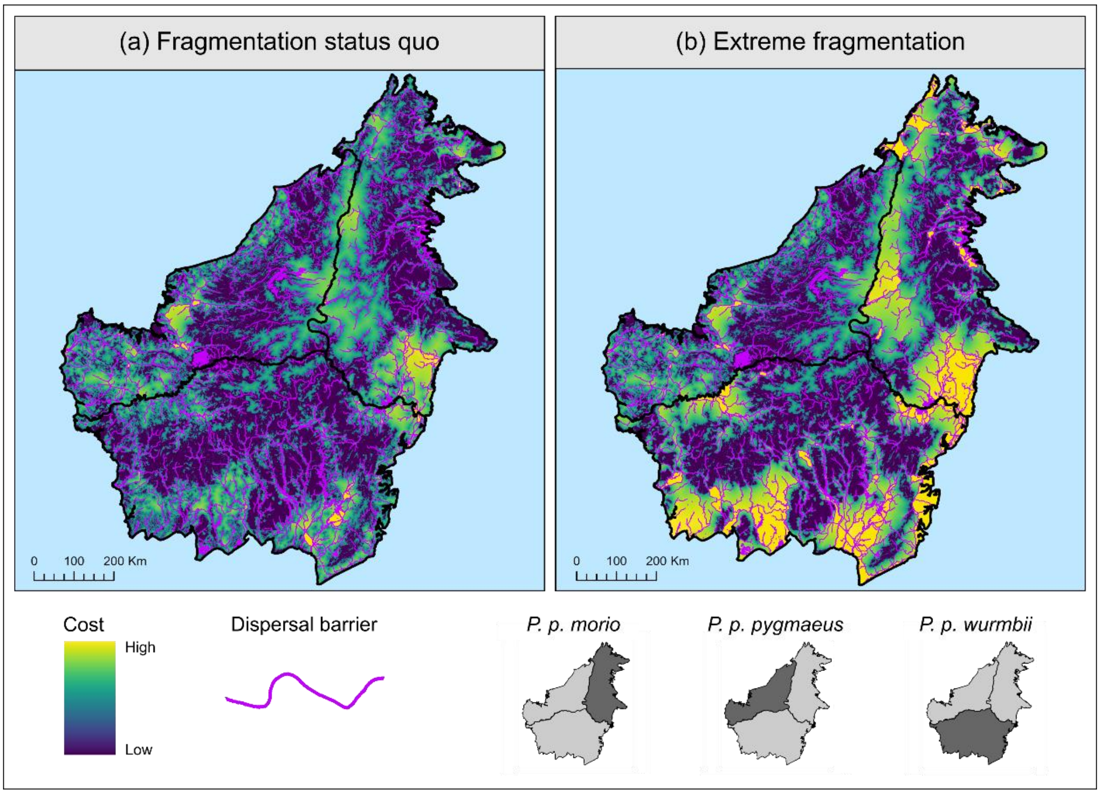

Figure SI 5.2: Cost surface for both landscape scenarios (a) Fragmentation status quo and b) Extreme fragmentation) and each of the three orangutan subspecies.

We produced two cost surfaces for use in RangeShifter 2.0, one for each fragmentation scenario (Figure SI 5.2), using the Distance Accumulation tool in ArcGIS pro (*v*2.6.0; ESRI, 2020) In addition to barriers, the Distance Accumulation tool can incorporate impediments to movement in the form of a “resistance surface”, where each landcover type can have a different resistance or difficulty in moving across. We used expert informed resistance values for each landcover type, which we ranked to provide relative difficulty of moving for each landcover type (Table SI 5.1).

Table SI 5.1 Expert informed resistance values

Expert informed resistance values for each landcover type and ranked resistance values, providing relative difficulty of moving for each landcover type

Landcover type	Expert informed resistance	Ranked resistance
Large scale palm plantation	85	17
Lowland evergreen	5	1
Lowland montane evergreen	25	5
Lowland mosaic	40	8
Lowland open	80	16
Mangrove	75	15
Montane open	90	18
Montane mosaic	50	10
Peat swamp	10	2
Regrowth/plantation	55	11
Upper montane evergreen	50	10
Urban	99	20

5.7.4 Sensitivity analysis

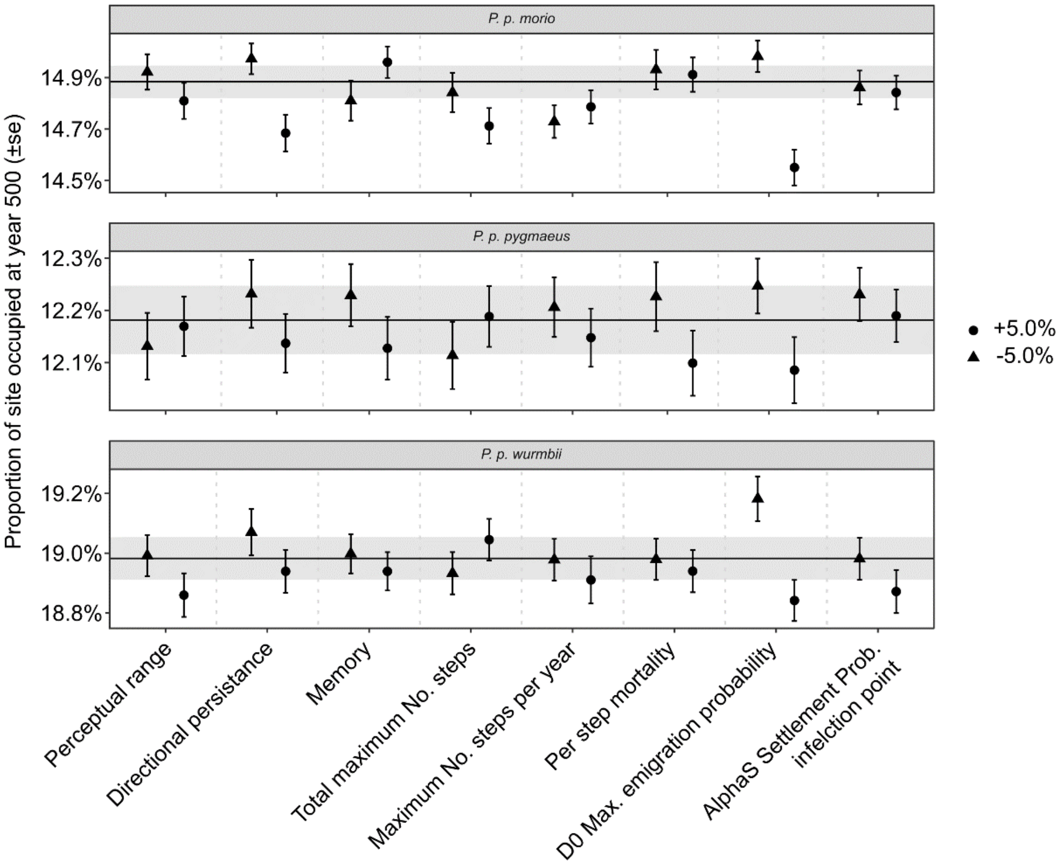

Figure SI 5.3: Sensitivity analysis – proportion of sites occupied.
The values for each parameter tested for sensitivity were varied positively and negatively by 5%, whilst keeping all other values static. The models were run for 500 years over 100 iterations for each subspecies, with points showing the mean value for each parameter permutation and error bars denote one standard error. The solid line shows the mean value for the baseline scenario (Fragmentation status quo and 0% offtake) and shaded area is one standard error.

Table SI 5-2: Summaries of change in female abundance over time. Including results from both fragmentation and offtake scenarios.

				Year 250		Year 500	
Subspecies	Landscape	Offtake rate	Starting population at year (±se)	Mean population (±se)	Mean percentage change (±se)	Mean population (±se)	Mean percentage change (±se)
P. p. morio	Status quo	0.0%	39,773	42,691	7.33%	62,139	56.23%
			(24)	(73)	(0.18)	(424)	(1.06)
	Extreme fragmentation		36,619	38,875	6.16%	54,606	49.12%
			(22)	(63)	(0.17)	(463)	1.27%
P. p. pygmaeus	Status quo		25,660	26,987	5.17%	34,429	(34.17)
			(17)	(48)	(0.19)	(55)	0.21%
	Extreme fragmentation		22,728	23,653	4.07%	30,360	33.58%
			(14)	(47)	(0.21)	(117)	(0.51)
P. p. wurmbii	Status quo		155,478	157,326	1.19%	188,699	21.37%
			(38)	(87)	(0.06)	(1172)	0.75%
	Extreme fragmentation		146,501	147,688	0.81%	169,782	(15.89)
			(41)	(69)	(0.05)	(930)	0.63%
P. p. morio	Status quo	1.0%	39,773	31,066	-21.89%	32,406	-18.52%
			(24)	(29)	(0.07)	(63)	(0.16)
	Extreme fragmentation		36,619	28,648	-21.77%	29,892	-18.38%
			(22)	(28)	(0.08)	(45)	(0.12)

P. p. pygmaeus	Status quo		25,660	19,912	-22.36%	20,617	-19.6%
			(17)	(21)	(0.08)	(45)	(0.18)
	Extreme fragmentation		22,728	17,664	-22.24%	18,274	-19.55%
			(14)	(17)	(0.07)	(36)	(0.16)
P. p. wurmbii	Status quo		155,478	119,985	-22.84%	120,973	-22.21%
			(38)	(45)	(0.03)	(76)	(0.05)
	Extreme fragmentation		146,501	113,460	-22.56%	114,332	-21.97%
			(41)	(46)	(0.03)	(59)	(0.04)
P. p. morio	Status quo	2.0%	39,773	12,062	-69.65%	3,333	-91.61%
			(24)	(27)	(0.07)	(19)	(0.05)
	Extreme fragmentation		36,619	10,989	-69.99%	3,113	-91.5%
			(22)	(23)	(0.06)	(18)	(0.05)
P. p. pygmaeus	Status quo		25,660	7,777	-69.7%	2,211	-91.38%
			(17)	(20)	(0.08)	(14)	(0.06)
	Extreme fragmentation		22,728	6,722	-70.39%	1,838	-91.9%
			(14)	(18)	(0.08)	(13)	(0.06)
P. p. wurmbii	Status quo		155,478	45,462	-70.76%	11,907	-92.34%
			(38)	(52)	(0.03)	(37)	(0.02)
	Extreme fragmentation		146,501	42,748	-70.82%	11,540	-92.12%
			(41)	(57)	(0.04)	(35)	(0.02)
P. p. morio	Status quo	4.0%	39,773	701	-98.24%	3	-99.99%
			(24)	(5)	(0.01)	(0)	(0)
	Extreme fragmentation		36,619	639	-98.25%	3	-99.99%
			(22)	(4)	(0.01)	(0)	(0)

P. p. pygmaeus	Status quo		25,660 (17)	451 (4)	-98.24% (0.01)	3 (1)	-99.99% (0)
	Extreme fragmentation		22,728 (14)	388 (4)	-98.29% (0.02)	3 (1)	-99.99% (0)
P. p. wurmbii	Status quo		155,478 (38)	2,631 (9)	-98.31% (0.01)	6 (0)	<99.99% (0)
	Extreme fragmentation		146,501 (41)	2,487 (9)	-98.3% (0.01)	5 (0)	<99.99% (0)
P. p. morio	Status quo	10.0%	39,773 (24)	1 (0)	-99.99% (0)	0 (-)	-100.00% (-)
	Extreme fragmentation		36,619 (22)	1 (0)	-99.99% (0)	0 (-)	-100.00% (-)
P. p. pygmaeus	Status quo		25,660 (17)	1 (1)	-99.99% (0)	0 (-)	-100.00% (-)
	Extreme fragmentation		22,728 (14)	2 (0)	-99.99% (-)	0 (-)	-100.00% (-)
P. p. wurmbii	Status quo		155,478 (38)	1 (0)	-99.99% (0)	0 (-)	-100.00% (-)
	Extreme fragmentation		146,501 (41)	2 (0)	-99.99% (0)	0 (-)	-100.00% (-)

Table SI 5-3: **Change in area occupied.**

				Year 250			Year 500		
Subspecies	Landscape	Offtake rate	Starting area occupied km^2	Mean area occupied km^2 (±se)	change in area km^2 (±se)	Mean percentage area occupied (±se)	Mean area occupied km^2 (±se)	change in area km^2 (±se)	Mean percentage change in area occupied (±se)
P. p. morio	Status quo	0.0%	24,874	40,522	+15,648	+63%	40,761	+15,886	+64%
				(52)	(52)	(0.21)	(57)	(57)	(0.23)
	Extreme fragmentation		22,261	35,334	+13,073	+59%	35,524	+13,263	+60%
				(96)	(96)	(0.43)	(99)	(99)	(0.44)
P. p. pygmaeus	Status quo		13,231	18,266	+5,036	+38%	18,652	+5,421	+41%
				(11)	(11)	(0.08)	(133)	(133)	(1.01)
	Extreme fragmentation		11,389	16,009	+4,620	+41%	16,026	+4,637	+41%
				(14)	(14)	(0.12)	(21)	(21)	(0.18)
P. p. wurmbii	Status quo		61,792	88,684	+26,892	+44%	89,197	+27,406	+44%
				(357)	(357)	(0.58)	(321)	(321)	(0.52)
	Extreme fragmentation		56,812	79,079	+22,266	+39%	81,649	+24,837	+44%
				(471)	(471)	(0.83)	(511)	(511)	(0.9)
P. p. morio	Status quo	1.0%	24,874	40,616	+15,741	+63%	40,826	+15,951	+64%
				(47)	(47)	(0.19)	(51)	(51)	(0.2)
	Extreme fragmentation		22,261	35,440	+13,179	+59%	35,740	+13,479	+61%
				(94)	(94)	(0.42)	(36)	(36)	(0.16)

P. p. pygmaeus	Status quo		13,231	18,172 (45)	+4,941 (45)	+37% (0.34)	18,344 (103)	+5,114 (103)	+39% (0.78)
	Extreme fragmentation		11,389	15,962 (33)	+4,572 (33)	+40% (0.29)	16,031 (8)	+4,641 (8)	+41% (0.07)
P. p. wurmbii	Status quo		61,792	88,859 (272)	+27,067 (272)	+44% (0.44)	89,124 (183)	+27,333 (183)	+44% (0.3)
	Extreme fragmentation		56,812	78,198 (382)	+21,386 (382)	+38% (0.67)	80,602 (190)	+23,790 (190)	+42% (0.34)
P. p. morio	Status quo	2.0%	24,874	41,329 (33)	+16,455 (33)	+66% (0.13)	39,496 (53)	+14,621 (53)	+59% (0.21)
	Extreme fragmentation		22,261	36,011 (20)	+13,750 (20)	+62% (0.09)	35,379 (37)	+13,117 (37)	+59% (0.16)
P. p. pygmaeus	Status quo		13,231	18,327 (6)	+5,097 (6)	+39% (0.05)	17,702 (12)	+4,472 (12)	+34% (0.09)
	Extreme fragmentation		11,389	16,063 (4)	+4,673 (4)	+41% (0.04)	15,912 (12)	+4,523 (12)	+40% (0.11)
P. p. wurmbii	Status quo		61,792	90,012 (18)	+28,220 (18)	+46% (0.03)	87,751 (252)	+25,959 (252)	+42% (0.41)
	Extreme fragmentation		56,812	79,380 (66)	+22,567 (66)	+40% (0.12)	78,797 (167)	+21,984 (167)	+39% (0.29)
P. p. morio	Status quo	4.0%	24,874	36,182 (275)	+11,308 (275)	+45% (1.11)	1,926 (226)	-22,948 (226)	-92% (0.91)
	Extreme fragmentation		22,261	32,899 (254)	+10,638 (254)	+48% (1.14)	1,721 (228)	-20,540 (228)	-92% (1.02)
P. p. pygmaeus	Status quo		13,231	16,786	+3,555	+27%	3,978	-9,253	-70%

				(77)	(77)	(0.58)	(615)	(615)	(4.65)
	Extreme fragmentation		11,389	15,069	+3,679	+32%	3,678	-7,712	-68%
				(97)	(97)	(0.86)	(536)	(536)	(4.71)
P. p. wurmbii	Status quo		61,792	81,724	+19,932	+32%	13,977	-47,815	-77%
				(656)	(656)	(1.06)	(1,047)	(1,047)	(1.69)
	Extreme fragmentation		56,812	76,594	+19,782	+35%	11,868	-44,945	-79%
				(334)	(334)	(0.59)	(937)	(937)	(1.65)
P. p. morio	Status quo	10.0%	24,874	2,337	-22,538	-91%	0	0	-100%
				(130)	(130)	(0.52)	(-)	(-)	(-)
	Extreme fragmentation		22,261	664	-21,597	-97%	0	0	-100%
				(491)	(491)	(2.21)	(-)	(-)	(-)
P. p. pygmaeus	Status quo		13,231	3,573	-9,658	-73%	0	0	-100%
				(3,260)	(3,260)	(24.64)	(-)	(-)	(-)
	Extreme fragmentation		11,389	5,925	-5,464	-48%	0	0	-100%
				(-)	(-)	(-)	(-)	(-)	(-)
P. p. wurmbii	Status quo		61,792	15,136	-46,656	-76%	0	0	-100%
				(1,180)	(1,180)	(1.91)	(-)	(-)	(-)
	Extreme fragmentation		56,812	12,800	-44,012	-77%	0	0	-100%
				(1,158)	(1,158)	(2.04)	(-)	(-)	(-)

Chapter 6 General discussion

In this thesis I explore how Bornean orangutans persist in human-modified landscapes, with the aim to increase our knowledge of this understudied subject and help guide management interventions and further applied conservation research. As large amounts of orangutan habitat has undergone some degree of disturbance and degradation, orangutan conservation initiatives within human-modified landscapes are essential to ensure positive outcomes for the species (Santika, Ancrenaz, *et al.*, 2017; Spehar *et al.*, 2018; Voigt *et al.*, 2018). A major impediment to establishing these conservation initiatives is a substantial lack of information on orangutan habitat use and movement within these landscapes (Ancrenaz *et al.*, 2021) and thus, the research I present here provides valuable scientific knowledge. In **Chapter 2,** I used nest count data from across a disturbance gradient in Sabah to produce density estimates and explore links between orangutan abundance and environmental and anthropogenic covariates.

With habitat loss and fragmentation being a major conservation concern to the species, the lack of data, particularly on abundance but also information on movement, creates challenges in understanding how Bornean orangutans might be using these landscapes. To begin to understand this, in **Chapter 3** I modelled population dynamics and connectivity at the landscape scale and applied a scenario analysis to explore the impact of environmental policies on the viability of the population. In **Chapter 4**, I integrated my nest count data with orangutan bycatch from camera trap surveys, showing the potential for this method to be applied to fine scale assessments, but also some limitations in agricultural landscapes. Finally, in

Chapter 5, I expanded the individual-based modelling approach applied in Chapter 3 to the entire species range over Borneo, explicitly considering the role of fragments and hunting in population connectivity and dynamics.

6.1 Contribution to the field

Although there is anecdotal evidence and a small number of publications suggesting orangutans can persist in human-modified landscapes (Meijaard *et al.*, 2010; Ancrenaz *et al.*, 2015; Spehar and Rayadin, 2017; Milne *et al.*, 2021), there are relatively few published data and abundance estimates in these habitats, particularly from oil palm plantations (Voigt *et al.*, 2018). In **Chapter 2,** I provide, to the best of my knowledge, the first published orangutan density estimates from remnant forest in oil palm landscapes in Sabah and link density estimates to anthropogenic covariates and forest structural metrics derived from LiDAR. Contrary to previous research by Davies *et al.*, (2017) who found orangutans prefer to nest in uniform forest canopies, I showed that orangutan density was positively associated with variation in tree canopy height in highly disturbed forest and demonstrated no discernible effect of isolation, differing to Spehar and Rayadin, (2017). These contradictory results are likely due to differences in landscapes and disturbance histories, with Davies *et al.*, (2017) research originating in heavily disturbed but relatively large continuous blocks of forest and Spehar and Rayadin, (2017) from acacia and eucalyptus plantations. The subsequent paper from **Chapter 1** complements existing research from heavily degraded landscapes, demonstrating the resilience of orangutans to habitat disturbance, provided some natural forest remains over a landscape. These results, therefore, provide valuable data on the persistence of orangutans in oil palm plantations and highlights the need for increased research focus on these landscapes, to expand our understanding and ability to produce robust management recommendations.

For **Chapters 3** and **5**, I collaborated with researchers from the University of Aberdeen to modify the RangeShifter individual-based population modelling platform, in order to better represent orangutan population dynamics than the base version. Utilising RangeShifter provides several advantages over existing Population Viability Analysis (PVA) software. For instance, the orangutan Population and Habitat Viability Analysis (PHVA; Utami-Atmoko et al., 2019), which informs government policies on orangutan conservation, uses the PVA tool Vortex. Vortex uses averaged parameter inputs on, among other things, survival, reproduction and emigration, which can vary in time, but not spatially. Conversely the individual-based modelling approach utilised by RangeShifter allows for two major advantages; inter-individual variation among parameters and spatially-explicit individual-based stochastic movement (Palmer, Coulon and Travis, 2011; Bocedi et al., 2021). Combined and run over multiple iterations, these advances produce probabilistic outcomes which may align more closely with reality, particularly in cases such as ours where individual are naive to the landscape (Aben et al., 2016).

Understanding how orangutans can utilise forest remnants in oil palm landscapes will be vital to effectively manage these areas for the species. In **Chapter 4**, I apply the modified RangeShifter model to four potential landscape management scenarios for an oil palm landscape in Sabah, Borneo. One of these management scenarios uses the High Carbon Stock (HCS) approach. This approach has been incorporated into the Roundtable on Sustainable Oil Palm (RSPO) but has received very little research into its effectiveness at facilitating connectivity, despite this being one of its key objectives (Rosoman *et al.*, 2017; Scriven *et al.*, 2019). This chapter demonstrated that maximising forest cover, through the HCS methodology, has the potential to support orangutan populations in excess of an oil palm plantations rotation period (25 – 30 years: Rahman *et al.*, 2018) and may facilitate movement among large protected areas. This is in keeping with multiple datasets collated from several oil palm landscapes, which found female orangutans are commonly present and reproduce in remnant oil palm plantations for up to 20 years (the maximum research period reported) (Ancrenaz *et al.*, 2021). Through publishing these results, I provide early evidence that the HCS approach has the potential to offer tangible benefits for orangutan populations.

Integrative modelling, although well established in statistics, is a rapidly evolving field in ecology (Zipkin, Inouye and Beissinger, 2019) and has the potential to maximise the information that can be drawn from field data (Miller *et al.,* 2019). In **Chapter 4,** I collaborated with Dr Diana Bowler [German Centre for Integrative Biodiversity Research (iDiv)], who has pioneered integrative modelling approaches to investigate fine-scale drivers of species habitat use (Bowler *et al.*, 2019). In this chapter, I integrated targeted nest count data and non-targeted orangutan data, using bycatch from camera traps. Data integration has been applied to investigate orangutan population trends across Borneo, using various data sets targeted at orangutans (Santika, Ancrenaz, *et al.*, 2017; Santika *et al.*, 2019). Although there is relatively little targeted orangutan sampling in human-modified landscapes, there are existing data sets, such as from camera traps (Spencer *et al.*, unpublished data), which have the potential to augment targeted orangutan data, through the use of integrated modelling. Here, I highlight how different ecological processes (terrestrial habitat use vs nesting behaviour) which the data result from, will need to be fully considered, to effectively integrate data and highlight how models with spatially correlated random effects may best be suited to this in future applications.

Increasing evidence indicates small forest fragments are likely to play an important role in maintaining orangutan populations and facilitating movement between meta-populations (Gregory *et al.*, 2014; Ancrenaz *et al.*, 2021). Despite this, range wide population viability assessments do not take these remnant forest areas into account when delineating sub-populations (Utami-Atmoko *et al.*, 2019). In **Chapter 5**, I applied the modified RangeShifter individual-based model to simulate orangutan habitat use across Borneo. As well as investigating how the removal of fragments affects large-scale population connectivity and viability, I used an additional model component (RangeShifter Contain) to simulate how offtake rates, i.e. the killing or removal of individual orangutans from the population, also affect population dynamics and dispersal. Our models suggest that without pressure from hunting, persecutions or translocations, these landscapes should be able to support orangutan populations in the long-term (over ca. 40 generations). However, even with moderate offtake (>2%), orangutan population suffer substantial declines, reducing their long-tern viability. This research not only corroborates existing studies, which highlight the vulnerability of orangutan populations to even small amounts of offtake (Marshall *et al.*, 2009; Utami-Atmoko *et al.*, 2019) but also makes a substantial advance in modelling orangutan population viability, through including inter-individual variability and spatially explicit dispersal.

6.2 Recommendations for future research

The lack of research in human-modified landscapes makes understanding and managing orangutans in these areas extremely challenging. Some of this difficulty stems from limitations with the traditional way orangutan surveys are conducted. Orangutan abundance estimates are derived from nest density; however, it has been shown in multiple publications that nest decay rates (one of the parameters used to convert nest density to orangutan density) can vary considerably and can generate significant difference in population abundance and density estimates (Mathewson *et al.*, 2008; Marshall and Meijaard, 2009). Nest decay rates are difficult to approximate, especially with the differing environmental condition in oil palm landscapes such as, temperatures or tree species community composition (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004). Nest decay rates can therefore deviate significantly across localities and necessitate consequently more realistic estimates within specific landscapes.

Alternatively, researchers in these areas could use different survey methods, such as repeat surveys and calculate a more robust “new nest production rate” as an alternative to decay rate (Spehar *et al.*, 2010). Nevertheless, this is no silver bullet as this approach also has drawbacks, requiring multiple surveys of each transect and may be biased by seasonal variation in orangutan movement (Marshall and Meijaard, 2009; Marshall *et al.*, 2021). The use of camera traps and direct observations, either from field observations or derived from interviews with farmers and plantation workers, are also alternative data sources for monitoring orangutans in these areas. The use of integrative models (such as those introduced in **Chapter 4**) within these landscapes, if coupled with additional methods to minimise nest decay rate bias, such as using tree species community composition and rain fall to apply correction coefficients to decay rates (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004), has the potential for expanding our knowledge in these landscapes. Although there may be questions on the validity of abundance estimates derived from this methods until additional research is done, using this approach may provide a powerful tool for investigating population trends in these areas (Santika *et al.*, 2019).

For conservation initiatives to be successful in human-modified landscapes, promoting and maintaining functional connectivity will be vital. In **Chapters 3 and 5** I used information on orangutan dispersal from relatively undisturbed areas (e.g. Nietlisbach *et al.*, 2012; van Noordwijk *et al.*, 2018). However one could assume, knowing the high behavioural plasticity of the species (Delgado and Van Schaik, 2000), that individuals may respond differently in these landscapes when faced with limited options for settling close to the mother’s home range. For instance, if female orangutans are more inclined to disperse in heavily disturbed areas, this may have led to an underestimation in the ability of corridors and stepping-stones in aiding movement across landscapes. The research I present in **Chapters 3 and 5** begin to shed light on these processes, but also highlight several research areas for future development of this modelling application:

First, for orangutans, increasing our knowledge of their movement poses several challenges, both logistical and ethical perspectives. Habituating orangutans is highly time consuming and in human-modified landscapes may exacerbate negative human-orangutan interactions. Although there is rapid growth in species tracking technology (McGowan *et al.*, 2017), from an ethical perspective some may question whether it is appropriate to anaesthetise individual orangutans purely to attach a tracking device, and especially when they may already be highly stressed from persecution and capture. Moving forward, there should be an increased emphasis on improving and implementing post-release monitoring of orangutans, as animals are regularly anaesthetised during rescue and translocation from oil palm plantations (Rayadin and Spehar, 2015; Sherman, Ancrenaz and Meijaard, 2020). Tracking released individuals will not only be vital to assess the success of translocations but in turn, provide movement data which can help further refine models such as those presented in **Chapters 3 and 5**. Secondly, non-invasive genetic analysis has been underutilised in the study of orangutan movement to date. Orangutan faeces and hairs, which can be collected from nests, can provide sources of non-invasive genetic data (Goossens *et al.*, 2005). These data can then be used to assess patterns of gene flow and drift, and hence infer population connectivity, which in turn can be used to validate spatial modelling and assess the success of conservation initiatives aimed at promoting connectivity. Advancing this research further is vital, as insights into patterns of movement of orangutans in anthropogenic landscapes is crucially important to enhance models and improve their ability to forecast outcomes of management and environmental scenarios.

6.3 Limitations, caveats, and way forward

A key finding of this thesis is that, although at reduced densities, orangutans are frequently observed in oil palm plantations. While these results from **Chapters 2** and **4** are consistent with previous research from plantations elsewhere on Borneo (Meijaard *et al.*, 2010; Ancrenaz *et al.*, 2015; Spehar and Rayadin, 2017; Milne *et al.*, 2021) and anecdotal evidence from researchers working in other oil palm landscapes (Ancrenaz *et al.*, 2021), caution needs to be taken when interpreting our findings. For instance, the case-study landscape I utilised – in Tawau district, - borders a large (ca. 1 million ha) contiguous block of protected forest, which has a large and stable orangutan population (Ancrenaz *et al.*, 2004, 2010; Simon, Davies and Ancrenaz, 2019). There may, therefore, be a degree of spillover of individuals into the plantations and equally, the recent disturbance may have displaced individuals. Combined, this may have inflated the occurrence and density estimates of orangutans in the landscape at the time of the study.

Additionally, Marshall *et al.*, (2021) found that over 99 consecutive months of surveying, orangutans moved across their study site characterised by continuous but differing forest types in West Kalimantan, Indonesia, tracking forest fruiting phenology. This synchronised movement suggests orangutans may utilise forest remnants in human dominated landscapes at times of high fruit availability, but that the same remnants may be less able to support individuals at times of low resource availability. Anecdotally, camera traps deployed by Deere *et al.*, (2018), captured a female orangutan with a very young offspring in a riparian forest remnant in mature oil palm, to the west of my study landscape. Two years after this camera trap study, I also observed a female orangutan with a dependant offspring of a consistent age in the same remnant, implying that these may well have been the same animals. Although we could not confirm this with certainty, it does hint that this may be a resident female within the oil palm plantation.

Orangutans are a classic “flagship species”, being large, charismatic and able to attract large sums of conservation funding each year (Morgans *et al.*, 2018; Santika, Sherman, *et al.*, 2021). With emphasis now on creating multi-functional landscapes in which humans and orangutans can co-exist (Spehar *et al.*, 2018), an additional argument could be made for orangutans being used as “umbrella species” and thus, protecting orangutans will, in turn lead to positive conservation outcomes for the wider biodiversity. There is precedent for this, for example 96% of protected areas created for giant pandas *(Ailuropoda melanoleuca)*, another large and charismatic mammal, also include at least one highly threatened endemic bird, mammal and amphibian species (Li and Pimm, 2016). However, caution will need to be taken if orangutan conservation is to be heralded as a panacea. No two species are equal, and the importance of small forest patches and riparian reserves are likely to differ greatly among taxa. For instance, a recent meta-analysis demonstrated that although increasing riparian reserve width was beneficial for most taxa in an oil palm landscape in Sabah, there was substantial variation in the degree to which species utilise these areas among birds, mammals, herptiles and invertebrates (Deere *et al*., In Press). Equally, Vanthomme *et al*., (2019) modelled movement behaviour for African forest elephants (*Loxodonta cyclotis*), forest buffalos (*Syncerus caffer nanus*), western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) between protected areas in Gabon. All four are considered umbrella species, however the authors found limited overlap in corridor use among the species. Conservation initiatives, such as reforesting patches to increase their core areas at the expense of smaller but more mature patches may have positive conservation outcomes for edge intolerant species. Conversely, for species which require tree cavities for nesting and roosting, such as hornbills or numerous bat species, there may be a negative effect without additional mitigation (e.g. the installation of nest boxes; Kaur *et al*., 2020). On the other hand, if remnant forest fragments are maintained and strict protection limits hunting activities, there may well be highly positive conservation outcomes for other species. Researching the effects of orangutan conservation measures, such as those recommended in this thesis and currently being undertaken by Pongo Alliance, on the wider biodiversity, could add additional justification for such conservation activities.

6.4 Conservation and policy implications

With the increasing need for agricultural production, further investment, and expansion of globally important crops is inevitable. This growth will be particularly true for tropical vegetable oils, such as oil palm, soya, maze and coconut (Meijaard *et al.*, 2020). In a bid to prevent further forest loss associated with agricultural expansion, tools such as the RSPO and the HCS approach have been established to prioritise forest for conservation. In addition, social corporate responsibility is increasing the number of producers making zero-deforestation commitments (Garrett *et al.*, 2019). Whilst zero-deforestation pledges are aimed at preventing further loss of intact forest, loss and degradation of already disturbed forest is likely to continue. Whilst the potential conservation value of degraded tropical forests has long been recognised (e.g. Bicknell and Peres, 2010; Edwards *et al.*, 2011), it has only been relatively recently that these areas are being included into policy, aimed at reducing biodiversity loss, such as the HCS approach. Throughout this thesis, I highlight the importance of these areas of degraded forest within oil palm estates for orangutans, showing orangutans can be found in remnant forest across oil palm landscapes and that these areas have the potential to facilitate connectivity. Yet, orangutans are only one species in a highly diverse community. Attention and funding for orangutan conservation is higher in comparison to most other species (Santika, Sherman, *et al.*, 2021), and if orangutans can be used as a driving force to implement policy changes, the wider species community may benefit. However, these wider positive outcomes will only be achieved if additional actions are taken to prevent species loss. For instance, hunting of wildlife for consumption is widespread across the tropics (Azhar *et al.*, 2013) and has caused substantial loss of species and is likely to be prevalent across agricultural landscapes where access to remnant forests is comparatively easy (Deere *et al.*, 2019).

Even with the prioritisation and conservation of forest in agricultural landscapes, the inevitable forest loss and fragmentation associated with agricultural expansion will still pose a substantial threat to species through increasing isolation. Therefore, as well as forest protection, an equally important conservation focus is maximising connectivity. The HCS approach thus explicitly includes connectivity among its aims to maintain landscape-level ecosystems (HCV 2) (Rosoman *et al.*, 2017). In **Chapters 3** and **5**, I demonstrate the potential for the HCS approach to facilitate connectivity both at the local and macro scales. Despite this, a limitation remains that the HCS approach identifies conservation set asides in relation to connectivity through proximity-based parameters, such as inter-patch distance, but does not provide a comprehensive framework for improving connectivity through forest restoration. However, for Borneo, forest cover and quality within plantations will need to increase, if connectivity and biodiversity targets are to be met (Scriven *et al.*, 2019). Although orangutans, particularly males, are likely to be willing to move across relatively large areas of monoculture (Ancrenaz *et al.*, 2015), our simulation suggest dispersing individuals are more likely to closely follow areas of natural forest, which is also supported by anecdotal field observations (Ancrenaz *et al.*, 2021). This dependence on natural forest will be exacerbated for more forest dependant species who are likely to be less willing to cross large forest gaps. The

HCS protocol could therefore be further enhanced by also incorporating a methodology for increasing the matrix permeability, through identifying areas for restoration, as well as protection.

A common theme throughout this thesis is the paucity of data regarding orangutans within human-modified landscapes. Surveys of other oil palm landscapes in Borneo and Sumatra, and the establishment of longitudinal research in human-modified landscapes more broadly, is now urgently needed to establish the degree to which remnant forests can alone support orangutan populations. One initiative that is taking the lead on this is Pongo Alliance, which is a conglomerate of businesses, oil palm growers, and NGOs supporting and implementing conservation initiatives within agricultural landscapes in Borneo (https://www.pongoalliance.org/). Projects include supplement planting fruiting trees in forest fragments, aimed at increasing resource availability, as well as planting and restoring forest areas to establish corridors or stepping-stones. Additional research from these areas can then further aid in informing these initiatives and provide evidence which can be used to lobby for additional uptake of sustainability certification such as the RSPO.

Within the current scientific literature on connectivity, there is a strong bias towards Europe and North America (Carroll *et al.*, 2015). Published studies from tropical regions tend to use methods from circuit or graph theory and do not incorporate population dynamics or have modelled simulated species using generalised parameters. **Chapter 3** was published in the journal Landscape Ecology and provides early evidence of the potential effectiveness of sustainability certification, at maintaining viable populations and increasing functional connectivity. However, we also highlight the paucity of data, even for a well-funded, charismatic species such as orangutans, will limit the use of these models in tropical regions, until more data on species movement are available.

6.5 Conclusion

In this thesis, I undertook both empirical and theoretical approaches to increase our understanding of orangutans within human-modified landscapes. Orangutans are understudied in these landscapes, and I highlight the need for an increased research agenda, particularly in terms of movement behaviour, to further refine models and improve our ability to forecast responses to future management. In addition, I show how existing data may be utilised to increase our understanding of the drivers of orangutan abundance across these landscapes through data integration and provide recommendations for future applications, particularly where differing ecological processes are being modelled. Overall, the results I present add support for the increasing awareness, that remnant forest in human-modified landscapes is of high conservation value for orangutans. However, conservation initiatives, such as promoting sustainability certification standards, will need to go hand-in-hand with additional measures to encourage co-existence and promote tolerance towards orangutans.

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Appendix I Co-authored publications

Here, I provide the titles and abstracts for peer-reviewed journal articles to which I contributed to during the course of my PhD programme and which are supplementary to the research manuscripts present in the main thesis text. These are presented in reverse chronological order and full texts are available online.

Research article: Effectiveness of 20 Years of Conservation Investments in Protecting Orangutans

Current Biology (in review)

Truly Santika, Julie Sherman, Maria Voigt, Marc Ancrenaz, Serge A. Wich, Kerrie A. Wilson, Hugh Possingham, Emily Massingham, **Dave J. I. Seaman,** Alison M, Ashbury, Taufiq Siddiq Azvi, Graham L, Banes, Elizabeth J. Barrow, David F. R. P. Burslem, Robert A, Delgado, Andi Erman, Gabriella Fredriksson, Benoit Goossens, Max Houghton, Tito P. Indrawan, Ricko L. Jaya, Tomoko Kanamori, Cheryl D. Knott, Ashley Leiman, Darmawan Liswanto, Martin Mach, Andrew J. Marshall, Julien G. A. Martin, Lelyana Midora, Adam Miller, Sol Milne, Courtney Morgans, Nardi Nardiyono, Dyah Perwitasari-Farajallah, Dolly Priatna, Robert Risch, Galuh Mochammad Riyadi, Anne E. Russon, Juhardi Sembiring, Endro Setiawan, Mohammad Sidiq, Donna Simon, Stephanie Spehar, Matthew J.Struebig, Ibrahim Sumardi, Albertus Tjiu, Rizki Wahyudi, Achmad Yanuar and Erik Meijaard

Abstract: Using data on the iconic orangutan (Pongo spp.), we developed a novel spatiotemporal framework for evaluating conservation investments. We show that around USD 1 billion was invested between 1999 and 2019 into orangutan conservation by governments, non-governmental organizations, companies and communities. Broken down by allocation to different conservation strategies, we find that habitat protection, patrolling and public outreach had the greatest return-on-investment for maintaining orangutan populations. Given variability in threats, land-use opportunity costs, and baseline remunerations in different regions, there were differential benefits-per-dollar invested across conservation activities and regions. We show, for the first time, that, while challenging from a data and analysis perspective, it is possible to fully understand the relationships between conservation investments and outcomes, and the external factors that influence these outcomes. Such analyses can provide improved guidance towards more effective biodiversity conservation, an increasingly urgent global challenge. Insights into the spatiotemporal interplays between the costs and benefits driving effectiveness can inform decisions about the most suitable orangutan conservation strategies for halting population declines. While our study focuses on the three extant orangutan species of Sumatra and Borneo, our findings have broad application for evidence-based conservation science and practice.

Research article: Disease Risk and Conservation Implications of Orangutan Translocations

Frontiers in Veterinary Science (2021)

Julie Sherman, Steve Unwin, Dominic A. Travis, Felicity Oram, Serge A. Wich, Ricko L. Jaya, Maria Voigt, Truly Santika, Emily Massingham, **Dave J. I. Seaman**, Erik Meijaard and Marc Ancrenaz

Abstract: Critically Endangered orangutans are translocated in several situations: reintroduced into historic range where no wild populations exist, released to reinforce existing wild populations, and wild-to-wild translocated to remove individuals from potentially risky situations. Translocated orangutans exposed to human diseases, including Coronavirus Disease 2019 (COVID-19), pose risks to wild and previously released conspecifics. Wildlife disease risk experts recommended halting great ape translocations during the COVID-19 pandemic to minimize risk of disease transmission to wild populations. We collected data on orangutan releases and associated disease risk management in Indonesia during the COVID-19 pandemic, and developed a problem description for orangutan disease and conservation risks. We identified that at least 15 rehabilitated ex-captive and 27 wild captured orangutans were released during the study period. Identified disease risks included several wild-to-wild translocated orangutans in direct contact or proximity to humans without protective equipment, and formerly captive rehabilitated orangutans that have had long periods of contact and potential exposure to human diseases. While translocation practitioners typically employ mitigation measures to decrease disease transmission likelihood, these measures cannot eliminate all risk, and are not consistently applied. COVID-19 and other diseases of human origin can be transmitted to orangutans, which could have catastrophic impacts on wild orangutans, other susceptible fauna, and humans should disease transmission occur. We recommend stakeholders conduct a Disease Risk Analysis for orangutan translocation, and improve pathogen surveillance and mitigation measures to decrease the likelihood of potential outbreaks. We also suggest refocusing conservation efforts on alternatives to wild-to-wild translocation including mitigating human-orangutan interactions, enforcing laws and protecting orangutan habitats to conserve orangutans in situ.

Research article: Importance of Small Forest Fragments in Agricultural Landscapes for Maintaining Orangutan Metapopulations

Frontiers in Forests and Global Change (2021)

Marc Ancrenaz, Felicity Oram, Nardiyono Nardiyono, Muhammad Silmi, Marcie E. M. Jopony, Maria Voigt, **Dave J. I. Seaman**, Julie Sherman, Isabelle Lackman, Carl Traeholt, Serge A. Wich, Truly Santika1, Matthew J. Struebig and Erik Meijaard

Abstract: Historically, orangutans (Pongo spp.) lived in large contiguous areas of intact rainforest. Today, they are also found in highly modified and fragmented landscapes dominated by oil palm or industrial timber plantations; a situation that calls for new conservation approaches. Here we report signs of orangutan presence in more than 120 small forest fragments of <500 ha in size and isolated in extensive oil palm plantations across Borneo. We confirmed the long-term presence of adult resident females with dependent young in 42% of the fragments assessed by ground survey (n = 50), and the regular sightings of males traveling across the landscape. We argue that orangutans using and living in small isolated forest patches play an essential part in the metapopulation by maintaining gene flow among larger sub-populations distributed across multiple-use landscapes. In some cases, translocations may be necessary when the animals are in imminent danger of being killed and have no other refuge. However, the impacts of removing animals from spatially dispersed metapopulations could inadvertently decrease critical metapopulation functionality necessary for long-term viability. It is clear that orangutans need natural forest to survive. However, our findings show that forest fragments within agricultural landscapes can also complement conservation areas if they are well-distributed, properly connected and managed, and if orangutan killing is prevented. Efforts to better understand the dynamics and the functionality of an orangutan metapopulation in forest-farmland landscape mosaics characteristic of the Anthropocene are urgently needed to design more efficient conservation strategies for the species across its range.

Research article: Riparian reserves promote insectivorous bat activity in oil palm dominated landscapes

Frontiers in Forests and Global Change (2020)

Mullin, Katherine E., Natalie Yoh, Simon L. Mitchell, Saloni Basrur, **Dave J. I. Seaman**, Henry Bernard, and Matthew J. Struebig

Abstract: The expansion of oil palm agriculture has contributed to biodiversity loss in Southeast Asia and elsewhere in the tropics. Riparian reserves (areas of native forest along waterways) have the potential to maintain forest biodiversity and associated ecological processes within these agricultural landscapes. Using acoustic sampling, we investigated the value of riparian reserves for insectivorous bats in oil palm plantations in Sabah, Malaysian Borneo. We compared general bat activity, foraging activity, and species occupancy between riparian areas in forest and riparian reserves in oil palm plantations. Overall bat activity varied little between riparian reserves in oil palm and riparian forest. Rather, activity was greatest in areas with a high forest canopy, irrespective of how much forest was available within or outside the riparian reserve. Bat foraging activity, as well as the occupancy of two species, was greatest in the forest sites, and while bats were detected in the oil palm riparian reserves, both foraging and occupancy were more associated with topographic ruggedness than forest amount or height. Our results indicate that habitat structure within riparian reserves may be more important than reserve size for supporting insectivorous bat diversity within oil palm landscapes. These findings provide important insights into the extent of the ecological benefits provided by conservation set-asides in forest-agricultural landscapes in the tropics.

Research article: Implications of zero-deforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes

Conservation Letters (2020)

Nicolas J. Deere, Gurutzeta Guillera-Arroita, Philip J. Platts, Simon L. Mitchell, Esther L. Baking, Henry Bernard, Jessica K. Haysom, Glen Reynolds, **Dave J. I. Seaman**, Zoe G. Davies, Matthew J. Struebig

Abstract: Zero-deforestation commitments seek to decouple agricultural production and forest loss to improve prospects for biodiversity. However, the effectiveness of methods designed to meet these commitments is poorly understood. In a highly fragmented tropical landscape dominated by oil palm, we tested the capacity for the High Carbon Stock (HCS) Approach to prioritize forest remnants that sustain mammal diversity. Patches afforded high priority by HCS protocols (100 ha core area) provided important refuges for IUCN-threatened species and megafauna. However, patch-scale HCS area recommendations conserved only 35% of the mammal community. At least 3,000 ha would be required to retain intact mammal assemblages, with nearly 10 times this area needed if hunting pressure was high. While current HCS protocols will safeguard patches capable of sustaining biodiversity, highly fragmented tropical landscapes typical of zero-deforestation pledges will require thinking beyond the patch toward strategically configured forest remnants at the landscape level and enforcing strict controls on hunting.