Promoting resilience and biodiversity in tropical agricultural landscapes

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Abstract

Tropical species are facing multiple environmental pressures, whereby agricultural expansion is causing rainforest loss and climate warming is resulting in range shifts to higher elevations. In Southeast Asia, biodiversity is severely threatened by oil palm expansion and much of the remaining lowland rainforest persists within isolated fragments and protected areas (PAs). I assessed the permeability of oil palm plantations to forest dependent species by examining boundary crossing abilities of fruit-feeding butterflies. I showed that crossing was dominated by species that could potentially breed within oil palm plantations, suggesting that plantations may act as dispersal barriers to forest species. Using the PA network on Borneo as a model system, I examined the spatial distribution of climate within PAs in future, and examined the connectedness of PAs along elevation gradients. For the majority (~60-90%) of PAs, which were predominantly situated at low elevation, analogous climates in future will only be available at higher elevation, requiring species to move in order to track cooler climates. However, over half (~60-82%) of these PAs were too isolated for species with poor dispersal abilities to reach cooler, higher elevation PAs. Finally, I used a novel modelling approach based on electrical circuit theory to identify important areas of rainforest connecting PAs along elevation gradients, and showed considerable spatial overlap in expansion routes under contrasting projections of warming. Protected area extent on Borneo will need to increase by approximately one fifth (~17%) to conserve all important rainforest connections between PAs. I conclude that rainforest species may be particularly vulnerable to the impacts of continued agricultural expansion and climate change, as they may be unable to move across fragmented landscapes due to lack of connecting rainforest habitat. Management to improve linkage of PAs and ensure protection of important dispersal routes along elevation gradients should be a conservation priority.

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Author's declaration

I declare that the work presented in this thesis is my own. This thesis has not been submitted for any other award at this or any other institution.

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Chapter 3

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Chapter 1 – General introduction

Sunrise over the Danum Valley rainforest

1.1. Tropical biodiversity

The term ‘biodiversity’ intends to encompass all of nature’s variety (Begon *et al.* 2006), and was formally defined at the 1992 United Nations Conference on Environment and Development in Rio de Janeiro (Davies & Cadotte 2011; http://www.cbd.int). Since then, the term has been used frequently in the conservation literature to represent a number of levels of ecological complexity, ranging from genetic variation within populations, to species diversity, to community diversity across landscapes and ecosystems (Sala *et al.* 2000, Begon *et al.* 2006, Davies & Cadotte 2011). ‘Biodiversity’ is also used in its simplest form in reference to species richness, which represents the number of species in a given geographical area (Myers *et al.* 2000, Townsend *et al.* 2003). Recent estimates suggest that there are approximately 8.7 million eukaryotic species on Earth (Mora *et al.* 2011), the vast majority of which are undescribed (Stork *et al.* 2015). However, biodiversity is not distributed evenly across the globe, with the highest concentrations found predominantly in tropical regions (Willig *et al.* 2003, Brown 2014).

Within tropical systems, rainforests are areas with particularly high biodiversity (Connell 1978), containing at least half of the Earth’s known species of plants and animals, despite only covering approximately 8% of the land area (Wilson 1989; Park 1992). More specifically, rainforests are thought to contain as many as 80% of all described insect species, more than 60% of all known plant species and around 90% of the world’s primates (Park 1992). Many rainforest ecosystems fall within the world’s ‘biodiversity hotspots’: areas identified as having exceptional concentrations of species richness and endemicity (Myers *et al.* 2000). Rainforests account for 15 of the original 25 biodiversity hotspots identified by Myers *et al.* (2000), with some, including the Tropical Andes, Madagascar and Sundaland, accounting for a disproportionate number of endemic plant and vertebrate species. High concentrations of endemism mean that loss of species through continued environmental change could result in widespread global extinctions and biodiversity losses (Brook *et al.* 2003, Koh & Sodhi 2010, Mittermeier *et al.* 2011).

A number of studies suggest that biodiversity is an important determinant of ecosystem functioning (Biodiversity-Ecosystem Function (BEF) relationship) (e.g. Philpott & Armbrecht 2006, Lefcheck *et al*. 2015, Poorter *et al*. 2015, Gould *et al*. 2016, but see Grime 1997, Eisenhauer *et al*. 2016), and it is often thought to be a key feature that underpins the resilience of ecosystems, i.e. how well an ecosystem absorbs changes in order to maintain its function and structure (Holling 1973, Mori 2016). The definition of 'resilience' as described by Holling (1973) (and subsequently referred to in this thesis) is widely used in the ecological literature and is multidimensional, integrating 'persistence', 'resistance' and the presence of asymptotic stability at multiple equilibria (see Donohue *et al*. 2016 for definitions). Thus, as tropical rainforests are currently under severe pressure from multiple environmental stressors including agricultural expansion (Laurance *et al.* 2014, Newbold *et al.* 2014, 2015) and climate change (Colwell *et al.* 2008, Corlett 2012, Perez *et al.* 2016) (see section 1.2.), maintaining this kind of ecological resilience may allow these systems the capacity to absorb some anthropogenic changes. Hence by conserving rainforest species and the connectivity of their rainforest habitats, the vulnerability of these ecosystems to disturbance may be reduced (Wiens 2016).

1.2. Environmental threats to rainforest biodiversity

1.2.1. Land use change

1.2.1.1. Selective logging

An important driver of land use change in tropical regions is commercial selective logging (Asner *et al.* 2005, Edwards *et al.* 2011a, Edwards *et al.* 2014a, Kleinschroth *et al.* 2016), and it is estimated that over 4 million km^2 of tropical forests globally are within permanent timber estates (Blaser *et al.* 2011). During commercial logging practices, large, profitable trees are removed, leaving smaller ones of low commercial value (Van Gardingen *et al.* 2003). Selective logging changes forest quality and structure (Whitmore 1984, Wilcove *et al.* 2013, Gatti *et al.* 2015), reducing canopy height and cover, and increasing gaps and understory light levels (Okuda *et al.* 2003), which can result in degraded habitats with a high abundance of bamboos and lianas (Edwards *et al.* 2011b). These structural changes can lead to reduced species richness, and changes to species community composition compared with primary forest for a number of taxa (e.g. butterflies: Hamer *et al.* 2003, Dumbrell & Hill 2005, Barlow *et al.* 2007a, 2007b; but see Hill & Hamer 2004, fruit- and insect- eating birds: Burivalova *et al*. 2015; as well as trees and lianas: Okuda *et al*. 2003, Barlow *et al*. 2007a). Hence, logged forests usually contain more light-tolerant ‘gap’ species (Hamer *et al*. 2003), and logging benefits species that are associated with non-forest or disturbed forest habitats (Burivalova *et al.* 2015, Tobias 2015).

Despite reductions in species richness, logged forests can support a large number of species and much functional diversity (Dunn 2004, Peh *et al.* 2005, Edwards *et al.* 2009, Berry *et al.* 2010, Edwards *et al.* 2013, Moura *et al*. 2013, Edwards *et al*. 2014a, Costantini *et al.* 2016). For example, an analysis of multiple taxa by Edwards *et al*. (2011b) in Borneo suggests that more than 75% of primary forest species persist after two rotations of high-intensity selective logging. However, biodiversity differences between logged and primary forests have been shown to vary considerably in relation to geographic region, taxonomic group and ecological metric used (e.g. see Barlow *et al*. 2007a, Gibson *et al*. 2011), and may also be dependent on sampling strategy (e.g. space-for-time (SFT) or before-after control-impact (BACI) experimental approaches; see França *et al*. 2016). Nonetheless, logging is generally much less detrimental for biodiversity than other land uses, such as conversion of rainforest to agricultural plantations (Fitzherbert *et al.* 2008, Turner & Foster 2008, Edwards *et al.* 2010, Moura *et al*. 2013, Laurance *et al.* 2014), where reduction in species richness can exceed 50% (e.g. for reptiles: Gallmetzer & Schulze 2015; and birds: Azhar *et al*. 2011 in oil palm plantations, and for dung beetles in *Eucalyptus* plantations: Gardner *et al*. 2008a). Unprotected selectively logged forests should therefore be a priority for conservation in tropical ecosystems where little primary rainforest remains (Edwards *et al.* 2011b).

1.2.1.2. Agriculture

The expansion and intensification of agriculture in tropical regions to meet rising demands for food, animal feed and fuel are key drivers of biodiversity loss and rainforest degradation (Laurance *et al.* 2014, Milder *et al.* 2015). Between 1980 and 2000, up to 83% of new agricultural lands came at the expense of rainforests (both intact and disturbed) (Gibbs *et al.* 2010), and further forest loss is expected as the amount of land needed for agriculture is set to increase (Laurance *et al.* 2014). One of the key aspects of agricultural intensification is landscape simplification, where previously heterogeneous landscapes contain increasingly fewer non-crop habitats (Landis 2017). The detrimental effects of such intensification on tropical ecosystems can occur directly, by the conversion of natural habitats to croplands and pastures, and indirectly due to the effects of habitat fragmentation (see section 1.2.1.3.), water pollution and invasive species (Brühl & Eltz 2010, Geissen *et al.* 2010, Laurance *et al.* 2014, Milder *et al.* 2015). Conversion of rainforests to agriculture also disrupts a number of important ecosystem services and functions such as water cycle regulation, soil protection and fertility, pollination, pest suppression and carbon storage (Potts *et al.* 2010, Milder *et al.* 2015, Dislich *et al.* 2016, Drescher *et al.* 2016, Milligan *et al.* 2016), many of which are essential for food production and human well-being (Milder *et al.* 2015).

It is widely accepted that conversion of rainforest to agricultural plantations results in the loss of rainforest species (e.g. see Donald 2004, Barlow *et al*. 2007a, Fitzherbert *et al*. 2008, Foster *et al*. 2011, Laurance *et al*. 2014). Such losses can generally be attributed to reductions in habitat heterogeneity, changes in forest structure and altered abiotic conditions and local microclimates (Gallina *et al*. 1996, Aratrakorn *et al.* 2006*,* Gordon *et al.* 2007, Foster *et al*. 2011, Luskin & Potts 2011, Gillespie *et al*. 2012). However, the extent to which rainforest species richness is reduced depends on the agricultural system involved, management strategy, and taxon being studied. For example, low intensity agricultural systems such as shade coffee are capable of supporting much higher levels of biodiversity than more intensive monocultures (e.g. Caudill *et al*. 2015); whilst some crop monocultures (e.g. oil palm plantations) support fewer forest species than other crops (e.g. rubber, acacia, and cocoa: see review by Fitzherbert *et al*. 2008, section 1.4.3. below, and Chapter 2/Scriven *et al*. 2017) for information on oil palm agriculture). Maintaining resilience and biodiversity in tropical landscapes requires an understanding of the responses of forest biota to different agricultural systems, and developing effective conservation strategies for these systems (Laurance *et al.* 2014).

1.2.1.3. Habitat fragmentation

Forest conversion to agriculture and other land uses results in a matrix of modified habitats, containing isolated forest fragments of different shapes and sizes, and that have different amounts of forest disturbance and levels of protection (Curran *et al.* 2004, Sodhi *et al.* 2004, Broadbent *et al.* 2008, Laurance *et al.* 2014). Effects of fragmentation on biodiversity are underpinned by fundamental ecological theories, including the

Equilibrium Theory of Island Biogeography (MacArthur & Wilson 1967) and Species-Area Relationships (SARs) (Preston 1962). These theories predict increased species richness with increasing area, whereby larger, less isolated fragments support more species due to increased colonisation rates and reduced rates of extinction (MacArthur & Wilson 1967). There is a large literature supporting these relationships in tropical fragmentation studies, showing that species richness increases with forest fragment size, but decreases with distance to continuous forest (Brühl *et al.* 2003, Hill & Curran 2003, Benedick *et al.* 2006, Martensen *et al.* 2008, Lucey *et al.* 2014, Almeida-Gomes *et al.* 2016). However, agricultural matrices often differ in their permeability to forest species (e.g. see Aguiar *et al*. 2015), which can affect area and isolation effects (Ewers & Didham 2006). Strategies to improve the permeability of agricultural matrices is a key knowledge gap for many taxa (Koh 2008, Yue *et al*. 2015), and this topic is addressed in Chapter 2, in relation to forest-dependent butterflies within oil palm plantations.

Metapopulation theory (Hanski 1994, 1999) is linked with Island biogeography and focuses on species population dynamics and persistence in fragmented landscapes. Sustaining viable metapopulations is dependent on the ability of individuals to move between habitat fragments, which is affected by their dispersal and colonisation capabilities (Hansson 1991). The size and isolation of habitat fragments affects metapopulation dynamics and landscape connectivity (Hanski 1994, Moilanen & Nieminen 2002), and matrix permeability is also important (Stevens *et al.* 2005) (see Chapter 3 for information on metapopulation dynamics and section 1.3. for details on landscape connectivity). Theories of island biogeography and metapopulation dynamics can be applied to landscape conservation planning and the optimal configuration of reserves (Tjørve 2010), but have given rise to debates, including land sparing versus land sharing (Green *et al*. 2005) and 'SLOSS' ('Single Large Or Several Small' sites; Higgs & Usher 1980) (Fischer *et al.* 2014). In tropical ecosystems, some studies have shown that small fragments have little benefit for biodiversity conservation, and advocate land sparing strategies (i.e. when high intensity agriculture is kept separate from larger areas of natural habitat), as opposed to land sharing strategies (i.e. 'wildlife friendly' approaches combining low intensity agriculture with conservation strategies such as forest corridors and fragments) (Edwards *et al.* 2010, Phalan *et al.* 2011, Lamb *et al.* 2016). However, beta diversity can be higher among rainforest fragments compared with continuous tracts of forest (Benedick *et al.* 2006), and small fragments may act as 'stepping stones' for species moving through fragmented landscapes (Falcy & Estades 2007, Slade *et al.* 2013), potentially facilitating long distance dispersal, range expansion and species persistence (Hodgson *et al.* 2011, Saura *et al.* 2014).

1.2.2. Climate change

The global atmosphere is undergoing a period of rapid anthropogenic change; levels of greenhouse gases such as CO_2 are rising, temperatures are warming and precipitation rates are changing (IPCC 2013). There are many examples of the ecological impacts of climate change on species and ecosystems, which include distribution changes and range shifts to track climate (Parmesan *et al*. 1999, Thomas 2010, Chen *et al*. 2011a, Freeman & Class Freeman 2014, Morueta-Holme *et al*. 2015, Scheffers *et al.* 2016; also see section 1.2.2.3.), as well as changes in phenology (Fitter & Fitter 2002, Parmesan 2006, Butt *et al.* 2015, Green 2017). However, whilst the greatest temperature rises may be at higher latitudes (IPCC 2013), it is anticipated that the most detrimental impacts on biodiversity may occur in the tropics (Bush & Hooghiemstra 2005, Tewksbury *et al.* 2008, Perez *et al.* 2016). This is in part due to rainforest systems containing exceptional concentrations of biodiversity (Myers *et al.* 2000), but also because many tropical species are thought to have narrowly restricted niches in terms of specific moisture requirements, limited elevational/ geographical ranges and specialist food plants/hosts etc. (Bush & Hooghiemstra 2005, Dyer *et al*. 2007, but see Novotny *et al*. 2002). Therefore, small changes in climatic conditions may have deleterious consequences for a large number of tropical species, especially in relation to rising temperatures because many have relatively narrow thermal tolerances (Colwell *et al.* 2008, Deutsch & Tewksbury 2008, Chan *et al.* 2016, Perez *et al.* 2016) (see section 1.2.2.1 below). However, the impacts of climate change on tropical species are complex, and depend not only on the magnitude of environmental change but the specific behaviour, physiology and ecology of different species (Tewksbury *et al.* 2008); impacts are also compounded by the synergistic effects of land use change (Nowakowski *et al*. 2017).

1.2.2.1. Vulnerability of tropical species to rising temperatures

Recent experimental evidence suggests that tropical animals may be particularly vulnerable to rising temperatures due to a limited capacity to acclimate (García-Robledo *et al.* 2016, Gutiérrez-Pesquera *et al.* 2016, Piantoni *et al.* 2016), and because of narrow margins between their upper thermal limits and the thermal environment of their habitats (Huey *et al.* 2009, Llewelyn *et al.* 2016). For example, tropical forest ectotherms show a tendency to thermoconform (i.e. they lack behavioural temperature regulation; Herczeg *et al*. 2003), and so may have limited capacity to cope with warming (Huey *et al.* 2009). Operative temperatures of terrestrial ectotherms (i.e. the 'null' distribution of body temperatures experienced in their microhabitats; see Hertz 1993, Piantoni *et al*. 2016) are determined by a number of interacting factors. These factors include: convection (heat transfer between the body and air), conductance (direct transfer of energy between physical objects), evaporation, metabolic heat, as well as radiation (Harrison *et al.* 2012, Kaspari *et al.* 2015). Hence, if ambient temperatures rise, resulting in operative temperatures exceeding the range of preferred body temperatures (i.e. the target range of body temperatures for a population that would be achieved when the cost of thermoregulation is zero; see Hertz 1993), thermoconformity is likely to reduce the hours of activity and lead to a greater risk of overheating (see Piantoni *et al*. 2016).

Rainforest-dependent species may be especially vulnerable to warming (Huey *et al.* 2009, Kaspari *et al.* 2015, Nowakowski *et al.* 2017) because they persist in conditions where temperatures are relatively constant with little annual or diurnal variation. Increases in temperature could reduce species' thermal performance and fitness if they are unable to adapt or acclimate to changing environments (Colwell *et al.* 2008, Tewksbury *et al.* 2008), and may increase local extinction risk (Sinervo *et al.* 2010, Brusch *et al.* 2016). However, the sensitivity of tropical species to warming is likely to vary across tropical taxa (Pincebourde & Suppo 2016), and some species may be able to adapt to environmental changes (Logan *et al.* 2014). Impacts of increasing temperatures may also be less detrimental for species if they are associated with higher rainfall, although predictions of rainfall changes are uncertain (Hijioka *et al.* 2014). In addition, intact primary forest may thermally buffer the impacts of regional or macrohabitat temperature changes and provide more microhabitats and microclimate refuges for rainforest-dependent species (Scheffers *et al*. 2014a, Scheffers *et al*. 2014b).

1.2.2.2. Vulnerability of tropical species to changing rainfall patterns

The effects of climate change on tropical ecosystems will not solely be through rising temperature, as tropical species are also thought to be highly sensitive to altered precipitation patterns (e.g. see Lewis *et al.* 2005, Condit *et al.* 2013), despite limited empirical evidence in relation to anthropogenic climate change. Increased frequency and severity of extreme droughts during certain seasons are expected as a consequence of climate change (IPCC 2013), and tropical trees may experience water stress if conditions become too hot, or if monthly rainfall falls below 100 mm (Meir & Grace 2005). Water availability manipulations in tropical forests have shown reduced tree growth rates in response to drought (Nepstad *et al.* 2002), and elevated mortality of both seedlings and mature trees has been associated with decreased water availability (Meir & Grace 2005). High temperatures that accompany drought also have consequences for photosynthesis, respiration and stomatal regulation that limit carbon assimilation (Santiago *et al.* 2016). These conditions could be especially detrimental for species residing in regions with a prolonged wet season, i.e., *Dipterocarpus* tree species in Peninsular Thailand, as drought tolerance is limited due to less desiccant tolerant leaves and wood properties (Trisurat *et al.* 2011). In addition, physiological processes of tropical trees have been shown to be sensitive to changing rainfall regimes; for example, the mast fruiting of Dipterocarp trees in Southeast Asia is correlated to drought during El Niño-Southern Oscillation (ENSO) events (Williamson & Ickes 2002). The capacity of these species to fruit is likely controlled by the carbon resources of the individual tree, and so extreme or repeated ENSO events may lead to failure in fruiting. In the long term, sensitivity to changing rainfall patterns may result in changes to the composition of tropical forests globally, and so complete or partial changes in vegetation may be a consequence of shifting climate regimes (Meir & Grace 2005).

El Niño-induced droughts during ENSO events can lead to widespread forest fires and have detrimental effects on both plants and animals (Barlow *et al*. 2003, Hill *et al*. 2003, Cleary & Genner 2004, Cleary & Grill 2004, Fredriksson *et al*. 2007). For example, in Indonesian Borneo following the 1997/98 ENSO event, more than 5 million ha of rainforest burned, which resulted in butterfly species richness declining from 211 species pre-ENSO to just 39 species post-ENSO (Cleary & Grill 2004). In the Brazilian Amazon, droughts during El Niño events also brought about low intensity ground fires that markedly increased the mortality of large trees between 1 and 3 years post-burn (Barlow *et al*. 2003). However, not all detrimental effects of ENSO events are associated with increased drought. For example, following heavy rainfall during the 2010-2012 La Niña, leaf litter frog abundance and diversity in Costa Rica was found to decline up to 12 months after the event, suggesting that excess moisture can also cause ecological cascades that are detrimental for certain species, at least in the short term (Ryan *et al*. 2015). Such findings attest to the sensitivity of rainforest species globally to changing rainfall regimes. Current evidence suggests that ENSO events may be increasing in both severity and frequency (Holmgren *et al*. 2001, Cai *et al*. 2014), but more research is needed globally to determine how rainfall patterns may vary with future climate change, and the subsequent impacts on the distributions of tropical species.

1.2.2.3. Range shifting

Temperature gradients contribute strongly to species distributions (Brown 1984, Merriam 1984), and future distribution shifts and migrations are a likely consequence of anthropogenic climate change (e.g. see Colwell *et al.* 2008, Chen *et al.* 2009, Feeley *et al*. 2011). A relative paucity of studies from low latitude regions means that there is currently limited understanding of how climate change is affecting tropical species (Perez *et al.* 2016), although recent studies show responses of tropical species to rising temperatures (e.g. see Chen *et al*. 2009, Freeman & Class Freeman 2014, Moret *et al*. 2016). Current evidence suggests that tropical species are responding to warming by shifting upslope to higher elevations, and this has been shown for a number of tropical taxa and regions (e.g. see Raxworthy *et al.* 2008, Chen *et al.* 2009, Feeley *et al.* 2011, Freeman & Class Freeman 2014). For example, distributions of 102 montane Geometrid moth species on Borneo shifted upwards by an average of 67 m over a 42 year period (Chen *et al.* 2009); whilst birds on two mountains in Papua New Guinea shifted upslope by an average of 113-152 m over ~40 years (Freeman & Class Freeman 2014) (Figure 1.1.). Current evidence also suggests that upslope shifts by tropical montane species track local temperature increases more closely than do temperate species (Freeman & Class Freeman 2014, but see Rehm 2015). Furthermore, evidence of range shifting is not just limited to insects and birds, but also evident in trees, as shown by Feeley *et al.* (2011) in the tropical Andes.

Current empirical evidence focuses on the impact of rising temperatures on tropical species (e.g. Freeman & Class Freeman 2014), whereas the direction and magnitude of precipitation-induced range shifts are currently unclear (IPCC 2013). Downslope range shifts could be driven by altered precipitation regimes, water balance and seasonality, and unexpected range shifts may be a consequence of complex environmental interactions between these climate parameters (Lenoir *et al.* 2010) and the sensitivities of species to different components of climate (i.e. temperature versus rainfall). For example, plant species in the Eastern Arc Mountains of Africa are predicted to move downslope due to changes in seasonality and water availability, although the direction of shifts are species specific (Platts *et al.* 2013). Changes in precipitation may also affect cloud forest ecosystems, by increasing water stress and fire frequency close to tropical tree lines. This may prevent range shifts of forest species into drier, more seasonal grasslands at higher elevations despite rising temperatures (Rehm & Feeley 2015).

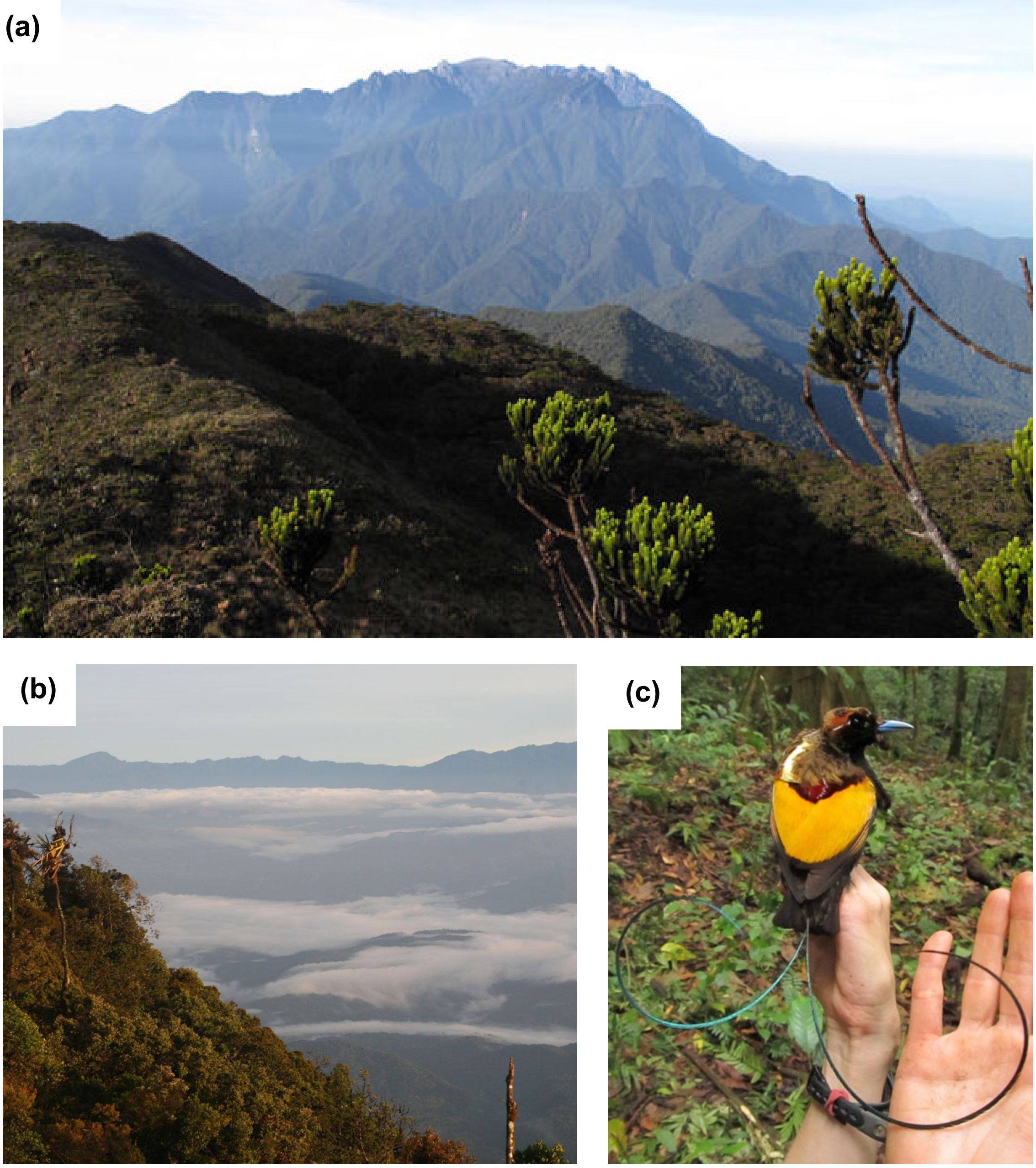

Figure 1.1. (a) Mount Kinabalu in Sabah, Borneo, is a center of endemism, and contains more than 4000 species of vascular plants in an area of only 1200 km^2 (Baeman 2005). Montane Lepidoptera found on this mountain have shifted their distributions upslope in association with climate warming (Chen *et al*. 2009); (b) Mount Karimui in Papua New Guinea, a diverse tropical mountain where bird communities are also shifting their distributions upslope in response to climate change; and (c) *Diphyllodes magnificus*, the Magnificent bird-of-paradise, has shifted its range upslope by more than 100 m on Mount Karimui in recent decades (Diamond 2014, Freeman & Class Freeman 2014). Photographs (b) and (c) are taken directly from Diamond (2014).

1.2.2.4. Threats to montane species and lowland biotic attrition

Tropical mountains contain large numbers of endemic species (Yeates *et al.* 2002, Burwell & Nakamura 2015), and many have extremely narrow elevational distributions (Harris *et al.* 2014). One consequence of montane species shifting to higher elevations to track climate is that range expansions may be constrained by a lack of vegetation due to slow succession on bare rock at high altitudes, as well as reductions in land area (Chen *et al.* 2009). Thus, montane species with distributions near to the tops of mountains may face extinction if they do not also occur on higher mountains elsewhere or at cooler latitudes (Williams *et al.* 2007, Colwell *et al.* 2008, Freeman & Class Freeman 2014). In some locations, upslope movements of montane species may be balanced by colonisations of lower elevation species adapted to warmer climates (Colwell *et al.* 2008), maintaining overall levels of biodiversity. Hence, tropical mountains may provide important climate refugia for lowland species (Chen *et al.* 2009), but only if lowland species are able to track climate via habitat corridors or stepping stone habitats within lowland agricultural landscapes (Colwell *et al.* 2008).

Another important consequence of anthropogenic warming may be 'lowland biotic attrition', i.e. the net loss of species from lowland areas due to upslope range shifts to higher elevations (Colwell *et al.* 2008, Gardner *et al.* 2009). Globally, there are no hotter places than the equatorial low-lying tropics that also maintain relatively constant temperatures during both annual and diurnal timescales (see Park 1992); hence there is unlikely to be a pool of suitably-adapted species able to replace those that shift to higher elevations and vacate lowland areas (Colwell *et al.* 2008). Lowland biotic attrition assumes that lowland species exist near the upper limits of their thermal tolerances, and cannot persist as climate warms (Colwell *et al.* 2008, Burwell & Nakamura 2015). Upper thermal tolerance seems to be have been conserved across many species (e.g. Sunday *et al.* 2011, Grigg & Buckley 2013, Piantoni *et al*. 2016), and so species may be unable to evolve physiological tolerances to rapidly rising temperatures (Araújo *et al.* 2013). However, if the upper thermal tolerances of tropical species are greater than currently thought, persistence of lowland species *in situ* may ameliorate biotic attrition in lowland ecosystems (Feeley & Silman 2010a). In tropical regions, it has been proposed that estimated climatic niches may underestimate fundamental thermal niches (sensu Hutchinson 1957) in many taxa if species' ranges are truncated due to the absence of any higher temperature areas under current climates. Thus, tropical species may be more capable of persisting in lowland areas despite rising temperatures (Feeley & Silman 2010a), but information is lacking.

1.2.2.5. Land use change and range shift gaps

In tropical regions, the impacts of climate change for biodiversity may be particularly severe as they will be projected onto ecosystems whose resilience is already depleted by other human activities (Gardner *et al.* 2009), most notably through deforestation and habitat degradation (Laurance *et al.* 2014). Whilst there are few data on the synergistic effects of climate change and habitat loss on tropical species, current projections for a number of tropical regions suggest that climate change will exacerbate the effects of deforestation for many taxa by reducing the availability of suitable habitat in future (Colwell *et al*. 2008, Brodie *et al.* 2015, Struebig *et al.* 2015a, Struebig *et al.* 2015b, Nowakowski *et al.* 2017), or by changing the location of conservation priority areas (Smith *et al*. 2016). In cases where global climate change might allow species to expand their range, such benefits may be offset by habitat destruction and degradation within their ranges. For species whose current distributions do not overlap with the distribution of suitable conditions in future (i.e. 'range-shift gaps'; see Colwell *et al*. 2008), likelihood of extinction may be exacerbated if areas of connecting habitat have already been converted to agriculture, especially for species with poor dispersal abilities. It is therefore imperative to find ways of maintaining and improving connectivity between remaining areas of rainforest (i.e. protected areas (PAs)) in order to conserve species that are under threat from habitat loss and climate change.

1.3. Maintaining connectivity to provide resilience

1.3.1. Landscape connectivity

Conservation of biodiversity in human-dominated landscapes that face pressure from both land-use and climate change require habitat networks that connect areas of suitable habitat (Rayfield *et al.* 2016). Landscape connectivity, 'the degree to which the landscape facilitates or impedes movements among resource patches' (Taylor *et al.* 1993), allows the movement of species and affects the spatial distribution of ecological and evolutionary processes (Gonzalez *et al.* 2011). Connectivity of local habitat patches allows species to colonise habitat patches and maintain source-sink dynamics, whilst connectivity at landscape scales enables long-distance movements such as climate-induced range expansions (see Rayfield *et al*. 2016). Habitat loss increases the distances between habitat patches (e.g. rainforest fragments) and generally decreases the size of habitat patches. This reduces population sizes, leads to fewer migrants, lowers colonisation success and hence reduces connectivity (Kindlmann & Burel 2008). The composition of the surrounding matrix can influence species dispersal (Ricketts 2001, Jules & Shahani 2003), and landscapes dominated by inhospitable matrices that impede movement have low connectivity (Kindlmann & Burel 2008).

The term 'connectivity' can be divided into two basic definitions: (1) structural connectivity, where connectivity is based on the physical structure of the landscape, and (2) functional connectivity where the behavioural responses of organisms and their dispersal abilities are considered in relation to landscape elements such as habitat patches and edges (see review by Kindlmann & Burel 2008). Functional connectivity may be affected by high mortality risks of organisms temporarily moving into unsuitable habitat in order to reach adjacent habitat patches (Stevens *et al.* 2005, Baguette & Van Dyck 2007, Hadley & Betts 2009); whilst behavioural responses at habitat boundaries may alter emigration rates (Ries & Debinski 2001). Connectivity can be measured in a number of ways, which can include the presence and absence of corridors between habitat patches (Danielson & Hubbard 2000) or the Euclidean distance between patches (Winfree *et al.* 2005) at the most basic level. These are opposed to integrated measures that take into account distance and size of all surrounding habitat patches within a set dispersal distance (e.g. Proctor *et al*. 2011).

Metapopulation ecology focuses specifically on habitat patch connectivity when determining metapopulation persistence (Tischendorf *et al*. 2001), and metapopulation models are frequently used to examine the connectedness of patches in a habitat network (e.g. see Ovaskainen & Hanski 2004, Wilson *et al*. 2009, Hodgson *et al*. 2012). For example, a type of metapopulation model known as IFMs (Incidence Function Models: Hanski 1994, Moilanen & Nieminen 2002) model connectivity based on colonisation and extinction dynamics, taking into account patch size, distance to all surrounding patches, as well as species-specific parameters such as fecundity and dispersal ability (e.g. Hodgson *et al*. 2011; also see Chapter 3/Scriven *et al*. 2015 for details on IFMs). In Chapter 3, I use spatially-explicit IFM simulations to examine the connectedness of PAs on Borneo along elevation gradients, for range shifting species under multiple warming scenarios.

1.3.2. Species movement through fragmented landscapes

The responses of tropical forest species to climate change are projected to depend on their dispersal ability (Anderson *et al.* 2012), and how they move through non-forest habitats in fragmented landscapes (Colwell *et al.* 2008, Gregory *et al.* 2012, Brodie 2016). Many rainforest species are unable to persist in agricultural areas across a number of tropical regions due to lack of breeding habitat or unsuitable microclimates (e.g. dung beetles: Davis & Phillips 2005; mammals: Yue *et al*. 2015; ants: Perfecto & Vandermeer 2002, Brühl & Eltz 2010; birds: Greenberg *et al.* 1997 Edwards *et al*. 2010; and herpetofauna: Gardner *et al*. 2007, Gillespie *et al*. 2012), but there are limited data on the movement of forest species within agricultural areas. Whilst some mobile taxa such as orchid bees in the neotropics move frequently between forest and agricultural plantations (Livingston *et al.* 2013), integrating multiple forest fragments within their foraging ranges (Tonhasca *et al.* 2002), there are few data for other tropical species. There are also limited data on the costs of dispersal through tropical agricultural landscapes for rainforest species, whereby environmental change can dissociate habitat quality from dispersal leading to 'ecological traps' (see Kokko & López-Sepulcre 2016). The presence of an ecological trap in a landscape is generally predicted to drive a local population to extinction (Battin 2004, Kokko & López-Sepulcre 2016); however, few empirical studies show clear evidence of ecological traps and most are limited to a small number of taxa (e.g. birds: Demeyrier *et al.* 2016, Hale & Swearer 2016). If high numbers of rainforest species disperse into unsuitable (i.e. non-forest) habitats and suffer high mortality rates, it is likely that populations may decline, but more research is needed to determine the likelihood of ecological traps in these landscapes.

Some tropical taxa have been shown to 'spillover' from rainforest into adjacent agricultural plantations (e.g. oil palm and coffee) in Southeast Asian and neotropical landscapes, implying they can disperse through non-forest habitats (e.g. butterflies: Lucey

& Hill 2012; ants: Lucey *et al*. 2014, but see Lucey & Hill 2012; dung beetles: Gray *et al*. 2016; and bees: Ricketts *et al*. 2004, Livingston *et al.* 2013), although boundary crossing was not quantified directly. The ability of species to cross habitat boundaries may be an indicator of species' dispersal ability in fragmented landscapes (Kallioniemi *et al.* 2014), and help our understanding of whether agricultural matrices act as barriers to the dispersal of rainforest species. Such information is required to develop effective conservation strategies to promote movement, and more information is needed on boundary crossing behaviour for different species. I address this knowledge gap in Chapter 2 by examining the movement of forest butterflies across rainforest-agricultural plantation boundaries, to determine whether agricultural areas are barriers to the dispersal of rainforest species in fragmented landscapes.

1.3.3. Conservation strategies to maintain connectivity

There is debate surrounding the best strategies for maintaining connectivity in tropical agricultural landscapes, and how to incorporate connectivity criteria into spatial conservation planning (Kool *et al.* 2013, Rayfield *et al.* 2016). Protected areas have been described as the main strongholds of biodiversity in tropical regions (Bruner *et al.* 2001, Curran *et al.* 2004, Hole *et al*. 2009), especially in multifunctional landscapes, i.e. landscapes that simultaneously provide food, livelihood opportunities, biodiversity and the maintenance of ecological functions (O'Farrell & Anderson 2010). In these landscapes tropical species are affected by both continued agricultural expansion and climate warming, and so approaches to assess the connectivity of PAs under multiple climate change and landcover scenarios are needed (see Chapter 3). A number of tropical studies have examined the ability of PAs to support biodiversity under future climate scenarios (e.g. Hole *et al.* 2009 Klorvuttimontara *et al*. 2011, Struebig *et al*. 2015b, Feeley & Silmon 2016), and have assessed the extent to which PAs protect highly-connected forest habitats (e.g. Proctor *et al*. 2011). However, there is limited information addressing the connectivity of PAs for species tracking climate change, or studies that identify the most important areas of remaining unprotected rainforest for conserving current levels of connectivity.

Computational models are becoming increasingly important decision support tools for conservation and have been used to determine ways of improving landscape connectivity under climate change (Hodgson *et al*. 2011, 2012, Brodie *et al*. 2015; also see Chapter 4 for details of software tools that examine connectivity). Such tools offer novel strategies for addressing connectivity of isolated PAs, and provide effective recommendations for focusing limited conservation effort (Hodgson *et al.* 2016). Focusing on Borneo, in Chapter 4 I use a novel modelling approach based on electrical circuit theory and metapopulation dynamics, combined with forest-cover information and climate data, to identify areas of rainforest that form important habitat connections linking PAs for range shifting species.

1.3.4. Butterflies as model species for investigating habitat connectivity

Butterflies have been used to study movement and connectivity in tropical agricultural landscapes (Fermon *et al*. 2003, Benedick *et al.* 2006, Marini-Filho *et al*. 2010, Lucey & Hill 2012, Marchant *et al.* 2015) and elsewhere (e.g. Brückmann *et al*. 2010, Leidner & Haddad 2011, Bergerot *et al*. 2013, Kuussaari *et al*. 2014). Butterflies are relatively mobile and so can often survive as metapopulations in habitat patch networks (e.g. see Hanski 1999). They also have short generation times and so are likely to respond to habitat fragmentation effects more rapidly than longer-lived species (Speight *et al.* 1999). Butterflies are also sensitive to changes in abiotic conditions such as temperature, humidity and light, and so are affected by fragmentation effects (Benedick *et al.* 2006), as well as the impacts of climate change (Parmesan *et al.* 1999, Thomas *et al.* 2006, Chen *et al.* 2011a, Thomas *et al.* 2011). There have been many studies examining butterfly movement in relation to metapopulation dynamics (Ovaskainen & Hanski 2004, Wilson *et al.* 2009, Bennie *et al.* 2013), behaviour at habitat patch edges (Ries & Debinski 2001, Kallioniemi *et al.* 2014, Mair *et al.* 2015) and spillover into adjacent agricultural areas (Lucey & Hill 2012). Whilst data from tropical regions are lacking, butterfly dispersal is still better studied compared with many other tropical taxa (e.g. see Benedick *et al.* 2007a, Marchant *et al.* 2015), and their ecology is relatively well-known (Owen 1971, Hill *et al.* 2001, Hamer *et al.* 2003, Pardonnet *et al.* 2013). Hence, in Chapter 2, I use forest-dependent butterflies as model organisms for field studies examining barriers to movement of forest species in agricultural landscapes. I also use data on forest dependent butterflies to parameterise connectivity and conductivity models in Chapters 3 and 4.

1.4. Southeast Asia as a study region

Southeast Asia harbours four of the world's biodiversity hotspots, including Indo-Burma, Philippines, Sundaland and Wallaceae (Myers *et al.* 2000, Mittermeier *et al.* 2004, 2011) (Fig. 1.2.), and some of the most threatened species on Earth (Sodhi *et al.* 2004, Koh & Sodhi 2010). Sundaland – comprising Malaysia, Singapore, Brunei and Indonesia (Sumatra, Java, Borneo and Palawan), is one of the 'hottest' biodiversity hotspots, supporting more than 15,000 endemic plant and vertebrate taxa (Myers *et al.* 2000). For example, the lowland rainforests of Borneo support more than 10,000 species of plant, higher than all other tropical regions (Kier *et al.* 2005). However, biodiversity within this region is under severe threat due to unprecedented levels of habitat loss, primarily due to industrial-scale agricultural expansion of crops such as oil palm in recent decades (Koh & Sodhi 2010, Miettinen *et al.* 2011, Richards & Friess 2016). On average, there has been an overall 1% yearly decline in rainforest cover within insular Southeast Asia (including Indonesian Papua New Guinea) during 2000-2010, although certain areas of Sundaland including the Eastern lowlands of Sumatra and peatlands of Sarawak (Borneo) have experienced deforestation rates of more than 5% per year (Miettinen *et al.* 2011).

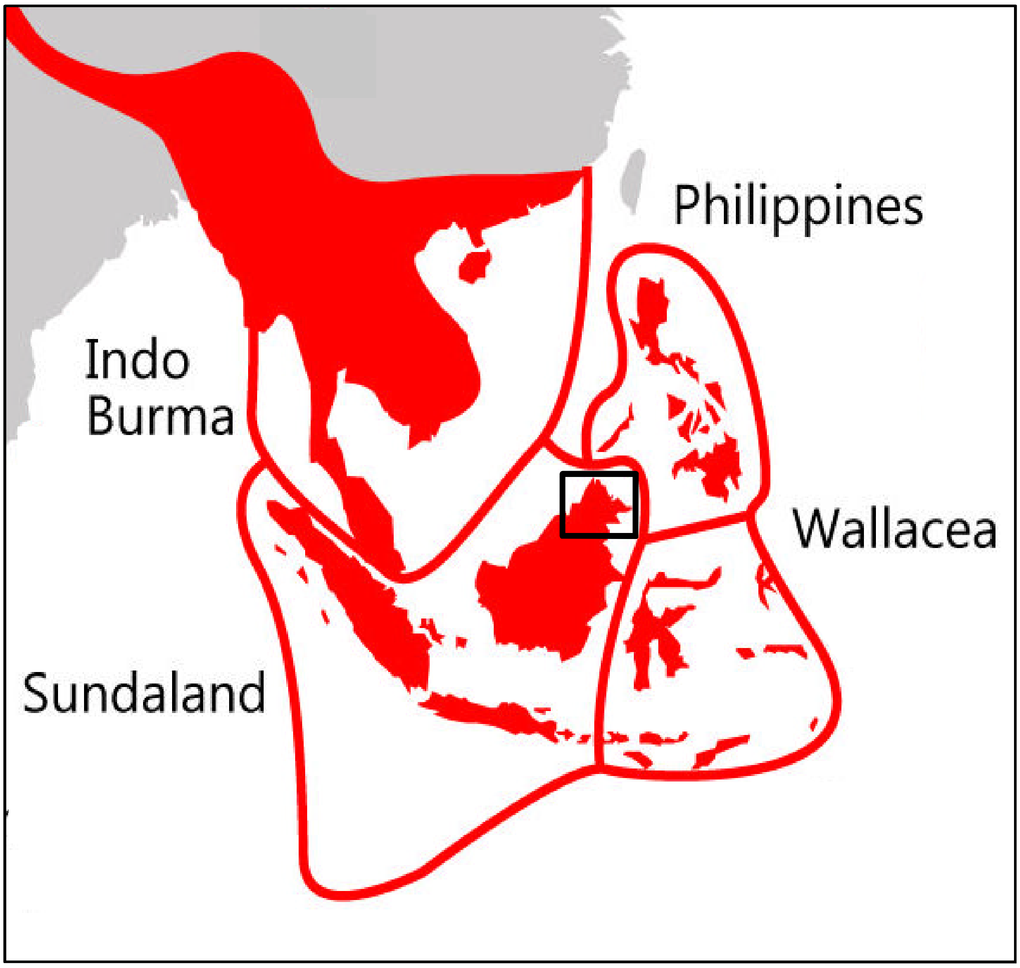

Figure 1.2. Outline map of Southeast Asia showing the four biodiversity 'hotspots'. Figure adapted from Conservation International (http://www.conservation.org). Box shows Sabah, Malaysian Borneo, where empirical data were collected in Chapter 2.

1.4.1. Southeast Asian rainforests

Within Southeast Asian rainforests there is considerable variation in rainforest types (often referred to as 'formations'), which differ in their structure, physiognomy and floristic composition (Whitmore 1984). The dominant rainforest formation is lowland evergreen rainforest (<1200 m a.s.l.), of which lowland dipterocarp forests are a major component and are the dominant rainforest type in many regions, including Borneo (Whitmore 1984, Richards 1996). These rainforests conventionally consist of three layers, whereby a top layer of giant emergent trees (>45-60 m) is found over a main stratum (>24-36 m) that covers smaller, shade-tolerant trees below (Whitmore 1984). Lowland dipterocarp forests are specifically dominated in their upper and emergent canopy by Dipterocarpaceae trees (Newbery *et al.* 1992), which make up more than 50% of the total volume of large trees (Marsh & Greer 1992) (Figure 1.3). These forests are characterised by intermittent mass flowering and fruiting events of the Dipterocarpaceae and other tree species at intervals of one to many years, triggered by El Niño-Southern Oscillation (ENSO) events (Sakai 2002).

Lowland dipterocarp rainforests within Southeast Asia contain the greatest number of species of any rainforest formation (Whitmore 1984), including many unique and endemic flora and fauna (Curran *et al.* 2004, Davies *et al.* 2005). Whilst, species-specific distribution maps for most rainforest taxa are severely lacking, a number of species, including several birds and mammals (e.g. black hornbills, black-headed pittas, flat-headed cats and proboscis monkeys: see https://www.iucn.org/) are thought to be restricted to low-lying forests (e.g. due to proximity of lowland rivers). Distributions of many Dipterocarpaceae tree species are also related to soil type (e.g. see Palmiotto *et al*. 2004, Russo *et al*. 2005), and so may be confined to specific low-lying habitats. Both tree species composition and forest structure have been shown to vary dramatically across edaphic (soil-type) gradients, and subsequently reflect habitat-driven floristic patterns (Potts *et al*. 2002). Other forest types, such as peatswamp forests, constitute important habitats within lowland evergreen rainforests (Koh *et al*. 2011) and not only contain high concentrations of region endemic plant and freshwater fish species, but act as reservoirs for both peat and carbon (Yule 2010, Posa *et al*. 2011). High numbers of species across several taxa have been found within peatswamp forests, but no terrestrial vertebrates appear to be entirely dependent on these habitats (Posa *et al*. 2011), which suggests that many vertebrate taxa may be able utilize different types of forest (e.g. orangutans: Ancrenaz *et al*. 2004 and large flying foxes: Posa *et al*. 2011). Being able to utilize a number of habitat types may be beneficial under climate change if lowland species need to shift or expand their distributions to forests at higher altitudes (see section 1.2.2. above), which may differ in their structural composition.

Other major rainforest types within Southeast Asia include lower (1200-1500 m a.s.l.) and upper (>1500-3000 m a.s.l.) montane rainforests, and these rainforests differ from lowland evergreen rainforest in both structure and community composition. At higher elevations, rainforests are shorter (15-33 m and 1.5-18 m in lower and upper montane rainforests, respectively) and have a flatter canopy surface; they are also dominated by more slender tree species with denser sub-crowns (Whitmore 1984). Montane species often occupy narrow niches spanning specific elevation gradients, and so these rainforests are associated with a relatively high number of endemic specialists (Baeman 2005, Chen *et al*. 2009). However, due to limited distribution data for tropical taxa, the proportions of endemic species restricted to either montane or lowland rainforests are relatively unknown. Whilst a number of locally endemic montane species on Borneo have shown significant elevation increases due to rising temperatures (Chen *et al.* 2009), it is unclear whether endemic species restricted to specific lowland habitats have the capacity to track climate change if suitable habitats do not exist at higher elevation (e.g. peatswamp forests).

Unfortunately, Southeast Asian rainforests, particularly lowland dipterocarp forests, are under severe threat from a number of anthropogenic pressures (Sodhi *et al.* 2004). Due to the high commercial value of many dipterocarp tree species, extraction rates are among the highest globally and have exceeded 100 m^3/ha (Collins *et al.* 1991), resulting in many areas of lowland rainforests that are now severely degraded (Gaveau *et al*. 2014). Lowland dipterocarp forests are also under threat from the continued expansion of oil palm plantations (Carlson *et al.* 2012), and a substantial proportion of regional peatswamp forest has already been cleared and converted to plantations (Koh *et al*. 2011). Many areas of remaining lowland forest now exist in small, isolated forest fragments or within protected areas (PAs), and few areas of unlogged (primary) rainforests in the lowlands now exist outside of PAs (Reynolds *et al.* 2011). Given their exceptional biodiversity, but dramatic decline over recent decades (e.g. see Gaveau *et al*. 2014), lowland dipterocarp forests provide a suitable study system to examine the movement behaviour of forest species at habitat boundaries (see Chapter 2), and such information is important for developing more sustainable agricultural practices that reduce biodiversity losses. These rainforests also constitute important lowland reserves that may be under threat from climate change (see section 1.4.2.1), and so their effectiveness to conserve tropical species in future needs to be examined (Chapter 3).

Figure 1.3. Lowland dipterocarp rainforest in Sabah, Borneo; (a) emergent trees in the upper canopy; (b) dipterocarps in flower during 2015-16 ENSO event; and (c) inside a lowland dipterocarp rainforest. These rainforests have an upper canopy that reaches ~45 m, with individual emergent trees (such as Dipterocarpaceae in the genera *Dipterocarpus*, *Dryobalanops* and *Shorea*) reaching up to ~60 m tall (Whitmore 1984). Photographs taken by S. A. Scriven.

1.4.2. Climate

In lowland equatorial rainforests within Southeast Asia, temperatures remain relatively constant throughout the year and are generally between 25°C and 26°C (Kira 1991), with an absence of low (<18°C) and high (>36°C) temperature extremes (Corlett 2014). Thus, temperature variations are generally greater from day to night than they are between months (Park 1992). Temperatures also decline as elevation increases at a rate of ~0.6°C for each 100 m increase in altitude (‘environmental lapse rate’) (Corlett 2014), which is important in the context of climate warming (Colwell *et al.* 2008, Chen *et al.* 2009). Unlike temperature, rainfall patterns across the Southeast Asian tropics are highly variable and complex due to the large-scale Asian monsoon system, inter-tropical convergence zone movements and topography (Wangwongchai *et al.* 2005, Corlett 2014). Inter-annual variation in precipitation in equatorial parts of Southeast Asia is also affected by ENSO events, the Indian Ocean Dipole (IOD) as well as the Pacific Decadal Oscillation effect (Corlett 2014). ENSO events in particular cause disruption to this monsoonal pattern, whereby approximately every 4-6 years (during the 20th and 21st Centuries; e.g. 1997-8, 2006-7, 2015-16) there is increased drought and higher fire frequency (Taylor 2010) (also see section 1.2.2.2. above).

1.4.2.1. Anthropogenic climate change

Across Southeast Asia, temperatures have been rising at a rate of between 0.14°C and 0.2°C per decade since the 1960s, and there has been an increase in the number of hot days and warm nights, along with a decline in the number of cool days (Hijioka *et al.* 2014). Mean changes in temperature (across all AR5 model scenarios; IPCC Fifth Assessment Report) are projected to be above 3°C for South and Southeast Asia compared to 21st Century baseline temperatures (Hijioka *et al.* 2014). Thus by 2100, tropical temperatures globally may have moved outside the natural range of variability of the last two million years (Phillips & Malhi 2005). Conversely, projected precipitation trends show strong variability, and both increasing and decreasing trends are predicted in different parts of the region, as well as between seasons. Future increases in rainfall extremes during the monsoons are likely in many areas, and 95% of AR5 models project an increase in heavy precipitation events during the summer monsoons (Hijioka *et al.*

2014). However, there is still a lack of consensus on how climate phenomena such as ENSO will affect rainfall patterns in Southeast Asia (Christensen *et al.* 2013), and so prolonged or more intense droughts during El Niño years may also be a consequence of anthropogenic change (Lewis *et al.* 2005, IPCC 2013).

1.4.3. Oil palm agriculture

Oil palm agriculture is a major driver of rainforest loss in Southeast Asia (Sodhi *et al.* 2004). In Malaysia and Indonesia alone, oil palm plantations expanded from 2.4 million ha in 1990 to 7.2 million ha in 2012, at the expense of rainforest (Koh & Wilcove 2008). When rainforest is converted to oil palm plantations there is a loss of habitat heterogeneity (Foster *et al.* 2011), as natural vegetation is cleared before the soil is terraced and roads and drainage ditches are created. Oil palm seedlings are then planted, which results in highly ordered monocultures with rows of oil palm trees ~10 m apart that have a 25-30 year life cycle (Luskin & Potts 2011) (Figure 1.4.). The reduced structure and altered microclimate of oil palm plantations are detrimental for both ecosystem functioning and biodiversity, and many forest species are unable to persist in such habitats (Aratrakorn *et al.* 2006, Fitzherbert *et al.* 2008, Edwards *et al.* 2010, Gillespie *et al*. 2012, Senior *et al*. 2013), although a few generalist species become hyper-abundant (Ickes 2001, Senior *et al.* 2013).

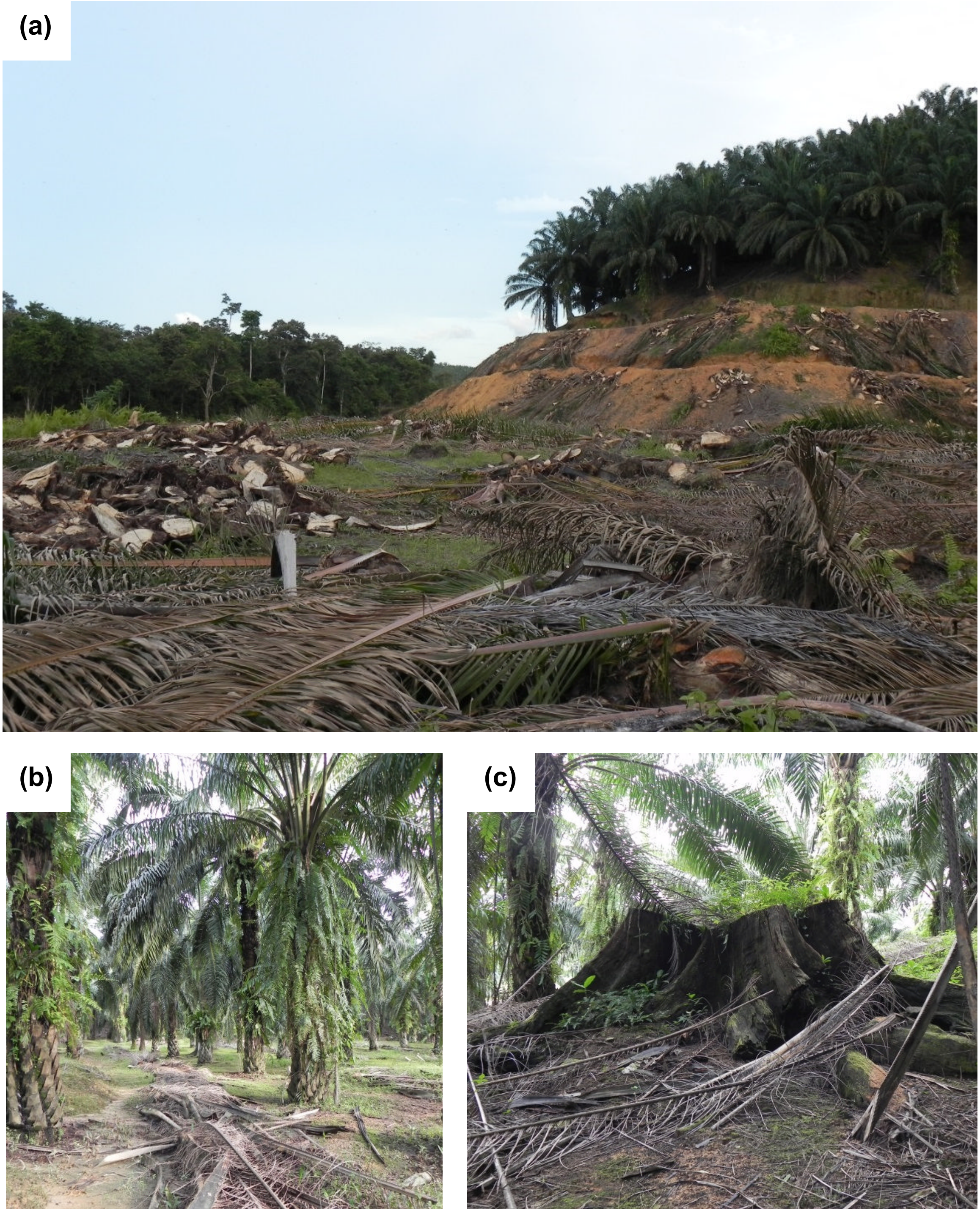

Figure 1.4. (a) Clearing of mature oil palm trees next to the Kinabatangan Wildlife Sanctuary in Sabah, Borneo, prior to re-planting. During clearing of plantations, oil palm trees are mechanically cut into smaller pieces (Luskin & Potts 2011); (b) inside a mature oil palm plantation, dead palm fronds are collected into piles by oil palm workers; and (c) the remains of a rainforest tree within an oil palm plantation. Photographs taken by S. A. Scriven.

1.4.4. Conserving Southeast Asian biodiversity

Oil palm expansion is projected to continue in Southeast Asia due to the rising global demand of palm oil for food and biofuel (Fitzherbert *et al*. 2008, Carlson *et al*. 2012). Therefore many species, particularly those dependent on remaining lowland dipterocarp forests, are threatened by deforestation and climate change (e.g. see recent studies by Struebig *et al*. 2015, Brodie 2016). Protected areas are likely to provide the mainstay of biodiversity conservation in this region (Sodhi *et al.* 2004), and conservation strategies are urgently needed to determine the effectiveness of PAs to conserve biodiversity under changing climate and landcover scenarios. Some estimates suggest that Southeast Asia could lose 13-42% of local populations of forest species by the end of this century, of which at least half could represent global species extinction (Brook *et al.* 2003). It is therefore vital to examine ways to promote connectivity, and thus maintain resilience and biodiversity in these ecosystems.

1.5. Thesis aims and rationale

The main aims of this thesis are (1) to improve our understanding of how to promote resilience and biodiversity in tropical landscapes that are under threat from agricultural expansion and climate change, and (2) to provide an evidence-base for conservation strategies that maintain rainforest connectivity. To achieve these aims, I focus specifically on Borneo. Firstly, I collected empirical data on butterfly movement at rainforest-plantation boundaries to examine the permeability of oil palm plantations to forest-dependent butterflies. I conclude that oil palm plantations may act as barriers to the dispersal of rainforest species. Secondly, I used metapopulation models to determine the connectedness of PAs along elevation gradients, and I show that many PAs are too isolated for poor dispersers to reach PAs at higher elevation due to lack of intervening forest habitat. Finally, I used models based on electrical circuit theory to identify the most important forest connections between PAs for range shifting species, and I quantify the extent to which new PAs are required to maintain current levels of connectivity. In the General Discussion, I synthesise this information in order to recommend conservation strategies to maximise connectivity in fragmented landscapes. The specific objectives of the main data chapters are outlined below:

Chapter 2 – **Barriers to dispersal of rainforest butterflies in tropical agricultural landscapes**

In order to improve connectivity and develop conservation strategies in fragmented landscapes, it is important to understand the movement behaviour of forest species at habitat boundaries. The conversion of rainforest to oil palm plantations reduces biodiversity, and investigating the permeability of forest-agricultural boundaries to rainforest species will help determine the conservation value of forest fragments within agricultural landscapes. If forest species (i.e. species that are dependent on rainforest habitat to breed) are unable to cross agricultural areas, plantations will form barriers to their dispersal and landscape connectivity will be reduced. By carrying out new field studies in Sabah (Borneo) on fruit-feeding Nymphalid butterflies, the main objectives of this chapter were to: (1) determine the net direction of butterfly movement across forest-oil palm boundaries, (2) compare overall movements of individuals from forest into plantations, compared with movements only in forest, and (3) examine whether larval host plant availability in plantations and other species specific traits (including forewing length, larval host plant specificity and geographical range size) are predictors of boundary crossing.

Chapter 3 – **Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change**

Protected areas are key for conserving rainforest species, but many PAs are becoming increasingly isolated within agricultural landscapes and studies that examine their connectivity are lacking. Hence, the effectiveness of tropical PA networks to conserve rainforest species under climate change is unclear, and there are few data on whether the spatial location of PAs will facilitate range shifting of species under climate warming. Focusing on Borneo, the main objectives of this chapter were to: (1) identify PAs that will not retain analogous climate conditions in future, and examine the characteristics of these PAs (e.g. size, elevation and isolation), and (2) determine the connectivity of PAs along elevation gradients under multiple assumptions of warming (IPCC RCP scenarios) and forest cover, as well as for species with different dispersal abilities and population densities.

Chapter 4 – Identifying important habitat connections for range shifting species in tropical agricultural landscapes

Maintaining connectivity between PAs will be vital for range shifting species, and ongoing habitat loss makes it important to identify areas of rainforest that form important connections linking PAs so that they may receive higher levels of protection. Using a novel modelling approach based on electrical circuit theory, and again focusing on Borneo, the main objectives of this chapter were to: (1) calculate the connectivity of PAs from which analogous climates may shift to cooler PAs at higher elevation using conductivity models; (2) identify the spatial locations of expansion routes between PAs along elevation gradients; (3) examine the spatial agreement in these expansion routes under two warming scenarios (mitigation scenario: RCP2.6 and business-as-usual scenario: RCP8.5); (4) overlay model outputs of expansion routes and identify the spatial location of the most important areas of rainforest habitat that connect PAs along elevation gradients on Borneo; and (5) determine the area of rainforest that would need protecting in order to conserve these important habitat connections.

Chapter 2 – Barriers to dispersal of rainforest butterflies in tropical agricultural landscapes

Lexias dirtea; marked with a unique number to study its dispersal

2.1. Abstract

Fragmentation of natural habitats can be detrimental for species if individuals fail to cross habitat boundaries to reach new locations, thereby reducing functional connectivity. Connectivity is crucial for species shifting their ranges under climate change, making it important to understand factors that might prevent movement through human-modified landscapes. In tropical regions, rainforests are being fragmented by agricultural expansion, potentially isolating populations of highly diverse forest-dependent species. The likelihood of crossing habitat boundaries is an important determinant of species' dispersal through fragmented landscapes, and so we examined movement across rainforest-oil palm plantation boundaries on Borneo by using relatively mobile nymphalid butterflies as our model study taxon. We marked 1666 individuals from 65 species, and 19 percent (100/527) of recaptured individuals crossed the boundary. Boundary crossing was relatively frequent in some species, and net movement of individuals was from forest into plantation. However, boundary crossing from forest into plantation was detected in less than 50 percent (12/28) of recaptured species, and was dominated by small-sized butterfly species whose larval host plants occurred within plantations. Thus, whilst oil palm plantations may be relatively permeable to some species, they may act as barriers to the movement of forest-dependent species (i.e. species that require rainforest habitat to breed), highlighting the importance of maintaining forest connectivity for conserving rainforest species.

2.2. Introduction

Across the globe, natural habitats are being fragmented by human activities with detrimental consequences for biodiversity (Canale *et al.* 2012, Melo *et al.* 2013, Almeida-Gomes *et al.* 2016). Habitat connectivity is important for population persistence (Hanski 1999), and species are predicted to shift their ranges in response to climate change (Chen *et al.* 2011a), making it important to understand the permeability of fragmented landscapes (Hodgson *et al.* 2011) and to maintain landscape connectivity (Martensen *et al.* 2008). Loss of connectivity is of particular concern in tropical regions (Wade *et al.* 2003) because rainforests are global hotspots for biodiversity but have already experienced extensive deforestation (Gibbs *et al.* 2010). For example, in parts of SE Asia, fragmentation of lowland forest is primarily due to the expansion of large-scale oil palm plantations (*Elaeis guineensis* Jacq.) (Gaveau *et al.* 2014), which can lead to the isolation of populations of forest-dependent species in the remaining areas of forest within these landscapes (Scriven *et al.* 2015/Chapter 3).

The ability of species to move between habitat patches depends on species' dispersal ability, a complex process that integrates the physical costs of movement through preferred habitat (Bonte *et al.* 2012), the response of species to habitat boundaries (Kallioniemi *et al.* 2014), and the permeability of the matrix (Perfecto & Vandermeer 2002). For tropical forest species to disperse successfully through fragmented habitats they need to cross forest-non forest edges, which are frequently avoided by forest specialists (e.g. Laurance 2004, Watson *et al*. 2004). Thus, an important component of dispersal involves species' behaviour upon reaching the forest edge, and responses to habitat boundaries affect emigration rates from suitable habitat (Ries & Debinksi 2001). Boundary crossing by individuals (e.g. butterflies) may be part of a random walk or movement (e.g. see Schultz *et al*. 2012), although it is also likely that crossing may represent an active decision by an individual to leave areas of suitable habitat, and so the likelihood of crossing an edge may be an indicator of dispersal ability. However, leaving areas of suitable habitat may not always indicate longer distance dispersal (see review by Stevens *et al.* 2010), but boundary crossing is a prerequisite for individuals moving through highly fragmented landscapes.

Whilst some tropical forest species avoid forest edges (Hansbauer *et al.* 2008), there is little information on the variation in boundary crossing among species. In temperate regions, species have been shown to recognise boundaries between suitable and unsuitable habitat and can actively control their rate of boundary crossing (Conradt & Roper 2006), and modify their movement behaviour in response to boundaries (e.g. birds: Rodríguez *et al*. 2001, butterflies: Schultz & Crone 2001, bush crickets: Berggren *et al*. 2002, and salamanders: Rittenhouse & Semlitsch 2006). Several temperate studies of butterflies have also reported species-specific differences in boundary crossing ability (e.g. Haddad 1999, Ries & Debinski 2001, Kallioniemi *et al*. 2014), and differences among species in their overall levels of activity can also affect rates of boundary crossing (Mair *et al.* 2015). Thus, current evidence implies that tropical species may vary in their sensitivity to habitat boundaries, and hence to rainforest fragmentation effects, but data quantifying movement of species across rainforest boundaries and how ecological traits influence edge-crossing behaviour are lacking.

The movement of individuals across a habitat boundary is predicted to follow productivity (Rand *et al.* 2006) and population source-sink (Pulliam 1998, Tscharntke *et al.* 2005) gradients. In both tropical (e.g. Lucey & Hill 2012) and temperate (e.g. González *et al*. 2015) regions, there is evidence of spillover from natural habitats into managed systems, although spillover can also occur in the opposite direction (Barcelos *et al.* 2015). Studying net movement of individuals across rainforest-agricultural boundaries is important for understanding species diversity and ecosystem functioning; for example, if forest pests move into plantations and reduce crop yields, or if crop-dwelling predators move into forests and reduce biodiversity (Rand *et al.* 2006).

Conversion of rainforest to oil palm agriculture reduces tropical biodiversity (Fitzherbert *et al.* 2008) and remaining tracts of rainforest become isolated within agricultural landscapes (Scriven *et al.* 2015/Chapter 3). In order to develop effective conservation management there is a pressing need to determine the permeability of forest-oil palm plantation boundaries to forest-dependent species (i.e. species that are dependent on forest habitat to breed). If forest species are unable to cross forest boundaries, then plantations will form barriers to the movement of individuals among forest patches thereby reducing habitat connectivity for these species. We investigated the movement of species at forest-oil palm plantation boundaries, and tested the hypotheses that net flow of individuals is from forest into plantations, and that plantations are barriers to movement of many forest-dependent species, hence we predicted fewer overall movements of species from forest into plantations compared with movements within forest. In addition, we predicted that plantations will be less of a barrier to species whose larval host plants occur within the plantation, and we also examined whether other species' traits (forewing length, larval host plant specificity and geographical range size) affected boundary crossing. We selected these traits for study because they have previously been shown to affect the sensitivity of tropical butterfly species to forest fragmentation (Benedick *et al.* 2006). Our study taxon was nymphalid butterflies, which are diverse (Benedick *et al.* 2006), relatively mobile (Marchant *et al.* 2015) and many species are dependent on closed-canopy forest (Hill *et al.* 2001). Butterfly distributions have also been shown to correlate well with observed patterns in other taxa (Schulze *et al*. 2004, Thomas 2005, Gardner *et al.* 2008) and so butterflies are considered sensitive ecological indicators of environmental changes (Cleary 2004).

2.3. Methods

2.3.1. Study sites

Butterflies were sampled at four sites spanning forest-oil palm plantation boundaries in Sabah (Malaysian Borneo) between June-September 2013 and April-July 2014 (Fig. 2.1a). Our sampling design comprised two groups of two sites; groups were ~115 km apart, and sites within each group were more than 5 km apart (Fig. 2.1a). Sites were located at boundaries between mature fruiting oil palm (cleared and planted between 1998-2000) and production forest that had been selectively logged at least twice (Appendix 1A: Fig. A1.1), representing habitat mosaics and boundaries typical of plantation landscapes (Tawatao *et al.* 2014). We selected four forest sites that had experienced similar levels of disturbance (due to repeated commercial selective logging) and that were adjacent to oil palm plantations of similar age (~13-16 years since planting). Thus, we minimised site-level differences in habitat structure, allowing us to focus on general patterns of boundary crossing. Oil palm plantations at sites 3 and 4 (adjacent to Tabin Wildlife Reserve; Nakashima *et al*. 2010) were members of the Roundtable for Sustainable Palm Oil (RSPO), but sites 1 and 2 (adjacent to the Ulu Segama Forest Reserve; Hector *et al*.

2011, Reynolds *et al*. 2011) were not (Fig. 2.1a). To characterise the structure of forest-oil palm plantation boundaries at the four study sites we measured a number of variables in the two habitat types (detailed descriptions of structural habitat and abiotic measurements taken at study sites are given in Appendix 1A). Differences in the means and standard errors of these variables among the four sites were small, showing that boundary characteristics were broadly similar (Appendix 1A: Table A1.1.), thus minimising any influence of site effects on our results.

2.3.2. Sampling techniques

At each of the four sites, 24 banana-baited traps (Dumbrell & Hill 2005, Benedick *et al.* 2006) were set up 50 m apart in a grid design spanning the boundary (Fig. 2.1b) and sampled for a total of 18 d per site (1728 trap-days in total). Traps were checked daily and trapped individuals were identified (following Otsuka 1988, Corbet & Pendlebury 1992), uniquely marked (Lucey & Hill 2012), and released. Some *Tanaecia* and *Euthalia* species cannot be identified in the field and so were grouped for analysis as *Tanaecia/Euthalia* sp.

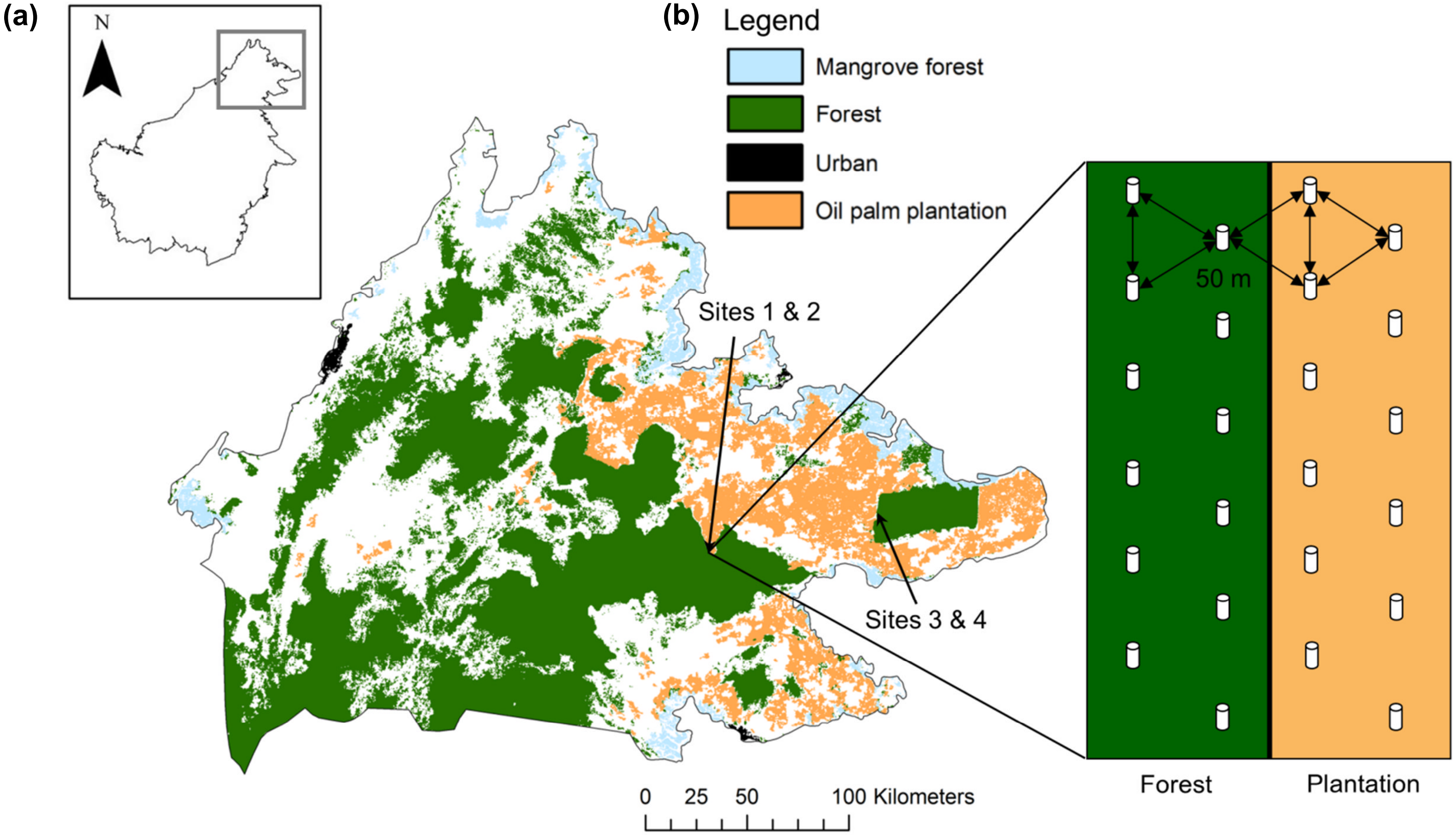

Figure 2.1. (a) Map of Sabah (North Borneo), arrows show study sites. The landcover category 'forest' consists of peatswamp forest, lowland evergreen forest, and lower and upper montane forest, and the category 'oil palm plantation' shows the extent of mature fruiting oil palm plantations (see Miettinen *et al*. 2012 for details); (b) Sampling design comprising 24 fruit-baited butterfly traps placed 50 m apart and sampled for a total of 18 d at each site.

2.3.3. Species traits

To investigate factors affecting the likelihood of species crossing the forest boundary, we examined the importance of four species traits that are associated with dispersal and with specialist-generalist characteristics. Traits examined were: (1) forewing length (mm), computed as the mean of male and female values quoted in Otsuka (1988), who measured the distance from the base of the forewing to the apex with a ruler; (2) larval host plant diet breadth (subsequently termed 'specificity') computed as the ln-transformed number of larval host plant genera each butterfly species has been recorded feeding on, based on information in Robinson *et al*. (2001); (3) presence/absence of larval host plants in oil palm plantations (subsequently termed 'availability') based on data from Lucey and Hill (2012), who recorded butterfly larval host plants in oil palm plantations in Sabah and assigned butterflies according to the presence/absence of host plant families occurring in plantations; and (4) geographical range size, analysed according to three categories: narrow (restricted to Sundaland – Borneo, Sumatra, Java and West Malaysia), intermediate (restricted to the Oriental region) and widespread (all other species), using species' distribution information in D'Abrera (1985) and Otsuka (1988), and following Benedick *et al*. (2006). Rainforest is the main natural habitat on Borneo and historically covered most of the island (Gaveau *et al.* 2014), and so we assumed that larval host plants were present in forest habitats and that species with no larval host plants in plantations could breed only in forest habitats. We refer to species without larval host plants in plantations as 'forest-dependent' species.

In our analysis of species traits (see below) we included only those species with ≥ two individuals recaptured moving between traps. Of these species, larval host plant data were not available for *Junonia atlites,* because this species was not recorded by Lucey and Hill (2012). Larvae of this species feed on species of grasses (family Poaceae, formerly *Gramineae;* Robinson *et al*. 2001), and grass is abundant in oil palm plantations, so we assumed that larval host plants of *J. atlites* were present in plantations. There was also no host plant information for two species of *Mycalesis* (*M. anapita* and *M. orseis*) in relation to the number of larval host plant genera used, and so we assigned them a value based on the average number of host plant genera used by other *Mycalesis* species (*M. horsfieldi* and *M. mineus*; Table 2.1). Larval host plants of *Bassarona dunya* are not known and so we excluded this species from our trait analysis.

2.3.4. Data analysis

For our analyses, we combined species data from the four sites because there were insufficient boundary crossing events from any single site to provide robust estimates of species movements per site. However, to check for any site-level effects, we re-ran analyses with species data split by site, and included site identity as a random factor (see Appendix 1B and Table A1.2). This did not alter our main conclusions, although the local abundance of species became more important in the trait analyses (see below) because of low sample sizes per species per site, and so we only report findings from analyses based on combined data from all four sites. We report the number of individuals marked, the habitat they were marked in (forest or plantation; subsequently termed 'forest individuals' and 'plantation individuals'), if they were subsequently recaptured, and whether the recapture was in the same habitat or if the butterfly had crossed the boundary. Only a small number of individuals (14/100) were recaptured crossing the boundary more than once, and only two individuals crossed more than twice. Thus, the vast majority of individuals that crossed the boundary did so on only one occasion and so for consistency we only analysed the first recapture, which corresponded to the direction moved after the individual was initially marked. Repeating our analysis using the last direction of recapture did not affect our results and so we only present results for the first recapture. We used chi-squared tests to examine whether the habitat (forest or plantation) an individual was marked in affected its likelihood of crossing the boundary, and of moving between traps. For forest individuals, we compared the number of individuals marked in forest that crossed the boundary into plantation with the number that only moved within forest. We also used a Mann-Whitney U test to compare distances moved by forest and plantation individuals.

We used Generalised Linear Mixed Models (GLMMs) with a logit link and binomial errors to examine whether the proportion of individuals per species crossing the habitat boundary was influenced by species' traits and habitat of first capture (excluding species with < two individuals recaptured moving between traps, and excluding species without larval host plant data; 16 species analysed). The dependent variable in these GLMMs comprised proportion data for each of the 16 study species, computed as the total number of individuals of a species crossing the boundary as a proportion of all recaptured individuals of that species that moved to a different trap. Data for each species comprised separate information for forest and plantation individuals, hence our GLMMs comprised two sets of proportion data for each of the 16 study species: one set of data for the total number of within-forest recaptures and boundary crossing events by forest individuals and another set of data for the total number of within-plantation recaptures and boundary crossing events by plantation individuals. This statistical design, where movement data per species from all four study sites are summed for forest and plantation individuals before analysis, provides reliable species-specific estimates of boundary crossing, but more detailed information such as the precise location on the study grid of original capture, capture day or site were not included. To avoid over-fitting models, we could not include multiple traits within a single model. Therefore, to determine which trait was most important for boundary crossing, we fitted four separate GLMMs (examining the importance of forewing length, host plant availability in plantations, diet specificity and geographical range size) and we included only a single trait predictor variable in each model. In addition, we also fitted a separate model that included a measure of species abundance (ln-transformed number of individuals marked in each habitat) as a fixed effect to control for variation in local density and recapture rates of species. Our predictor variables were weakly correlated, i.e. the smallest species were generally the most abundant, and had host plants present in plantations (see Fig. 2.2 for relationships between species traits), but we ran separate models for all four traits in order to explore the relative importance of traits on the probability of boundary crossing. In addition, we also incorporated an obligate habitat (of first capture) covariate into each of the models, interacting with each trait variable and species abundance, in order to control for the different numbers of individuals marked in forest or plantation habitats. Butterfly Subfamily was included as a random factor to control for phylogeny.

We compared the difference in the corrected Akaike information criterion (ΔAICc) and models where ΔAICc < 2 were considered to be no better than a ‘habitat-only’ model (i.e. a model including only habitat of first capture and butterfly Subfamily) (Burnham & Anderson 2004). We compared models that included species traits and abundances to habitat-only models in order to determine the influence of each trait on boundary crossing, whilst accounting for the effect of the habitat individuals were marked in. For each of the four trait models where ΔAICc > 2 compared to the habitat-only model, we calculated four movement probabilities: forest to plantation, plantation to forest, forest to forest and plantation to plantation. To aid interpretation of model outputs, we report the logit probabilities of movement between and within habitats for the smallest and largest species (forewing lengths = 19 mm and 54.5 mm, respectively) and for species with larval host plants present and absent in plantations. We also calculated 95% CIs for all logit movement probabilities to assess the relative importance of the species traits. All statistical analyses were carried out in R statistical software version 3.2.0 (R Core Team 2015).

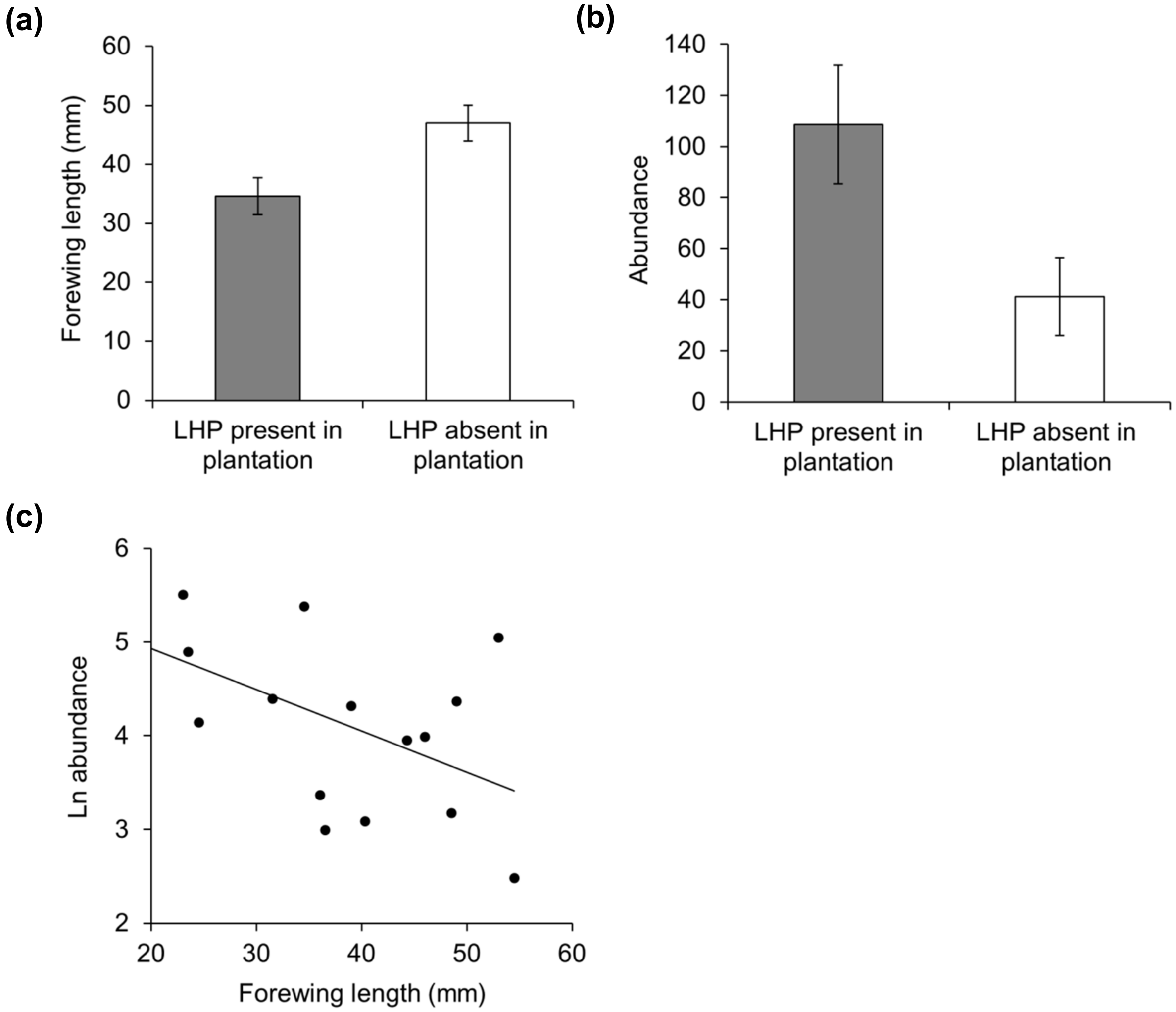

Figure 2.2. Relationships between species traits for 16 species included in our trait analyses (see Table 2.1). (a) Forewing length (mm) vs. larval host plant (LHP) availability (presence and absence in oil palm plantations); (b) abundance vs. larval host plant availability; and (c) ln-transformed abundance vs. forewing length (mm); trend line shows significant correlation between ln-transformed abundance and forewing length (mm) (Pearson's correlation *r* = -0.53; *p* = 0.04).

2.4. Results

2.4.1. Boundary crossing by species

We marked a total of 1666 individuals from 65 species, of which 527 individuals from 28 species were recaptured (recapture rate of individuals = 31.6%; see Appendix 1C: Table A1.3 for summary data of butterfly recaptures). Of the 28 species recaptured, 11 species had larval host plants present within oil palm plantations, whilst eight species did not, and so were assumed to be forest-dependent; for nine species there was no host plant information (see Appendix 1C: Table A1.4 for full species list). Boundary crossing was relatively common in some species, and 100 individuals from 13 species crossed the boundary (Table 2.1), corresponding to 19 percent (100/527) of all individuals recaptured. Overall, individuals from a total of 12 species (42.9% of the 28 species recaptured) crossed the boundary from forest into plantation (Table 2.1). Even though more individuals and species were marked in plantation (1105 individuals, 51 species) compared with forest (561 individuals, 42 species), individuals were 5.6 times (odds ratio test; 95% CIs: 3.4, 9.1) more likely to move across the boundary if they were originally marked in forest (57/139 recaptured individuals) than if they were originally marked in plantation (43/388 recaptured individuals; $\chi^2(1) = 59.6$, $p < 0.0001$) (Fig. 2.3). Thus, net flow of movement of individuals was from forest into plantation.

A higher proportion of individuals was recaptured in plantation compared with forest (Fig. 2.3a), but only 18 percent (43/243) of plantation individuals that were recaptured in a different trap crossed the boundary into forest. By contrast, forest individuals that were recaptured in a different trap had an approximately equal chance of moving to plantation (52.8%; 57/108 recaptured individuals) as moving within forest (47.2%; 51/108 recaptured individuals). This implies that most forest individuals did not perceive the boundary as a barrier. However, there was considerable variation among species marked in forest in relation to boundary crossing (Table 2.1), and larval host plant availability, forewing length and abundance were important factors affecting these movements (Table 2.2). Crossing from forest into plantation was more than twice as likely for species with larval host plants present in plantations (ten species crossed) than for species without host plants present (only two species crossed) (Fig. 2.4a). Boundary crossing from forest into plantation was also more than twice as likely by small species than large species (Fig. 2.4b).

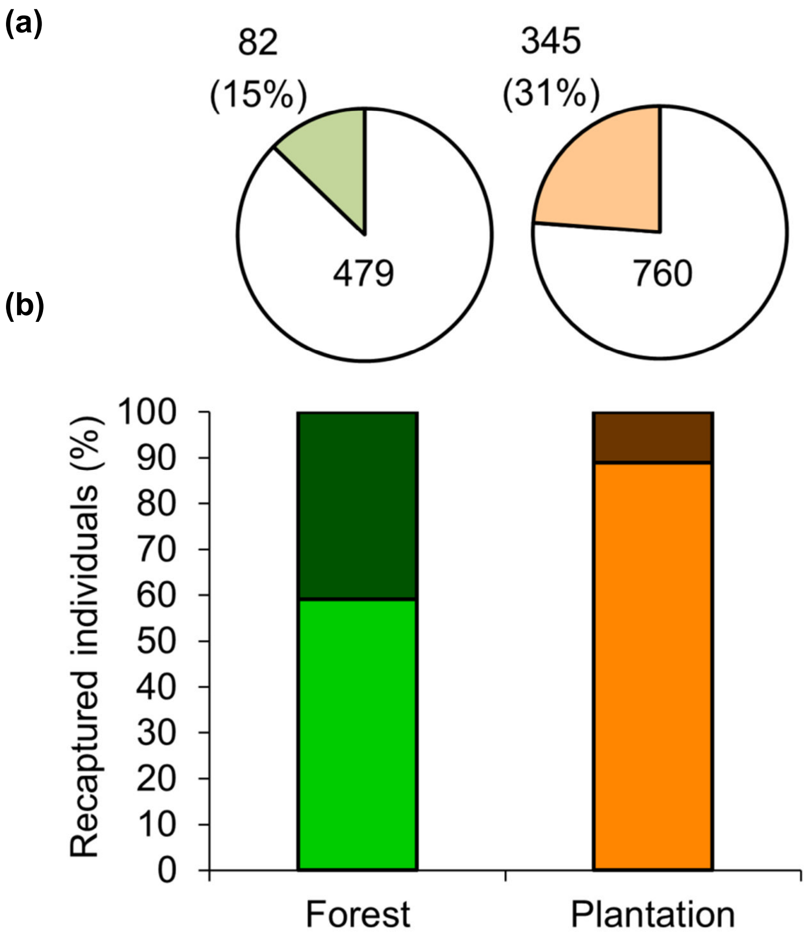

Figure 2.3. (a) Pie charts showing number of all individuals initially marked in forest or plantations, and the number subsequently recaptured at least once in the same habitat (shaded portion; i.e. excluding individuals that crossed the boundary). (b) Stacked bar chart showing percentage of all individuals marked in forest (*n* = 139 marked individuals) and plantations (*n* = 388 marked individuals) that were subsequently recaptured in the same habitat (medium shading; either within the same trap, or a different trap), or crossed the boundary (dark shading). Forest individuals were more likely to cross the boundary compared with plantation individuals ($\chi^2(1) = 59.6$, $p < 0.0001$).

Table 2.1. Summary data and trait information for butterfly species sampled during the study for which individuals were originally marked in either forest ('forest individuals') or plantation ('plantation individuals'); only species with ≥ two individuals recaptured moving between traps were included.

Species	**Subfamily**	**# Individuals that moved between traps**	**# F to P movements**[a]	**# P to F movements**[b]	**# Forest individuals**	**# Plantation individuals**	**Forewing length (mm)**	**LHP specificity**[c]	**LHP availability**[d]	**Geographical range size**
Agatasa calydonia	Charaxinae	2	0	0	6	6	54.5	1	Absent	Intermediate
Charaxes bernardus	Charaxinae	6	1	0	22	30	44.3	13	Absent	Intermediate
Prothoe franck	Charaxinae	7	0	1	19	3	40.3	2	Absent	Intermediate
Amathusia phidippus	Morphinae	20	2	3	46	110	53	10	Present	Intermediate
Discophora necho	Morphinae	7	1	1	22	32	46	1	Present	Narrow
Bassarona dunya	Nymphalinae	9	0	0	19	2	45.3	-	-	Intermediate
Dophla evelina	Nymphalinae	17	4	5	42	37	49	4	Absent	Intermediate
Hypolimnas bolina	Nymphalinae	4	0	0	0	29	36	28	Present	Wide
Junonia atlites	Nymphalinae	3	0	0	0	20	36.5	13	Present	Intermediate
Neorina lowii	Nymphalinae	7	1	1	19	5	48.5	1	Present	Narrow
Elymnias nesaea	Satyrinae	16	3	4	13	62	39	4	Present	Intermediate
Elymnias panthera	Satyrinae	13	2	2	23	58	31.5	3	Present	Narrow
Melanitis leda	Satyrinae	43	11	8	78	139	34.5	25	Present	Wide
Mycalesis anapita	Satyrinae	65	15	11	66	137	19	-[e]	Present	Intermediate
Mycalesis horsfieldi	Satyrinae	70	9	6	40	207	23	3	Present	Intermediate
Mycalesis mineus	Satyrinae	47	6	0	7	127	23.5	8	Present	Intermediate
Mycalesis orseis	Satyrinae	11	2	1	50	13	24.5	-[e]	Present	Intermediate

[a] Number of movements by forest individuals moving into plantation (F to P movements)

[b] Number of movements by plantation individuals moving into forest (P to F movements)

[c] Larval host plant (LHP) diet breadth

[d] Presence/absence of larval host plants in oil palm plantations. We classified species that were unable to breed in plantation habitat as forest-dependent.

[e] There was no information on the number of larval host plant genera used by these species, and so they were assigned a value based on the average number of host plant genera for other species within the same genus that were included in our analyses (*Mycalesis horsfieldi* and *M. mineus*).

Table 2.2. Model comparisons for binomial logistic regression models (GLMMs) determining the effect of species traits (forewing length, larval host plant (LHP) specificity, larval host plant availability and geographical range size) and abundance on probability of crossing the boundary for forest and plantation individuals.

Model	Direction[a]	K[b]	LL[c]	AICc[d]	ΔAICc[e]	w_i[f]
LHP availability * Habitat	+	5	-60.32	132.94	-	0.372
Forewing length * Habitat	-	5	-60.51	133.32	0.38	0.307
Ln habitat abundance * Habitat	+	5	-61.03	134.37	1.43	0.182
Ln LHP specificity * Habitat	NA	5	-61.68	135.67	2.73	0.095
Habitat-only model	NA	3	-65.34	137.53	4.59	0.037
Geographical range size * Habitat	NA	7	-61.15	140.96	8.02	0.007

[a] Positive (+) or negative (-) relationship between each trait and boundary crossing probability from forest into plantation for each model that was better (Δ Akaike information criterion (AICc) > 2) than the habitat-only model. NA = not computed.

[b] Number of estimated parameters in the fitted model.

[c] Log likelihood (LL): overall model fit.

[d] A measure of model fit corrected for sample size.

[e] Change in AICc from that of the best model.

[f] Akaike weight, representing the model's relative strength compared to other best models.

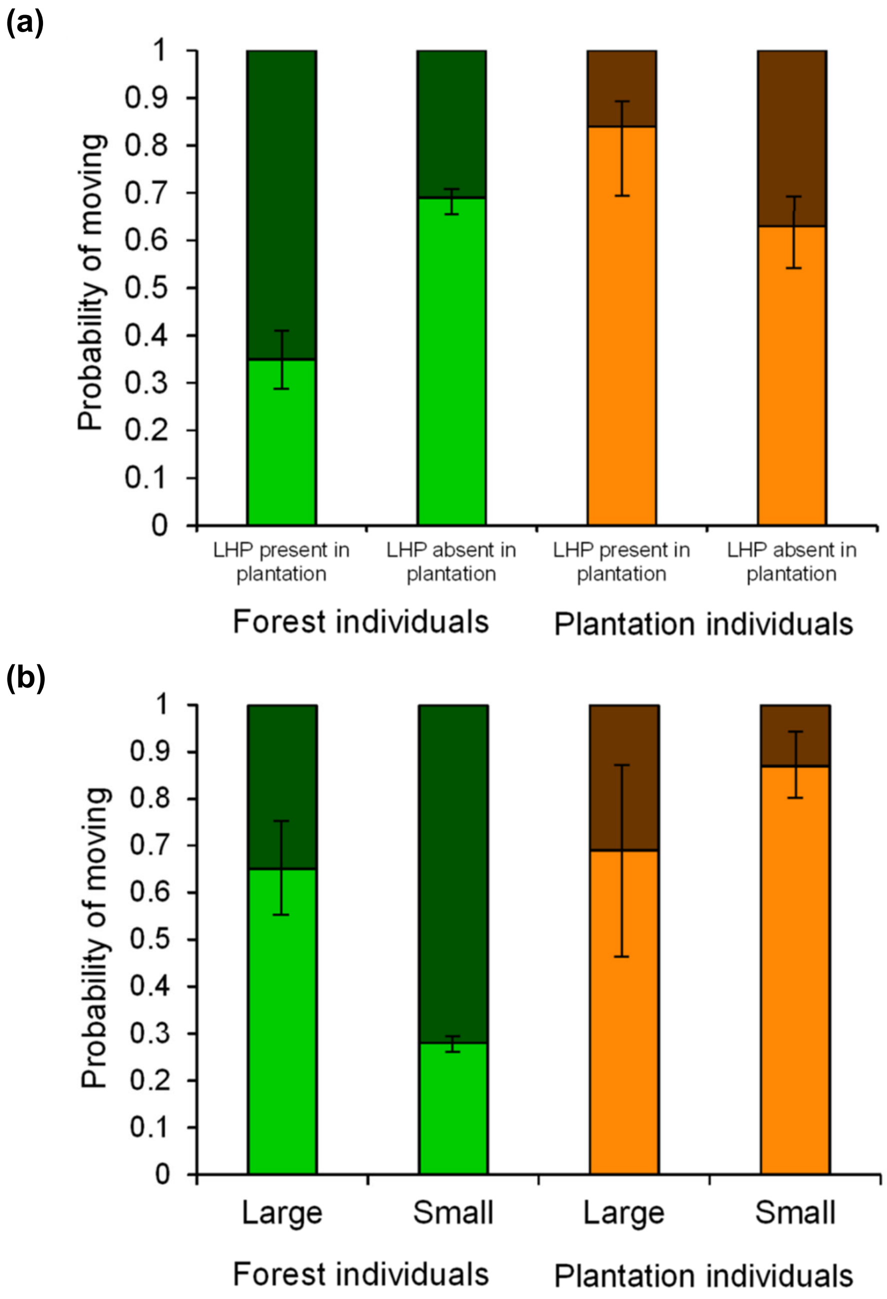

Figure 2.4. Probabilities (logit probability from binomial GLMMs) of individuals moving within the same habitat (medium shading) or crossing the boundary (dark shading) for forest and plantation individuals. Separate probabilities are calculated for species with (a) larval host plants (LHP) present (*n* = 12 species) and absent (*n* = 4 species) in plantations, and (b) for the smallest (19 mm forewing length) and largest (55 mm forewing length) species with ≥ two individuals recaptured. Error bars show 95% CIs, and traits with bars that do not overlap are significant factors affecting boundary crossing (i.e. forest individuals with host plants present in plantations (A) and small forest individuals (c).

2.4.2. Movement within habitats

Plantation individuals were less likely to move between traps (243/388: number of individuals marked in plantations that moved traps/total number of plantation individuals recaptured; 62.6%) than forest individuals (108/139 individuals moved traps; 77.7%; χ^2 (1) = 10.45, p = 0.001; n = 20 species, including individuals that crossed the boundary). Moreover, plantation individuals were 2.1 times (odds ratio test; 95% CIs: 1.3, 3.3) more likely to be recaptured in the same trap compared with those marked in forest, and moved shorter distances when they did move (plantation individuals: mean distance moved = 114 m; forest individuals: mean = 121 m; Mann-Whitney U test: W = 14,813; p = 0.047). This finding was qualitatively the same if we restricted our analyses to only those species with individuals that were recaptured in both habitats (n = 12 species; plantation: 234/367 (63.8%) of recaptures in a different trap, mean distance moved = 116 m; forest: 90/111 (81.1%) of recaptures in a different trap, mean distance moved = 128 m; p < 0.02 for both analyses). Thus, we conclude that butterflies were more sedentary in oil palm plantations compared with forest.

2.5. Discussion

2.5.1. Boundary permeability and factors affecting crossing

We found that boundary crossing was relatively frequent at our study sites for some species, although crossing from forest into plantations occurred in only 12 (43%) of the 28 species that were recaptured. Small species with larval host plants present in plantations were most likely to cross from forest into plantations, whilst species dependent on rainforest habitat to breed were recorded crossing the boundary less frequently. We deemed species to be rainforest dependent if their larval host plants were not found in plantation habitats and hence the species could not breed there (see Lucey & Hill 2012), and we assumed that species whose larval host plants were found in the plantation matrix did not solely rely on forest habitat to breed. Therefore, boundary crossing was dominated by species that could potentially breed within both rainforest and plantation habitats. These species included several in the genus *Mycalesis* (Satyrinae), whose larval host plants include a variety of grasses (Robinson *et al.* 2001). *Mycalesis* species are often found in gap sites within forest habitats (Hill *et al.* 2001), and these high-light conditions are typical of habitats within oil palm plantations (Luskin & Potts 2011). In many insect groups, body size is a good proxy for mobility (Nieminen *et al.* 1999, Greenleaf *et al.* 2007, Kuussaari *et al.* 2014), but this relationship was not evident in our study, because boundary crossing was dominated by small Satyrinae species. Whilst we included Subfamily as a random factor in our models to control for phylogeny, it is likely that phylogenetic relatedness among species within the genus *Mycalesis* was an important determinant of edge crossing, and edge crossing ability may also have been influenced by common traits within this group that we did not consider (e.g. thermal tolerances, visual abilities suited to high light environments and ability to feed upon a diverse range of adult food sources).

Boundary crossing into plantations occurred less often in forest-dependent species whose larval host plants did not occur in plantations. Conversion of rainforest to oil palm plantations is accompanied by considerable changes in habitat structure, vegetation and microclimatic characteristics (Foster *et al*. 2011, Luskin & Potts 2011; see Appendix 1A: Table A1.1; Fig. A1.2 for habitat characteristics at forest boundaries at our study sites), which make plantations unsuitable for the persistence of many forest species (e.g. for ants: Fayle *et al*. 2010 and frogs: Gillespie *et al*. 2012, Gallmetzer & Schulze 2015). Oil palm plantations have more extreme diurnal temperature variation, higher light levels, increased evaporation rates and lower humidity compared with forest (Luskin & Potts 2011), and so forest-dependent species that prefer shaded, cooler conditions may actively avoid crossing boundaries. However, compared to other types of habitat boundaries (e.g. forest-grassland: see Ries & Debinski 2001, Rittenhouse & Semlitsch 2006, Schultz *et al.* 2012), structural differences between selectively-logged rainforest and oil palm plantations may be less severe. For example, mature oil palm plantations (>10 years) provide some shade cover (Table A1.1; Fig. A1.2), an understory shrub/herb layer (Aratrakorn *et al.* 2006), and support epiphyte species that are important for some forest species (e.g. birds: Koh 2008). In our study, some species with larval host plants restricted to forest were nonetheless captured in plantation in relatively high abundance, despite being recorded crossing the boundary less frequently than some species that could breed within the plantation matrix (Table 2.1). This implies that some forest-dependent species (e.g. *Charaxes bernardus* and *Dophla evelina;* Table 2.1) are more capable of crossing the boundary than we recorded, and hence may be able to move through the oil palm matrix, particularly strong fliers such as *C. bernardus* (S.A.S. pers. obs.).

Boundary crossing from forest to plantations is likely influenced by both internal (e.g. genetic dispersal cues and behaviour) and external factors (e.g. vegetation structure, abiotic conditions and habitat quality). Certain butterfly species have been shown to actively avoid habitat edges, and may respond by modifying their movement behaviour when within close proximity to the boundary, likely due to 'edge effects' penetrating the forest habitat (Haddad 1999, Ries & Debinski 2001). Our study focussed on butterflies, but active avoidance of rainforest edges has been shown by other tropical taxa (e.g. birds: Laurance 2004), and is likely to be particulary pronounced for forest species that are sensitive to changes in abiotic conditions (e.g. amphibians: Gillespie *et al*. 2012). Such behavioural avoidance of boundaries may arise if individuals use previous knowledge to avoid crossing habitat boundaries, or if individuals perceive sensory cues of changing habitat structure (Rittenhouse & Semlitsch 2006), e.g. light hue and polarisation (Douglas *et al.* 2007) as they approach the boundary. Our study grid sampled up to ~65 m from the boundary, and edge effects may have permeated even further into the forest (Ewers & Didham 2008). Thus, the area of forest habitat sampled in our study may have already been avoided by forest-dependent species, and this may explain the low diversity of species recorded in forest traps, and why we only recaptured a relatively small number of forest species during the study. In addition, butterflies show vertical stratification in forest habitats (Fordyce & DeVries 2016) and canopy species may have been under-represented in our ground-level forest traps (Dumbrell & Hill 2005).

There is little information on whether trap efficiency varies among habitat types for tropical butterflies. We captured more species and individuals in plantations, even though plantations have greatly reduced diversity compared with primary forest (Fitzherbert *et al*. 2008), and this might reflect increased efficiency of traps within plantations if there are fewer adult food sources in plantations. It is also possible that increased fermentation of the banana bait due to higher temperatures in plantations (see Appendix 1A: Fig. A1.2) may have increased the attractance of plantation traps, and this topic requires further study.

From of a total of 65 species captured during our study, there were only 17 species with multiple individuals recaptured in a different trap (of which larval host plant information was available for 16 species), and so our analyses of species traits were based on a relatively small number of species. In addition, the small number of species meant we could not include multiple species traits in models because of over-fitting, yet it is likely that there are interactions among traits that may affect movement (i.e. the smallest species are also the most abundant; Fig. 2.2). Our experimental design allowed us to examine general patterns of boundary crossing, but future work examining factors such as trap-location, distance from edge, 'hardness' of the edge, or time of day on boundary crossing would be interesting new topic areas for study.

2.5.2. Movement in forest versus plantation habitats

Forest individuals were more mobile than those in plantations. However, all our forest traps were relatively close to the forest edge, and so these mobility levels may not be representative of movement within closed-canopy interior forest. Over half of all species we marked were not subsequently recaptured, likely reflecting high mobility, large home ranges and lack of territoriality in our study species (Marchant *et al.* 2015), as well as short adult lifespans in some species potentially leading to low survival rates between recapture events. Tropical forest taxa typically have high species richness but occur at low density, and so high mobility detected in our study may reflect tracking of low density resources (e.g. host plants, mates). Species were apparently more sedentary in the plantation and tended not to cross into forest, which may reflect high availability of certain resources in oil palm plantations, leading to a few species achieving very high levels of abundance (e.g. *Amathusia phidippus* whose larvae feed on palms). Extremely high abundances of some species in oil palm plantations are also evident in other taxa such as termites (Hassall *et al.* 2006), birds (Senior *et al.* 2013) and rats (Wood & Fee 2003), where species presumably exploit hyper-abundant resources, such as palm fronds and fruit, present in plantations. Thus, species apparently modify their behaviour within plantations, being more sedentary and less likely to cross the boundary than when in forest.

2.5.3. Conservation implications

Our results suggest that boundary crossing was more frequent from forest into oil palm plantations and was dominated by species whose larval host plants occurred within the plantation matrix, and thus may be capable of breeding within plantations. Failure of forest-dependent species to cross plantation boundaries in high numbers may result in limited dispersal of these species through fragmented tropical agricultural landscapes, and these species are likely to become confined to increasingly isolated forest fragments. Future conservation effort to improve habitat connectivity may help to reduce extinction risks of species in isolated populations, and facilitate range shifting of species under climate change (Scriven *et al.* 2015/Chapter 3). Forest connectivity may also be improved by making non-forest areas more hospitable (Azhar *et al.* 2013), and by improving quality of remaining forest areas (Mair *et al.* 2014), thereby helping to reduce biodiversity losses in tropical agricultural landscapes.

2.6. Acknowledgements

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2.7. Data availability

The data used in this chapter are archived at the Dryad Digital Repository (doi:10.5061/dryad.2m19h).

Chapter 3 – Protected areas in Borneo may fail to conserve tropical rainforest biodiversity under climate change

Lowland rainforest-oil palm plantation boundary

3.1. Abstract

Protected areas (PAs) are key for conserving rainforest species, but many PAs are becoming increasingly isolated within agricultural landscapes, which may have detrimental consequences for the forest biota they contain. We examined the vulnerability of PA networks to climate change by examining connectivity of PAs along elevation gradients. We used the PA network on Borneo as a model system, and examined changes in the spatial distribution of climate conditions in future. A large proportion of PAs will not contain analogous climates in future (based on temperature projections for 2061-2080), potentially requiring organisms to move to cooler PAs at higher elevation, if they are to track climate changes. For the highest warming scenario (RCP8.5), few (11-12.5%; 27-30/240) PAs were sufficiently topographically diverse for analogous climate conditions (present-day equivalent or cooler) to remain in situ. For the remaining 87.5-89% (210-213/240) of PAs, which were often situated at low elevation, analogous climate will only be available in higher elevation PAs. However, over half (60-82%) of these PAs are too isolated for poor dispersers (<1 km per generation) to reach cooler PAs, because there is a lack of connecting forest habitat. Even under the lowest warming scenario (RCP2.6), analogous climate conditions will disappear from 61% (146/240) of PAs, and a large proportion of these are too isolated for poor dispersers to reach cooler PAs. Our results suggest that low elevation PAs are particularly vulnerable to climate change, and management to improve linkage of PAs along elevation gradients should be a conservation priority.

3.2. Introduction

Protected areas (PAs) have been established globally to help conserve biodiversity, and now cover over 10% of the Earth's land surface (Chape *et al*. 2005, Soutullo 2010). Targets under the Convention on Biological Diversity (CBD) aim to expand this protection to 17% by 2020 (CBD 2010). In tropical regions, current conversion of natural habitat to other land uses is particularly high, and PAs are especially important for protecting high levels of biodiversity (Curran *et al*. 2004, Klorvuttimontara *et al*. 2011, Laurance *et al*. 2012), but PAs are becoming increasingly isolated within human-modified landscapes (Curran *et al*. 2004).

Climate change drives geographic range shifts in plants and animals (Thomas 2010, Thomas *et al*. 2012), and tropical species are shifting to higher elevations in response to warming temperatures (Pounds *et al*.1999, Colwell *et al*. 2008, Chen *et al*. 2009, Chen *et al*. 2011b, Feeley *et al*. 2011, Forero-Medina *et al*. 2011, Laurance *et al*. 2011, Freeman & Class Freeman 2014). Rainfall may also affect the responses of tropical species to climate change (Colwell *et al*. 2008, Corlett 2012), although future projections are more uncertain for precipitation than for temperature (Corlett 2011, 2012, IPCC 2013). Species' abilities to shift their ranges will also be limited by the availability and distribution of suitable habitat (Chen *et al*. 2009, Hodgson *et al*. 2009, Feeley & Silman 2010b), and species that fail to shift their ranges may face increased likelihood of extinction (Thomas *et al*. 2004). The effectiveness of PAs to conserve tropical species under climate change has been questioned (Marini *et al*. 2009, Klorvuttimontara *et al*. 2011, Vieilledent *et al*. 2013), and if the connectivity of PAs is reduced due to land-use change, it may become difficult for species to track climate changes and move between PAs. In temperate regions, PAs have been shown to be effective in facilitating latitudinal range expansions (Thomas *et al*. 2012), but the effectiveness of PAs to conserve tropical biota responding to climate changes along elevation gradients has received little attention.

We address this issue by studying PAs on Borneo. As is typical of tropical regions across Southeast Asia, Borneo is extremely biologically diverse but facing severe pressure due to loss of forest habitats. Rainforest now covers only approximately 50% of Borneo, with most extensive areas of remaining forest occurring in the central montane region and many coastal forest areas now fragmented and isolated due to conversion to oil palm

(*Elaeis guineensis* Jacq.) plantations (Proctor *et al*. 2011). Lowland Dipterocarpaceae forests support exceptionally high levels of species diversity, and in many low-lying areas remaining dipterocarp forest is confined to PAs, which are therefore vital for conserving rainforest species within human-modified landscapes (Curran *et al*. 2004). Protection is clearly important to prevent habitat conversion, but the extent to which PAs are sufficiently well connected to allow biota to move between them in order to track climate change is unknown.

We examined the connectivity of PAs along elevation gradients using a spatially-explicit metapopulation model (Incidence Function Model (IFM); Hanski 1994). We focus specifically on temperature changes, based on current empirical evidence from tropical studies (e.g. Laurance *et al*. 2011, Freeman & Class Freeman 2014) and the limited understanding of species' responses to other climate variables. We do not model responses of individual species because distribution data are very incomplete for tropical taxa, and often available only for iconic species (e.g. Struebig *et al*. 2015a), and so we describe changes in the distribution of climate conditions within PAs and the connectivity of PAs (e.g. see Ohlemüller *et al*. 2006, Ackerly *et al*. 2010). We determined which PAs will not retain analogous climate conditions (present-day temperature or cooler) in future and the characteristics of these PAs (area, mean elevation and amount of forest in the surrounding landscape). Organisms in these PAs may need to reach cooler PAs if they are to keep track of climate, and we modelled whether or not PAs are sufficiently well connected for organisms to successfully reach cooler PAs at higher elevation (for different dispersal abilities, population densities and forest covers within PAs). We ran models primarily for the highest ('business-as-usual') warming scenario (IPCC Fifth Assessment Report (AR5), RCP8.5), but compared our results with the lowest ('mitigation') warming scenario (RCP2.6), to highlight common patterns.

3.3. Methods

3.3.1. Data sources

The locations of PAs on Borneo (IUCN; World Conservation Union) were downloaded from the World Database of Protected Areas (WDPA; http://www.protectedplanet.net; including designated and proposed PAs, but excluding offshore islands). Only PAs that had complete boundaries were used, and PAs that were duplicated or overlapping other PAs were excluded. Forest cover was obtained at a grid cell resolution of 250 m (Miettinen *et al*. 2012). We extracted data for peatswamp forest, lowland forest, and lower and upper montane forest, subsequently termed ‘forest’, and all other remaining land categories were termed ‘non-forest’. Our ‘forest’ category included selectively logged forests that have reached structural characteristics similar to those of primary forest. Elevation data as well as current and future annual climate data for 1950-2000 and 2061-2080 were obtained (http://www.worldclim.org) at a 30 arc-second grid cell resolution. We used a nearest neighbour interpolation method to convert gridded climate and elevation data from 30 arc second resolution (approx. 0.86 km grid) to 1 km grid cells. Future climate data were for IPCC AR5 Representative Concentration Pathways (RCP) 8.5 and 2.6, HadGEM2-AO general circulation model (GCM). RCP8.5 represents the most severe (‘business-as-usual’) IPCC scenario, and projects global mean surface temperature to increase between 2.6-4.8°C in 2081-2100, relative to 1986-2005; whilst RCP2.6 represents the least severe (‘mitigation’) scenario (0.3-1.7°C increase) (IPCC 2013). RCP8.5 predicts mean temperature for Borneo to rise by 3.2°C (mean difference between 1950-2000 annual mean temperature and 2061-2080 predicted annual mean temperature at a 1 km grid cell resolution), whereas RCP2.6 predicts a rise of only 0.9°C (Appendix 2A) (Appendix 2B shows precipitation projections for Borneo for these scenarios).

Gridded annual temperature data from 1950-2000 (current) and 2061-2080 (future) were used in our model simulations (see section 2.3 below) at a 1 km grid cell resolution. Forest grid cells at 250 m resolution were also converted to 1 km grid cells, and assigned a value between 0-16 representing the number of aggregated 250 m forest cells within each 1 km grid cell. Each 1 km forest grid cell was also specified as ‘protected’ or ‘not protected’ depending on whether or not it fell within a PA polygon. Small PAs <1 km^2 (29 PAs in total) were represented by a single 1 km grid cell. For PAs that contained no forest according to Miettinen *et al*. (2012), we added one 250 m forest grid cell to the centre of each PA so that all PAs could be included in our simulations.

3.3.2. PA characteristics

All spatial data were analysed in ArcGIS Version 10. WDPA listed 223 PAs, corresponding to 240 spatially independent polygons, and so we based our subsequent analyses on these 240 PA units (henceforth termed PAs). For each PA we calculated the area (km^2), the percentage of forest it contained, mean elevation (m a.s.l.), elevation range (m), current (1950-2000) mean temperature range (°C), and percentage of forest in a surrounding 10 km buffer (‘surrounding forest’), all at a 250 m (62,500 m^2) grid cell resolution.

3.3.2.1. Source and refuge PAs

We described the spatial distribution of climate conditions within PAs, and categorised PAs into ‘source’, ‘refuge’ or ‘target’ PAs in relation to whether or not analogous climate conditions were projected to remain in PAs in future (using predicted temperature of forested grid cells within PAs in 2061-2080). The current (1950-2000) mean temperature of forested grid cells within each PA was used as our measure of climate conditions. If a PA contained at least one forested grid cell in future that was cooler than, or the same as, the current mean temperature of forested grid cells within the PA, we assumed that analogous climate conditions remained in situ, and so we did not examine connectivity of these PAs (termed ‘refuge’ PAs) to other PAs. For all other PAs, termed ‘source’ PAs, we carried out simulations to determine whether or not organisms from these PAs could reach cooler ‘target’ PAs. Target PAs were defined as PAs containing analogous climate conditions in future; i.e. protected and forested grids cells with temperatures that were cooler than, or the same as, the current mean temperature of the focal source PA. In this way, each source PA had its own specific set of target PA grid cells. Thus, our approach focused on whether PAs were projected to lose analogous climate conditions in future, and if so, whether connectivity of PAs was sufficient to facilitate organisms moving from source PAs to cooler target PAs. Therefore, we examined the connectivity and relative vulnerability of PAs to climate change impacts, based on changes in the locations of analogous climate conditions, and in the absence of species-specific information required for climate-envelope modelling (e.g. Thomas *et al*. 2004).

3.3.3. Modelling PA connectivity with the IFM

We used a patch-based metapopulation model (IFM; Hanski 1994) (R code in Appendix 2C) to examine connectivity of source and target PAs. The IFM assumes that (a) extinction risk of populations in grid cells is inversely related to population size and habitat patch area (amount of forest cells at a 250 m grid cell resolution contained within a 1 km grid cell), and (b) colonisation probability of forest habitat patches within grid cells is positively related to habitat patch connectivity; where connectivity is a function of the distance to other occupied forest cells and the amount of forest they contain (Hanski, 1994). Specifically, connectivity (S_i) for a habitat patch (a spatially discrete forest grid cell(s)) *i*, is defined as:

$$A_i \frac{R\alpha^2}{2\pi} \sum_{j \neq i} p_j A_j \, e^{-\alpha d_{ij}}$$

where *A* = area of habitat (km^2) in cell *i* or *j*, *R* = population density (number of emigrants produced per generation per occupied km^2 grid cell), α = slope of a negative exponential dispersal kernel, p_j = occupancy of *j* (1 if cell *j* is occupied, 0 if not) and d_{ij} is the Euclidean distance between the centre of cells *i* and *j*. As our measure of PA connectivity, we simulated the likelihood of individuals successfully reaching cooler target PAs from every source PA, at a 1 km grid cell resolution.

Model simulations were run separately for each source PA, with the focal source PA initially occupied (i.e. seeding all forest grid cells at maximum carrying capacity) at the start of each simulation. Movement of organisms from source PAs could potentially occur in any direction, organisms could reproduce in forest grid cells on route to the target PA regardless of whether or not the forest was protected, but we constrained reproduction to occur only in forested cells that were cooler than, or the same as the current (1950-2000) mean temperature of forest grid cells in the focal source PA (Fig. 3.1). Thus, organisms were constrained to disperse to target PAs through forest habitats that were not hotter than the PA they were leaving. We assumed that dispersal could occur across non-forest areas, but that organisms did not survive if they landed in a non-forest grid cell. For each source PA the model simulation could be unsuccessful, when a target PA was not reached (Fig. 3.1a), or successful, when a target PA was reached (Fig. 3.1b).

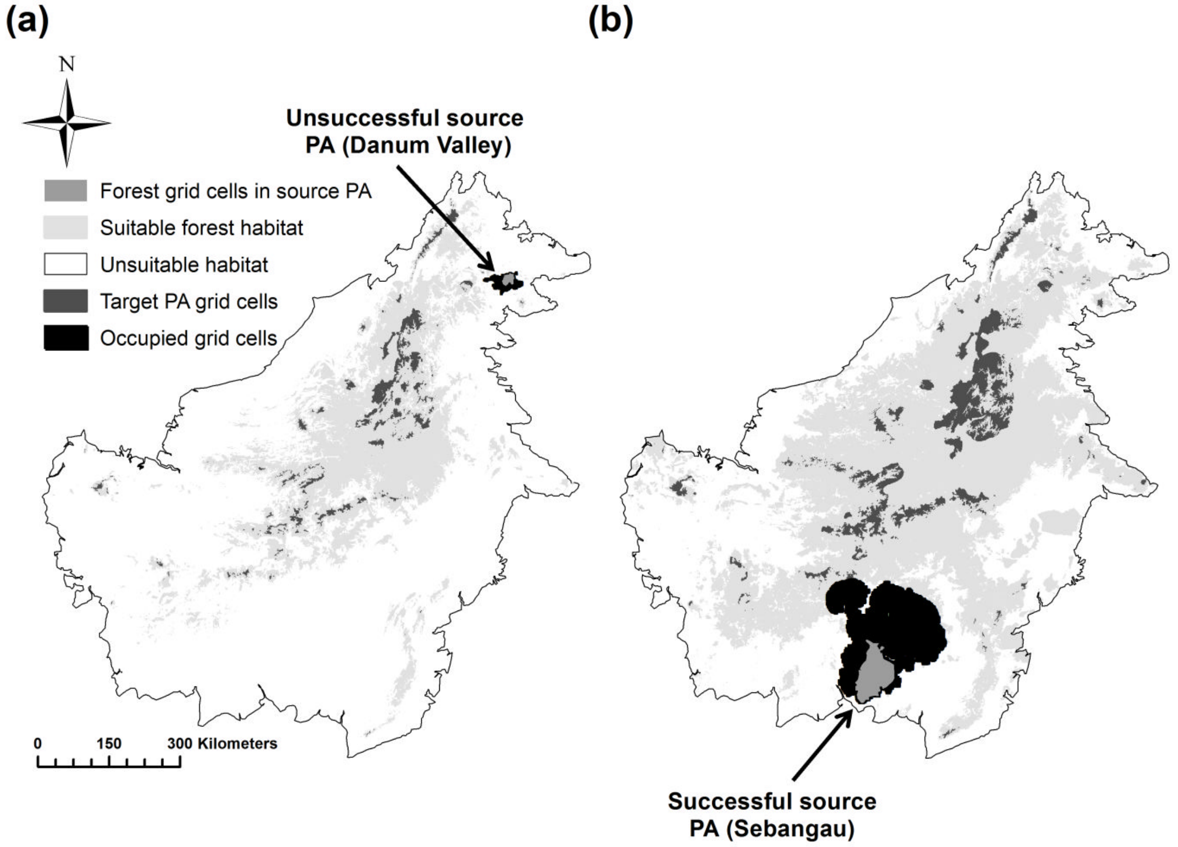

Figure 3.1. Examples of simulations illustrating the connectedness of two source PAs (RCP8.5 temperature projections). In (a) individuals did not reach a cooler target PA grid cell within 600 generations, whilst in (b) individuals reached a target PA grid cell after 55 generations. Simulations assumed 1 km dispersal ability, a population density of 125 individuals per 250 m forest grid cell and 100% forest cover within all PAs. Medium grey shading = forested grid cells within the source PA from which populations were seeded; light grey = forested grid cells containing analogous climate conditions, i.e. that were the same temperature, or cooler, than the current (1950-2000) mean temperature of the PA, and through which organisms could potentially disperse to reach a target PA; white = unsuitable habitat, either non-forest grid cells, or forested grid cells that were too warm; dark grey = target PA grid cells, and black = occupied grid cells.

3.3.3.1. Future climate scenarios, dispersal, and model parameter values

Using RCP8.5 temperature projections, we varied population density in occupied habitat and dispersal ability (representing plausible parameter ranges for winged invertebrates, e.g. tropical butterflies; Benedick *et al*. 2006, 2007b). Population density was set as either 12.5, 125 or 1250 individuals per 250 m forest grid cell (corresponding to 2, 20 and 200 individuals per ha^{-1}). Dispersal ability was varied by altering α (the slope of a negative exponential dispersal kernel) within the model (Hodgson *et al*. 2011). We examined 10 dispersal values corresponding to maximum dispersal distances from 0.5 to 10 km per generation, spanning a wide range of mobilities. Tropical butterflies can develop through 6 generations y^{-1} (Azerefegne *et al*. 2001), and so we ran models for 600 generations to represent approximately 100 years of climate warming. Whilst we assume six generations per year, species with fewer generations per year are likely to take much longer to reach target PAs, and so our findings may be conservative for these types of organisms. The amount of forest within each 1 km grid cell was multiplied by the population density to estimate the carrying capacity of each cell, and the extinction probability was 1/carrying capacity of each habitat patch at each time step (generation). In order to assess the degree to which forest management within PAs might benefit conservation we examined two forest cover scenarios; assuming current levels of forest cover within PAs, and assuming forest cover in all PAs was improved to 100%. Increasing forest cover to 100% caused three source PAs to become refuge PAs. A total of 34,873 km^2 (in 250 m grid cells) was added to PAs to increase forest cover to 100%; this corresponded to 10% of existing forest cover on Borneo.

In total, for each source PA, we ran models for 10 dispersal scenarios, three population densities and two forest cover scenarios (i.e. 60 treatments in total per source PA). Our model is stochastic and so we ran five repeat runs for each treatment (i.e. 300 simulations per source PA in total). Model simulations were terminated once any individual reached a target PA grid cell, or if the seed population failed to expand, or went extinct, or after a maximum of 600 generations (i.e. 100 years). Only when a target PA had been reached in three or more of the five repeat runs, did we consider the outcome ‘successful’. To assess the impact of different warming scenarios, we also ran models using RCP2.6

temperature projections. We simulated expansion from source PAs for all dispersal distances, but only one population density (125 individuals per 250 m forest grid cell), and one landcover scenario (100% forest cover in PAs; i.e. 10 treatments per source PA for RCP2.6). The number of source and refuge PAs was dependant on the RCP scenario (RCP8.5 and 100% forest cover; refuge PAs =30, source PAs = 210; RCP2.6 and 100% forest cover; refuge PAs = 94, source PAs = 146).

3.3.4. Analysis of model outputs

All statistical analyses were performed in R statistical software, version 3.0.2. We used a Generalised Linear Model (GLM, binomial logistic regression), with a logit link function and binomial error distribution to analyse whether individuals successfully reached target PAs from source PAs for each of the 60 model treatments for the RCP8.5 warming scenario. Population density (3 categories), forest cover in PAs (current/100%), and dispersal distance (10 values, continuous variable) were included as predictor variables of connectivity success/failure. To evaluate the importance of each parameter on connectivity, we calculated partial McFadden's r^2 values (Menard 2000) for each predictor by sequentially removing the variable of interest from the model and comparing the change in the r^2 between the full model and reduced model. For each source PA in the RCP2.6 warming scenario, we ran models for 10 dispersal distances, one population density and one forest cover scenario (i.e. 10 treatments and 50 simulations per source PA). To examine the importance of RCP scenario in relation to dispersal ability on connectivity success/failure, we used a GLM (binomial logistic regression), with a logit link function and binomial error distribution. We included 20 model treatments, comprising RCP scenario (2 categories) and dispersal distance (10 values, continuous variable), which were both included as predictor variables of success/failure. We calculated partial McFadden's r^2 values to determine the importance of each parameter.

We also used GLMs (binary logistic regression) to examine the probability of a source PA being connected to a target PA ('successful' versus 'unsuccessful' movement of individuals; RCP8.5 scenario) in relation to PA elevation, area, and percentage cover of forest within a 10 km buffer zone surrounding the source PA boundary (termed 'surrounding forest'). We computed the percentage of forest within a 10 km buffer zone to coincide with maximum dispersal distance examined in our models. We also included the straight-line distance (km) of the source PA to the nearest target PA to account for the spatial locations of source and target PA grid cells. We analysed the characteristics of successful versus unsuccessful source PAs separately for each dispersal distance (0.5-10 km). We used a binomial error distribution and a probit link function, which consistently provided the lowest AIC and residual deviances. We also square root transformed data for surrounding forest cover to improve model parsimony. In order to improve the interpretation of regression coefficients, all predictor variables were centred and standardised (Schielzeth, 2010), and 95% confidence intervals were calculated for each coefficient estimate. To control for effects of variation in forest cover within PAs, we only analysed data from simulations with 100% forest cover in all PAs (n = 210 source PAs). We also only analysed outputs for models with intermediate population density (125 individuals per 250 m forest grid cell). To evaluate the importance of each parameter on determining the connectivity of PAs, we calculated partial McFadden's r^2 values for each predictor.

3.4. Results

3.4.1. PA characteristics

There is considerable variation in the topography of PAs on Borneo; mean elevation range of the 10% of PAs (n = 24) with the lowest topographical heterogeneity is 3.1 m, but 1536.8 m for the most heterogeneous 10% of PAs (Fig. 3.2). The 10% of PAs with the lowest topographical heterogeneity had a current mean temperature range of 0.1°C, compared with 8.4°C for the most heterogeneous 10% of PAs. As mean elevation of all PAs (including both sources and refuges) increased, surrounding forest around each PA increased (Spearman correlation: $r_s = 0.53$, $n = 240$, $p < 0.0001$), as did percentage forest within PAs ($r_s = 0.58$, $n = 240$, $p < 0.0001$) and PA area (km^2) ($r_s = 0.18$, $n = 240$, $p = 0.004$), consistent with the fact that higher elevation forests on Borneo are more likely to be intact and protected (Appendix 2D).

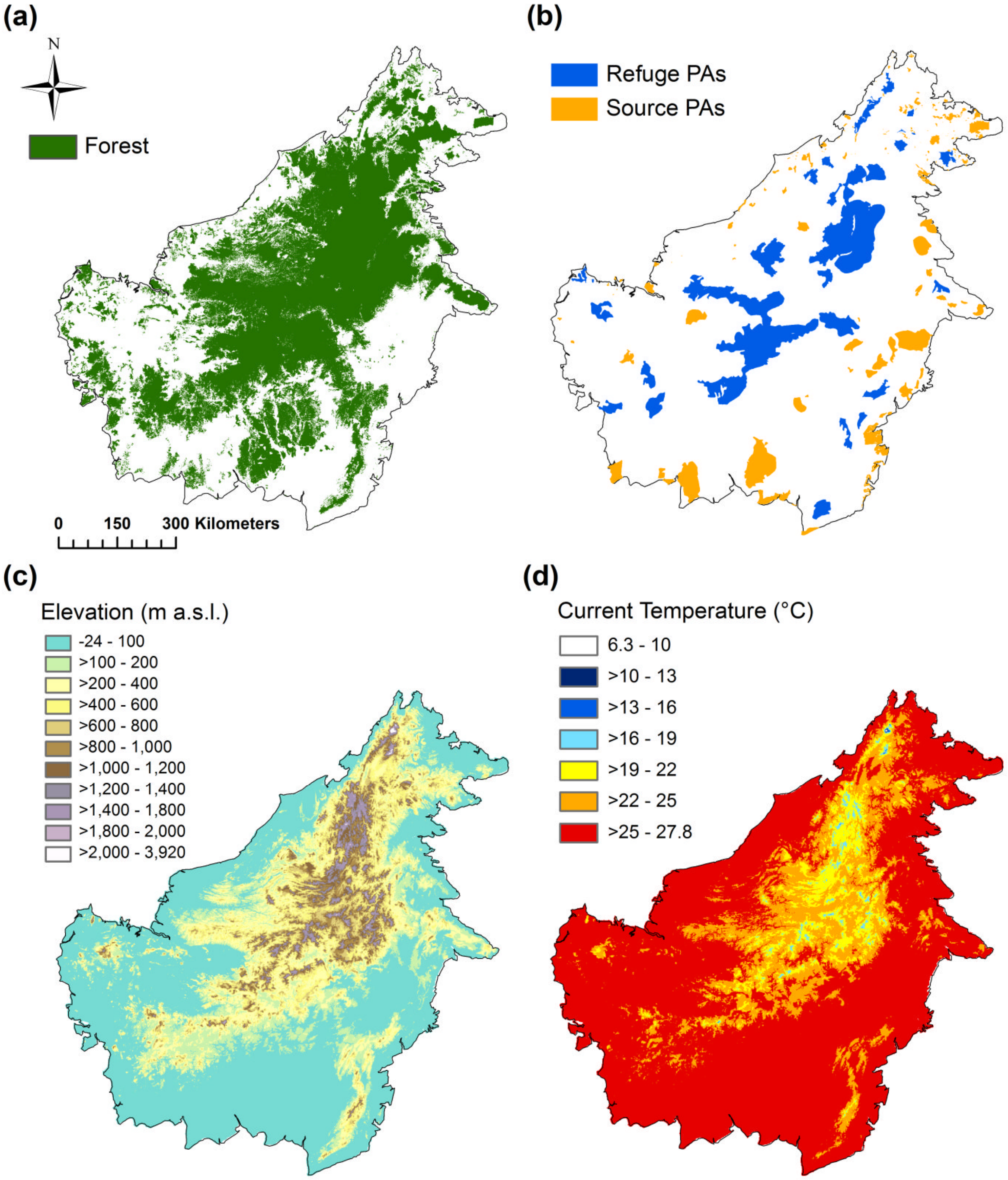

Figure 3.2. Maps of Borneo showing baseline data for simulations. (a) Distribution of forest cover (250 m grid cell resolution), where approximately 48% remains; (b) locations of refuge and source PAs (see main text for definitions; assuming current forest cover within PAs and using RCP8.5 temperature projections), which cover approximately 16% of Borneo's total land area; (c) elevation (1 km grid cell resolution); and (d) current (1950-2000) temperature (1 km grid cell resolution).

3.4.1.1. Source and refuge PAs

Our analyses of the RCP8.5 temperature projections revealed that only 11-12.5% (27-30/240; current and 100% forest cover in PAs, respectively) of PAs were refuges and the vast majority of PAs (87.5-89%; 213/240) were source PAs (Fig. 3.2b), which will not retain analogous climate conditions in future, and from which individuals may need to move if they are to track future climate change and reach cooler locations. Under the RCP2.6 scenario (assuming 100% forest cover in PAs), slightly more PAs were refuges (39%; 94/240) but again, the majority of PAs were source PAs. Source PAs were generally much smaller than refuge PAs, situated at lower elevation, and with low topography (Appendix 2E).

3.4.2. Simulations of PA connectivity

Dispersal ability was the most important factor determining whether or not a source PA was connected to a target PA (partial McFadden r^2 = 0.843), and forest cover within PAs (current or 100% cover; partial McFadden r^2 = 0.095), population density (partial McFadden r^2 = 0.029) and RCP scenario (partial McFadden r^2 = 0.978 for dispersal versus r^2 =0.003 for RCP) were less important. The relationship between PA connectivity and dispersal ability was non-linear for both RCP scenarios, initially increasing rapidly with increased dispersal, but then reaching an asymptote where further increased dispersal ability had little additional impact on the success of dispersers (Fig. 3.3).

Across all RCP8.5 model scenarios (60 treatments) the percentage of source PAs connected to target PAs ranged from a minimum of 18% (n = 39/213 PAs; lowest forest cover, dispersal and density treatments) to a maximum of 99% (n = 208/210 PAs; highest forest cover, dispersal and density treatments) (Fig. 3.3a). Across these scenarios, 60-82% of source PAs were not successfully connected to target PAs for the poorest dispersers (<1 km dispersal ability), depending on forest cover and population density values (Fig. 3.3a; Appendix 2F: Table A2.2). Figure 3.4 shows the minimum dispersal ability required for organisms to reach a target PA from each source PA, and shows the three PAs which were never connected to target PAs even at the highest (10 km per generation) dispersal ability.

The time taken (in generations) to reach target PAs generally decreased with increasing dispersal ability (Fig. 3.3b). Improving forest cover within PAs to 100% increased the percentage of source PAs connected to target PAs by 6-30%, depending on population density and dispersal ability (Fig. 3.3a). Reforestation within PAs had the greatest benefit on source PA connectedness when organisms with low population densities and/or intermediate dispersal abilities were used (Fig. 3.3a).

In the RCP2.6 scenario, the percentage of source PAs connected to target PAs ranged from a minimum of 36% (*n* = 53/146 PAs; lowest dispersal treatment) to a maximum of 100% (*n* = 146/146 PAs; highest dispersal treatments) (Fig. 3.3c). However, the majority (61-64%) of source PAs were not connected to target PAs for poor dispersers (<1 km dispersal ability; Fig 3.3c), highlighting the vulnerability of many PAs under even the lowest warming scenario. Overall, there was little difference in success rates of dispersers between the lowest or highest RCP scenarios (Fig. 3.3c; difference ranged from -0.9% to +6%), or the time taken to reach target PAs (Appendix 2F: Figure A2.5).

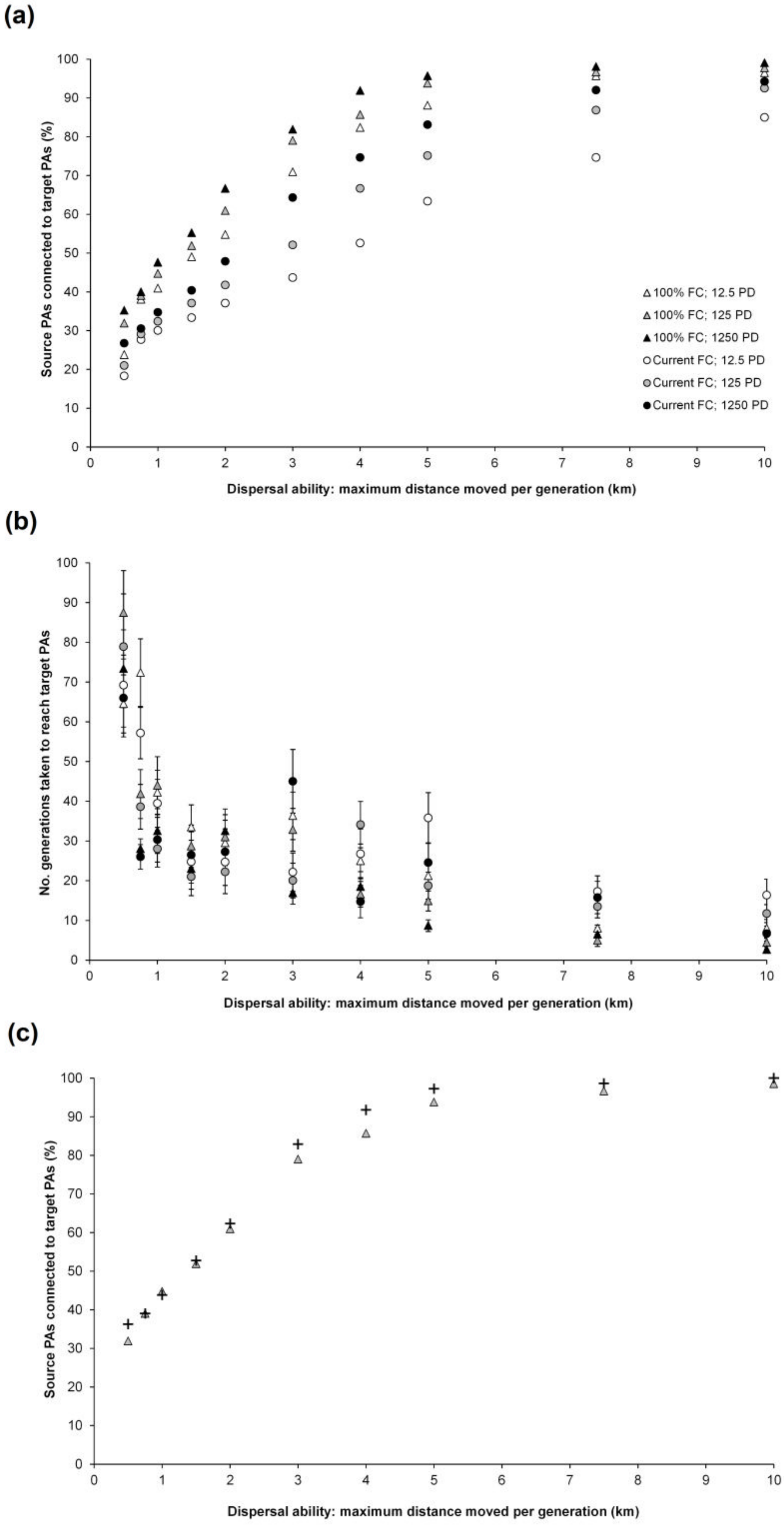
(a)
Source PAs connected to target PAs (%)
0
10
20
30
40
50
60
70
80
90
100
Dispersal ability: maximum distance moved per generation (km)
0
1
2
3
4
5
6
7
8
9
10
△ 100% FC; 12.5 PD
△ 100% FC; 125 PD
▲ 100% FC; 1250 PD
○ Current FC; 12.5 PD
● Current FC; 125 PD
● Current FC; 1250 PD
(b)
No. generations taken to reach target PAs
0
10
20
30
40
50
60
70
80
90
100
Dispersal ability: maximum distance moved per generation (km)
0
1
2
3
4
5
6
7
8
9
10
(c)
Source PAs connected to target PAs (%)
0
10
20
30
40
50
60
70
80
90
100
Dispersal ability: maximum distance moved per generation (km)
0
1
2
3
4
5
6
7
8
9
10

Figure 3.3. Incidence function model (IFM) outputs. (a) Percentage of source PAs (current forest cover (FC): *n* = 213; 100% forest cover: *n* = 210) connected to cooler target PAs for organisms with different dispersal abilities and population densities (PD) (individuals per 250 m forest grid cell) (RCP8.5 temperature projections); (b) mean number of elapsed generations for organisms at each dispersal distance to reach cooler target PAs (of those successful in Fig. 3.3a); standard error bars illustrate the error across all successful source PAs at each dispersal distance; and (c) percentage of source PAs (100% forest cover; 125 individuals per 250 m forest grid cell) connected to cooler target PAs for organisms with different dispersal abilities under the low (RCP2.6) (crosses; *n* = 146) and high (RCP8.5) warming scenarios (triangles; *n* = 210). Ten dispersal distances were examined (see Table 3.1; 0.5 km - 10 km per generation).

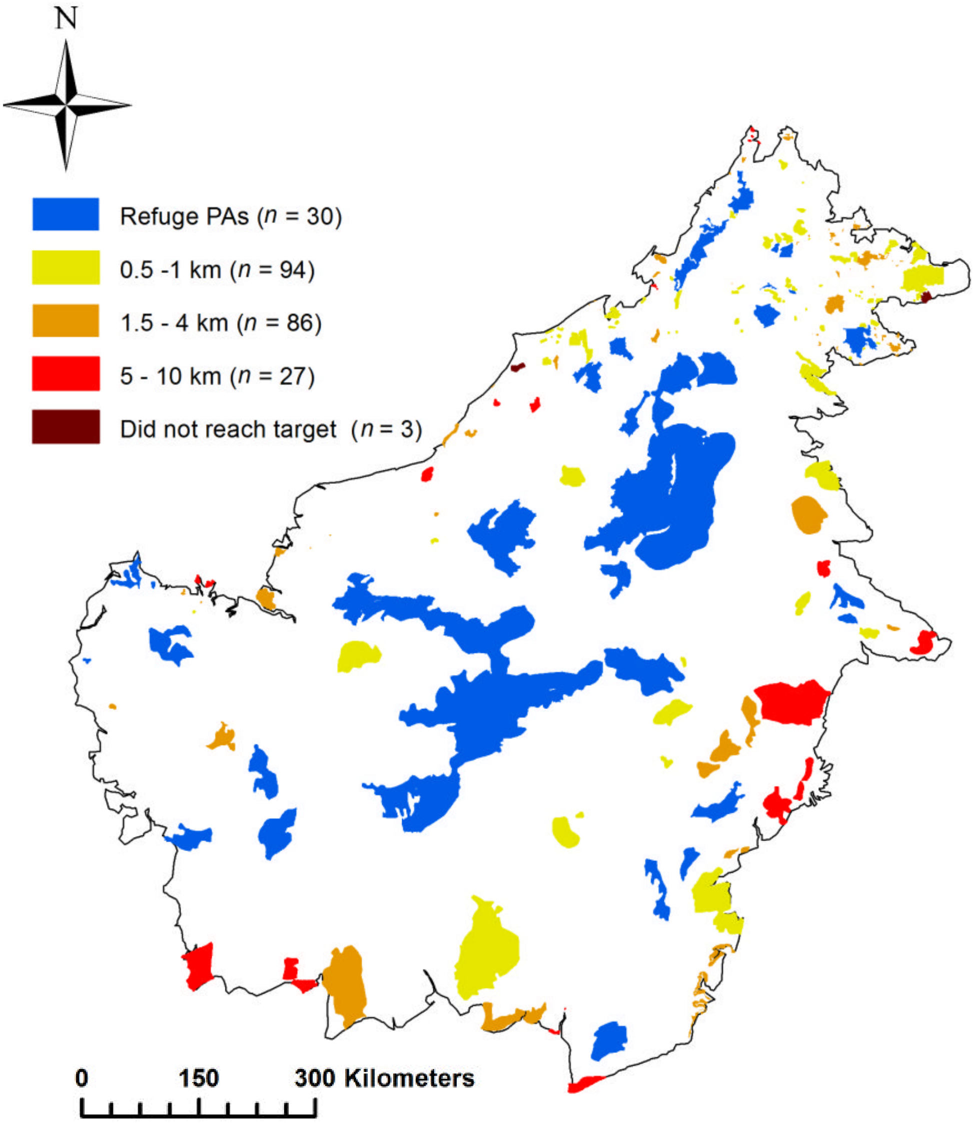

Figure 3.4. Map of Borneo showing location of refuge (*n* = 30) and source PAs (*n* = 210). Source PAs are shaded according to the minimum dispersal ability required for individuals to successfully reach target PAs (assuming 100% forest cover in PAs, a population density of 125 individuals per 250 m forest grid cell and using RCP8.5 temperature projections).

3.4.3. Characteristics of successful and unsuccessful source PAs (RCP8.5 scenario)

The relative importance of elevation, area, distance to nearest target PA and surrounding forest on the likelihood of a source PA being connected to a target PA (*n* = 210 source PAs) differed according to dispersal ability. For organisms with low-medium dispersal abilities (≤4 km per generation) surrounding forest was most important for source PA connectivity, followed by distance to target PA, while elevation and area of source PAs were of less importance (Table 3.1). Thus, for organisms with poorer dispersal ability, source PAs were more likely to be connected if they were surrounded by high forest cover and the target PA was nearby. At intermediate dispersal distances, surrounding forest became less important for connectivity, and straight-line distance to target PA increased in importance. In simulations with highly mobile organisms (≥5 km per generation), source PAs were nearly always connected regardless of the characteristics of the PAs (Table 3.1).

Table 3.1. Standardised regression coefficients and McFadden's partial r^2 values from binary logistic regression models of whether or not source PAs (n = 210) were connected to target PAs for organisms with different dispersal abilities. The analysis assumed 100% forest cover in PAs, a population density of 125 individuals per 250 m forest grid cell and used RCP8.5 temperature projections

		No. of connected source PAs (/210)	**Predictors in model**							
			Area (km^2)		**Surrounding forest (%)**		**Mean elevation (m a.s.l)**		**Distance to target (km)**	
Dispersal[a]	**α**[b]		**Coefficient**	**r^2**	**Coefficient**	**r^2**	**Coefficient**	**r^2**	**Coefficient**	**r^2**
0.5	9.40	67	0.168	0.008	1.059*	0.309	-0.213*	0.016	-0.300*	0.023
0.75	6.27	82	0.203	0.010	1.203*	0.337	-0.226*	0.015	-0.543*	0.066
1	4.70	94	0.170	0.007	1.244	0.334	-0.283*	0.020	-0.676*	0.096
1.5	3.13	109	0.327*	0.019	1.386*	0.335	-0.286*	0.016	-1.005*	0.171
2	2.35	128	0.197	0.009	1.210*	0.280	-0.362*	0.027	-0.896*	0.168
3	1.57	166	0.076	0.001	1.538*	0.271	-0.524*	0.032	-0.879*	0.186
4	1.18	180	0.068	0.002	1.113*	0.188	-0.419*	0.027	-0.652*	0.145
5	0.94	197	0.032	0.001	0.844*	0.127	-0.476*	0.058	-0.602*	0.163
7.5[c]	0.63	203	-	-	-	-	-	-	-	-
10[c]	0.47	207	-	-	-	-	-	-	-	-

[a] Maximum dispersal distance (km)

[b] Slope of negative exponential dispersal kernel

[c] Results from GLMs not computed due to small number of unsuccessful source PAs (i.e. very high connectivity in all simulations).

[*] 95% confidence intervals that do not overlap with zero

3.5. Discussion

3.5.1. Characteristics of PAs

Climate change is resulting in the distributions of tropical species shifting to higher elevations (Corlett 2011, 2012, Freeman & Class Freeman 2014). Protected areas are vital for in situ biodiversity conservation (Chape *et al*. 2005), but our Borneo study highlights the isolation of many low-lying PAs. The majority (60-82%) of source PAs under the highest warming scenario (RCP8.5) were not connected to target PAs for poor dispersers (i.e. <1 km per generation), meaning that poor dispersers may fail to reach cooler PAs at higher elevation from these PAs. Broadly similar findings were also evident for the lowest scenario (RCP2.6), despite a much lower predicted temperature change. Even though more than 16% of Borneo’s land area is currently protected, and more than 48% still covered in forest (Fig. 3.2), our study reveals that populations of forest species within many lowland PAs on Borneo may be isolated from cooler locations in future and so could be vulnerable to climate change (Appendix 2G). Poor dispersers, which may represent a high proportion of tropical species, may be particularly vulnerable to the consequences of low connectivity of PAs.

Assuming full forest cover in PAs, our study suggests that 61-87.5% of PAs on Borneo may not be sufficiently topographically diverse to retain analogous climate conditions in future*,* even under low levels of warming. These source PAs with low topographic diversity were primarily in low-lying areas, often close to the coast and in regions where most conversion to oil palm plantations has occurred (Reynolds *et al*. 2011). Thus, in order to track climate, we predict that populations of forest species within these PAs will have to cross large expanses of inhospitable agricultural habitat, which may be barriers to dispersal for many species. Failure of organisms to track climate may result in local extinctions of range-restricted species as climate conditions become unsuitable for them (Deutsch & Tewksbury 2008). Low connectivity of PAs may also reduce gene flow and genetic diversity of populations, and/or reduce the distribution extent of species depending on their thermal limits in relation to the location of source and target PAs (Appendix 2G). Our study has focussed on temperature, but other climate variables such as precipitation may also determine the viability of populations of tropical species in PAs (Colwell *et al*. 2008, Corlett 2012), and species in locations that become both too hot and too dry may be particularly vulnerable, although future precipitation changes are uncertain (Appendix 2B). Thus, biodiversity may decline in many low-lying regions, especially if there is no pool of colonising species adapted to higher temperatures/drier conditions to replace species shifting uphill (Colwell *et al*. 2008). If species fail to extend their leading-edge range margins uphill, the species richness of sites at intermediate and higher elevation may also decline as trailing-edge margins of montane species retract upslope (Chen *et al*. 2009, Freeman & Class Freeman 2014); therefore, improving linkage of PAs along elevation gradients may help conserve regional tropical diversity.

3.5.2. Factors affecting PA connectivity

The amount of forest surrounding source PAs was important in influencing whether or not they were connected to cooler target PAs, and neither PA size nor mean elevation strongly influenced connectivity if the PA had little surrounding forest habitat (Table 3.1). Therefore, whilst cooler, higher elevation PAs appeared to be well located to receive organisms from warmer habitats, many low-lying PAs were topographically homogeneous and too isolated from tracts of continuous forest or patches of stepping stone habitats linking to cooler habitats. Whilst our analysis specifically focused on Borneo, similar patterns are likely elsewhere. In Thailand for example, extensive areas of forest at high elevation are protected, but organisms in low-lying areas are likely to experience similar difficulties reaching higher elevations from isolated PAs (Klorvuttimontara *et al*. 2011); similarly, PAs in Sumatra also tend to be at higher elevations (Gaveau *et al*. 2009). Other studies in Southeast Asia have shown that upland and montane rainforests have encountered relatively low levels of deforestation compared with lowland areas (Miettinen *et al*. 2011, Margono *et al*. 2014, Miettinen *et al*. 2014), and so our findings concerning low connectivity of low-lying PAs are likely to be relevant throughout the region.

3.5.3. Conservation implications

Source PAs that were not connected to cooler target PAs were primarily located around the coastal regions of Borneo. This finding is worrying because low-lying forests not only contain high numbers of endemics, but also contain the majority of vertebrate species (Curran *et al*. 2004); species richness of some taxa can also peak at low elevation (Ashton 2010). For example, 50% of the 40 endemic Bornean bird species and over 35% of endemic mammal species depend upon lowland forests (MacKinnon *et al*. 1996, Lambert & Collar 2002). Highest tree diversity is also found at low elevation (<300 m a.s.l.) along with high levels of dipterocarp endemism (Ashton 2010). In many lowland landscapes, little forest habitat now remains outside of PAs and so they are increasingly important strongholds for biodiversity in these regions (Curran *et al*. 2004).

The inaccessibility and remoteness of central Borneo means that extensive tracts of relatively undisturbed forest remain at high elevation, of which a large proportion is protected (Appendix 2D). Thus, the future prospects for conserving low-mid elevation species under threat from climate change that reside within, or are well connected to, this central montane region remain promising, as long as current levels of forest cover outside PAs remain. An analysis to examine consequences of loss of all forest outside current PAs, suggests that connectivity of source PAs could decrease by up to 50% under a worse-case deforestation scenario (Appendix 2H). Species with high dispersal abilities (>5 km) may still be able to track climate, providing that the agricultural matrix does not prevent dispersal across the landscape, but most lowland species with poor dispersal abilities will fail to track climate due to lack of forest. Therefore, conservation efforts should also focus on the preservation of remaining forest outside PAs, which often retains high biodiversity value (Edwards *et al*. 2011b), including the increased protection of forest ‘corridors’ that play an important role in linking forest areas along elevation gradients.

Replanting and forest management may be required to improve connectivity in some very heavily degraded landscapes, and our study suggested that improving forest cover within existing PAs increased PA connectivity by up to 30% in some instances (Fig.3.3a). Improving habitat quality and increasing population growth rates of species within PAs may help promote dispersal (Mair *et al*. 2014). Thus, forest management within existing PAs may be more cost-effective in the immediate term given the high economic returns from oil palm plantations. However, certification criteria for sustainable oil palm agriculture require riparian forest strips and 'High Conservation Value' (HCV) forest areas to be retained within plantations (RSPO 2013). Such forest fragments may help link PAs in human-dominated landscapes; although studies that address this issue are lacking.

3.5.4. Conclusions

Assuming our findings for Borneo are typical for many parts of Southeast Asia, we conclude that analogous climate conditions will disappear from a large number of tropical PAs, particularly those in the lowlands, even under modest warming. PAs are crucial for preserving tropical biodiversity in human-modified landscapes, but low connectivity of PAs will mean that many forest-dependent species, particularly poor dispersers, may fail to track climate. Increasing demand for agricultural lands, especially in tropical lowlands is likely to further increase the isolation of lowland PAs; thus, the connectivity of PAs along elevation gradients should be increased in order to enhance the effectiveness of tropical PA networks for conserving biodiversity under climate change.

3.6. Acknowledgements

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Chapter 4 – Identifying important habitat connections for range shifting species in tropical agricultural landscapes

Large-scale oil palm plantation monoculture

4.1. Abstract

Protected Areas (PAs) support high levels of biodiversity and maintaining connectivity of PAs is important for conserving species, particularly those species shifting their ranges in response to climate change. Ongoing habitat loss makes it important to identify areas that are important habitat connections linking PAs, so that these areas might be prioritised for protection. We focused on Borneo, where PAs are becoming increasingly isolated within agricultural landscapes, and used a new modelling approach (based on the ‘Condatis’ model) that uses electrical circuit theory to identify important areas of rainforest connecting PAs. We assumed that future climate changes will result in tropical species shifting to cooler PAs at higher elevation, and we modelled range expansion of species from focal ‘source’ PAs (*n* = 146 PAs) to cooler ‘target’ PAs under two contrasting RCP scenarios. We parameterised our model for a mobile insect species (e.g. a butterfly species dispersing ~4 km per generation). There was considerable spatial overlap in the locations of expansion routes under the different climate scenarios, implying that increased protection of these routes may be effective under different assumptions of future climate change. When model outputs from all source PAs were overlaid, in order to determine the most important habitat connections, some connections fell within existing PAs because species expanded through intermediate PAs on route to target PAs. However, about two thirds (~62%) of important connections were not protected. We estimated that PA extent would need to increase from ~17% (123,958 km^2) of Borneo’s land area to ~20% (144,583 km^2) to maintain current levels of PA connectivity. Thus, PA cover would need to increase by almost one fifth (i.e. ~17%; an additional 20,626 km^2 of protected forest). Greatest increases in this PA cover are needed at low elevation, where expansion of agriculture (particularly oil palm plantations) over the last few decades has fragmented remaining areas of lowland forest. Models, such as Condatis, that can identify important habitat connections and locate the best sites for enhanced protection (and for habitat re-creation to improve PA connectivity) may be vital for landscape conservation planning to ensure the safeguarding of important dispersal routes under climate change.

4.2. Introduction

Climate change is an increasing threat to species globally (Thomas *et al.* 2004), and is driving geographic range shifts of plants and animals (Parmesan 2006, Chen *et al.* 2011a, Thomas *et al.* 2012). Moreover, climate change interacts synergistically with other threats such as habitat loss and fragmentation (Bennie *et al.* 2013, Mair *et al.* 2014, Struebig *et al.* 2015b), which may lead to the extinction of many species if they are unable to track climate change (Thomas *et al.* 2004). In tropical regions, species are shifting to higher elevation in response to warming temperatures (Colwell *et al*. 2008, Chen *et al*. 2009, 2011b, Forero-Medina *et al*. 2011, Freeman & Class Freeman 2014), but may be prevented from doing so due to lack of suitable connecting rainforest habitat along elevation gradients (Scriven *et al.* 2015/Chapter 3, Struebig *et al.* 2015b). Thus, it is important to identify areas of habitat that are important for connectivity, so that these areas can receive increased protection and hence aid the conservation of species under climate change.

Protected areas (PAs) are strongholds of biodiversity in many tropical regions (Lee *et al.* 2007, Klorvuttimontara *et al.* 2011, Laurance *et al.* 2012), where conversion of rainforest to other lands uses is especially high (Laurance *et al.* 2014). In temperate regions, PAs have been shown to be effective at facilitating latitudinal range expansions (Thomas *et al.* 2012, Hiley *et al.* 2013, Gillingham *et al.* 2015, Thomas & Gillingham 2015), but the effectiveness of PAs in conserving tropical biodiversity under threat from climate change has received much less attention. In many parts of the tropics, PAs are becoming increasingly isolated due to continued land use change (e.g. Curran *et al*. 2004), and so PA networks may not be functionally connected for many species. Rainforest habitat located outside PAs has been shown to be important for maintaining connectivity in fragmented landscapes for range shifting species (Scriven *et al.* 2015/Chapter 3), but unprotected forest is under pressure from continued degradation and deforestation (Laurance *et al.* 2014, Brodie 2016). Deciding where to place additional legislative protection, or where to retain important areas of rainforest (i.e. with High Conservation Values, see RSPO 2013 and https://www.hcvnetwork.org/), to ensure well-connected PA networks will be challenging; especially in light of uncertain future climate projections (Corlett 2011, 2012, IPCC 2013) and altitudinal expansion of agriculture brought about by rising temperatures (e.g. oil palm: *Elaeis guineensis*; Brodie 2016). Thus, effective spatial planning of future reserves and remaining areas of forest to create robust habitat networks will be essential in order to conserve tropical species under threat from climate change.

Species' ability to track climate change will be limited by the availability and distribution of suitable habitat in their current and future ranges (Hodgson *et al.* 2009, Feeley & Silman 2010b), species dispersal ability (Anderson *et al.* 2012) and the permeability of non-forest habitat (e.g. agricultural landscapes) to rainforest species (Scriven *et al*. 2017/Chapter 2). Island biogeographic and metapopulation dynamic theories suggest that greater habitat availability leads to increased population sizes, reduced extinction risk and faster expansion through fragmented landscapes (Hanski 1999, Kinezaki *et al.* 2010). However, the spatial arrangement of habitat as a functionally connected network is also important for effective conservation, and so conservationists urgently need to determine whether such networks can facilitate range shifts (Hodgson *et al.* 2011), and identify important areas of connecting habitat within these networks (Hodgson *et al.* 2016). Computational models are important decision support tools for conservation, to determine optimal spatial habitat configurations for improving landscape connectivity (e.g. Goodwin & Fahrig 2002) and facilitating range shifts (e.g. Hodgson *et al*. 2011, 2012, 2016), as well as locating the best areas in a landscape to protect (e.g. Carroll *et al*. 2012, Brodie *et al*. 2015).

There are a number of computational tools that can be used to examine the functional connectivity of habitat networks (e.g. least cost models: Adriaensen *et al*. 2003, McRae & Kavanagh 2011; and circuit analysis: McRae *et al*. 2008 , McRae & Shah 2011, Brodie *et al*. 2015). These tools highlight important connections but usually assess how habitat fragmentation affects movement within a single generation of the focal species (e.g. McRae *et al*. 2008), rather than examining whether species can colonise and persist over multiple generations, which is critical for the survival of species under climate change (see Hodgson *et al*. 2012, 2016, also see McRae *et al*. 2008 for a comparision of least cost and electrical cicuit theory approaches). Recent studies (Hodgson *et al*. 2012, 2016) have combined habitat patch-based metapopulation dynamics with electrical circuit theory in order to model the colonisation of a species through patchy landscapes ('Condatis' model; Hodgson *et al*. 2016). This integration of electrical circuit theory with metapopulation dynamics produces a model whereby electrical current flowing through the landscape represents colonisation. High flow of current through particular locations identifies important areas that should be priorities for conservation in order to maintain connectivity for range-shifting species under climate change.

In this study, we used this approach of integrating electrical circuit theory with metapopulation dynamics to assess whether there was spatial consensus in range expansion routes by species under different assumptions of warming, and to identify the most important areas of rainforest connecting protected areas (PAs) on Borneo. Borneo is extremely biologically diverse, but rainforest is being lost through land-use change and large-scale agricultural expansion of oil palm plantations (Proctor *et al.* 2011). Rainforest now covers less than 50% of Borneo (Gaveau *et al.* 2014), with much of the remaining primary forest confined to the central montane region, or occurring as isolated PAs within agricultural landscapes (Curren *et al*. 2004, Proctor *et al*. 2011). Many areas of forest outside PAs have been repeatedly commercially logged (Reynolds *et al.* 2011) and are vulnerable to clear felling and conversion to agriculture. However, these logged forests may contain high levels of biodiversity (Edwards *et al.* 2011b) and are vital for maintaining landscape connectivity (Scriven *et al.* 2015/Chapter 3), and hence need increased protection. Analogous climates are predicted to shift out of a large number of lowland PAs, particularly those in coastal regions. Many PAs may therefore be poorly connected along elevation gradients due to lack of forest in oil-palm dominated landscapes (Scriven *et al.* 2015/Chapter 3), making it important to identify and protect important connections before they are lost due to further land-use change. We focus on Borneo because it provides a model system to examine connectivity, and it is typical of other Southeast Asian regions, where many lowland PAs are isolated but there are still opportunities to increase the protection of remaining areas of relatively intact forest (e.g. see Gaveau *et al*. 2009, Klorvuttimontara *et al*. 2011).

We used our model, combined with land-cover information and climate data, to examine the connectedness of rainforest habitat linking PAs along elevation gradients. We ran models parameterised for relatively mobile winged insects that may be capable of dispersing relatively large distances (e.g. butterflies; Benedick *et al*. 2006, 2007a, Marchant *et al*. 2015), and can persist in habitat patch networks (Hanski 1999). We focused solely on temperature, because responses of tropical species to other climate variables (e.g. precipitation) are more uncertain (Corlett 2011, 2012), but realise that tropical species are also likely to be highly sensitive to changing rainfall patterns (e.g. see Meir & Grace 2005, Trisurat *et al*. 2011 and General introduction section 1.2.2.2.). We identified those PAs that are projected to lose analogous climates in future (i.e. PAs that will not contain current (or cooler) temperatures; subsequently termed ‘source’ PAs), and the future locations of analogous climates within higher elevation PAs (termed ‘target’ PAs). We ran models to represent range expansion of species from individual source PAs to target PAs, and calculated the overall landscape conductance (analogous to range expansion speed) for each model run. For each source PA, we mapped expansion routes (areas of high electrical flow) under two climate change scenarios and examined the spatial overlap in these routes. We then overlaid model outputs from all source PAs to generate a single map for Borneo of ‘important habitat connections’ linking these PAs, and calculated the amount of rainforest habitat within these connections (and hence the amount of habitat requiring protection). In this way, our study addressed five main objectives, to: (1) calculate how well connected each source PA is to its target PAs (i.e. the overall landscape conductance); (2) identify the spatial locations of expansion routes between source PAs and cooler target PAs at higher elevation; (3) examine the spatial agreement in these expansion routes under two warming scenarios (mitigation scenario: RCP2.6 and business-as-usual scenario: RCP8.5); (4) overlay model outputs of expansion routes from all source PAs, and identify the spatial location of the most important areas of rainforest that connect PAs along elevation gradients (subsequently termed ‘important habitat connections’) on Borneo; and (5) determine the area of rainforest that would need protecting in order to conserve these important connections.

4.3. Methods

4.3.1. Sources of data on forest cover, PA locations and climate

The locations of 240 spatially discrete PAs on Borneo (IUCN; World Conservation Union: all PA Categories) were downloaded as shapefiles from the World Database of Protected Areas (WDPA; http://www.protectedplanet.net) in AcrGIS version 10, following methods in Scriven *et al*. (2015) (Chapter 3). Forest cover for Borneo was downloaded at a 250 m grid cell resolution (Miettinen *et al*. 2012). Peatswamp forest, lowland forest and lower and upper montane forest were combined into a single ‘forest’ landcover category, which included both primary and high quality secondary (selectively logged) rainforest, and we assumed that our modelled ‘populations’ could utilize these different types of forest. All other landcover categories were termed ‘non-forest’ and were representative of the agricultural matrix (e.g. large scale oil palm plantations), urban areas and severely degraded areas of forest. Gridded elevation data, as well as gridded current (1950-2000) and future (2061-2080) annual climate data were downloaded (from http://www.worldclim.org) at a 30 arc second (~0.86 km) grid cell resolution, and converted to 1 km grid cells. In order to examine the impacts of different assumptions of climate warming, we used climate data from IPCC AR5 Representation Concentration Pathways (RCP) 2.6 and 8.5, from HadGEM2-AO general circulation model (GCM) (IPCC 2013). The RCP2.6 represents the least severe (‘mitigation’) climate scenario and projects a mean surface temperature increase for Borneo of 0.9°C in future (mean temperature difference between annual mean temperature in 1950-2000 and 2061-2080 at 1 km grid cell resolution); whilst RCP8.5 is the most severe (‘business-as-usual’) climate scenario and projects a temperature increase for Borneo of 3.2°C. Thus, this choice of future climate data allowed us to examine the likely range of projected warming across all scenarios. This not only allows for more uncertainty compared to just selecting one intermediate scenario, but also allows for a comparison across contrasting scenarios to highlight common patterns. Forest grid cells at 250 m resolution were converted in ArcGIS to 1 km grid cells, to match the grid resolution of the climate data, and given a forest cover value of between 0 and 16 to represent the number of aggregated 250 m grid cells per 1 km grid cell that were forested. Each 1 km forest grid cell was also specified as ‘protected’ or ‘not protected’ depending on whether it occurred within a PA polygon.

4.3.2. Selecting PAs to study: refuge, source and target PAs

We categorised PAs on Borneo as either ‘refuges’ or ‘sources’ in relation to whether or not analogous climate conditions were projected to remain in a particular PA in 2061-2080 (following Scriven *et al*. 2015/Chapter 3; according to RCP 2.6 and 8.5 scenarios) (Appendix 3A: Fig. A3.1). If the PA contained at least one forested grid cell in future that was either cooler, or the same temperature as the current (1950-2000) mean temperature of forested grid cells within the PA, then it was assumed that analogous climate conditions would remain. Thus, we assumed that species could potentially shift their ranges within the PA to track warming, and the PA was subsequently termed a ‘refuge’ PA (Fig. A3.1; *n* = 94 PAs). For all other PAs (termed ‘source’ PAs; *n* = 146 PAs)

(Fig. A3.1), analogous climate conditions were predicted to shift out of these PAs in future, and thus species may need to colonise other cooler PAs to track climate. We used our model to represent range expansion from source PAs to cooler target PAs, and used model outputs to identify important habitat connections linking source and target PAs (see below) (Fig. 4.1). Target PAs were defined as protected and forested grid cells that contained analogous climates in future, i.e. cells that were cooler than, or the same temperature as, the current mean temperature of the focal source PA. Thus, each focal source PA had its own sets of target PAs (which differed according to the RCP scenario being examined), and we were interested in identifying the range expansion routes (i.e. forest areas with the most electrical flow, see section below) between each source PA and its nearest target PAs. Range expansion was constrained to forested areas, and could occur through both unprotected and protected forest if intermediate PAs were colonised on route to target PAs. A number of source PAs apparently contained no forest according to Miettinen *et al*. (2012), but to enable us to consider all source PAs, we assumed all 1 km grid cells within all PAs (n = 240) were 100% forested.

4.3.3. Modelling landscape connectivity using electrical circuit theory

The Condatis model has been described in detail elsewhere (Hodgson *et al*. 2016) and here we briefly explain how we applied a version of this model to the Borneo landscape. We ran the model at 5 km grid cell (habitat patch) resolution, and information for forest cover, PA cover and climate (1 km resolution; see above) were aggregated into 5 km grid cells (in R version 3.2.0; R Core Team 2015). Grid cells were given values for the proportion of the cell that was forested, protected, and the average current and future temperature (all values computed from aggregated 1 km grid cells). The model assumed all 5 km grid cells (habitat patches) within a source PA were initially occupied by the ‘species’, and we modelled range expansion to target PAs through forested grid cells that were cooler, or the same temperature as the mean current temperature of the source PA. We assumed that populations needed to reach cells that were cooler than (or the same temperature as) the mean current temperature of the source PA, to allow them to reach areas where they may be able to persist in future following our modelled warming period (i.e. after 2080). In this way, the distribution and amount of forested grid cells in our

Borneo ‘landscape’ was different for each model run because the availability of forest was dependent on the location and temperature of the focal source PA (Fig. 4.1).

Models were run separately for each source PA, whereby the poles in the electrical circuit (habitat network) were individual source PA grid cells and their specific set of corresponding target PA grid cells. Our approach includes metapopulation dynamics, and takes into account both the rates of colonisation for dispersers between all grid cells and the rates at which suitable grid cells produce new emigrants (see Hodgson *et al*. 2012). Colonisation of a grid cell was determined by habitat patch connectivity, whereby connectivity is a function of the distance to other occupied forest cells and the amount of forest they contain (Hanski 1994). The model assumes a uniform dispersal process, where every disperser has an equal chance of colonising a new forest grid cell if they land on it (but they cannot colonise non-forest cells), and dispersal can occur in any direction. Every 5 km grid cell is a node in the habitat network, and the cost (resistance) of each link between grid cells is the expected time for a population to colonise one grid cell from another occupied cell. Every grid cell (node) is connected to all other cells in the network, but there are no direct links between source and target PA grid cells. For each run of the model, positive flows through all links going into each grid cell (excluding grid cells in source and target PAs) are summed to give a measure of absolute ‘flow’ for that grid cell, which provides a measure of the importance of each cell in the circuit. Flow through each grid cell is a measure of the likelihood that a given cell is part of the colonisation chain of cells that reaches a target PA first (Fig. 4.1).

For each model run, we computed a single value representing the overall landscape conductance, which is analogous to range expansion speed and important for determining the overall connectedness of the source and target PAs (Hodgson *et al.* 2016). To aid interpretability of our model outputs and compare outputs from different model runs, we also converted absolute flow of each grid cell to a percentage value. Hence, for each model run (i.e. for each source PA) we summed all flow values in the Borneo landscape and divided each individual 5 km forested grid cell value by total flow. Thus, each model run produced a map of Borneo, with a value for the percentage flow in each 5 km grid cell. For all 146 source PAs, we ran two models corresponding to the two RCP climate projections (RCP2.6 and RCP8.5; i.e. 292 model runs in total).

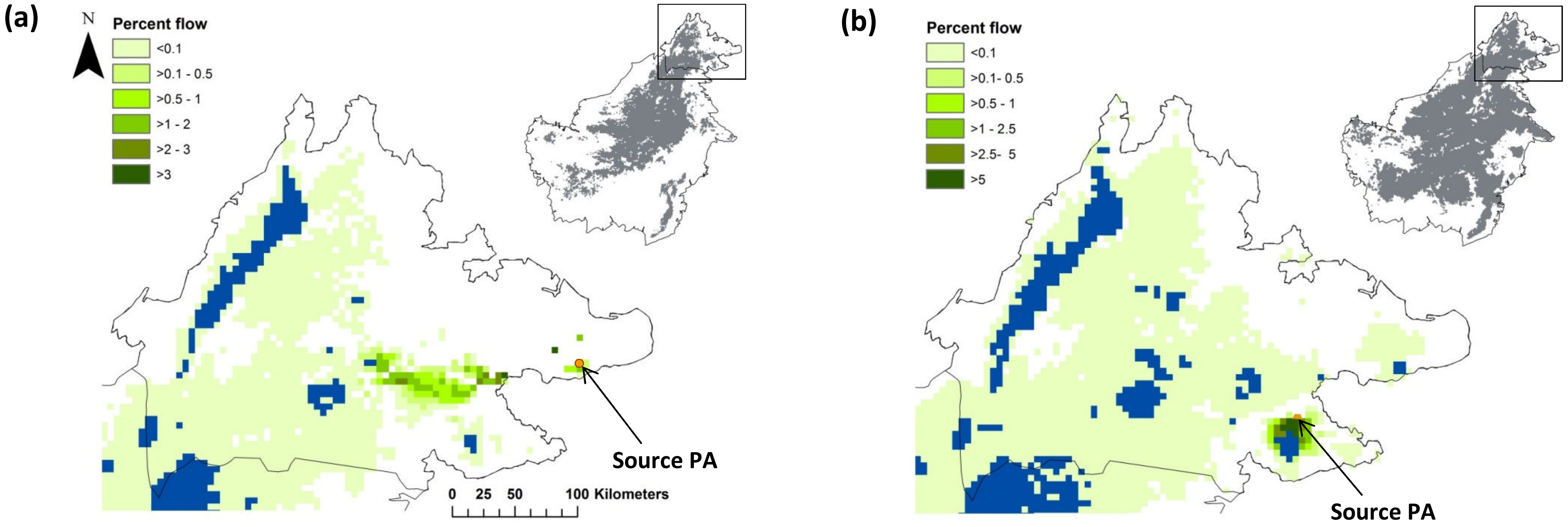

Figure 4.1. Model outputs (RCP8.5) for source PAs that are: (a) poorly connected to cooler target PAs in future (e.g. Silabukan PA; overall landscape conductance = 4.17×10^{-6}), and (b) well connected to cooler target PAs in future (e.g. Madai-Baturong PA; overall landscape conductance = 143,282). Conductance is the inverse of resistance, which is analogous to the time taken (in generations) until the first grid cell within a target PA is colonised. Thus, landscape conductance is analogous to range expansion speed, and an overall measure of how well connected a source PA is to suitable target PAs. Each 5 km forested grid cell (excluding cells within focal source and target PAs) in the landscape had a value according to approximately how much overall landscape conductance would decline if that cell was removed. The scale bar represents percentage flow; light green = lowest flow, dark green = highest flow. Inserts show forest cover that is cooler or the same temperature as the current mean temperature of the focal source PA; arrows show location of source PAs (orange) and blue grid cells show location of target PAs. Silabukan PA (a) is represented by a filled circle due to its small size (<1 km^2).

4.3.4. Parameterising the model for winged insects

The rate of emigration from each focal source PA was determined by population density, which we set at 2000 individuals per 1 km forest grid cell (corresponding to 20 individuals ha^{-1}, typical of rainforest butterflies; Benedick *et al*. 2006, 2007a). We selected a dispersal ability with a mean distance of ~4 km per generation and maximum distance of ~10 km per generation, representing a relatively mobile insect, such as a forest-dependent butterfly (Marchant *et al.* 2015). This dispersal distance was chosen to represent organisms that may be capable of moving through fragmented landscapes. Hence, our model outputs are most relevant to fairly mobile forest-dependent animal species that are neither very sedentary nor highly dispersive (e.g. see Corlett 2009 for examples), and whose range expansions have the potential to be adversely affected by loss of habitat connectivity.

4.3.5. Spatial agreement in expansion routes under different RCP scenarios

Outputs of each model run produced values for the percentage flow in each 5 km grid cell across Borneo. For each source PA (*n* =146 PAs), we used Spearman's rank correlations to determine the agreement between RCP 2.6 and RCP 8.5 in the amount of flow (%) through each 5 km grid cell (excluding source and target PA cells specific to each model run). In order to focus on the grid cells with the greatest flow, we specifically ran pairwise Spearman's rank correlations on flow values for all grid cells that cumulatively contained 99.99% of flow, and subsequently termed these cells 'expansion routes'. To select these expansion routes, we ranked the grid cell flow values in each model run from high to low, and then cumulatively summed values for all cells to a 99.99% cut-off, and then analysed only these cells. We chose 99.99% as our threshold because in several model runs the vast majority of flow was contained in relatively few grid cells (Appendix 3B: Fig. A3.2). The total number of grid cells in the landscape was dependent on the RCP scenario, due to different numbers of target PA grid cells (Fig. 4.2), and so we only included grid cells present in both scenarios in these correlation analyses.

4.3.6. Identifying the location of important habitat connections

In order to map important habitat connections across Borneo, we integrated information from the expansion routes of all 146 source PAs. We focussed only on model outputs for RCP 8.5 (business-as-usual) climate projections because this scenario requires the greatest amount of range expansion by species. We overlaid 146 model output maps reporting percentage flow values for each 5 km grid cell for every source PA, and we assigned a value to each grid cell that corresponded to the maximum percentage flow value reported for any expansion route from a source PA (across all model output maps). Important habitat connections were subsequently defined as all 5 km forested grid cells that contained >0.5% flow. We then calculated the amount of forest habitat (km^2) found within these habitat connections. Thus, we produced a single map of Borneo that synthesised information from all source PAs, and that emphasised grid cells that were important connections. This revealed that most flow was contained in relatively few grid cells (see Appendix 3B: Fig. A3.3), making the identification of important connections straightforward. Out of a total of 22,501 forested 5 km grid cells across Borneo that connected PAs, only 8.7% (1952 cells) had values >0.5% flow (i.e. important habitat connections). We selected this relatively low threshold value for identifying important habitat connections in order to include all potentially important areas of forest, whilst maintaining some selectivity in the grid cells identified. We computed the forested extent of these grid cells to examine the amount of forest within important habitat connections in relation to elevation (Fig. A3.1), and determine the amount of additional protection required to conserve these forest areas of high flow. All statistical analyses were performed in R statistical software version 3.2.0 (R Core Team 2015).

4.4. Results

4.4.1. Landscape conductance

Among the 146 source PAs, there was considerable variation in the total amount of flow (i.e. overall landscape conductance) according to the focal source PA in each model run, and Figure 4.1 illustrates source PAs with high and low conductance. Variation in landscape conductance, which is analogous to the speed at which each ‘landscape’ facilitates expansion, means that some source PAs were much better connected (i.e. PAs with high landscape conductance; Fig. 4.1a) to target PAs than others (i.e. PAs with low landscape conductance; Fig. 4.1b).

4.4.2. Spatial agreement in expansion routes under different RCP scenarios

There was generally strong spatial agreement in expansion routes between the two RCP scenarios. This is despite different assumptions of warming resulting in different amounts and distributions of forested cells in the landscape for a species expanding from a source PA, and hence potentially different colonisation routes to target PAs. Spearman's rank correlations of percentage flow values from RCP 2.6 versus RCP 8.5 scenarios (for 5 km grid cells that cumulatively contained 99.99% of flow, and were present in both scenarios) ranged from $r_s = 0.348$ to 0.968 across all 146 source PAs (Spearman correlations, mean $r_s = 0.85 \pm$ SE 0.011; Fig. 4.2), but the majority of source PAs ($n = 121$) had r_s values >0.8 (Appendix 3C: Fig. A3.4). Thus, we conclude that range expansion routes from source PAs to target PAs were similar under the two warming scenarios. The few occasions where there was low agreement (Spearman $r_s < 0.5$; $n = 8$ source PAs) occurred when the specific spatial locations of target PAs varied considerably between RCP 2.6, and 8.6, and when there was low forest cover adjacent to the source PA, which resulted in range expansion (electrical flow) diverging along very different pathways towards target PA grid cells (Fig. 4.2d and e). These source PAs with lower agreement in expansion routes across RCPs tended to be located in coastal regions (Fig. A3.4).

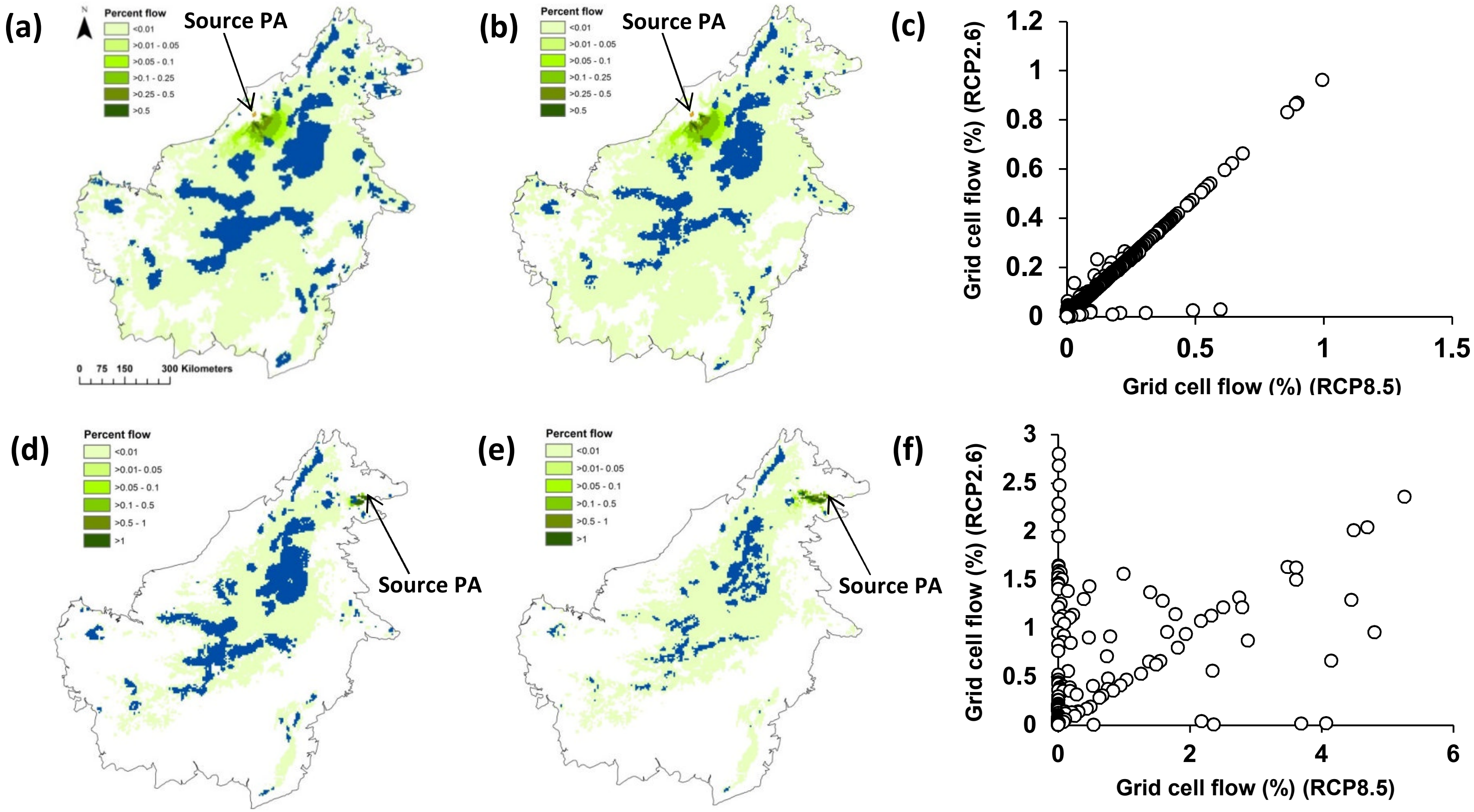

Figure 4.2. Model outputs for two exemplar source PAs that had: (i) strong spatial agreement in percentage flow of grid cells between the focal source and target PAs across RCP scenarios, e.g. Loagan Bunit PA, and (ii) weak spatial agreement in percentage flow of grid cells between the focal source and target PAs, e.g. Kawang Ginbong PA. Top panels show model outputs under RCP2.6 (a) and RCP8.5 (b), and correlation of grid cells within expansion routes (r_s = 0.97, n = 3199 grid cells) (c),whilst bottom panels shows model outputs under RCP2.6 (d) and RCP8.5 (e), and correlation of grid cells within expansion routes (r_s = 0.35, n = 135 grid cells) (f). Arrows show location of source PAs (orange) (note Kawang Ginbong reserve is <1 km^2) and blue grid cells show locations of target PA cells.

4.4.3. Location of important habitat connections

We mapped the locations of grid cells that contained the greatest percentage flow for any of the 146 source PAs (at a threshold of >0.5%), and across Borneo we identified 1952 grid cells that were important habitat connections (Fig. 4.3). These 1952 grid cells contained 33,303 km^2 of forest (according to Miettinen *et al*. 2012) of which ~62% (20,626 km^2) of forest area is not currently protected (Fig. 4.3; Table 4.1). The remaining forest forming important habitat connections was protected because it fell within the boundaries of intermediate PAs, on route for range expansion between source and target PAs. Hence, we estimate that the amount of protected forest on Borneo would need to increase from 123,958 km^2 to 144,583 km^2 in order to conserve all the important habitat connections we have identified. If this additional amount of forest was protected, it would increase the overall extent of protected areas from ~17% of Borneo's land area under protection, to ~20%. Thus, PA cover on Borneo would need to increase by almost one fifth (i.e. ~17%) which corresponds to an additional 20,626 km^2 of protected forest.

Forest cover on Borneo increases with elevation (Table 4.1 presents data for each 200 m elevation band on Borneo), but the proportion of forest within each elevation band that comprised important habitat connections was relatively constant (between 4-11% of forest area per elevation band; Table 4.1). Grid cells that were important habitat connections occurred at all elevations below 2000 m (Fig. 4.4), but the greatest absolute amount of forest within these cells (24,869 km^2; >75% of all forest within important connections) occurred in lowland forest below 400 m. However, less than half (10,852 km^2) of the forest contained within these lowland grid cells fell within the boundaries of PAs, and so we estimate that about 14,016 km^2 (~68%) of forest requires additional legislative protection in these lowland areas to ensure protection of important habitat connections. The spatial arrangement of these important habitat connections (i.e. 1952 forested 5 km grid cells that contained >0.5% maximum flow) were visualised on a regional map of flow, to identify connections of regional importance (Fig 4.3). The state of Sabah in particular, contained a disproportionate amount of important habitat connections, likely due to a high concentration of extremely isolated lowland PAs (Fig. 4.3; Appendix 3C: Fig. A3.4).

Table 4.1. Summary data for extent of rainforest on Borneo and important habitat connections (i.e. 5 km grid cells that contained >0.5% maximum flow for any source PA) across 200 m elevation bands. Model outputs assume 100% forest cover in all PAs and expansions are specific to locations of intervening forest habitat and target PAs assuming RCP8.5 temperature projections; see section 4.3.2. for PA definitions.

Elevation band (m a.s.l.)	Total forest area (km^2)	Protected forest area (km^2)	Area of important habitat connections (km^2)[a]	Forest within important connections in each band (%)[b]	Forest within important connections across all bands (%)[c]	Area of connections protected (km^2)[d]	Percentage of connections protected (%)[e]
<200	162,668	47,067	17,882	11	53.6	8273	46.3
>200 - 400	70,651	18,953	6986	9.9	21	2579	36.9
>400 – 600	50,444	16,331	3701	7.3	11.1	1223	33
>600 - 800	37,970	13,670	2187	5.8	6.6	309	14.1
>800 - 1000	27,634	11,467	1060	3.8	3.1	71	6.7
>1000 - 1200	18,451	8041	787	4.3	2.4	96	12.2
>1200 - 1400	10,095	4676	372	3.7	1.1	38	10.1
>1400 - 1600	5074	2378	195	3.8	0.59	18	9.2
>1600 - 1800	1940	1012	106	5.5	0.32	45	42
>1800 - 2000	382	217	25	6.5	0.08	25	100
>2000	191	146	0	0	0	0	0

[a] Absolute area of forest within important habitat connections in each elevation band.

[b] Calculated as a percentage of remaining forest within important habitat connections in each elevation band.

[c] Calculated as a percentage of the total forest within important habitat connections across all elevation bands.

[d] Absolute area of forest within important habitat connections that fell within the legislative boundaries of PAs in each elevation band.

[e] Calculated as a percentage of total forest within important habitat connections at each elevation band.

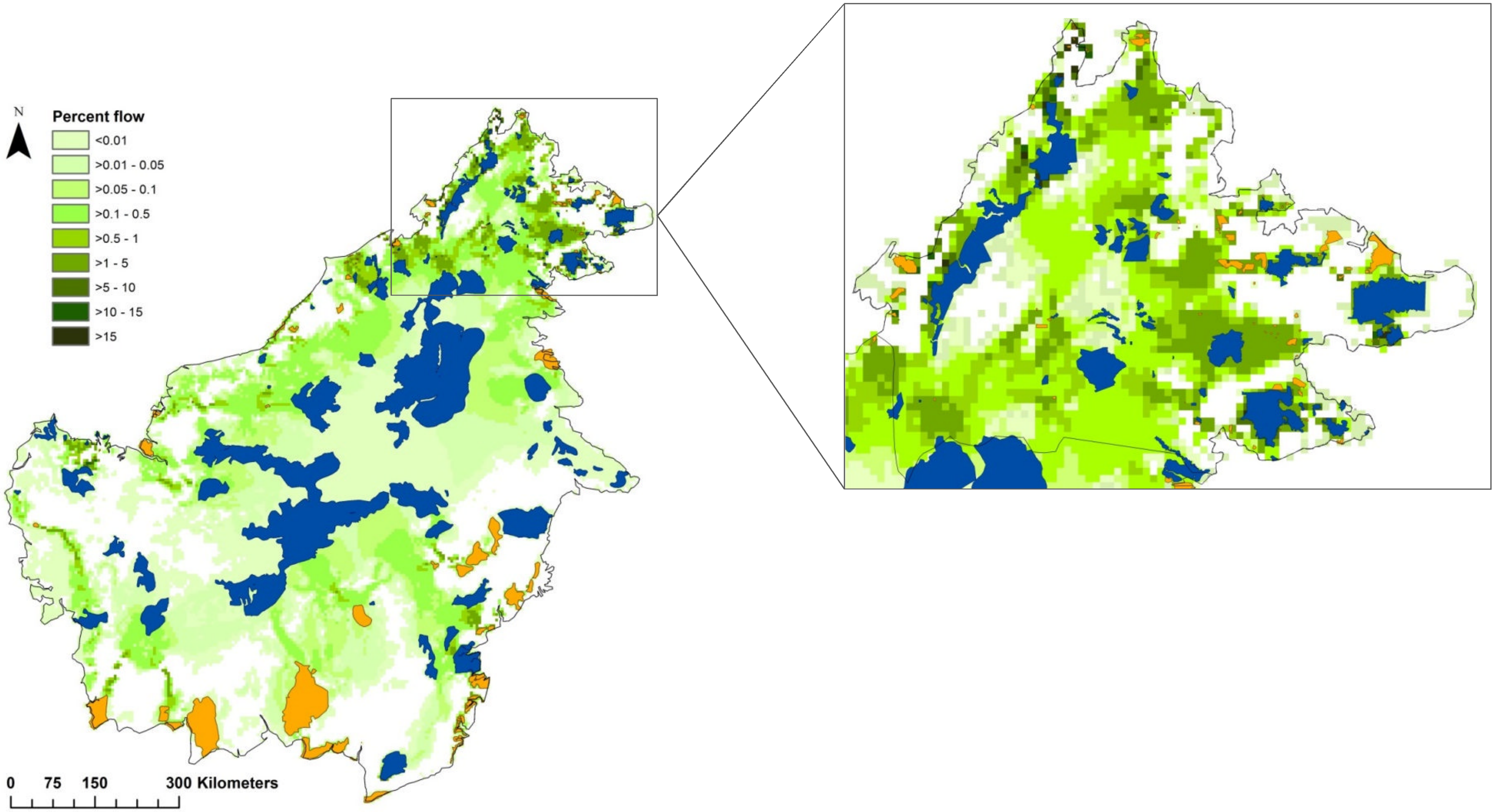

Figure 4.3. Map of Borneo highlighting important habitat connections integrating information for all source PAs and their corresponding target PAs, and assuming RCP8.5 temperature projections. Model output maps reporting percentage flow values for all 146 source PAs were overlaid, and each grid cell was assigned a value that corresponded to the greatest percentage flow value for any source PA. Habitat connections were then defined as 5 km forested grid cells containing >0.5% flow for any source PA. Locations of source (orange) and refuge (blue) PAs are overlaid. Insert shows Sabah, an area of regional importance due to a high concentration of important habitat connections.

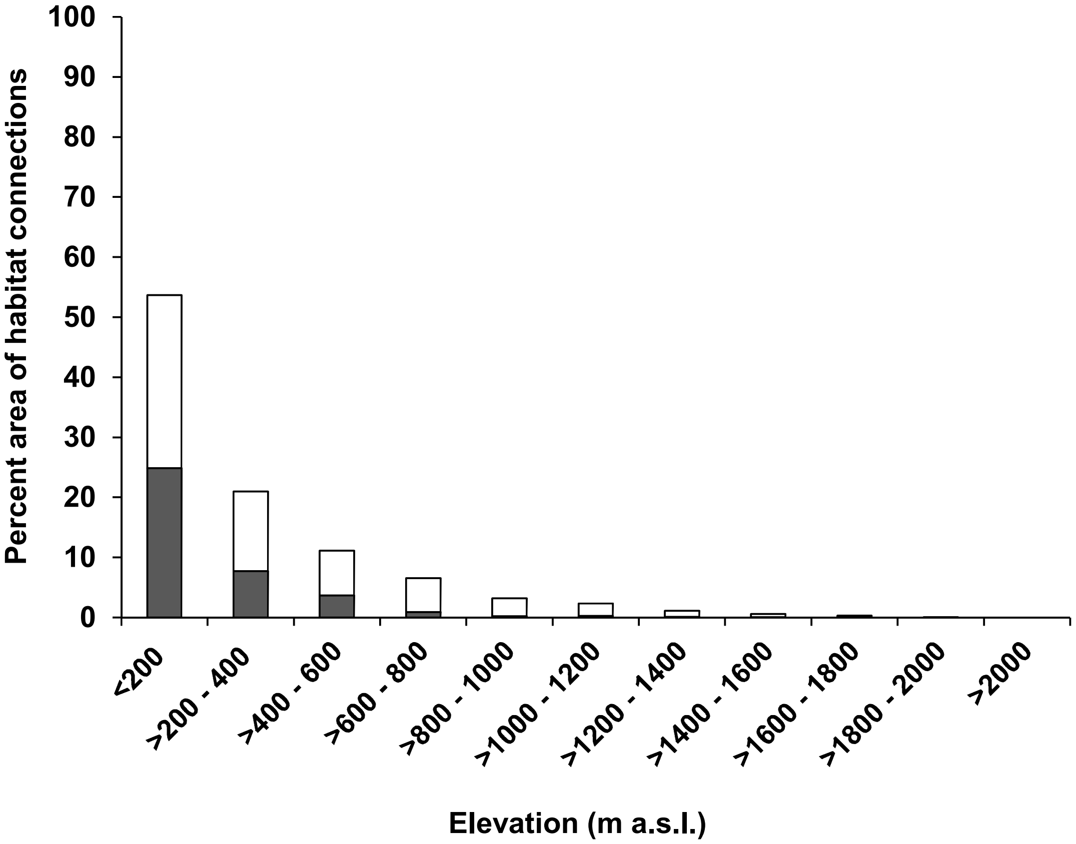

Figure 4.4. Area of forest within important habitat connections that are protected (grey shading) and unprotected (white shading) in each elevation band (i.e. all bars add up to 100% across all bands).

4.5. Discussion

4.5.1. Maintaining habitat connectivity in fragmented landscapes

Climate change is resulting in tropical species shifting their distributions uphill to track cooler climates (Chen et al. 2011b, Corlett 2011, Forero-Medina *et al.* 2011), and habitat connectivity will play an important role in facilitating climate-induced range shifts (Hodgson *et al.* 2009). Using Borneo as a model system within Southeast Asia, we identified 33,303 km^2 of rainforest that formed important habitat connections between source and target PAs, and about two thirds (20,626 km^2) of forest within these connections was not protected. The majority of important habitat connections were found at low elevation (<400 m a.s.l.), and the area of forest in important connections at higher elevation was small, as land area on Borneo decreases with elevation (Table 4.1;

Appendix 3A: Fig. A3.1). With deforestation in the region predicted to continue (Sodhi *et al.* 2004, Wilcove *et al.* 2013), these important areas of unprotected forest will be under threat from continued agricultural expansion, particularly from large scale oil palm plantations (Brodie 2016). If lowland tropical species fail to track cooler climates at higher elevation, they may face unsuitable conditions in lowland PAs (i.e. too hot or too dry) (Corlett 2011). We show that if legislative protection could strategically incorporate an additional 20,626 km^2 of Borneo's forest, the most feasible colonisation routes linking PAs under climate change could be maintained.

Our novel modelling approach based on electrical circuit theory identified regionally important areas of rainforest connecting PAs along elevational gradients (Fig. 4.3). Whilst we focus specifically on Borneo, our methodology could be used in other tropical regions, including different parts of Southeast Asia, where a large majority of landcover at low elevation has been converted to agriculture (Klorvuttimontara *et al.* 2011, Margono *et al.* 2014, Miettinen *et al.* 2014). Our approach takes into account both the rates of colonisation between grid cells and the rates at which occupied cells produce new emigrants (Hodgson *et al.* 2012, 2016). Thus, by using a model that is analogous to range expansion, we assessed colonisation and survival of species in new locations over multiple generations, as opposed to the movement of species within an individual's lifetime (McRae *et al.* 2008). It is important to incorporate population dynamics into studies of landscape connectivity in order to give more biological realism, especially with regard to the synergistic effects of habitat loss and climate change (Brodie 2016). In our study, we highlight areas of remaining rainforest habitat that may be particularly important for relatively mobile insects, such as butterflies that are typically diverse within tropical ecosystems (Benedick *et al.* 2006, Marchant *et al.* 2015). However, our approach could be easily adapted to represent other types of tropical species for which functional landscape connectivity, and thus the ability to move between PAs, may vary (see Brodie *et al*. 2015).

4.5.2. Spatial agreement of expansion routes across RCP scenarios

In general, there was strong spatial agreement (Spearman's $r_s > 0.8$ for 121 source PAs) in expansion routes, as determined by areas of high electrical flow between source and target PAs across different warming scenarios (RCP2.6 and RCP8.5). This shows that range expansion routes to target PAs were generally similar even though the amount of forest habitat that was available for colonising species in the landscape differed for each source PA under different RCP scenarios. This finding is important in the context of practical conservation planning, because our results suggest that increasing protection of these expansion routes may be beneficial for species under multiple assumptions of warming. However, our models highlighted weaker spatial agreement (Spearman's $r_s < 0.5$ for 8 source PAs) in the connectivity of grid cells between RCP scenarios for a few PAs, particularly those located in eastern Sabah (Fig. 4.3; Appendix 3C: Fig. A3.4). Different assumptions of warming resulted in very different spatial locations of target PAs, which led to range expansions taking different routes along elevation gradients, particularly when the forest in proximity to the source PAs was highly fragmented, as is the case in Sabah. It is likely that for some source PAs, the spatial agreement in range expansion routes across RCPs is idiosyncratic and depends not only on the amount of forest in the landscape, but also the precise spatial location of these grid cells, as well as the location of cooler target PA grid cells. In general, our model identified areas of remaining rainforest that would benefit from further protection across multiple RCP scenarios, but we did not explore whether there was spatial overlap in expansion routes for assumptions of different dispersal ability (see section 4.5.3. below). For PAs with low spatial agreement in connectivity across RCPs, deciding which areas of forest may be best to protect in future will be challenging, and may require multiple conservation strategies to account for different assumptions of projected warming and species dispersal.

4.5.3. Identifying important habitat connections

We used our modelling approach to identify important habitat connections between source and target PAs, and showed that most important habitat connections on Borneo were at low elevation. The majority of source PAs are primarily located at low elevation, whilst cooler target PAs at higher elevation are generally located within the central montane region of Borneo (Scriven *et al.* 2015/Chapter 3). Therefore, populations of species that may need to shift their ranges to track cooler climates are likely to primarily move towards the centre of the island. Hence, given the large amount of rainforest loss at low (<400 m a.s.l) elevation (Bryan *et al.* 2013), it is not surprising that important connections mostly occurred within the lowlands. Of the total area of rainforest that we identified as comprising important habitat connections, over half of this rainforest (20, 626 km^2; ~62%) did not fall within PAs. Given that the majority of important habitat connections occurred at low elevation, and that proportionally the greatest PA cover is at high elevation (see Scriven *et al.* 2015/Chapter 3), greatest efforts to increase protection of these connections are required within the lowlands. However, lowland areas of Borneo are under continued pressure from agricultural expansion due to high oil palm yields (Edwards *et al.* 2014b, Brodie 2016), and so increased protection may be vital in order to safeguard areas of forest that are likely to become increasingly important for conserving species under climate change. Our study focused on Borneo, but similar conservation recommendations likely apply to other parts of Southeast Asia. For example, in both Thailand and Sumatra more extensive areas of forest at higher elevation are protected, whilst conversion of rainforest to agriculture is highest in the lowlands (Gaveau *et al.* 2009, Klorvuttimontara *et al.* 2011). Therefore, it will be important to increase protection of habitat connections for range shifting species across a number of lowland regions within Southeast Asia.

Our modelling approach highlighted forested areas that form important habitat connections for species under climate change. Whilst a disproportionate number of these important connections occurred in Sabah, some parts of Brunei, Sarawak and West and East Kalimantan were also identified as having a high concentration of these connections (Fig. 4.3). It is common for conservation features to span multiple countries, but conservation efforts and programmes often stop at international and state borders (Kark *et al.* 2015). On Borneo, integrated conservation planning across international and state borders has been proposed to protect habitats for key megafauna (Runting *et al.* 2015). Similar conservation efforts will be needed in order to protect important habitat connections and routes for range shifting species, but such international conservation planning may prove challenging.

Legislative protection of Borneo's forest needs to increase by approximately one-fifth in order to conserve important habitat connections, and over half of this protection is required in low lying areas (<400 m a.s.l.). However, in our study we used only one dispersal distance (a mean distance of ~4km per generation), which was chosen to represent species that would probably benefit most from improvements to landscape connectivity because they are relatively mobile, and so may be able to move between patches of forest. The most important habitat connections may be similar for other species with different dispersal abilities; although more isolated connections may not be reached by species that are very sedentary, for which even high levels of connectivity may fail to allow expansion. Hence, an important extension to the current study would be to examine the spatial overlap of range expansion routes for species with different dispersal abilities. In addition, we parametrised our model with only one population density value, which was representative of forest butterflies (Benedick *et al*. 2006, 2007a), rather than species such as forest mammals that occur in lower abundances.

Given recent evidence from temperate systems (e.g. see Thomas *et al.* 2001, Davies *et al*. 2006, Pateman *et al*. 2012), we assumed that dispersal of our ‘populations’ was not restricted by the distribution of associated plant species (i.e. larval host plants). Species were therefore capable of tracking climate, providing that there was sufficient rainforest habitat along elevation gradients between PAs. Hence, the location of important habitat connections and the area of forest that will require additional protection may change if models are run with different combinations of species traits, such as dispersal ability and population density, and if range shifting was dependent on the distributions of other forest taxa (i.e. larval host plants or adult food plants). Another important consideration or our modelling approach, is that we combined all forest cover types into a single landcover category (i.e. ‘forest’) (see Klorvuttimontara *et al*. 2011, Proctor *et al*. 2011, Brodie *et al*. 2015), and hence did not take into account rainforest type or condition, both of which may limit the distribution of tropical species (Clements *et al*. 2006, Posa *et al*. 2011, Barlow *et al*. 2016). Hence, important habitat connections identified in this study are most relevant to species that have distributions limited by temperature, rather than by a specific habitat type (e.g. endemic peatswamp or limestone specialists), and that can utilize forest habitats of different conditions (i.e. butterfly species found in both logged and primary rainforests; e.g. see Hamer *et al.* 2003).

To identify important habitat connections for range shifting species, we chose to select the maximum flow (%) in a grid cell for any given expansion route from a source PA. This approach emphasises cells that are important connections for at least one source PA, and in this way all important habitat connections for all source PAs are given priority. An alternative approach could be to give priority to only those grid cells that form important connections for a larger number of source PAs (i.e. ‘conservation triage’; e.g. see Bottrill *et al*. 2008). This approach could be achieved from our model outputs by calculating the mean percentage of flow within each grid cell across all model runs, rather than select only the single greatest flow value as we have done (Appendix 3D: Fig. A3.5). This approach would assign higher importance to areas with more source PAs (i.e. Sabah), and might be appropriate if deforestation projections are extremely severe, or if future legislative protection is severely limited.

4.5.4. Relevance to policy and legislation

Less than half of all important habitat connections in the lowlands (<400 m a.s.l.) fell within the boundaries of PAs, and so our study showed that a relatively large amount (14,016 km^2) of forest requires additional legislation in lowland areas to ensure protection of these forests in future. In both Malaysia and Indonesia, specific laws and procedures ultimately promote the transformation of rainforest habitat to agriculture (Brockhaus *et al*. 2012), but land use allocation is highly complex, involves numerous stakeholders at multiple levels, and can often fall victim to corruption (Ancrenaz *et al*. 2016). A large proportion of Indonesia’s forests are state owned (Cotula *et al*. 2015, Sumarga & Hein 2016), and government owned forested areas that are not within ‘Forest Zones’ (i.e. assigned as reserves or production forest) are generally allocated for agriculture. In Malaysia, private ownership of forest is not permitted (Cotula *et al*. 2015), and long term land titles have previously allocated many forested areas for conversion that are deemed suitable for agriculture. In Eastern Sabah, where much of the landscape has already been converted to oil palm, conservation efforts would be best focused on managing forest within existing PAs and increasing protection of any remaining large forest tracts, especially those that connect existing PAs. Whilst this process is both complex and lengthy, it can be achieved with pressure from multiple stakeholders. For example, in 2015, the state Government of Sabah enhanced the protection of 112,118 ha of forest forming an important corridor (‘corridor of life’) between several important PAs (Danum Valley, Maliau Basin and Imbak Canyon) (see http://www.forest.sabah.gov.my/), an area identified as containing important habitat connections by this study (Fig 4.2). In many parts of Indonesian Borneo however, where large-scale expansion of oil palm plantations is still continuing in the lowlands (Sumarga & Hein 2016), sustainability certification schemes such as the Roundtable of Sustainable Palm Oil (RPSO) or Indonesian Sustainable Palm Oil (ISPO: http://www.ispo-org.or.id/) may be best placed to provide strategies for maintaining landscape connectivity in the lowlands. For example, if both Environmental Impacts Assessments (EIAs) and HCV assessments for new planting procedures (NPPs: see RSPO 2015) promote the retention of forested areas that facilitate landscape connectivity between PAs (i.e. along elevation gradients or as riparian buffers), this may have significant benefits for lowland species and ensure that some important habitat connections remain, despite ongoing forest loss.

4.5.5. Future directions

There are several extensions to our modelling approach that could form important areas for future work regarding the optimisation of spatial habitat arrangements that will benefit species' range expansion. Firstly, our model could be adapted by using knowledge of locations of important connections to identify habitat 'bottlenecks' (areas of high flow in a link between grid cells) for reforestation programmes. By adding new habitat to these locations, the model could be used to investigate the most efficient places for adding forest in order to improve connectivity (see Hodgson *et al*. 2016). Secondly, we could also simulate deforestation*,* i.e. in areas most suitable for oil palm development (e.g. see Brodie 2016), to quantify the subsequent impacts on PA network connectivity, and determine whether the most important connections would change as habitat loss continues. Our models focus solely on temperature, but other climate variables such as precipitation are also likely to influence areas of suitable future habitat for tropical species (Corlett 2012). For example, downslope range shifts may be a consequence of changes in seasonality and water avaibility (Lenior *et al*. 2010, Platts *et al*. 2013), whilst favourable hydrological conditions may offset the detrimental impacts of rising temperatures (Johnson 2012). Thus, the locations of the most important habitat connections may change if rainfall projections are included in our modelling approach. Hence, we recognize that incorporating rainfall patterns into any future work would be an important area of further study. However, future precipitation changes for Southeast Asia are currently uncertain (Hijioka *et al.* 2014, Scriven *et al.* 2015/Chapter 3), making it extremely difficult to generate assumptions about directions of range shifting and potential locations of target PAs.

The quality and type of tropical agricultural matrices have been shown to affect species richness (Sheldon *et al.* 2010) and landscape connectivity (Goulart *et al.* 2015).

Variation in matrix quality was not considered in our study (and habitat was either suitable (i.e. forest) or unsuitable). Matrix quality may affect the specific spatial locations of important connections if the landscape which surrounds them is permeable to species, or facilitates breeding populations. In our modelling approach we assumed that species were relatively mobile and capable of crossing forest-non forest boundaries (e.g. into oil palm plantations). However, if forest species are unable to cross boundaries into non-forest habitat, or cross in low abundance (see Scriven *et al*. 2017/Chapter 2), the locations of the most important habitat connections may change, and isolated areas of forest may not be reached. Our models could be adapted to incorporate agricultural matrices of differing permeability, and this would be a key area of further research.

4.5.6. Conclusions

We highlight areas that are regionally important for maintaining connectivity on Borneo, and use a novel modelling approach that could be adapted for application in other regions, or at local spatial scales (Hodgson *et al.* 2016). Our findings suggest that PA cover needs to increase on Borneo by about a fifth, with greatest increases in PA cover needed in areas at low elevation. Increases in PA cover are necessary to conserve the most important habitat connections for range shifting species and to prevent further isolation of lowland PAs through continued deforestation. Increasing PA cover at this scale is likely to have large benefits for tropical biodiversity, but may be difficult to implement (Struebig *et al.* 2015b). Therefore, further work is needed to prioritise the most important areas of forest that require legislative protection; these include areas that will facilitate range shifting for multiple taxa, but are most threatened by conversion to agriculture.

4.6. Acknowledgements

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Chapter 5 – General discussion

Forest fragment surrounded by oil palm plantations

5.1. Summary of thesis findings

The aims of my thesis were to (1) improve our understanding of how to promote resilience and biodiversity in tropical landscapes that are under threat from agricultural expansion and climate change, and (2) provide an evidence-base for conservation strategies that maintain rainforest connectivity. I examined the permeability of rainforest-oil palm plantation boundaries to forest-dependent butterflies, and determined the number of protected areas (PAs) on Borneo from which analogous climates (specifically in relation to temperature changes) may shift in future. I also examined the connectedness of PAs for range-shifting species, identified the most important habitat connections along elevation gradients, and calculated the amount of forest within these connections that is not currently protected. In this final chapter, I present a summary of my findings in relation to the specific objectives of each chapter, discuss the wider implications of my research in relation to maintaining connectivity in tropical agricultural landscapes and discuss conservation strategies to protect tropical biodiversity under climate change, with reference to further research. Finally, I put forward my final conclusions.

Chapter 2 – Barriers to dispersal of rainforest butterflies in tropical agricultural landscapes

Main objectives:

1. Determine the net direction of butterfly movement across forest-oil palm boundaries
2. Compare overall movements of individuals from forest into plantation, compared with movements only in forest habitats.
3. Examine whether larval host plant availability in plantation along with species specific traits (including forewing length, larval host plant specificity and geographical range size) are predictors of boundary crossing.

In this chapter, I investigated the movement of fruit-feeding butterflies at forest-oil palm plantation boundaries in relation to species-specific traits. I established that the net flow of butterflies across forest-oil palm plantation boundaries was from forest into plantations, and that individuals marked in forest habitats and recaptured in a different trap had an approximately equal chance of moving into plantation compared to moving only within forest. However, not all species crossed the boundary in equal frequency, and boundary crossing was dominated by small-sized butterflies whose associated larval host plants occurred within the oil palm plantation matrix. More specifically, crossing from forest into plantations was more than twice as likely for (1) species with larval host plants present in plantation habitats compared to those with no larval host plants present, and (2) for small species compared to large species. I concluded that whilst oil palm plantations may be relatively permeable to some species, they may act as barriers to the movement of forest-dependent species across agricultural landscapes. My results therefore highlight the need to maintain rainforest connectivity in tropical agricultural landscapes in order to conserve rainforest species.

Chapter 3 – **Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change**

Main objectives:

1. Identify PAs that may not retain analogous climate conditions in future, and examine the characteristics of these PAs (e.g. size, elevation and isolation).
2. Determine the connectivity of PAs along elevation gradients under multiple assumptions of warming (IPCC RCP scenarios) and forest cover, as well as for species with different dispersal abilities and population densities.

I used the protected area (PA) network on Borneo as a model system to examine the connectedness of PAs under multiple warming and landcover scenarios. Under both IPCC RCP2.6 and RCP8.5 temperature projections, I revealed that a large number of PAs (~60% and ~90%, respectively) will not contain analogous temperatures in future (i.e. they will become too warm). Thus, in order to track cooler climates, species may need to move from these PAs to cooler PAs at higher elevation. Protected areas from which analogous climates may shift, were mostly situated at low elevation, were relatively small and were isolated from surrounding areas of forest. Over half of these PAs were not connected to cooler PAs for species with poor dispersal abilities (<1 km maximum dispersal per generation), because there was insufficient intervening forest habitat between PAs. Assuming that these findings for Borneo are representative of other parts of Southeast Asia, I concluded that many lowland PAs in the region may lose analogous climate conditions in future, even under relatively modest levels of warming (RCP2.6). Species within these PAs, particularly poor dispersers, may therefore be unable to track cooler climates due to lack of connecting rainforest habitat along elevation gradients. If species are unable to track cooler climates and fail to adapt to climate change *in situ* (i.e. within PAs), there may be detrimental consequences for rainforest biota. Thus, maintaining connectivity along elevation gradients should be a conservation priority to maximise the effectiveness of PA networks in Southeast Asia.

Chapter 4 – Identifying important habitat connections for range shifting species in tropical agricultural landscapes

Main objectives:

1. Calculate the connectivity of PAs from which analogous climates may shift to cooler PAs at higher elevation using conductivity models.
2. Identify the spatial locations of expansion routes between PAs along elevation gradients.
3. Examine the spatial agreement in these expansion routes under two warming scenarios (mitigation scenario: RCP2.6 and business-as-usual scenario: RCP8.5).
4. Overlay model outputs of expansion routes and identify the spatial location of the most important areas of rainforest habitat that connect PAs along elevation gradients on Borneo.
5. Determine the area of rainforest that would need protecting in order to conserve these important habitat connections.

Using Borneo as a model system, I used a novel modelling approach based on electrical circuit theory to identify important areas of rainforest connecting PAs along elevation gradients. The findings of this chapter revealed that there was considerable spatial overlap in the locations of expansion routes between PAs across different assumptions of warming. When expansion routes were overlaid for all PAs, almost two thirds (~62%) of forest habitat within important habitat connections was not protected, and I estimated that the PA extent of Borneo's land area would need to increase from ~17% to ~20% in order to maintain current levels of connectivity between PAs. This would mean that to conserve all habitat connections, current legislative protection would need to increase by approximately one fifth of current PA extent (increase of ~17%; 20,626 km^2). My results also revealed that the greatest proportion of additional protection (~68% of all habitat connections) would be needed at low elevation (<400 m a.s.l.). With deforestation in Southeast Asia set to continue, especially in the lowlands, important areas of rainforest connecting PAs will be under threat from continued oil palm expansion. Hence, I concluded that if future legislation could increase the protection of important habitat connections, the most feasible routes out of PAs to higher elevation could be conserved. This would help species track and adapt to climate change, potentially reducing the detrimental impacts of climate change for tropical biodiversity.

5.2. Range shifting, thermal limits and range boundaries

The modelling approaches used in both Chapters 3 (Scriven *et al*. 2015) and 4 examined the thermal conditions of protected areas (e.g. Ohlemüller *et al*. 2006), and did not use a species-based approach such as species bioclimate-distribution envelopes (e.g. see Klorvuttimontara *et al*. 2011, Trisurat *et al*. 2011). Hence, I assessed the degree to which PAs on Borneo were sufficiently connected to allow species to track temperature changes, and did not incorporate any data on species distributions (which are often poorly surveyed in tropical regions, with sparse and unreliable data). My modelling approaches were based on the assumption that tropical species may need to keep track of rising temperatures (see Colwell *et al.* 2008). The concept of range shifting, and expansion from PAs that may not contain analogous climates in future (termed source PAs) to cooler PAs at higher elevation (termed target PAs), is primarily based on evidence from empirical studies that show uphill shifts by a number of tropical species in response to recent warming (e.g. see Chen *et al*. 2009, Freeman & Class Freeman 2014, Moret *et al*. 2016). Empirical evidence is also supported by changes in the distribution of tropical species under past climate regimes (Bush 2002, Jaramillo *et al.* 2006), whereby certain species have moved upslope and downslope in response to past temperature changes (e.g. during the last glacial maximum; see Bush *et al*. 2004). Thus, with rainforests currently entering a set of climate conditions that have no past analogues during the past two million years (Colwell *et al.* 2008, Bush *et al.* 2011), future distribution shifts and migrations of rainforest species along elevation gradients are the most likely consequence of anthropogenic climate change (Chen *et al*. 2009), which is central to the modelling approaches used in this thesis.

The modelling approaches used in Chapters 3 and 4 examine the connectedness of PAs along elevation gradients using different temperature projections (RCP 2.6 and RCP 8.5), but do not include future projections for other climatic variables, including rainfall. It is well recognized that rainfall patterns play an important role in regulating rainforest structure and productivity (e.g. see Gentry 1988, Swaine 1996, Bongers *et al*. 1999, Condit *et al.* 2013), and species distributions can often be predicted by their sensitivity to drought (Engelbrecht *et al.* 2007, Condit *et al.* 2013). Thus, rainfall induced range shifts of many tropical species are a likely consequence of anthropogenic climate change (e.g. see Platts *et al.* 2013). However, there is limited empirical evidence into how tropical species will to respond changes in rainfall, and such responses are likely to be highly complex (Davies & Shaw 2001, Lenoir *et al*. 2010). What's more, there is significant uncertainty in projected rainfall patterns (IPPC 2013), particularly in Southeast Asia, and with respect to ENSO events (Hijioka *et al.* 2014, also see Chapter 1 section 1.4.2.1). Whilst increased rainfall may offset some of the detrimental impacts brought about by rising temperatures (i.e. fewer droughts) (Johnson 2012), a reduction in rainfall in combination with higher temperatures may significantly increase extirpation risk of certain species (McCain & Colwell 2011). Hence, conditions within source PAs may be more suitable than suggested by the results of Chapters 3 and 4 if increased rainfall ameliorates the detrimental effects of rising temperatures, but the opposite may be true if rising temperatures are accompanied by lower rainfall. Thus, I acknowledge that the results of Chapters 3 and 4 could change if climate suitability within PAs is substantially or disproportionately altered when changes in precipitation are considered.

Findings from Chapter 3 revealed that a large proportion of PAs on Borneo (~60% in RCP2.6 and ~90% in RCP8.5) will not contain analogous climates in future (source PAs), and so in order to track cooler climates species may need to move to PAs at higher elevation (target PAs). Whether or not particular species will shift or expand their distributions out of source PAs in response to future warming will be dependent on their specific thermal tolerances (Colwell *et al.* 2008), which may differ both intra-specifically (e.g. Llewelyn *et al*. 2016) and inter-specifically (e.g. Pincebourde & Suppo 2016). Rates of range expansion will also depend on the leading- (cool boundaries) and trailing- (warm boundaries) edge range dynamics of each species (Chen *et al.* 2011b). Whilst much empirical evidence suggests that tropical species, particularly ectotherms, may be sensitive to rising temperatures due to physiological constraints (Deutsch & Tewksbury 2008, Piantoni *et al.* 2016), there is much debate surrounding their ability to adapt to warming *in situ* (i.e. within PAs) (Feeley & Silman 2010a). What's more, species' ability to adapt to warming *in situ* may also depend on the level of disturbance they experience in their rainforest habitats. Whilst structurally complex rainforest environments (i.e. primary rainforests) may provide considerable thermal heterogeneity to some tropical species (see Scheffers *et al.* 2016), disturbance regime may alter abiotic conditions that worsen the impacts of rising temperatures (Laurance 2005). Under IPCC RCP8.5 projections, the results from Chapter 3 suggest that ~60-80% of source PAs on Borneo are not well connected to higher elevation PAs for species with poor dispersal abilities (<1 km maximum dispersal per generation). A large component of tropical biodiversity may have limited dispersal, and so experience high levels of PA isolation and poor PA connectivity. However, the consequences of poor connectivity along elevation gradients for tropical species will vary depending on their specific distributional extents, rainforest condition and ability to cope with changing abiotic environments.

There are limited data on both the thermal tolerances and distributional extents of many tropical species, and so in Chapter 3, I considered the potential outcomes of poor connectivity between PAs for taxa with different distributions and thermal limits (see schematic in Appendix 2G; Fig. A2.6). For example, a ubiquitous species may have thermal tolerances extending beyond the temperatures within an existing source PA, and so may be able to persist *in situ* following climate change, particularly under moderate warming (RCP2.6) (Appendix 2G; Fig. A2.6a). Other species however, may have relatively narrow thermal limits, and both their leading- and trailing- edge range boundaries may fall within a particular source PA, which could result in reduced range sizes or local extinctions as climates warm (Appendix 2G; Fig. A2.6d). If species disappear from low-lying regions (either by failing to acclimate or by shifting to higher elevation) because conditions become too hot or too dry, it is possible that they will not be not be replaced by species that are adapted to warmer climates (i.e. lowland biotic attrition; see Colwell *et al*. 2008). However, there is currently limited empirical data supporting the theory of lowland biotic attrition in tropical systems (Burwell & Nakamura 2015), and it is unlikely that the fundamental climatic niche of tropical species is fully represented by current distributions, suggesting some capacity for adaption (Feeley & Silman 2010a; Appendix 2G; Fig. A2.6). Hence, I focussed on PA connectivity, rather than range shifting directly, in order to make the results broadly applicable to forest-dependent taxa with different thermal limits.

Range retreats at species' trailing-edge range boundaries due to rising temperatures have been shown by a number studies (e.g. Thomas *et al*. 2006, Zuckerberg *et al*. 2009). However, there is some evidence that leading-edge boundaries may be expanding faster than trailing edge boundaries are retreating (Peh 2007, Chen *et al.* 2011b, Sunday *et al.* 2012, Freeman & Class Freeman 2014), which could allow time for mitigation of climate impacts (i.e. rising temperatures) if tropical species are capable of developing adaptation strategies (Chen *et al.* 2011b). One explanation for this is that microclimate effects may allow trailing-edge populations to survive, often in cooler or wetter 'microrefugia' (Hampe & Jump 2010, Maclean *et al.* 2015). Small tropical ectotherms (e.g. ants and other insects) for example, may be able to escape overheating by taking advantage of such thermal heterogeneity, e.g. in areas orientated away from the sun (Pincebourde & Suppo 2016). Fine-scale thermal heterogeneity created by different microclimates (e.g. see Bennie *et al.* 2013) could not be considered in the modelling approaches used in Chapters 3 and 4, due to the coarse resolution of available spatial datasets (~1 km grid resolution for temperature data). This is however an important area of future research fundamental to our understanding of whether tropical species will be able to adapt or acclimate to rising temperatures *in situ* (Tewksbury *et al.* 2008, Pincebourde & Suppo 2016).

5.3. Importance of connectivity in fragmented landscapes

5.3.1. Connectivity of PAs along elevation gradients

Many PAs on Borneo are projected to become too warm in future (source PAs), and one of the key findings of my thesis was that the majority of these PAs are not connected to cooler PAs at higher elevation (target PAs) for species with poor dispersal abilities (<1 km maximum dispersal per generation). This result was primarily due to lack of intervening forest outside PAs that connected forest habitat along elevation gradients (Chapter 3).

Many tropical species are poor dispersers (Corlett 2009), and so the results of Chapter 3 are concerning because many populations of forest species could be isolated in low-lying PAs and unable to shift or expand their ranges in response to climate warming. Nevertheless, findings from Chapter 3 did reveal that species with relatively high dispersal abilities (>5 km maximum dispersal per generation), may still be able to track cooler climates, as the connectedness of source and target PAs was higher for more mobile species. However, this result was dependent on current levels of forest cover remaining outside of PAs in future, and was markedly reduced when unprotected forest was removed, suggesting that forest outside of PAs is vital for maintaining connectivity (see Appendix 2H, Fig. A2.7).

My results from Chapter 4 revealed that about two thirds (62%) of forest habitat comprising important connections between source and target PAs is not currently protected. Hence, in order to maintain current levels of connectivity between PAs shown in Chapter 3, PA extent would need to increase from ~17% of Borneo's land area to ~20%. This equates to current PA cover increasing by approximately one fifth (17%; 20,626 km^2 increase in protected forest), and the greatest increases in this cover (68% of new protected areas; 14,016 km^2) are needed at low elevation (<400 m a.s.l.). It is unlikely that unprotected forest within these important habitat connections will remain unaffected by agricultural expansion, because oil palm plantations are predicted to expand in Southeast Asia, particularly within low-mid elevation areas where palm yields are high (Brodie 2016). Other studies on Borneo have also highlighted the importance of increasing PA cover in order to safeguard areas of forest that will become increasingly important for a number of species under climate change (e.g. for mammals: Struebig *et al.* 2015b). The results of Chapter 4 are representative of relatively mobile species (~4 km mean dispersal per generation), but assuming that the expansion routes between PAs may also be similar for species with low dispersal, PA connectivity may severely decline for a range of taxa if further deforestation affects these connections. In both Chapters 3 and 4, I therefore concluded that conservation efforts should focus on conserving unprotected areas of rainforest along elevation gradients. These forests may not only have high biodiversity value (Edwards *et al.* 2011b), but their protection could conserve connectivity along important routes used by species to track cooler climates.

In order to examine the connectivity of PAs along elevation gradients (Chapter 3) and identify the most important habitat connections between PAs (Chapter 4), I combined several different rainforest types into one overall ‘forest’ category (see Klorvuttimontara *et al*. 2011, Proctor *et al*. 2011, Brodie *et al*. 2015). Hence, what I classified as forest represented peatswamp forest, lowland forest and lower and upper montane forest, irrespective of soil type or forest condition. It is important to recognise that different rainforest types (formations) can vary considerably in their structure (Whitmore 1984, also see Chapter 1 section 1.4.1.), and that rainforest condition can vary substantially within the same forest type (Barlow *et al*. 2016), often resulting in distinct communities (Edwards *et al*. 2013). Soil type can also affect the distribution of tropical species (Potts *et al*. 2002), with certain taxa found to significantly aggregate on specific soils (Palmiotto *et al*. 2004, Russo *et al*. 2005). There is currently little information available on the distributions of tropical species within different rainforest types, but some endemic specialists are likely restricted to particular habitats, i.e. limestone formations (Clements *et al*. 2006), peatswamp forests (Posa *et al*. 2011) and primary forests (Barlow *et al*. 2007a, Barlow *et al*. 2016). In Chapter 4, I determined important areas of forest connecting PAs along elevation gradients, and whilst a number of taxa may be able to utilize connections that are comprised of different types of forest (e.g. wild felids: Cheyne & Macdonald 2011; orangutans: Felton *et al.* 2003, Ancrenaz *et al*. 2004; and certain butterflies: Häuser *et al.* 1997, Hamer *et al*. 2003, Ghani 2012), other highly specialized species may be unable to do so (Clements *et al*. 2006, Posa *et al*. 2011). Thus, the results of Chapters 3 and 4 will be less relevant for forest specialists fundamentally restricted to particular habitats, as there may not be suitable habitat within PAs at higher elevation (i.e. peatswamps), or suitable connecting habitats between PAs (i.e. primary forest tracts) to facilitate range shifts.

5.3.2. Matrix permeability

The results from Chapter 2 (Scriven *et al*. 2017) show that forest-dependent species (i.e. species reliant on rainforest habitat to breed) are less likely to cross rainforest-oil palm plantation boundaries compared with species that have their larval host plants present within the plantation matrix. Thus, my results suggest that large scale oil palm plantations may act as barriers to the movement of certain forest species in fragmented agricultural landscapes. In the computational models used in Chapters 3 and 4, I assumed that populations of species will be able to move through (but not breed in) agricultural matrices in order to reach connecting areas of forest; an approach used by other studies that model range advances in fragmented landscapes (e.g. Hodgson *et al.* 2011). Whilst some of the grid-cells classified as 'non-forest' in my study may have contained some areas of poor quality rainforest (i.e. regenerating or heavily logged areas), a large proportion of non-forest cells were representative of oil palm monocultures (see Miettinen *et al*. 2012). Thus, the connectedness of source PAs to cooler target PAs may have been overestimated in these models if forest species are unable to disperse across agricultural matrices (Chapter 3).

Some forest species have been shown to move into oil palm plantations (e.g. orchid bees: Livingston *et al*. 2013), but for most species there is limited consensus about the permeability of oil palm matrices for facilitating landscape-level movements. I showed in Chapter 2 that a small number of forest-dependent butterflies were captured in the plantation without being captured crossing the edge, and these species have been found in other studies to 'spillover' into oil palm plantations (see Lucey & Hill 2012). It is therefore possible that these species may be able to cross habitat boundaries more frequently than was detected in my study, although the distances that they can travel through oil palm plantations and the importance of 'hard' and 'soft' boundaries at forest edges are still currently unclear. Habitat management to make forest-plantation boundaries more permeable (e.g. by reducing microclimate gradients) may facilitate movements of forest species across non-forest habitats (Koh 2008). However, more empirical data are needed to address the dispersal abilities of tropical species in oil palm plantations, especially in relation to climate induced range shifts in agricultural landscapes.

In Chapter 2, data were collected from rainforest habitats that have been logged at least twice. Whilst selectively logged rainforests in Southeast Asia can support relatively high levels of biodiversity (Berry *et al.* 2010, Edwards *et al*. 2014a), species richness is generally lower than in unlogged (primary) rainforests (Edwards *et al*. 2011b), and vulnerable or threatened species are often lost from these disturbed habitats (Costantini *et al.* 2016). Hence, if a large number of forest specialists have already been lost from logged areas of rainforest, the overall proportion of these species crossing the boundary into oil palm plantations may in fact be lower than I recorded in Chapter 2. Thus, matrix permeability may have been overestimated. This may also affect the conservation value of many lowland PAs on Borneo (see Chapter 3); i.e. if lowland PAs have already lost high numbers of forest specialists because they are heavily degraded. Whilst these are important considerations, there are few areas of primary rainforest left in the lowlands of Borneo (Gaveau *et al.* 2016), and logged forests that remain have been shown to contain a number of rare and endemic species, as well as species of conservation concern (Cleary *et al*. 2007, Wells *et al*. 2007, Ancrenaz *et al.* 2010, Berry *et al*. 2010, Gillespie *et al*. 2012, Hearn *et al*. 2016). Furthermore, in other tropical regions, species abundance levels and community composition can start to recover following selective logging (Clarke *et al.* 2005, but see Gunawardene *et al*. 2010), and so I argue that it is still necessary to develop conservation strategies that improve the connectivity of disturbed lowland reserves.

5.3.3. Consequences of poor connectivity

Analogous climates may shift out of many PAs on Borneo (Chapter 3), giving tropical species a number of potential ‘options’: ‘acclimate, adapt, move or die’ (Corlett 2011). The potential for acclimation and adaption are dependent on the specific behaviours and thermal limits of organisms (e.g. see Deutsch & Tewksbury 2008), as well as microclimate heterogeneity (Pincebourde & Suppo 2016) (see section 5.2.). Even if species are able to acclimate or adapt to climate change *in situ*, poor connectivity may still result in reduced gene flow between metapopulations, and hence reduced genetic diversity (Bickel *et al.* 2006, but see Benedick*, et al*. 2007b), increasing the chances of local extinction (Reed 2004). Genetic erosion as a consequence of rainforest fragmentation may be particularly relevant for large mammals, because their area requirements for population persistence are greater, resulting in reduced breeding populations (Goossens *et al.* 2005). The ability of these species to move involves range shifting or range expansion in response to warming, and depends on both landscape connectivity and the extent of remaining rainforest. The findings of Chapter 2 suggest that the dispersal of forest-dependent species through agricultural plantations may be limited, and so connectivity may indeed be low in oil palm-dominated landscapes (Kindlmann & Burel 2008). This may therefore result in the limited capacity of forest species to move to cooler locations. In Chapter 3, I showed that many source PAs on Borneo are not connected to higher elevation PAs for species with poor dispersal, and so many species may be unable to track cooler climates. If species cannot move to cooler locations, and subsequently fail to adapt to new (and unsuitable) abiotic conditions then biodiversity could be lost from rainforest systems. Current local assemblages may also be shuffled and interspecific interactions between key species may be disrupted (Colwell *et al.* 2008, Corlett 2011). For example, the loss of species which function as plant dispersal agents from lowland rainforests could bring about cascading effects in plant population community dynamics, and have a major influence on plant population persistence (Corlett 2009, 2011). Therefore, the effectiveness and resilience of tropical PAs networks may decline in future if climate change brings about biodiversity losses as a consequence of poor connectivity.

5.4. Wider applicability of findings

5.4.1. Relevance to other taxa

In Chapter 2, I collected empirical data on forest-dependent butterflies, which are mobile, and have been shown to disperse relatively large distances in rainforest habitats (Benedick *et al*. 2007a, Marchant *et al.* 2015). Hence, the results of my study are most relevant to fairly mobile species (i.e. other winged insects, birds, bats etc.), as opposed to species with lower dispersal abilities such as ants (Corlett 2009) and flightless invertebrates, as their ability to occur in oil palm plantations is likely to depend on their ability to survive permanently in these habitats. The findings of Chapter 2 suggest that oil palm plantations may be permeable to certain generalist species such as small-sized satyrid butterflies in the genus *Mycalesis* (whose larvae feed on grasses). A similar result has also been shown by Barlow *et al*. 2007b, who found that Satyrid butterflies became hyper-abundant in *Eucalyptus* plantations in the Brazilian Amazon. However, my findings also suggest that oil palm plantations may be less permeable to those species that require forest habitat to breed (i.e. forest specialists). Whilst no other studies have quantified edge-crossing movements at rainforest-oil palm plantation boundaries, there are empirical data showing the persistence of generalist species within the oil palm matrix, which is accompanied by the loss of forest specialists (e.g. for birds, beetles and ants: Senior *et al*. 2013; as well as frogs: Gillespie *et al*. 2012). These findings support my conclusions from Chapter 2, which suggest that oil palm plantations may represent barriers to the dispersal of some (possibly many) rainforest species. Other taxa such as orchid bees in neotropical oil palm landscapes, have been shown to penetrate forest-oil palm boundaries relatively frequently, and plantations can have high compositional (>90%) overlap with forest species. However, species richness, abundance and community similarity still declined with increasing distance from forest, suggesting sensitivity of these species to oil palm disturbance (Livingston *et al.* 2013). More research is needed to understand the permeability of habitat boundaries for different taxa, and to determine the distances different types of species can disperse through agricultural matrices.

The modelling approaches I used in Chapters 3 and 4 were most relevant to winged insects (i.e. forest-dependent butterflies), and the conductivity models I used in Chapter 4 were specifically developed to be representative of relatively mobile insect species. It is likely that there is spatial agreement in the expansion routes across dispersal distances for many source PAs; yet, if source PAs are particularly isolated, due to large gaps of unsuitable non-forest habitat, spatial agreement may decline. This is because certain areas of forest that may be important for more mobile species may not have been reached by poor dispersers, and so the spatial locations of expansion routes may diverge. In the metapopulation models used in Chapter 3, dispersal distances moved by species were manipulated to represent a range of different motilities that could reflect a wide variety of rainforest taxa. However, the number of generations per year was specified to be representative of tropical butterflies, as was the population density within each ha^{-1} of forest (Azerefegne *et al.* 2001, Benedick *et al.* 2006, Benedick *et al.* 2007b). Organisms with fewer generations per year (e.g. many mammal species; Bruford *et al.* 2010, Stark *et al.* 2012), may have taken longer to reach target PAs, and so the connectedness of many source PAs was likely conservative for such taxa. Hence, the models I used in Chapter 3 are unlikely to be representative of tropical plant species, particularly long-lived trees that do not reach reproductive maturity for many years (e.g. species within the Dipterocarpaceae; Williamson & Ickes 2002). Precipitation data were also not included in the modelling approaches used in Chapters 3 and 4, due to the uncertainty of future projections (IPCC 2013; Appendix 2B Fig. A2.2). Changes in rainfall patterns are likely to be of particular importance to plants due to transpiration and water loss (Meir & Grace

2005), and drought stress is known to affect the dynamics of tropical lowland plant communities (Lewis *et al.* 2011). Thus, changes in rainfall are likely to be one of the most important drivers affecting patterns in future plant distributions (Platts *et al.* 2013, Rehm *et al.* 2015), but more research is needed to determine the likely impacts of future rainfall patterns on tropical species.

In both Chapters 3 and 4, I assumed that the dispersal of rainforest taxa (i.e. forest-dependent butterflies) along elevation gradients was not restricted by the distribution of specific larval host plants or adult food plants. Whilst there are few data detailing the specific distributions of larval host plants for tropical butterflies, research on temperate species suggests that climate-induced range shifts may not be limited by the availability of specific host plants (e.g. Thomas *et al.* 2001, Davies *et al*. 2006, Pateman *et al*. 2012). Thus, a number of temperate butterfly species have been able to expand rapidly through previously unsuitable landscapes as climates warm. However, it has been suggested that some plant species may lag behind climate change (Bertrand *et al*. 2011, Feeley *et al.* 2011, Dullinger *et al*. 2012), despite a number of studies showing significant elevational and latitudinal shifts in certain species (e.g. Lenoir *et al*. 2008, Chen *et al*. 2011). Some tropical plants also disperse relatively large distances (i.e. >10 km) depending on their specific dispersal agent (e.g. wind, fruit bats and megaherbivores) (Corlett 2009), and so may be capable of crossing fragmented landscapes and tracking cooler climates. It is currently unknown whether the larval host plants of many lowland butterfly species are lagging behind rising temperatures (i.e. if they do not already exist at higher elevation). Hence, more research is needed to determine whether the ability of tropical butterflies to track climate change will be limited by the distributions of their associated larval host plants.

5.4.2. Relevance to other tropical regions

In Chapter 3, I showed that ~60-90% (RCP2.6 and RCP8.5 projections, respectively) of PAs on Borneo may lose analogous climates in future (source PAs), and so conditions may become too warm for species residing within them. A number of studies in other tropical regions have also shown that analogue climates and current species' distributions may shift out of tropical PAs in future (e.g. Marini *et al.* 2009, Vieilledent *et al.* 2013, Baker *et al*. 2015, Feeley & Silman 2016), and the importance of connecting lowland habitats to highland refuges in tropical regions has been acknowledged (Colwell *et al.* 2008, Malhi *et al.* 2008, Perez *et al.* 2016). In Chapter 4, my results showed that landscape-level movements through unprotected forest habitats may be essential for the persistence of tropical species under climate change on Borneo, and this is also likely for other tropical regions, where temperature analogs in the near future will also shift to different PAs in the current PA network (e.g. in Amazonia: Feeley & Silman 2016). I therefore conclude that conservation effort needs to focus on preserving remaining areas of rainforest outside the boundaries of current PAs, and my conclusions are likely to be of global relevance - PA networks in all tropical regions need to be managed in the context of climate change (Avalos & Hernández 2015).

On Borneo, cooler, higher elevation (target) PAs are well placed to receive species that may need to move from lowland areas. However, I found that many lowland PAs are too isolated from remaining areas of forest to facilitate range shifting. In Chapter 3, I discussed the relevance of these results in relation to other regions of Southeast Asia and concluded that similar patterns were likely elsewhere (e.g. Thailand and Sumatra). This is because extensive areas of protected forest remain at higher elevation, whilst agricultural expansion has been most extensive in lowland areas of Southeast Asia (Gaveau *et al.* 2009, Klorvuttimontara *et al.* 2011), due to the suitability of these areas for growing oil palm (Edwards *et al.* 2014b). However, in some tropical regions such as the tropical Andes and parts of Central America, intense agricultural expansion has also occurred at mid-elevation, for other land uses including dairy farming and coffee plantations (Hannah *et al.* 2002). Thus, whilst the future prospects for conserving low-mid elevation species under threat from climate change on Borneo may be promising (given that they reside within PAs that are well connected to the central montane region), this conclusion may not be representative of other regions if mid-elevation PAs are isolated from connecting areas of forest at higher elevation. Hence, the connectedness of PAs and the amount of additional legislative protection needed to conserve PA connectivity may vary by tropical region, depending on current PA cover, the spatial locations of PAs and the physical geography of the system. The modelling approaches used in Chapters 3 and 4 could be easily adapted for other tropical regions (Hodgson *et al.* 2011, 2016), and examining whether there are contrasting patterns across different regions would be an important area of further research in order to design effective PA networks globally.

5.5. Recommendations for conservation and future research

The majority of PAs have been established based on information from static snapshots of species' distributions in the present day (Hole *et al.* 2009, Thomas & Gillingham 2015), which greatly increases the susceptibility of species to climate change (Gaston *et al.* 2006). In many cases, PAs are effective at protecting species from further deforestation and other land-use pressures (e.g. see Thomas & Gillingham 2015), but there is increasing evidence to suggest that current PA networks in tropical regions may not be sufficient to conserve tropical biodiversity. Hence, the effectiveness of tropical PAs under climate change is of global concern (Hannah *et al*. 2007, Klorvuttimontara *et al*. 2011, Feeley & Silman 2016). In Chapter 3, I showed that analogous climates (specifically in relation to temperature changes) are projected to shift out of many PAs on Borneo, and many low-lying PAs that are projected to become too warm are too isolated from continuous forest tracts or 'stepping stones' of suitable habitat to facilitate range shifting. I estimate that protected area cover will need to increase by almost a fifth (~17%; 20,626 km^2) in order to conserve the most important habitat connections for range shifting species on Borneo, and prevent further isolation of lowland PAs (Chapter 4). Further isolation of PAs may have detrimental consequences for PA connectivity, especially in areas where connectivity is already low. Protected areas currently cover >16% of Borneo's land area, which is close to the targets set by the Convention on Biological Diversity (CBD) that aim for 17% of PA cover by 2020 in terrestrial ecoregions (CBD 2010). Therefore, even though there have been some recent steps to designate new reserves on Borneo (e.g. the 'Heart of Borneo' trans-boundary initiative, see: http://www.heartofborneo.org; Proctor *et al.* 2011), increasing PA cover at the scale required to conserve all important habitat connections would be challenging to implement island-wide (Struebig *et al*. 2015b). I conclude that remaining areas of forest that are important for maintaining connectivity for multiple taxa under different assumptions of warming need to be prioritised (see Struebig *et al.* 2015b), and that future research is needed to determine the spatial overlap of expansion routes for different types of species.

Increasing PA cover is one strategy to maintain landscape connectivity, although increasing the number of tropical PAs strictly set aside for biodiversity may not always be feasible due to complex laws and political frameworks regarding land use (e.g. see Cotula *et al*. 2015). Even so, other conservation strategies exist that may also preserve landscape connectivity in fragmented landscapes. For example, downgrading reserves that may be 'underachieving' in their conservation objectives in order to provide additional land for conservation elsewhere has been suggested (e.g. see Alagador *et al.* 2014); although this is somewhat difficult to justify in hyper-diverse rainforest systems. A large proportion of forest outside of PAs on Borneo is under forestry jurisdiction and set aside for commercial logging (Gaveau *et al.* 2013, Struebig *et al*. 2015b). If managed appropriately, these areas also have the potential to provide considerable biodiversity benefits (Edwards *et al*. 2014a). The results of Chapters 3 and 4 suggest that unprotected forest areas may be important for tropical species under threat from climate warming, results supported by recent findings for mammals on Borneo (Struebig *et al*. 2015b). Unfortunately however, the long term persistence of production forests may be at risk, particularly in Indonesia, where 25% of forest areas once allocated for timber harvesting have been reclassified for agricultural development by the government between 2000 and 2010. This suggests that specific land classifications are easily changeable (Gaveau *et al.* 2013), and so urgent steps are needed to increase the protection of timber concessions from reclassification. The retention of state forests may not only have profound benefits for biodiversity and connectivity, but will also help Indonesia meet its pledge of reducing emissions from land use, land use change and forestry (LULUCF) by 2020 (Indrarto *et al*. 2012). In addition, conserving remaining forest areas would also have value under PES (Payments for Ecosystem Services) (e.g. see Duncan 2006) and REDD+ (Reducing Emissions from Deforestation and Forest Degradation and enhancing forest carbon stocks) schemes. The REDD+ mechanism in particular, offers the potential for financing local governments and community based resource management (Scheyvens & Setyarso 2010, Indrarto *et al.* 2012), although there is currently an urgent need to clarify land tenure and legal frameworks to ensure sustainable forest management in the long term (Indrarto *et al.* 2012).

Agricultural expansion in the topics is predicted to increase (Laurance *et al.* 2014), including large scale oil palm plantations in Southeast Asia (Brodie 2016). However, the modelling approaches used in both Chapters 3 and 4 did not take into account future projections of landcover change (i.e. the most likely areas in future to be converted to agriculture). This is an important area of further work, especially in relation to the likely altitudinal expansion of the cultivation zone for oil palm in future. If higher elevation areas become more suitable for oil palm through rising temperatures, the connectedness of both low and mid elevation PAs to PAs at higher elevation may be severely reduced, and many vulnerable biota on Borneo will be threatened (Brodie 2016). Thus, combining future landcover and climate projections (e.g. see Struebig *et al*. 2015b), may be an effective way of identifying rainforest within the most important habitat connections for range shifting species that are most at risk from future deforestation. What's more, the metapopulation and conductivity models used in Chapters 3 and 4 did not take into account improvements to habitat quality or reforestation outside of PAs. Improvements to habitat quality both within existing PAs and along important dispersal routes may help promote dispersal by boosting populations within PAs and increasing the number of migrants (Mair *et al.* 2014). Improving the condition of forest habitat within PAs may also reduce the synergistic effects of climate change and habitat loss, resulting in more favourable abiotic conditions in degraded forests (e.g. reduced edge effects etc.) (Laurance 2005), which may allow more species to adapt to climate change *in situ*. Furthermore, reforestation could help to improve important connections for low-lying PAs that may be too isolated to facilitate range shifting. One direct extension to my modelling approach in Chapter 4 would be to identify places where adding a small amount of habitat could markedly improve range expansion due to a current 'bottleneck' (see Hodgson *et al*. 2016). However, successful reforestation is dependent on species' dispersal ability, the permeability of the surrounding matrix, and the suitability of proposed locations for conversion into rainforest (Fagan *et al*. 2016). Hence, more research is needed to determine whether reforestation along elevation gradients in tropical agricultural landscapes will be an appropriate and effective conservation strategy.

The results of my empirical data collection in Chapter 2 suggest that some forest-dependent species (species whose larval host plants are restricted to forest) may become increasingly confined within isolated forest patches because they are unable to cross rainforest-oil palm plantation boundaries in high numbers. Therefore, when considering reforestation and conserving important areas of connecting forest, riparian forest strips and forest corridors may facilitate dispersal between PAs and larger areas of remaining forest through agricultural matrices (Gillies & St Clair 2008, Gregory *et al.* 2014, Brodie *et al.* 2015, Kormann *et al.* 2016). However, if tropical species are unable to cross habitat boundaries into oil palm plantations, retaining forest fragments may not be an effective conservation strategy in agricultural landscapes if they cannot support viable populations of species. A number of crop sustainability standards such as the Roundtable on Sustainable Palm Oil (RSPO; http://www.rspo.org) and Roundtable for Responsible Soy (RTRS; http://www.responsiblesoy.org) have been adopted by growers and users of certain crops to reduce biodiversity losses within agricultural matrices and promote the retention of forested areas with 'High Conservation Values' (HCVs; see http://www.hcvnetwork.org) within the plantation matrix (see RSPO 2013, RTRS 2013). Retaining these forested areas is a potential strategy for promoting 'wildlife-friendly' farming (see Green *et al*. 2005). However, my results suggest that more research is needed to determine whether these forest areas can provide resting and foraging sites, as well as support breeding populations (e.g. see Lees & Peres 2009), which could increase connectivity and promote movement of rainforest species through agricultural landscapes.

5.6. Conclusions

Tropical species under threat from climate change may need to move through fragmented landscapes in order to track cooler climates. On Borneo, and in other parts of Southeast Asia, this may require movement of species through large-scale oil palm plantations. Movement across rainforest-oil palm plantation boundaries was relatively infrequent for forest butterflies that require rainforest habitat to breed. Therefore, oil palm plantations may act as barriers to the dispersal of forest-dependent species in agricultural landscapes, potentially restricting forest species to isolated PAs. Analogous climates may shift out of the majority of lowland PAs on Borneo, and so species may need to move to higher elevation PAs to track cooler climates. Due to the loss of lowland rainforest by expansion of oil palm plantations, the majority of PAs from which analogous climates may disappear are likely to be too isolated to allow species with poor dispersal abilities to reach cooler PAs at higher elevation. Approximately two thirds of remaining rainforest within important connections linking these PAs along elevation gradients may not be protected for relatively mobile dispersers. Hence, PA extent may need to increase by approximately one fifth in order to conserve many important areas of rainforest on

Borneo, help maintain current connectivity and facilitate range shifting by rainforest species. Maintaining connectivity may be vital for promoting resilience and biodiversity in tropical agricultural landscapes, where rainforest systems are under threat from continued agricultural expansion and climate change.

List of Appendices

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Appendix 1 – Supporting information for Chapter 2

Appendix 1A. Measuring vegetation structure at study sites

Butterfly movement data were collected from four sites and combined for subsequent analysis. The four sites were chosen to be broadly similar in terms of forest disturbance, age and management of adjacent oil palm plantations, and hence the boundary characteristics. In order to assess the similarity of the four sites, we measured environmental characteristics of the forest-oil palm plantation boundaries at each site (Chapter 2: Fig. 2.1a; Fig. A1.1). A total of 13 variables were recorded in forest and five variables in plantation (see Table A1.1 for summary data for these variables). At each trap in forest habitat (n = 12 traps per site; 4 sites) (following Hamer *et al*. 2003) we measured the following: (1) temperature, using one HOBO® data logger placed at each trap recording at 30 min intervals (loggers were activated at the start of each sampling period and removed after sampling terminated; where possible, data loggers were placed at breast height on tree trunks in the shade); (2) shade cover (%), measured using a spherical densiometer (Model-C; a measure of all overhead vegetation, see Lemmon 1956) above each trap facing N, E, S and W; (3) ground cover (%), an estimation (by eye) of plant vegetation cover at ground level (< 1 m); (4) canopy cover (%), an estimation (by eye) of all vegetation > 15 m above ground; (5) sub-canopy cover (%), an estimation (by eye) of all vegetation < 15 m above ground (all estimations were made by the same observer in each of the four quadrants within a 10 m radius of each trap); (6) circumference at breast height (CBH) of the two nearest trees (CBH ≥ 0.6 m) and (7) saplings (CBH 0.1-0.6 m) in the four quadrants, measured within a 30 m radius of each trap; (8) distance from trap of two nearest trees and (9) saplings in each quadrant; (10) identity (family Dipterocarpaceae or other) of two nearest trees and (11) saplings in each quadrant; (12) point of inversion of two nearest trees in each quadrant (mean estimated height (m) from two observers of first major branch; see Torquebiau 1986); and finally, (13) number of fallen fruit species at beginning of sampling period, recorded during 2 min fallen fruit searches in each of the four quadrants, and within a 10 m radius of the trap station (fruits were later identified in the laboratory). From our measurements at forest traps, we then calculated a measure of tree and sapling density (number of trees or saplings measured/average distance of each from trap), the proportion of trees and saplings that were members of the Dipterocarpaceae (a family that comprises a dominant component of canopy trees in Bornean forests and used as an indicator of forest quality; Hamer *et al*. 2003), and the tree and sapling heights (calculated from the CBH measurements using logarithmic allometric equations generated by Morel *et al*. 2011).

At each trap in plantation habitat (*n* = 12 traps per site; 4 sites) we measured the following: (1) temperature; (2) shade cover (%); (3) ground cover (%) (using same methodology as in forest); (4) estimated height of ground cover (m) in each of the four quadrants within a 10 m radius of the trap station; and (5) number of plant species, recorded using 4 x 10 m transects facing N, E, S and W (centred on each trap) whereby any plants within 0.25 m of the tape were recorded at 0, 5 and 10 m (thus *n* = 9 samples per trap) (plants were later identified in the laboratory).

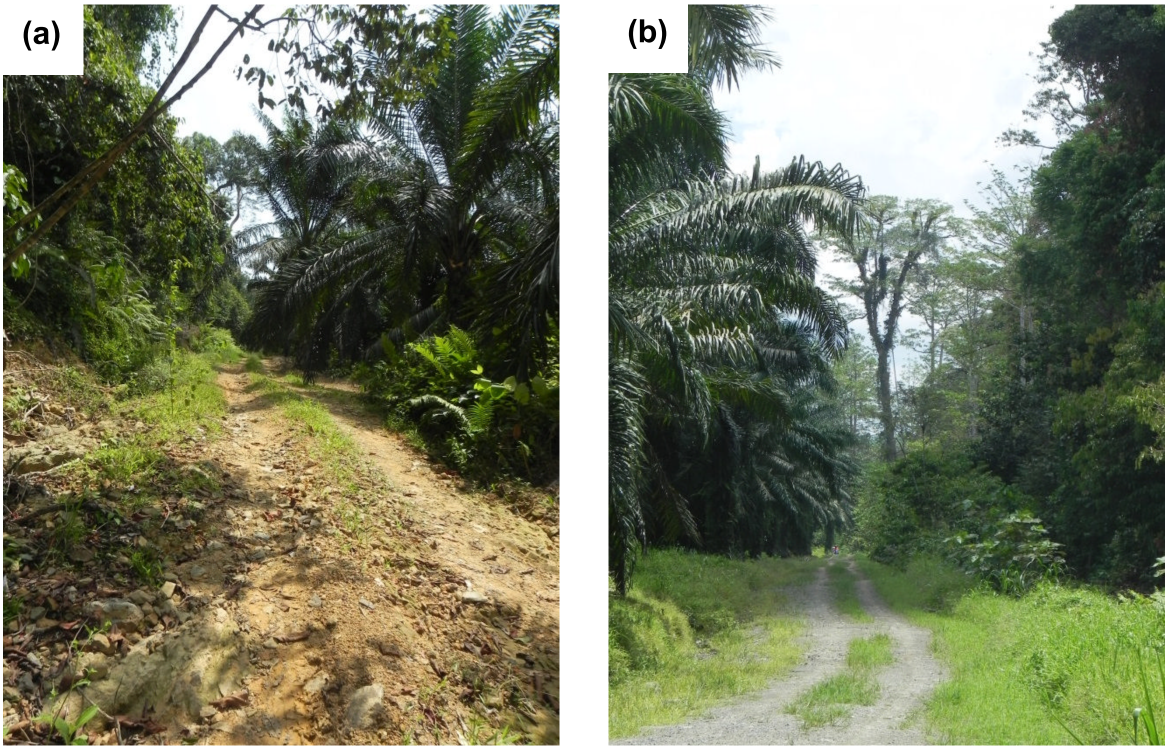


Figure A1.1. Photographs of forest-oil palm plantation boundaries at study sites; (a) site 1 adjacent to the Ulu Segama Forest Reserve, and (b) site 3 adjacent to the Tabin Wildlife Reserve**.**

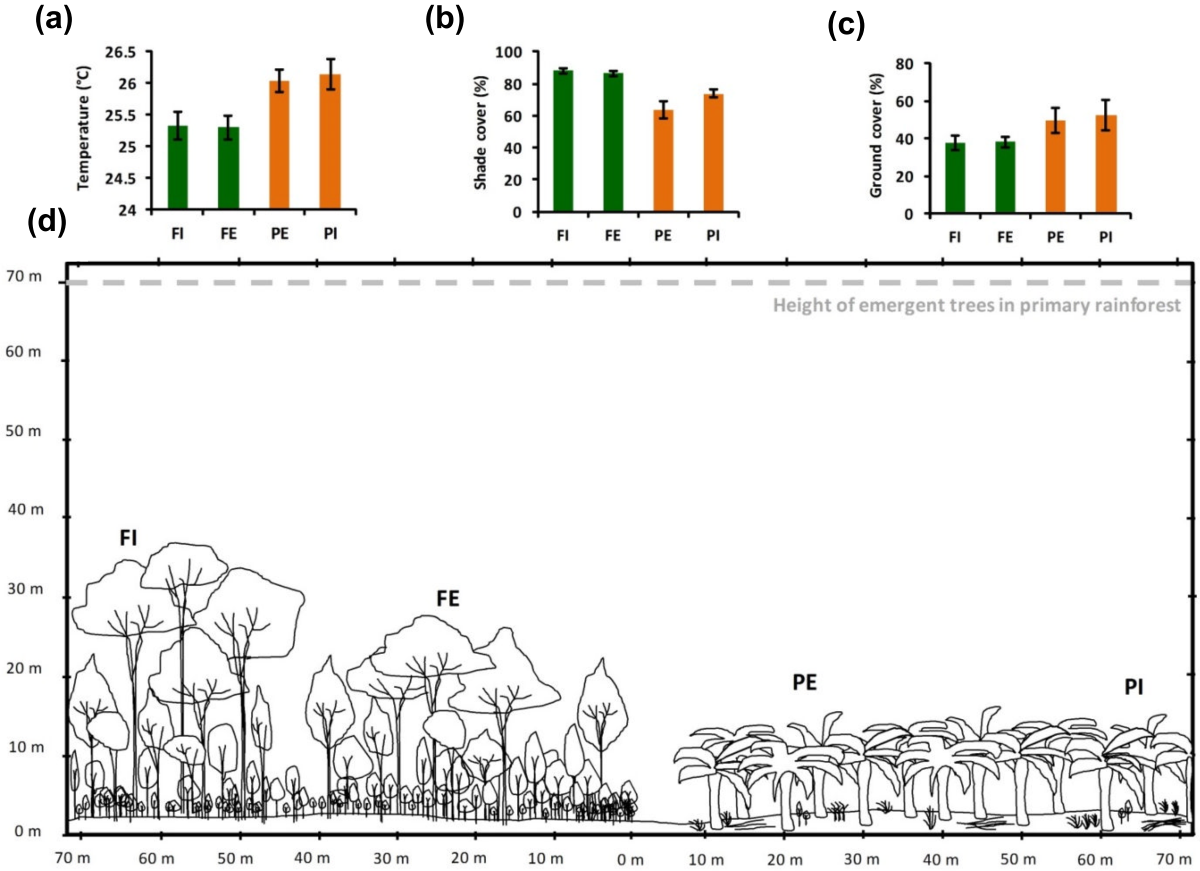


Figure A1.2. (a) Mean daily temperature (averaged across 18 d of sampling), (b) shade cover (%) and (c) ground cover (%), averaged across all study sites for traps located within forest interior (FI), forest edge (FE), plantation edge (PE) and plantation interior (PI) trap stations (see Chapter 2: Fig. 2.1 in for trap set up). Error bars represent standard errors. (d) Example of a lateral section (70 m in height; 140 m in width) through secondary forest (Ulu Segama Forest Reserve, Sabah) and adjacent oil palm plantation study site. Average tree (CBH ≥ 0.6 m) height across all forest sites was 26.5 m (SE ± 0.64 m); whilst in plantation habitats, palm trees were between 13-16 years old and approximately 10-15 m tall (to canopy top). Figure adapted from Foster *et al*. (2011).

Table A1.1. Habitat variables summarized across study sites for edge and interior trap stations. Temperature values are the mean, minimum and maximum daily temperatures averaged across 18 d of sampling for six interior trap stations and six edge trap stations at each study site; all others variables are the mean of measurements recorded at each of the six interior and six edge trap stations per study site. SE = standard erros.

Habitat variable:	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Mean (± SE)**	
Forest	**Edge**	**Interior**	**Edge**	**Interior**	**Edge**	**Interior**	**Edge**	**Interior**	**Edge**	**Interior**
Daily mean temperature (^{o}C)	24.58	24.49	24.76	24.75	26.16	26.07	25.76	25.83	25.31 (± 0.38)	25.29 (± 0.39)
Daily min temperature (^{o}C)	21.41	21.27	21.57	21.54	22.61	25.12	22.32	22.45	21.98 (± 0.29)	22.6 (± 0.88)
Daily max temperature (^{o}C)	30.88	33.71	31.14	31	36.77	32.24	31.86	31.8	32.66 (± 1.38)	32.19 (± 0.57)
Shade cover (%)	88.2	86.2	84	86.2	89.9	84.6	90.3	89.2	88.1 (± 1.44)	86.6 (± 0.96)
Ground cover (%)	37.9	44.2	39.8	37.5	31.7	26.5	41.3	45.0	37.7 (± 2.11)	38.3 (± 4.28)
Canopy cover (%)	21.3	36.7	35.4	42.1	20.4	30.4	29.2	57.3	26.6 (± 3.54)	41.6 (± 5.75)
Sub canopy cover (%)	55.4	56.3	57.1	60.8	49.8	48.3	58.5	52.7	55.2 (± 1.91)	54.5 (± 2.66)
Tree CBH (cm)	130.9	142.9	103.5	114.3	100.8	132.4	125.1	140.7	115.1 (± 7.57)	132.6 (± 6.5)
Tree density	0.71	0.67	1.25	0.97	0.98	0.93	0.89	0.90	0.96 (± 0.11)	0.87 (± 0.07)
Tree prop. dipterocarps	0.25	0.42	0.23	0.06	0.02	0.02	0.13	0.35	0.16 (± 0.05)	0.16 (± 0.09)
Tree height (m)	27.5	28.7	23.3	25.4	23.5	27.9	27.1	28.9	25.35 (± 1.10)	27.7 (± 0.80)
Tree inversion (m)	11.1	13.7	11.5	13.3	9.9	11.5	11.3	13.7	11.0 (± 0.36)	13.1 (± 0.53)
Sapling CBH (cm)	25.0	26.5	18.9	22.5	20.6	21.8	21.9	23.3	21.6 (± 1.29)	23.5 (± 1.04)
Sapling height (m)	9.0	9.4	6.5	7.9	7.2	7.6	8.8	8.3	7.88 (± 0.61)	8.3 (± 0.39)
Sapling density	2.77	2.46	2.35	2.15	2.08	2.64	2.12	2.15	2.33 (± 0.19)	2.35 (± 0.12)
Sapling prop. dipterocarps	0	0.17	0.04	0.13	0	0	0.02	0.17	0.015 (± 0.01)	0.12 (± 0.04)
No. fallen fruit species	1.3	1.8	2.7	2.3	4.7	3.3	2.3	5.3	2.75 (± 0.7)	3.18 (± 0.77)
Plantation	**Edge**	**Interior**	**Edge**	**Interior**	**Edge**	**Interior**	**Edge**	**Interior**	**Edge**	**Interior**
Daily mean temperature (^{o}C)	25.31	25.3	25.68	25.5	26.79	26.9	26.35	26.8	26.03 (± 0.33)	26.13 (± 0.42)
Daily min temperature (^{o}C)	21.89	21.92	21.84	21.82	23.5	23.65	23.02	22.66	22.56 (± 0.41)	22.57 (± 0.41)
Daily max temperature (^{o}C)	37.62	32.51	35.23	33.14	36.66	37.5	34.15	36.82	35.92 (± 0.77)	35.0 (± 1.27)
Shade cover (%)	61.4	75.3	63.4	66.9	62.7	76.7	66.6	76.2	63.5 (± 1.1)	73.8 (± 2.31)
Ground cover (%)	52.1	58.3	31.7	19.6	36.0	50.2	78.8	86.3	49.65 (± 10.7)	53.6 (± 13.7)
Ground cover height (m)	0.48	0.77	0.35	0.27	0.35	0.34	0.50	0.48	0.42 (± 0.04)	0.47 (± 0.11)
No. plant species	15.0	12.2	13.2	12.5	11.0	15.3	14.0	17.3	13.3 (± 0.85)	14.3 (± 1.21)

Appendix 1B. Additional statistical analyses with species data split by site

Our analyses in the main text of Chapter 2 are on species data combined across all four sites, but we carried out additional analyses to examine the influence of any site-level effect on our findings. To examine the influence of any site-level effects, we re-ran analyses with species data split by site. Thus, we computed recaptures and movement data separately for each species at each site. We used a Generalised Linear Mixed Model (GLMM) (see main text Chapter 2 for model details) and included site identity as a random effect. As in the main analyses on combined data, our additional analyses comprised two sets of proportion data for each of the 16 study species: one set of data for the total number of within-forest recaptures and boundary crossing events by forest individuals and another set of data for the total number of within-plantation recaptures and boundary crossing events by plantation individuals. However, in our additional analyses, these two sets of proportional data were computed separately for the 16 study species for each of the four study sites, representing the number of within-habitat movements and boundary crossing events at each of our sample sites (Table A1.1). See Table A1.2 below for GLMM results with species data split by site. For some species, there were few/no recaptures (or occurrences) per site, and so these data are not as robust as the analyses in the main text of Chapter 2, where combining data across the four sites provides a better overall assessment of boundary crossing for each species. These additional analyses did not alter our main conclusions, although the local abundance of species became more important than species traits (Table A2.2).

Table A1.2. Model comparisons for binomial logistic regression models (GLMMs) determining the effect of species traits (forewing length, larval host plant (LHP) specificity, larval host plant availability and geographical range size) and abundance on probability of crossing the boundary for forest and plantation individuals; species data are split by sample site.

Model	**Direction**[a]	**K**[b]	**LL**[c]	**AICc**[d]	**ΔAICc**[e]	**w_i**[f]
Ln habitat abundance * Habitat	+	6	-83.75	180.2	-	0.992
LHP availability * Habitat	+	6	-89.39	191.47	11.27	0.004
Forewing length * Habitat	-	6	-89.5	191.69	11.49	0.003
Ln LHP specificity * Habitat	NA	6	-90.76	194.21	14.01	0.001
Habitat-only model	NA	4	-93.81	195.95	15.75	0.000
Geographical range size * Habitat	NA	8	-90.22	197.66	17.46	0.000

[a] Positive (+) or negative (-) relationship between each trait and boundary crossing probability from forest into plantation for each model that was better (Δ Akaike information criterion (AICc) > 2) than the habitat-only model. NA = not computed.

[b] Number of estimated parameters in the fitted model.

[c] Log likelihood (LL): overall model fit.

[d] A measure of model fit corrected for sample size.

[e] Change in AICc from that of the best model.

[f] Akaike weight, representing the model’s relative strength compared to other best models.

Appendix 1C. Summary data of recaptures and full species list

Table A1.3. Summary data of butterfly recaptures across four forest-plantation boundary sites. Data from the four sites were combined for analysis. No. of individuals marked = number of unique individuals that were captured and marked; no. of individuals recaptured = number of individuals that were subsequently recaptured, regardless of the number of times they were recaptured (which ranged from 1–12 times); proportion crossing from forest = number of individuals that crossed the boundary into plantation (including data from only the first recapture for individuals that crossed the boundary on multiple occasions)/number of individuals marked in forest; proportion crossing from plantation = number of individuals that crossed the boundary into forest/number of individuals marked in plantation.

Summary statistics	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**All Sites**
Overall data					
No. of individuals marked	257	252	801	356	1666
No. of individuals recaptured	82	89	229	127	527
Individual recapture rate	31.9%	35.3%	28.6%	35.7%	31.6%
Species data					
No. of species marked	32	31	48	37	65
No. of species recaptured	15	16	20	18	28
Boundary crossing data					
No. individuals crossing boundary	22	18	49	11	100
No. species crossing boundary	7	8	10	6	13
Proportion crossing from forest	0.52	0.3	0.52	0.23	0.41
Proportion crossing from plantation	0.15	0.17	0.11	0.05	0.11
Habitat data					
No. individuals marked in forest	92	80	283	106	561
No. individuals marked in plantation	165	172	518	250	1105
No. species marked in forest	17	21	34	24	42
No. species marked in plantation	30	25	31	25	51

Table A1.4. Butterfly species list with trait and abundance information. Traits include: larval host plant (LHP) availability = presence or absence of host plants in oil palm plantations; larval host plant specificity = number of host plant genera that larva have been recorded feeding on; forewing length = average of males and females; and geographical range size = a measure of habitat specificity. Many species sampled were either data deficient for host plant information, or not found by Lucey and Hill (2012), hence the high number of missing values. See Methods of main text in Chapter 2 for trait details. Abundance in forest and plantation habitats represents the number of individuals marked in each habitat type

Subfamily	Genus	Species	LHP availability	LHP specificity	Forewing length (mm)	Geographical range size	Abun.	Abun. in forest	Abun. in plantation	No. Individuals Crossing
Charaxinae	*Agatasa*	*calydonia*	Absent	1	54.5	Intermediate	12	6	6	0
Charaxinae	*Charaxes*	*bernardus*	Absent	13	44.3	Intermediate	52	22	30	1
Charaxinae	*Charaxes*	*durnfordi*	-	-	51.5	Intermediate	9	8	1	0
Charaxinae	*Polyura*	*athamas*	-	10	32.3	Intermediate	8	2	6	0
Charaxinae	*Polyura*	*hebe*	-	5	35.0	Intermediate	1	0	1	0
Charaxinae	*Polyura*	*moori*	-	1	34.3	Intermediate	4	0	4	0
Charaxinae	*Prothoe*	*franck*	Absent	2	40.3	Intermediate	22	19	3	1
Morphinae	*Amathusia*	*masina*	-	-	54.0	Narrow	10	9	1	0
Morphinae	*Amathusia*	*phidippus*	Present	10	53.0	Intermediate	156	46	110	5
Morphinae	*Amathusia*	*schoenbergi*	-	1	62.0	Narrow	3	3	0	0
Morphinae	*Amathuxidia*	*amythaon*	-	-	57.0	Intermediate	2	2	0	0
Morphinae	*Discophora*	*necho*	Present	1	46.0	Narrow	54	22	32	2
Morphinae	*Thaumantis*	*klugius*	-	-	43.0	Intermediate	1	1	0	0
Morphinae	*Zeuxidia*	*amethystus*	Present	-	52.0	Intermediate	2	2	0	0
Morphinae	*Zeuxidia*	*aurelius*	Present	1	67.8	Narrow	2	2	0	0

Morphinae	*Zeuxidia*	*doubledayi*	Present	1	53.5	Intermediate	2	2	0	0
Nymphalinae	*Amnosia*	*decora*	Absent	1	41.5	Narrow	1	1	0	0
Nymphalinae	*Athyma*	*kanwa*	-	1	28.8	Intermediate	3	1	2	0
Nymphalinae	*Athyma*	*pravara*	Absent	1	24.5	Intermediate	2	1	1	0
Nymphalinae	*Athyma*	*reta*	-	1	28.3	Intermediate	1	0	1	0
Nymphalinae	*Bassarona*	*dunya*	-	-	45.3	Intermediate	21	19	2	0
Nymphalinae	*Bassarona*	*tueta*	-	-	36.5	Intermediate	4	1	3	0
Nymphalinae	*Cirrochroa*	*emalea*	Present	1	36.0	Intermediate	1	0	1	0
Nymphalinae	*Dichorragia*	*nesimachus*	-	1	41.5	Wide	13	7	6	0
Nymphalinae	*Dophla*	*evelina*	Absent	4	49.0	Intermediate	79	42	37	9
Nymphalinae	*Euthalia*	*aconthea*	-	9	29.0	Intermediate	1	0	1	0
Nymphalinae	*Euthalia*	*alpheda*	-	1	33.0	Intermediate	1	0	1	0
Nymphalinae	*Euthalia*	*iapis*	-	4	30.0	Narrow	2	1	1	0
Nymphalinae	*Euthalia*	*kanda*	-	-	31.5	Intermediate	1	0	1	0
Nymphalinae	*Euthalia*	*merta*	-	-	31.3	Intermediate	2	0	2	0
Nymphalinae	*Euthalia*	*monina*	Present	5	29.5	Intermediate	1	0	1	0
Nymphalinae	*Euthalia*	*djata*	-	1	30.5	Intermediate	2	0	2	0
Nymphalinae	*Hypolimnas*	*bolina*	Present	28	36.0	Wide	29	0	29	0
Nymphalinae	*Junonia*	*atlites*	-	5	36.5	Intermediate	20	0	20	0
Nymphalinae	*Kallima*	*limborgi*	-	5	53.5	Intermediate	2	2	0	0
Nymphalinae	*Lebadea*	*martha*	-	3	30.0	Intermediate	1	0	1	0
Nymphalinae	*Lexias*	*dirtea*	Absent	4	42.5	Intermediate	6	6	0	0
Nymphalinae	*Lexias*	*pardalis*	Absent	1	44.5	Intermediate	4	3	1	0
Nymphalinae	*Moduza*	*procris*	Absent	13	33.5	Intermediate	9	0	9	0
Nymphalinae	*Neorina*	*lowii*	Present	1	48.5	Narrow	24	19	5	2
Nymphalinae	*Neptis*	*clinia*	-	4	24.5	Wide	1	0	1	0
Nymphalinae	*Neptis*	*hylas*	Absent	27	26.5	Wide	18	0	18	0

Nymphalinae	*Paduca*	*fasciata*	Absent	2	22.3	Intermediate	1	1	0	0
Nymphalinae	*Pandita*	*sinope*	-	2	28.0	Narrow	2	0	2	0
Nymphalinae	*Parthenos*	*sylvia*	Absent	4	47.0	Wide	1	0	1	0
Nymphalinae	*Phalanta*	*alcippe*	-	2	23.5	Wide	1	1	0	0
Nymphalinae	*Rhinopalpa*	*polynice*	Absent	2	34.0	Intermediate	9	4	5	0
Nymphalinae	*Tanaecia/ Euthalia*	*species*	-	-	-	-	8	6	2	0
Satyrinae	*Coelites*	*epiminthia*	-	-	35.0	Intermediate	3	3	0	0
Satyrinae	*Elymnias*	*dara*	Present	-	30.5	Intermediate	2	0	2	0
Satyrinae	*Elymnias*	*nesaea*	Present	4	39.0	Intermediate	75	13	62	7
Satyrinae	*Elymnias*	*panthera*	Present	3	31.5	Narrow	81	23	58	4
Satyrinae	*Lethe*	*dora*	-	-	34.0	Narrow	1	0	1	0
Satyrinae	*Melanitis*	*leda*	Present	24	34.5	Wide	217	78	139	19
Satyrinae	*Melanitis*	*zitenius*	Present	2	39.0	Intermediate	5	3	2	0
Satyrinae	*Mycalesis*	*amoena*	-	-	31.0	Narrow	1	1	0	0
Satyrinae	*Mycalesis*	*anapita*	Present	-	19.0	Intermediate	203	66	137	26
Satyrinae	*Mycalesis*	*horsfieldi*	Present	3	23.0	Intermediate	247	40	207	15
Satyrinae	*Mycalesis*	*maianeas*	Absent	1	22.5	Narrow	1	1	0	0
Satyrinae	*Mycalesis*	*mineus*	Present	8	23.5	Intermediate	134	7	127	6
Satyrinae	*Mycalesis*	*orseis*	Present	-	24.5	Intermediate	63	50	13	3
Satyrinae	*Ragadia*	*makuta*	Absent	1	21.5	Narrow	16	15	1	0
Satyrinae	*Ypthima*	*baldus*	-	8	19.0	Wide	3	0	3	0
Satyrinae	*Ypthima*	*fasciata*	-	-	19.3	Narrow	2	0	2	0
Satyrinae	*Ypthima*	*pandocus*	-	4	21.5	Intermediate	1	0	1	0

Appendix 2 – Supporting information for Chapter 3

Appendix 2A.

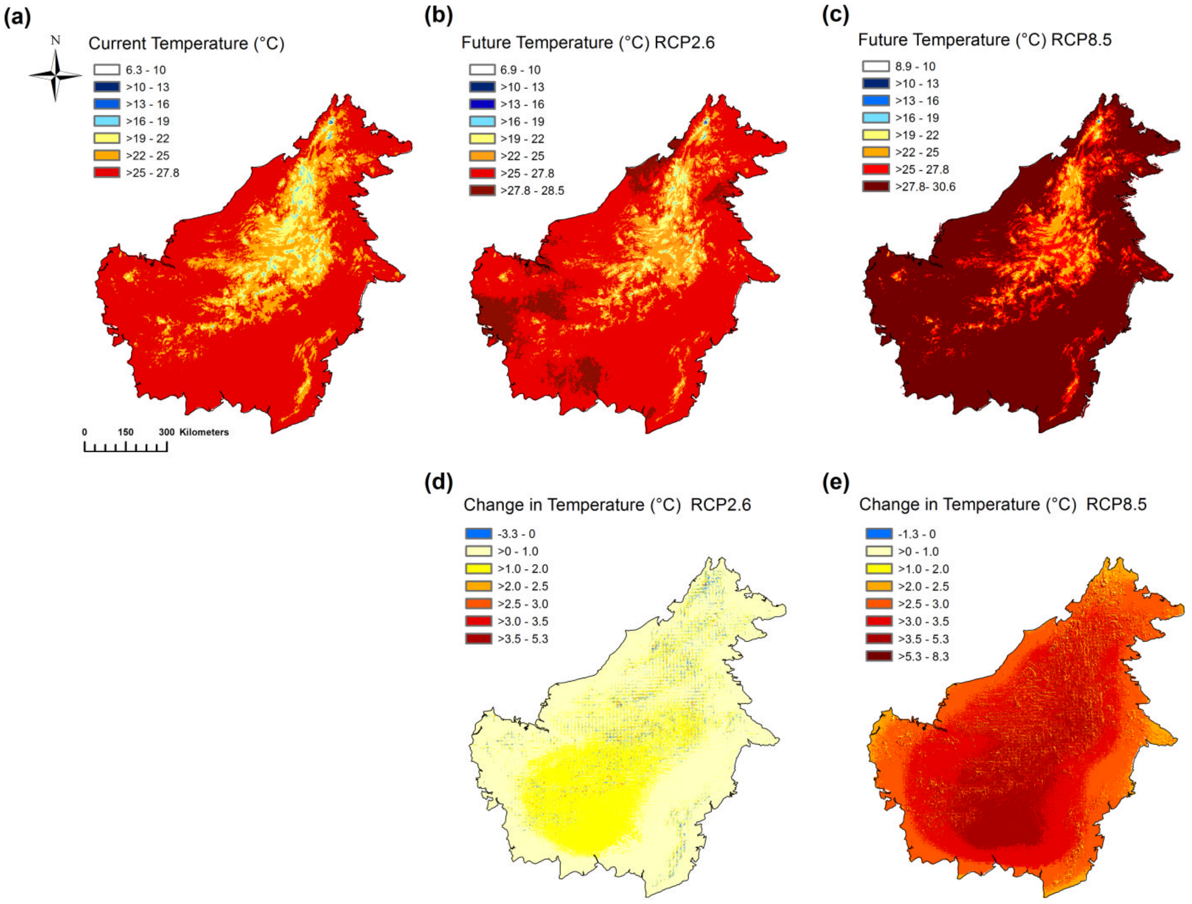


Figure A2.1. Temperature maps of Borneo showing (a) annual current (1950-2000) temperature in approximately 3°C temperature bands; (b) annual future temperature for RCP2.6 projections (2061-2080), in the same 3°C temperature bands; (c) annual future temperature for RCP8.6 projections (2061-2080), also in the same 3°C temperature bands; (d) annual temperature change between the projected RCP2.6 temperature and the current temperature; and (e) annual temperature change between the projected RCP8.5 temperature and the current temperature. All maps were created from gridded data at a 1 km grid cell size.

Appendix 2B.

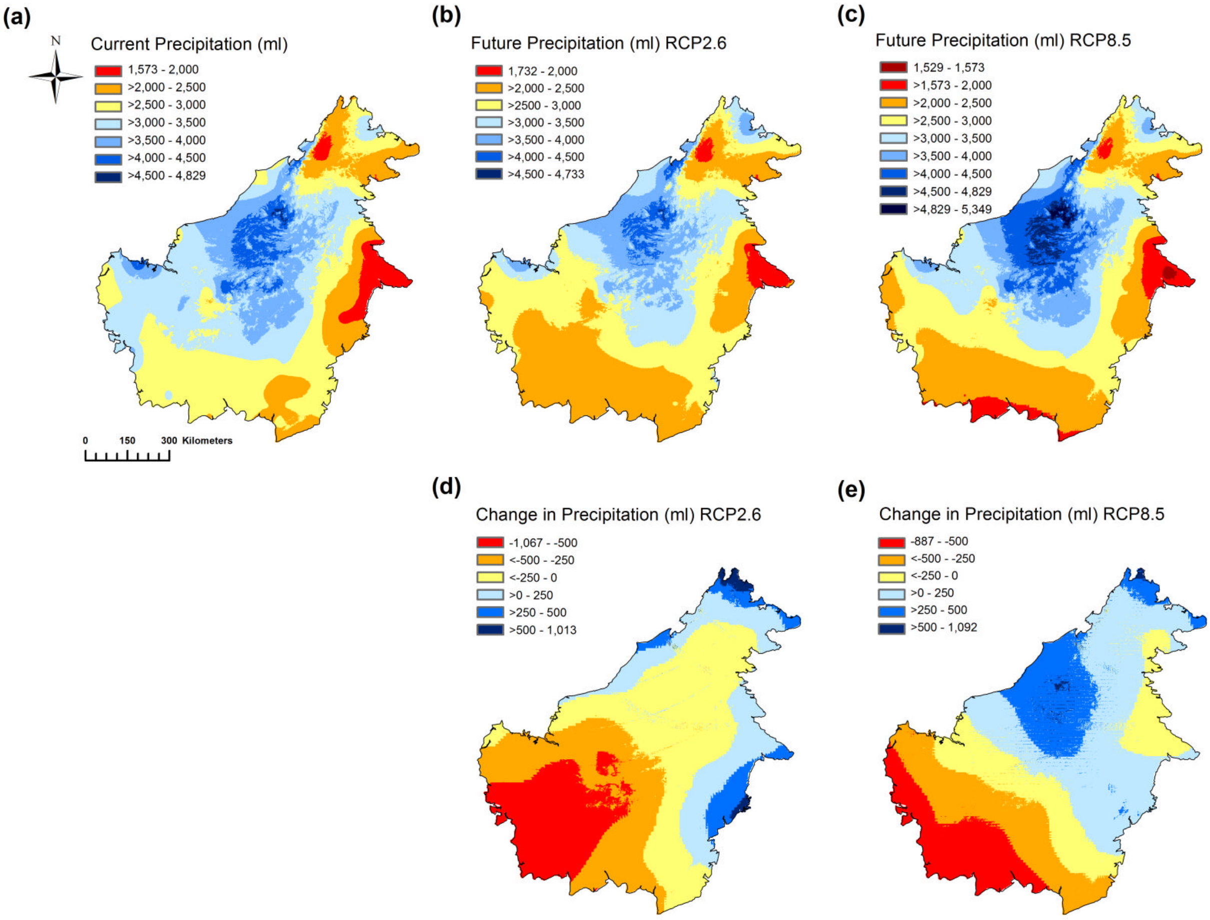


Figure A2.2. Precipitation maps of Borneo showing (a) annual current (1950-2000) precipitation in approximately 500 ml bands; (b) future precipitation for RCP2.6 projections (2061-2080) in the same 500 ml bands; (c) future precipitation for RCP8.6 projections (2061-2080), also in the same 500 ml bands; (d) precipitation change between the projected RCP2.6 future precipitation and the current precipitation; and (e) precipitation change between the projected RCP8.5 future precipitation and the current precipitation. All maps were created from gridded data at a 1 km grid cell size.

Appendix 2C. R code and information for running the Incidence Function Model (IFM)

Description

Function ‘ifm’ is an implementation of the incidence function model of a patch-based metapopulation.

Usage:

```
ifm(x,y,area,startocc,istarget,alpha,R,reportat,maxtime)
```

Arguments:

`x,y`	Vectors containing the x and y coordinates of the centres of the patches (grid cells). These must be the same length and should be measured in kilometres.
`area`	Amount of available habitat within each patch (grid cell). Area is multiplied by the population density to estimate the carrying capacity of each cell. This is used to calculate the extinction probability, which is 1/carrying capacity of each habitat patch at each time step.
`startocc`	Patches (grid cells) from which the metapopulation initially expands. Expansion can occur in any direction.
`istarget`	Patches (grid cells) that the metapopulation need to reach; simulations are terminated once they become occupied.
`alpha`	The parameter that sets the dispersal distance of the species, which is the slope of a negative exponential dispersal kernel.
`R`	The density of individuals in occupied habitat, which equates to the number of emigrants produced per generation per occupied grid cell.
`reportat`	When to produce reports of patch (grid cell) occupancy
`maxtime`	The number of generations for which to run the simulations. Simulations will terminate when this time has elapsed, if an `istarget` has not been occupied

Value

A list containing the following components:

tis	The time series of the simulation that is a data frame with columns headed t (time step) and no (the no of occupied patches).

`time`	The time step when model simulation is terminated.
`snapshots`	data frame where each column is a snapshot of patch occupancy at a given time, including time 0, every `reportat` years, and the end

Author

Jenny A. Hodgson (see Hodgson *et al*. 2011)

R Code:

```
ifm<-function(x,y,area,startocc,istarget,alpha,R,
reportat=10000, #this is how often you want reports of occupancy
maxtime=10000){

le<-length(x)
pex<- pmin(1,1/area/R) #baseline probability  of extinction
conn<-rep(0,le) #the connectivity

for(j in 1:le){
if( startocc[j] ){
conn[-j] <- conn[-j]+(area[-j])*alpha^2/2/pi*
area[j]*R*exp(-alpha*
sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
) #close kernel
} #close if
} #close j loop

########### output for t=0 #############
tis<- data.frame(t=0,no=sum(startocc))
snapshots<-data.frame(t0=startocc) #preparing a data frame to contain
snapshots
      occ0<-startocc

###### the actual simulation #######
for(i in 1:maxtime){
pcol<- 1-exp(-conn)
pext<- pex*(1-pcol) #extinction prob with rescue effect
occ1<- (occ0*(1-pext) + (!occ0)*(pcol)) > runif(le) #the new occupancy

tis<- rbind(tis,c(t=i,no=sum(occ1)))#the results, no. patches occupied

if( (i %% reportat)==0){ #snapshot of all patches at intervals of
'reportat'
snapshots[,paste("t",i,sep="")]<-occ1
}

########### test for ending ###########
if( sum(occ1)==0 ){break}
if( sum(occ1[istarget==1])>0 ){break}

########### update connectivity #######
for(j in 1:le){
if( occ0[j] & !occ1[j]){
conn[-j] <- conn[-j] - (area[-j])*
alpha^2/2/pi*area[j]*R*exp(-alpha*
```

```
sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
) #close kernel
} #close if
if( !occ0[j] & occ1[j]){
conn[-j] <- conn[-j] + (area[-j])*
alpha^2/2/pi*area[j]*R*exp(-alpha*
sqrt( (x[-j] - x[j])^2 + (y[-j] - y[j])^2 )
) #close kernel
} #close if
} #close j loop

occ0<- occ1
} #end time series

if( (i %% reportat)!=0){# snapshot at end if not already done
snapshots[,paste("t",i,sep="")]<-occ1
}
list(tis=tis,time=i,snapshots=snapshots)#return this
} end the function
```

Appendix 2D.

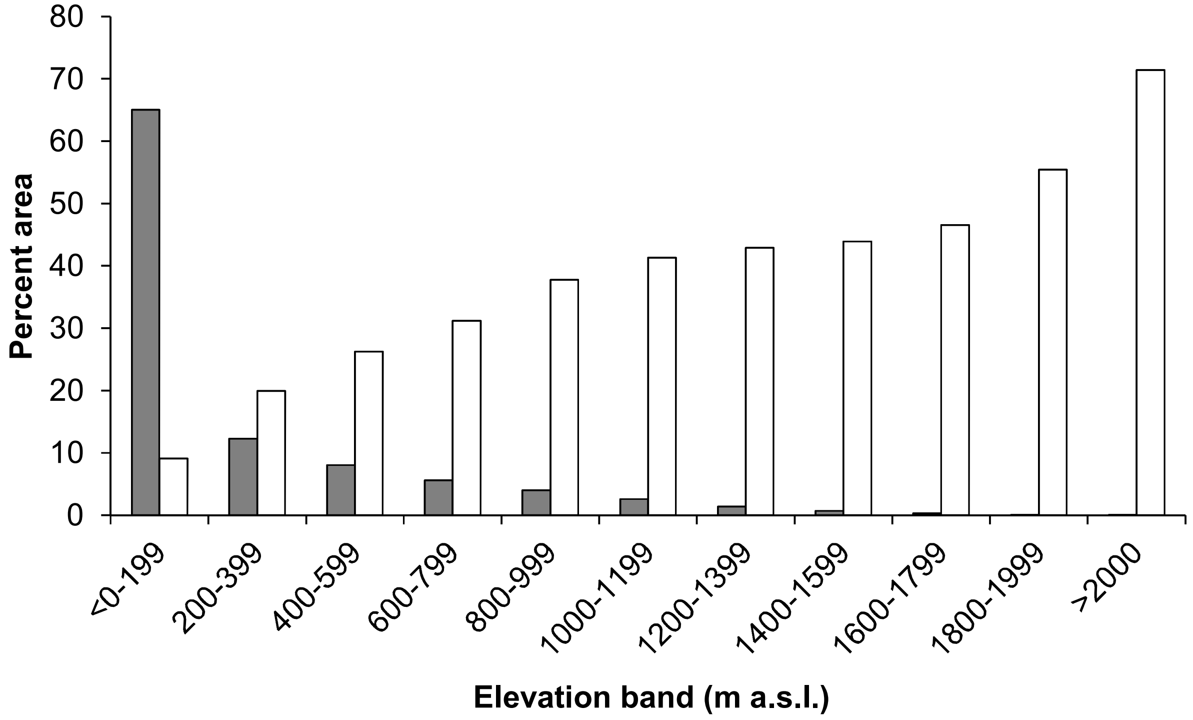


Figure A2.3. Land area in different elevation bands (m a.s.l.), expressed as a percentage of total land area (grey bars), and percentage of land in each elevation band that is protected (white bars).

Appendix 2E.

Table A2.1. Summary data describing the characteristics of source and refuge protected areas (PAs) for low (RCP2.6) and high (RCP8.5) warming scenarios (2061-2080). See Chapter 3 for definitions of 'source' and 'refuge' PAs.

Characteristic	**Source PAs RCP2.6**	**Refuge PAs RCP2.6**	**Source PAs RCP8.5**	**Refuge PAs RCP8.5**
n[a]	146	94	210	30
Total area (km^2)[b]	22 878	96 590	39 451	80 366
Mean area (km^2)[b]	157	1028	188	2679
Mean elevation (m a.s.l)[c]	83	370	150	512
Mean elevation range (m)[c]	64	744	181	1375
Mean temperature (°C)[c]	26.7	25.8	26.3	24.2
Mean temperature range (°C)[c]	0.36	4.0	0.98	7.53
Total forest area (km^2)[c,d]	9 585	79 499	16 139	72 945
Mean forest area (km^2)[c,d]	66	846	77	2431
Mean forest cover (%)[c,d]	22	60	31	77
Mean surrounding forest (km^2)[c,d,e]	94	765	146	1833
Mean surrounding forest cover (%)[c,d,e]	16	42	21	53

[a] Assuming 100% forest cover in PAs

[b] Calculated from PA polygons

[c] Calculated from raster grids with a grid cell size of 250 m

[d] Assuming current forest cover in PAs (but calculated for the number of source/refuge PAs determined using 100% forest cover in PAs)

[e] Calculated within a 10 km buffer surrounding the outer boundary of each source PA

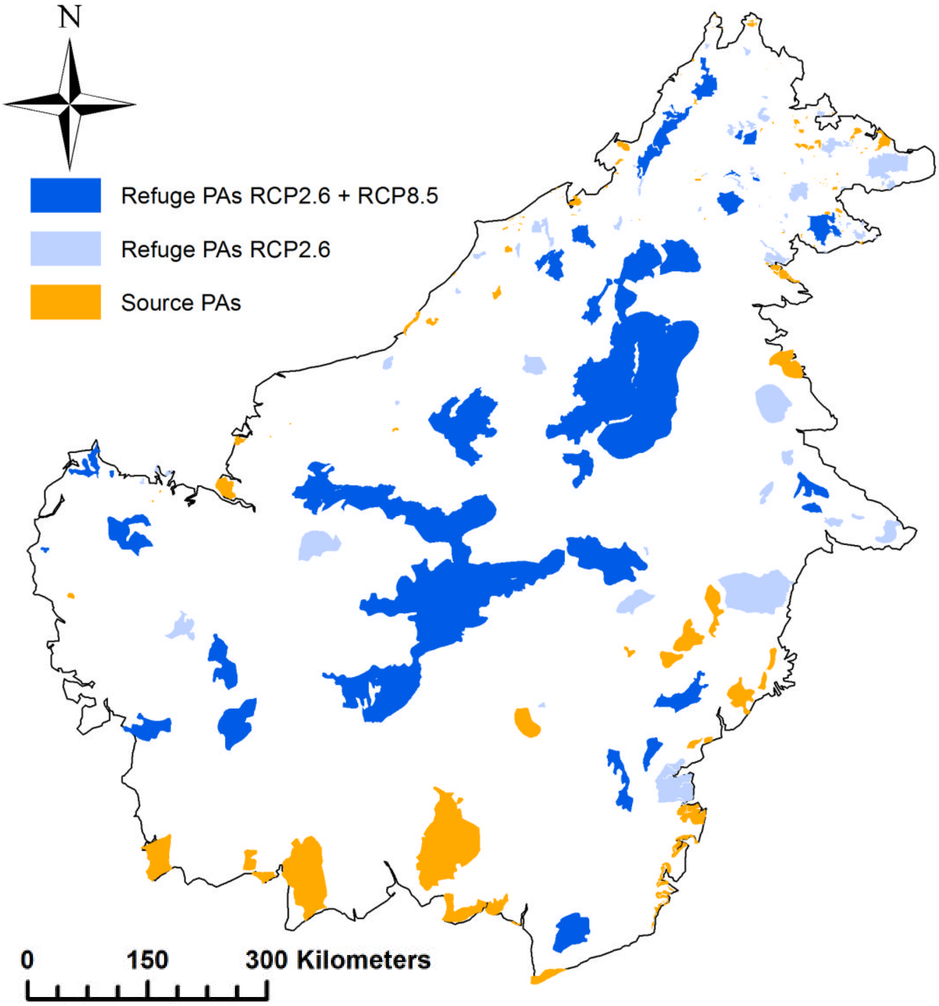


Figure A2.4. Map of Borneo showing location of refuge and source PAs for RCP2.6 (number of refuge PAs = 94; sources = 146) and RCP8.5 (number of refuges = 30; sources = 210) warming scenarios. Dark blue shading shows PAs that are refuges under both scenarios, and orange shading shows PAs that are sources in both scenarios. Pale blue shading shows PAs that are refuges under RCP2.6 but sources under RCP8.5. We assumed 100% forest cover in PAs in both scenarios.

Appendix 2F.

Table A2.2. Output from incidence function models (IFMs) to examine the connectivity of source PAs (n = 213-210, for current and 100% forest cover, respectively) to cooler target PAs for organisms with 10 different dispersal abilities (0.5 – 10 km dispersal ability per generation), three population densities (12.5, 125 and 1250 individuals per 250 m forest grid cell) and for two forest cover scenarios (current and 100% forest cover in PAs). The table shows the number of source PAs that were successfully connected to target PAs. The mean number of generations taken by organisms to reach these PAs, and standard errors, are shown in brackets. All models were run using RCP8.5 temperature projections.

		Current forest cover in PAs			**100% forest cover in PAs**		
		Population density[c]			**Population density**[c]		
Dispersal[a]	**α**[b]	**12.5**	**125**	**1250**	**12.5**	**125**	**1250**
0.5	9.40	39 (69 ± 11)	50 (79 ± 13)	57 (67 ± 10)	50 (67 ± 7)	67 (87 ± 11)	74 (73 ± 10)
0.75	6.27	59 (69 ± 6)	62 (39 ± 6)	65 (27 ± 3)	80 (72 ± 9)	82 (42 ± 6)	84 (27 ± 3)
1	4.70	64 (57 ± 6)	69 (29 ± 5)	74 (30 ± 6)	86 (42 ± 6)	94 (43 ± 7)	100 (32 ± 6)
1.5	3.13	71 (39 ± 5)	79 (23 ± 5)	86 (25 ± 6)	103 (33 ± 6)	109 (29 ± 5)	116 (24 ± 5)
2	2.35	79 (25 ± 6)	89 (22 ± 6)	102 (27 ± 6)	115 (30 ± 6)	128 (31 ± 6)	140 (31 ± 6)
3	1.57	93 (25 ± 5)	111 (20 ± 4)	137 (30 ± 8)	149 (37 ± 6)	166 (33 ± 5)	172 (17 ± 3)
4	1.18	112 (22 ± 6)	142 (34 ± 6)	159 (26 ± 4)	173 (26 ± 4)	180 (17 ± 3)	193 (18 ± 4)
5	0.94	135 (27 ± 6)	160 (19 ± 3)	177 (27 ± 5)	185 (21 ± 4)	197 (15 ± 3)	201 (9 ± 1)
7.5	0.63	159 (36 ± 4)	185 (13 ± 3)	196 (45 ± 4)	201 (7 ± 1)	203 (6 ± 2)	206 (6 ± 2)
10	0.47	181 (4 ± 4)	201 (12 ± 2)	205 (16 ± 2)	205 (8 ± 2)	207 (4 ± 1)	208 (3 ± 0.2)

[a] Maximum dispersal distance (km)

[b] Slope of negative exponential dispersal kernel

[c] Number of individuals per 250 m forest grid cell

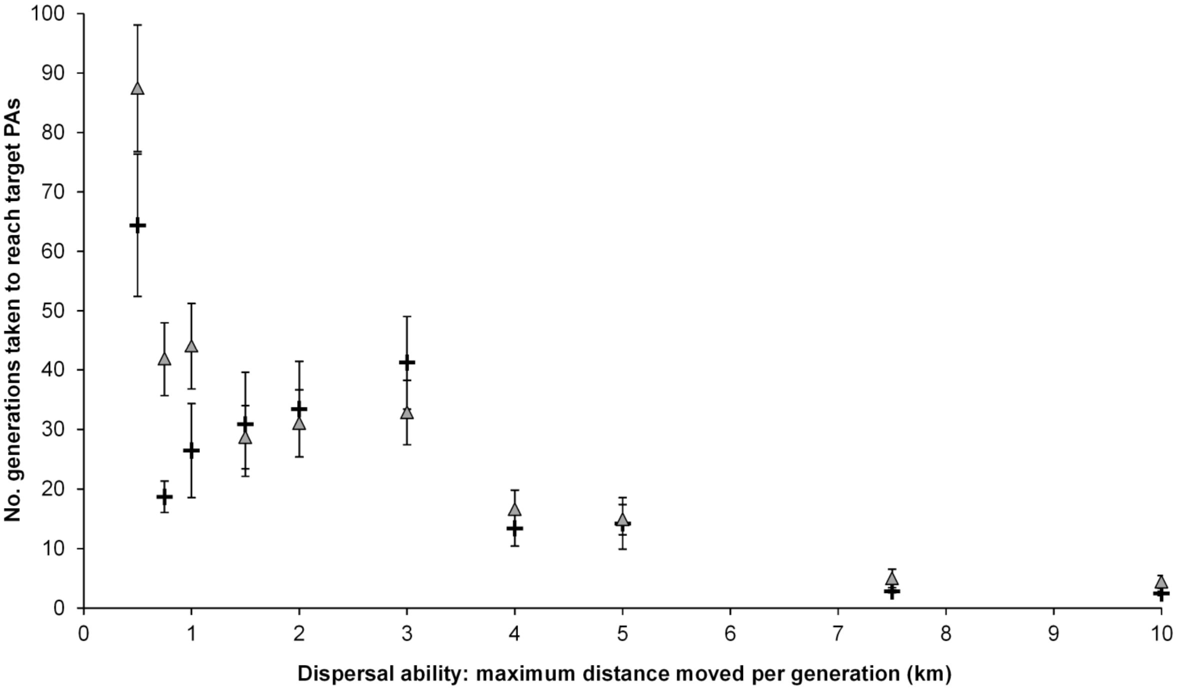
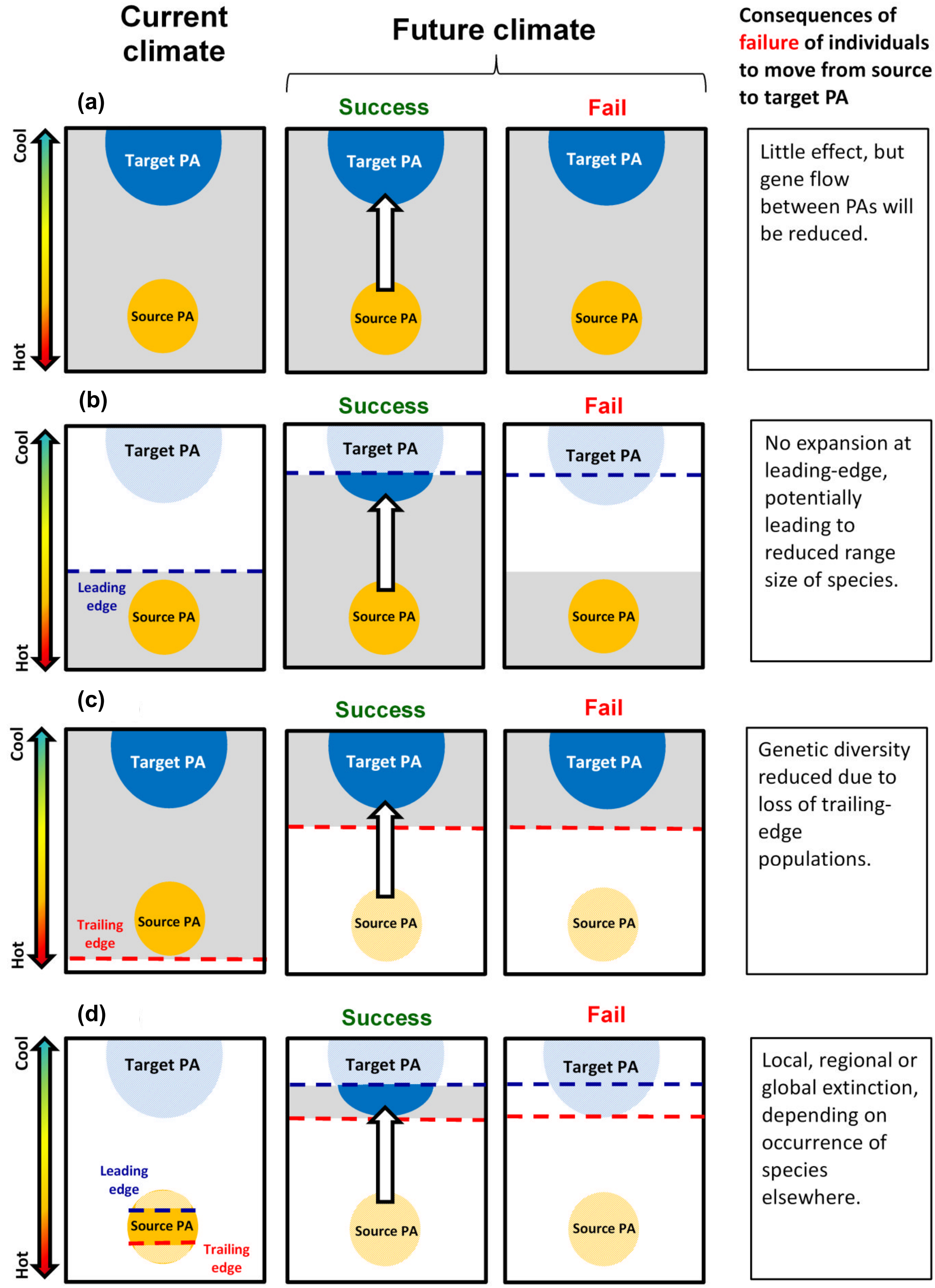


Figure A2.5. Output from incidence function models (IFMs) for the RCP2.6 (crosses; total source PAs = 146) and RCP8.5 (triangles; total source PAs = 210) warming scenarios showing mean number of elapsed generations for organisms at each dispersal distance to reach cooler target PAs from source PAs (for successful source PAs shown in Chapter 3 Fig. 3.3c). Standard error bars illustrate the error across all successful source PAs at each dispersal distance. Ten dispersal distances were examined (0.5 km – 10 km per generation) and we assumed 100% forest cover in PAs and 125 individuals per 250 m forest grid cell.

Appendix 2G.



Consequences of failure of individuals to move from source to target PA

(a) Little effect, but gene flow between PAs will be reduced.

(b) No expansion at leading-edge, potentially leading to reduced range size of species.

(c) Genetic diversity reduced due to loss of trailing-edge populations.

(d) Local, regional or global extinction, depending on occurrence of species elsewhere.

Figure A2.6. A schematic diagram to illustrate the potential consequences of lack of connectivity between source and target PAs for species which may need to shift their ranges upslope (from ‘hot’ to ‘cool’ temperatures) under future climate warming. We illustrate four exemplar types of ‘species’ with contrasting distributions and thermal range limits: (a) a ubiquitous species that does not have a thermal range margin in the study area; a species that has a (b) leading-edge and (c) trailing-edge range margin in the study area, and (d) an endemic species confined to source PAs. Under climate warming, we assume that species may need to move to higher elevations to track climate, and our main study examines the factors affecting the connectivity of source and cooler target PAs, and whether it is sufficient to facilitate the movement of organisms between PAs. For each exemplar species type, we show three panels (from left to right); its current distribution, and its future distribution assuming it succeeds (white arrow) or fails to move from source to target PAs. We show the extent of species’ occupied ranges (grey shading), and locations of trailing-edge (red dashed line) and leading-edge margins (blue dashed line). We assume that the exemplar species’ ranges are at equilibrium with current climate (left hand panels), but species may either track climate warming and reach target PAs (middle panels; white arrow), or fail to track climate and not reach target PAs in future (right hand panels). PAs are either occupied by the exemplar species (solid colour; source = yellow; blue = target), or un-occupied (hatched pattern). We briefly summarise the consequences of failure to reach target PAs. In our study, we assume species are restricted to forest, and may fail to reach target PAs if e.g. there is insufficient forest or poor dispersal ability, but for simplicity the distribution of forest cover is not shown in the schematic.

Appendix 2H. Examining the effects of deforestation outside PAs and the consequences of complete removal of all forest occurring outside PA boundaries on PA connectivity.

Appendix 2H.1. Methods

In order to assess the importance of forest occurring outside PAs on the connectivity of source and cooler target PAs, we ran models for a ‘worse-case’ landcover scenario whereby all 235 448 km^2 (in 250 m grid cells) of forest occurring outside PAs was removed (thus only forest within PAs remained). We used temperature projections for the highest warming scenario (RCP8.5), which corresponded to 210 source PAs. We ran simulations for all dispersal distances, but only for the intermediate population density (125 individuals per 250 m forest grid cell). We assumed 100% forest cover within PAs.

Appendix 2H.2. Results

Across all dispersal distances, the percentage of source PAs connected to cooler target PAs ranged from 4-87% (Fig. A2.7a).For the poorest dispersers (<1 km dispersal per generation) only 7% of source PAs were connected to target PAs, whereas for good dispersers (≥7.5 km dispersal ability per generation) up to 78% of source PAs were connected to target PAs (Fig. A2.7a). Overall, source and target PA connectivity was on average 33% lower when compared to the equivalent model scenario with current forest cover outside PAs. PA connectivity was most affected by the removal of forest cover outside PAs when organisms with intermediate dispersal distances were used; for example, PA connectivity decreased by 50% for organisms with dispersal abilities of 3 km per generation (A2.7a). The time taken to reach target PAs was <60 generations for all dispersers (Fig. A2.7b).

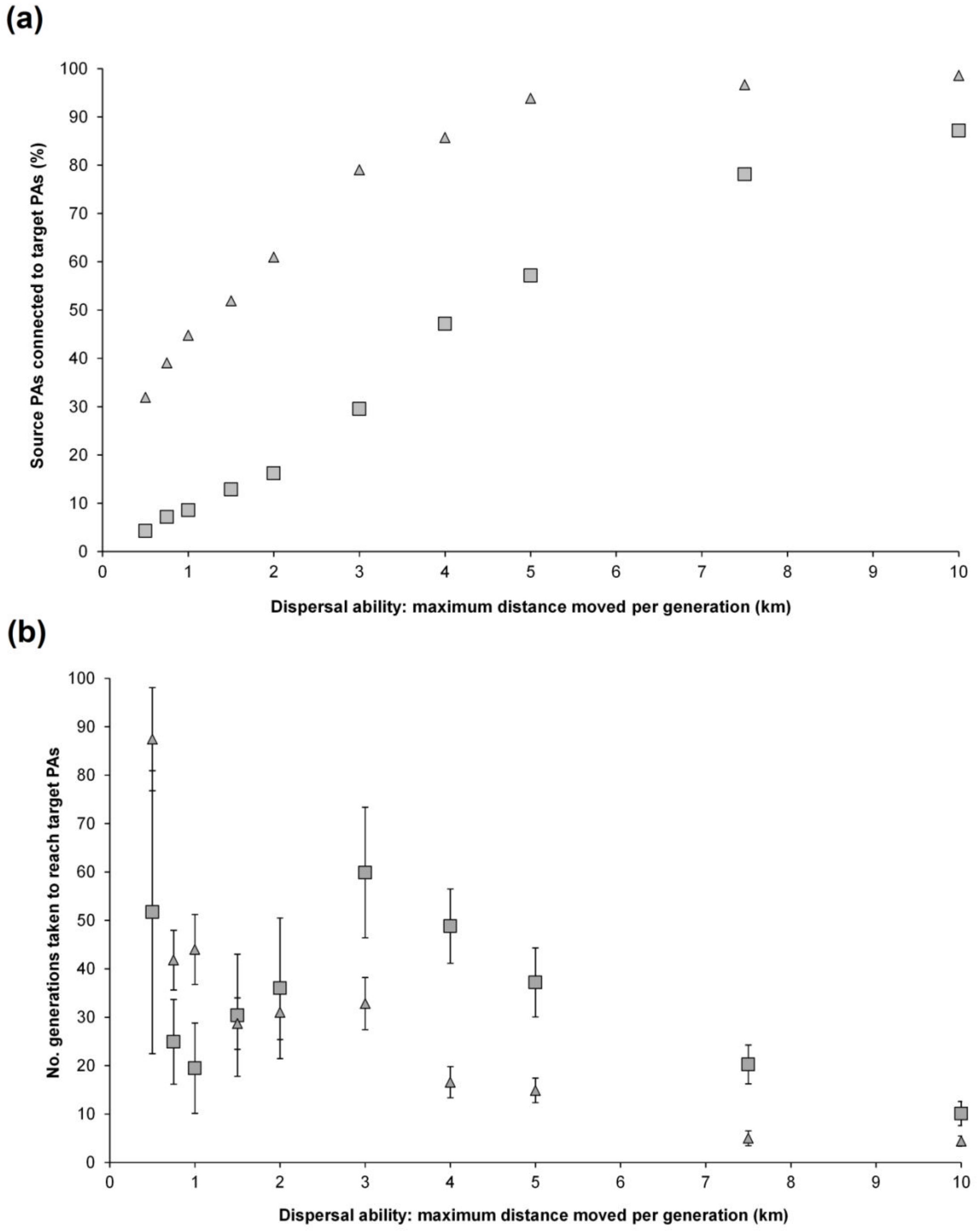


Figure A2.7. Incidence function model (IFM) outputs showing (a) percentage of source PAs (*n* = 210; 100% forest cover in PAs; 125 invidividuals per 250 m grid cell) connected to cooler target PAs for organisms with different dispersal abilities; and (b) mean number of elapsed generations (and standard errors) for organisms at each dispersal distance to reach cooler target PAs (of those successful in Fig. A2.7a). Triangles represent model scenarios assuming current forest cover outside PAs and squares represent a 'worse-case' scenario where all forest outside PAs was assumed to have been removed. We ran all models using RCP8.5 temperature projections.

Appendix 3 – Supporting information for Chapter 4

Appendix 3A.

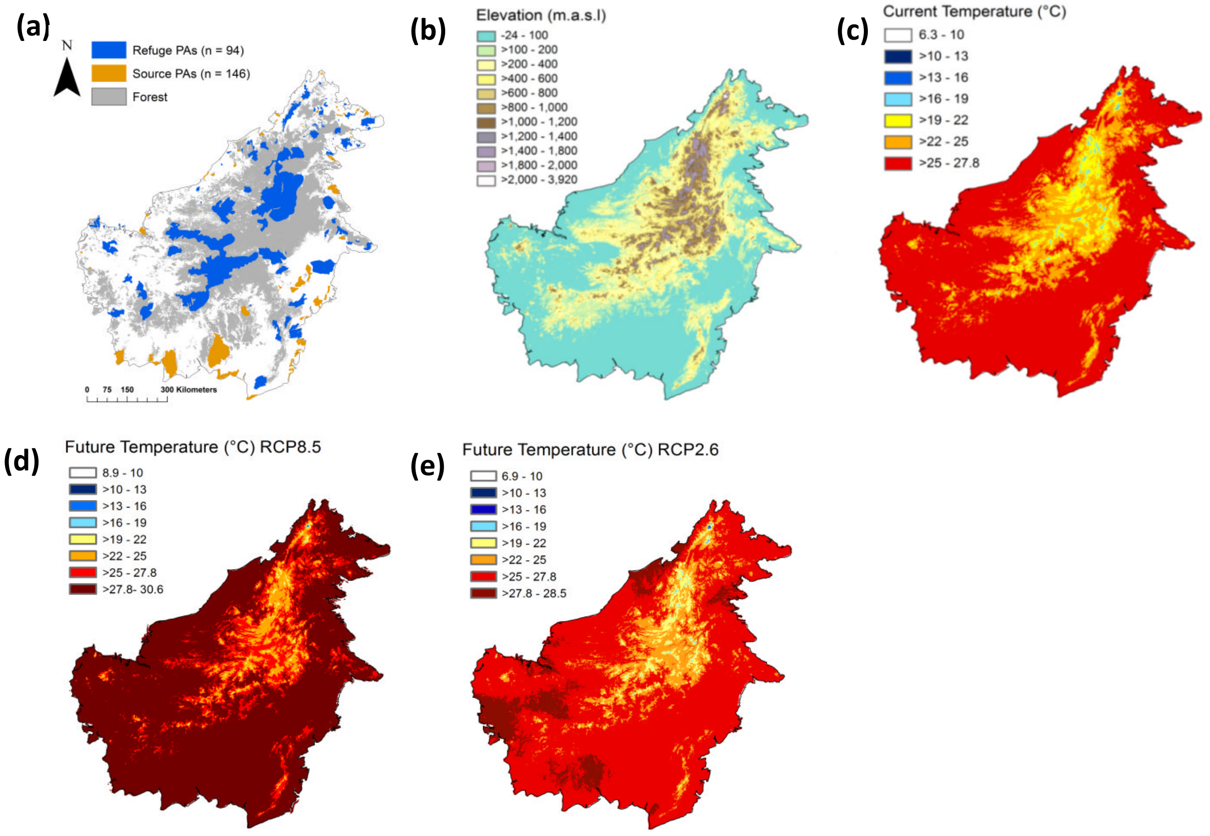


Figure A3.1. Maps of Borneo showing (a) source and refuge PAs (see Chapters 3 and 4 for PA definitions); (b) elevation in ~200 m bands; (c) annual current mean surface temperate (1950-2000) in ~3°C temperature bands; (d) future temperature for RCP8.5 projections (2061-2080), in the same 3°C temperature bands; and (e) future temperature for RCP2.6 projections (2061-2080). Maps (b) to (e) were created from gridded data at a 1 km grid cell size and adapted from Scriven et al. (2015) (Chapter 3).

Appendix 3B.

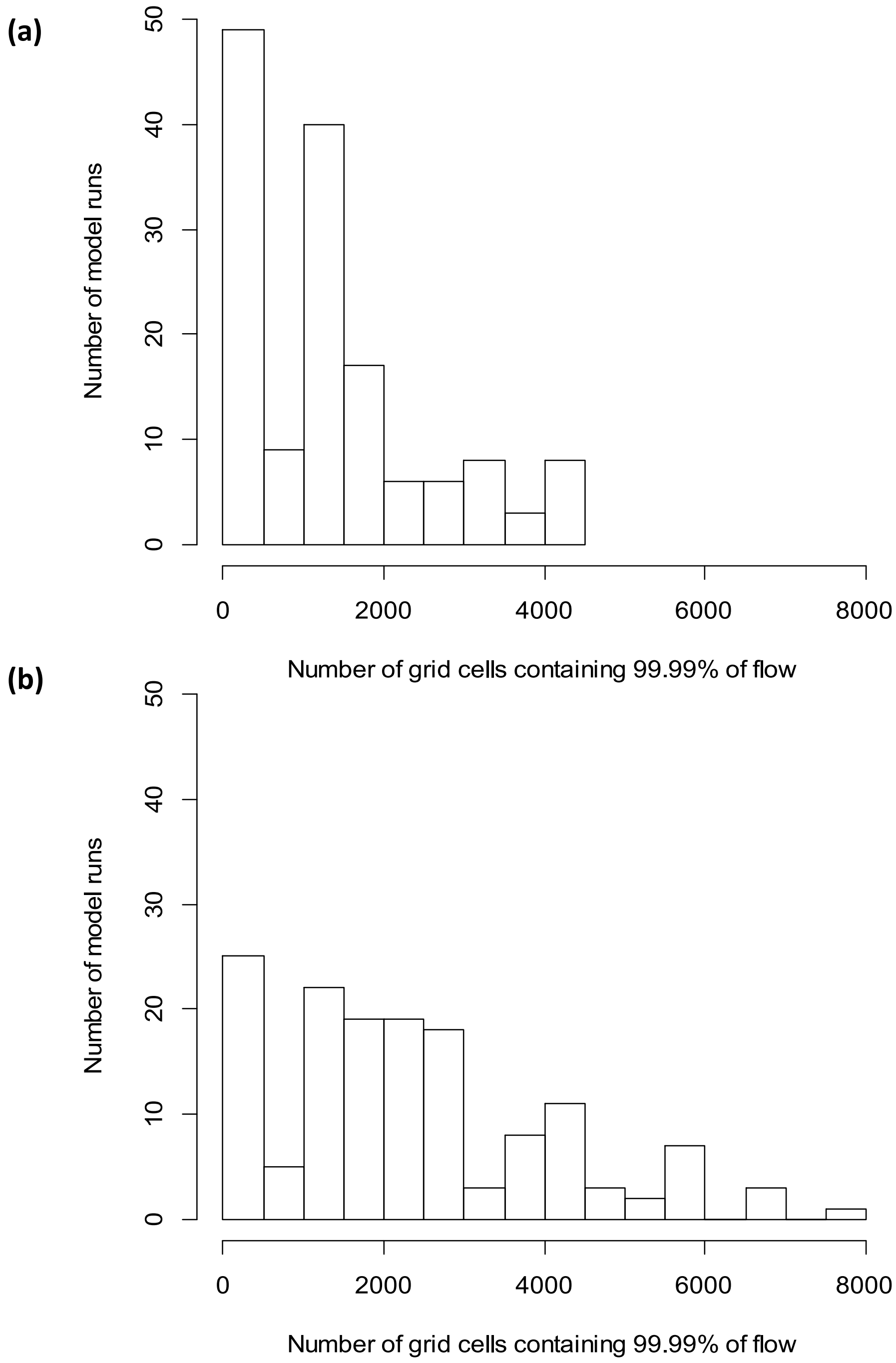


Figure A3.2. Histograms showing number of 5 km forested cells (excluding focal source and target PA grid cells) that contained 99.99% of flow per model run (*n* = 146 source PAs), assuming (a) RCP2.6 future temperature projections and (b) RCP8.5 future temperature projections. To select these grid cells (termed 'expansion routes'), we ranked the cell values in each model run from high to low, and then cumulatively summed values for all cells to a 99.99% cut-off. Hence, the majority of source PAs had relatively low numbers of grid cells (<2000) on route to their specific target PAs (i.e., expansion routes).

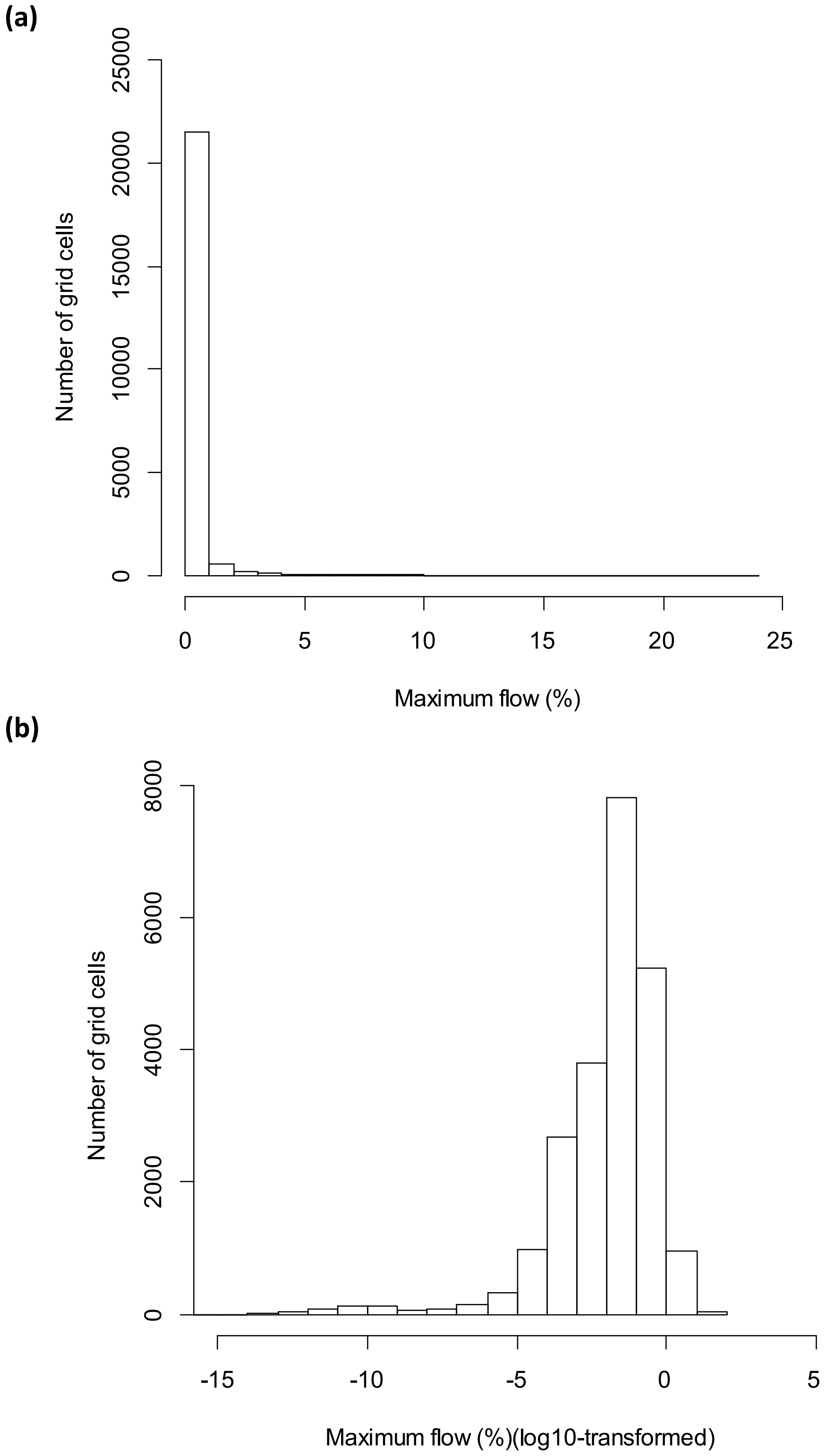


Figure A3.3. Histogram showing maximum flow (%) for any model run (*n* = 146 PAs) for (a) untransformed percentage flow values and (b) log10-transformed percentage flow values, assuming RCP8.5 temperature projections. Hence, across all PAs, the majority of grid cells contained very low flow.

Appendix 3C.

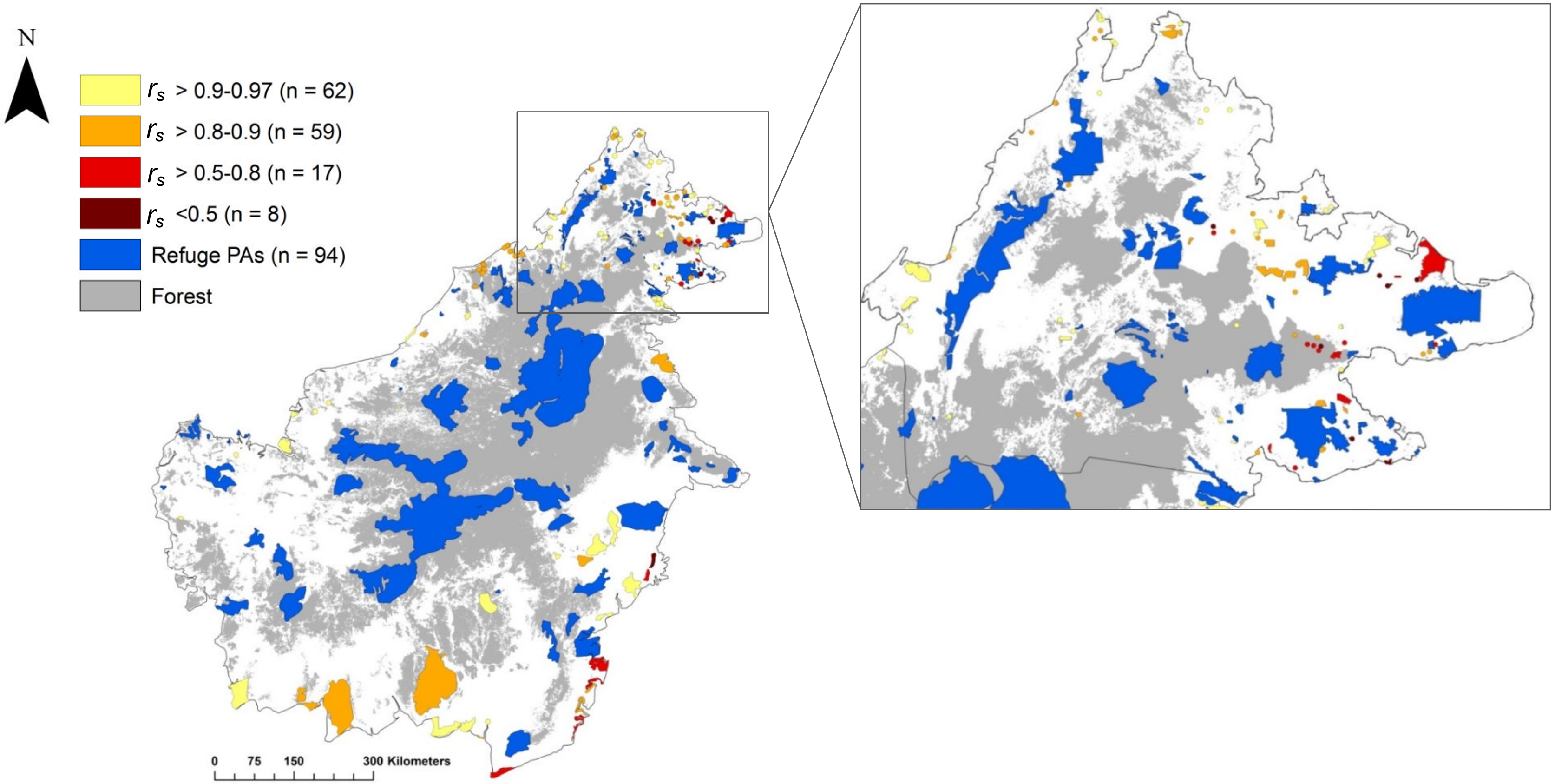


Figure A3.4. Map of Borneo showing location of refuge (*n* = 94) (blue shading) and source (*n* = 146) PAs (RCP2.6). Source PAs are shaded according to the spatial agreement in forested grid cells (Spearman's rank correlation (r_s) of cells with high flow between source and target PAs) across RCP2.6 and RCP8.5. Source PAs that were <4.5 km^2 are represented by shaded circles for clarity. Insert shows Sabah, an area of relatively low spatial agreement in high flow (i.e. expansion routes) across RCP scenarios.

Appendix 3D.

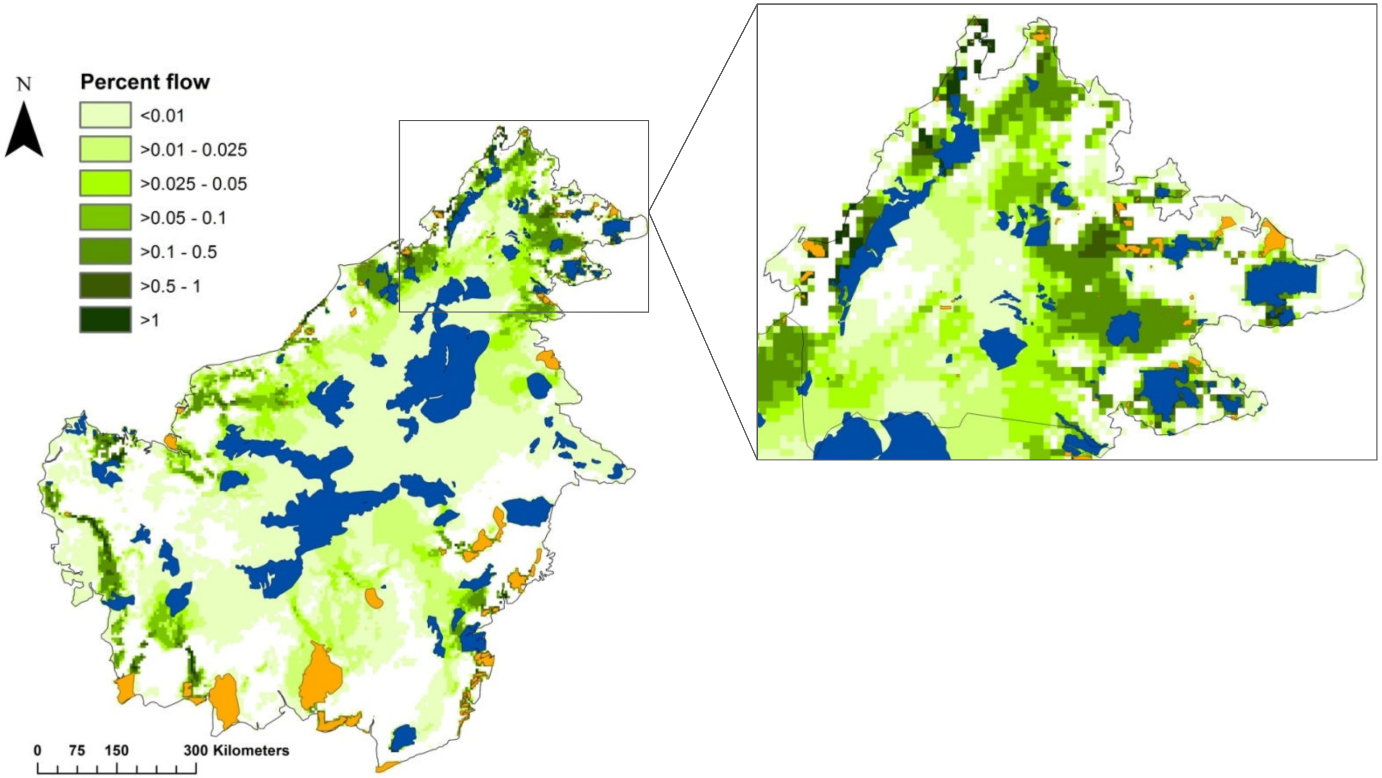


Figure A3.5. Map for Borneo, highlighting important habitat connections (assuming RCP8.5 temperature projections). To create this map, expansion routes (5 km forested grid cells that cumulatively contained 99.99% of flow) reporting percentage flow values for all 146 source PAs were overlaid, and each cell was assigned a value representing the sum of these flow values. Each value was then divided by the number of source PAs for which that grid cell was found to contribute to 99.99% of flow (i.e. mean flow). Habitat connections were then defined as cells containing >0.5% of mean flow. Locations of source (orange) and refuge (blue) PAs are overlaid. Insert shows Sabah, an area of regional importance due to a high concentration of habitat connections**.**

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