The effects of forest degradation on arboreal apes within Sikundur, the Gunung Leuser Ecosystem, Northern Sumatra

Christopher David Marsh

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Department of Life & Environmental Sciences
Faculty of Science and Technology
Bournemouth University

For my mother

Abstract

Tropical forests are being destroyed at a rate of 1.5 acres every second due to human activities, thereby accelerating climate change through impacts on the carbon cycle and causing the extinction of species dependent on these habitats. In the face of such immediate and globally significant issues, there is a lack of robust scientific knowledge on how tropical deforestation and degradation affects ecosystem stability and the fauna that inhabit tropical forests.

As anthropogenic disturbance removes available habitat for rainforest species and degrades remaining forests, a multitude of species are threatened. There is a need to develop methods to rapidly assess tropical forest structure and relate this to habitat quality for keystone species, like primates. Only upon understanding the impacts of degradation on forests and their inhabiting animals can effective conservation methods be planned. This project aims to investigate the effects of forest degradation on primates over a large study site using innovative data collection methods, as well as enabling the identification of areas of conservation importance and the modelling of future predicted climate change effects on the well-being of primates inhabiting degraded forests, addressing the possible synergistic effects of forest degradation and climate change on primate species at a landscape scale.

The findings of this project show that Sikundur in Northern Sumatra, a degraded tropical forest, is highly climatically variable. This climatic variability in turn alters how and when siamang range within the forest canopy. Due to the structural and climatic heterogeneity of the Sikundur landscape, different primate species are more abundant in different areas, with more morphologically and behaviourally specialist species dependant on specific structural elements with the forest. Although identifying historical forest degradation is problematic do to microtopography variation in Sikundur, modelling of future climate change shows that both anthropogenic disturbance and microtopographic variation may render some areas of Sikundur less suitable for primate species in the future. For species with narrower habitat requirements, climatic change is likely to have more impact, disproportionately effecting sympatric species.

This thesis contains four data chapters with an introductory chapter and a discussion chapter. Chapter 1 reviews the available literature on the potential impacts of forest degradation on arboreal primates within the study site. Chapter 2 assess the effects of forest structure on microclimates within tropical rainforest canopy, with detailed recording of temperatures within the canopy. Both data collection and microclimate modelling indicate a highly diverse climate environment in the Sikundur forest canopy, with vertical temperature gradients potentially having a substantial impact on arboreal primates. Chapter 3 relates the synergistic relationship between forest degradation and microclimate on the behaviour and ranging of siamang, *Symphalangus syndactylus*. Results suggest that siamang are limited in their ability to behaviourally thermoregulate effectively in low cloud cover due to the limiting factors of near-exclusive arboreality and territorial defence. Chapter 4 assesses the abundance of three primate species, Thomas's langur *Presbytis thomasi*, the lar gibbon *Hylobates lar verstitus,* and siamang, in relation to anthropogenic disturbance and forest structure at a landscape scale. In this study, the more behaviourally and ecologically specialist lar gibbons show clear habitat preferences. Thomas langur are seemingly adverse to anthropogenic disturbance whilst siamang habitat requirements, despite extensive vegetation surveys, remain unclear. Chapter 5 models the effects of future predicted climate change on the habitat suitability of siamang and Sumatran orang-utan, *Pongo abelii,* inhabiting the degraded forests of Sikundur. Results in this chapter indicate that areas of forest degradation and areas subject to intense solar radiation due to forest structure variation will be less suitable for arboreal primates in the future.

This research contributes to a greater understanding of the effects of selective logging and climate change on tropical forests, vegetation structure and climate change on primate behaviour and ranging, and sheds light on the prospect of primate species survival in the face of anthropogenic disturbance. Additionally, it provides innovative, cost effective methods for the study of 3-dimensional forest structure and arboreal microclimate and the analytical techniques that apply these data to potential conservation actions.

- SIKUNDUR - SUMATRA - LEAP - BOURNEMOUTH UNIVERSITY - SOCP - PROYEK OBSERVASI SIAMANG

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Abbreviations

cm - centimetre

cm^2 – centimetre squared

DBH – diameter at breast height

GLTCP - Golden Lion Tamarin Conservation Programme

GPS – global positioning system

ha – hectare

IUCN – International Union for Conservation of Nature

km – kilometre

km/h – kilometres per hour

km^2 – kilometre squared

kWH/m^2 – kilowatt hours per metres squared

mm/24hr – millimetres per 24 hours

^oC – degrees centigrade

RCP – representative concentration pathway

SfM – structure from motion

SOCP – Sumatran Orangutan Conservation Programme

SSC – Species Survival Commission

UAV – unmanned aerial vehicle

DNA –Deoxyribonucleic acid

Statement of originality

I confirm that the work presented in this thesis is my own work, with the following exceptions: UAV flights used throughout this study were conducted in collaboration with Graham Usher. Field data of orang-utan locations within Sikundur used in Chapter 5 was collected by the Sumatran Orangutan Conservation Program.

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Chapter 1. Introduction: Impacts of forest degradation on arboreal primates

A rising human population, together with increased affluence in post-industrial economies has caused a rise in the demand for luxury products such as tropical timber, biofuels and plant oils. In 2014, the International Tropical Timber Organization exported over 15.8 million tropical non-coniferous logs worth $5.9 billion (ITTO, 2014). As a consequence of this demand for tropical timber, only 18% of tropical nations report more primary than regenerating forest, due to logging events (FOA, 2010). Forest degradation, measured by partial canopy cover loss, affected 185 million hectares between 2000 and 2012, with over 156 million hectares within tropical forests (van Lierop et al., 2015). The effects of selective logging on the ecology of tropical forests and their inhabitants is still poorly understood, as most studies lack comparable pre- and post-logging data (Laufer et al., 2013). Quantitative measures of selective logging are equally challenging, through both the uneven distribution of valuable tree species and the collateral damage caused by "selective" logging. Historically logged forest cannot easily be classified as logged and non-logged, but rather exhibits heterogeneous gradients of degradation (Struebig et al., 2013). Selective logging can have a relatively low impact compared with other forms of anthropogenic disturbance, such as fragmentation and fire, in terms of reduced habitat (Chaves et al., 2012, Barlow et al., 2006) with most logged-over forests containing at least 50% of the biomass and more than 75% of the species compared to undisturbed forest (Berry et al., 2010, Putz, 2012). However, for long lived species inhabiting these forests, there may be a form of extinction debt hidden by this discrete form of habitat disturbance, the full effects of which have not yet become apparent (Tilman et al., 1994, Vellend, 2006).

Though species richness of tropical forests appears resilient to logging events (Edwards et al., 2011), the response of taxa varies widely (Berry et al., 2010, Marsh et al, 2016). Many studies show clear shifts in species composition (Hall et al., 2003, Ernst et al., 2006), but with few clear discernible patterns between those species most affected (bats, Peters et al., 2006; apes, insectivorous birds, Poulsen et al., 2011; butterflies, Summerville and Crist, 2002).

Whilst species composition can be strongly impacted by forest degradation, another defining aspect of modern anthropogenic land-use change and subsequent industrialisation is climate change, caused by an increase in "greenhouse" gases released into the atmosphere (Searchinger et al., 2008, Stainforth et al., 2005). Land-surface temperatures in tropical rainforest regions have risen by ~0.25^{o}C per decade since the mid-1970s (Malhi and Wright, 2004) and are projected to rise by 3-8 ^{o}C over the 21st century (Malhi et al., 2009). Tropical regions which are largely landlocked will experience higher rates of warming than those with large areas bordering oceans, such as Southeast Asia (Graham et al., 2016). However, as a consequence of the stable climates that Southeast Asia experiences, both over seasonal and millennial timescales, many organisms that inhabit these areas have narrow thermal niches (Tewksbury et al., 2008). These organisms may be close to a thermal threshold where only a moderate degree of warming would lead to a marked decline in fitness (Deutsch et al., 2008). The application of climate envelope models predicts large declines of tropical biodiversity in a warming world, especially in the lowland tropics (Colwell et al., 2008). These two effects, forest degradation and climate change, impacting in synergy, could have profound effects on organisms which have evolved to survive in tropical rainforest environments (Ahumada et al., 2011, Corlett, 2011). Species which have both narrow thermal thresholds and reliance on the complex homogenous structure of tropical forests could be most adversely affected by selective logging and climate change (Brodie et al., 2012). One taxonomic group that falls under this classification is the order Primates.

Previous research has shown that changes in forest structure due to selective logging alter the behaviour and densities of primates (Marshall et al., 2009). Similarly, microclimate changes in degraded areas have also been shown to drastically alter how and when primates use disturbed areas of forest (Suggitt et al., 2011, Takemoto, 2004). Garber et al. (2006) suggest that species-specific ecomorphological adaptations and social structures govern species' ability to survive in disturbed habitat, with frugivorous, large bodied primates found to be most adversely affected by habitat degradation and removal (Link et al., 2010, Marsh et al., 2016), whilst other, less specialised, behaviourally adaptive species are able to weather the effects of anthropogenic disturbance. These studies suggest that dietary and behavioural flexibility of some primate species may offer some resilience to anthropogenic disturbance.

The lowland equatorial forests of the Leuser Ecosystem, Northern Sumatra, home to a diverse range of primate species and subject of past logging events, offers an excellent location to study the responses of tropical forests and primates to anthropogenic disturbance. Multiple sympatric primate species have inhabited areas of lowland dipterocarp forest since the late Miocene, forcing each species to adopt separate ecological niches.

This study aims to explore the synergistic relationship between selective logging and microclimate changes within forest canopies on the behaviours and ranging of multiple primate species. This project will develop methods that can rapidly assess habitat quality over large areas and apply this to the behaviour and ranging, as well as abundance of primate species, enabling the prediction of how forest degradation and future climate change may affect primate communities that have evolved within narrow thermal thresholds. As well as exploring the interplay of ecological variables and anthropogenic disturbance on habitat quality for primates, this project will also develop a low-cost method that will enable this, and future projects, to conduct ecological surveys of large areas of tropical forest, evaluating levels of degradation and the effect this may have on the fauna inhabiting them.

1.2 Research Questions

The research questions of this project, in a broad sense are:

1. How are arboreal primates affected by inhabiting historically selectively logged forest?

And,

2. How will future climate change affect tropical forests and their primate inhabitants?

To address these, this project will relate gradients of anthropogenic disturbance to relative changes in primate abundance, behaviour and ranging, with an aim to highlight possible effective conservation actions.

The hypothesis that this project is testing is that multiple measurable ecological variables in tropical forests correlate, enabling detailed small-scale terrestrial data (vegetation plots, microclimates) to be predicted by large-scale aerial data (from Unmanned Aerial Vehicles - UAVs), which, in turn are determinants of the occurrence, abundance and behaviour of arboreal primates.

1.3 Research Objectives

To achieve these goals, the following objectives will be accomplished:

Objective 1. By conducting vegetation surveys and microclimate measurements, assess the impacts of forest structure on microclimate variability within the forest canopy (Chapter 2).

Objective 2. After habituating a group of siamang to the presence of researchers, collect behavioural and ranging data of the group to assess how forest structure and microclimate fluctuations impact their behaviour (Chapter 3).

Objective 3. Using wide ranging UAV vegetation surveys and surveys of primate abundance, explore how habit structure and disturbance affects gibbon, langur and siamang species abundance at the landscape scale (Chapter 4).

Objective 4. Using data obtained from O1 and O2, model various future scenarios of climate change to predict the response of primate species to possible environmental change (Chapter 5).

To achieve the objectives, two linked data collection regimes took place, one at the community scale and one at the landscape scale. Community-scale data collection focused on primate behavioural responses to forest structure and subsequent alterations in within-canopy microclimate in a small (6km^2) area. Landscape-scale data collection focused on primate abundance in relation to forest structure and gradients of forest degradation over a large (75km^2) area. Both data collection regimes provided data to inform a predictive model of canopy microclimates and primate habitat suitability, allowing a robust understanding of how future predicted climate change will affect primate species.

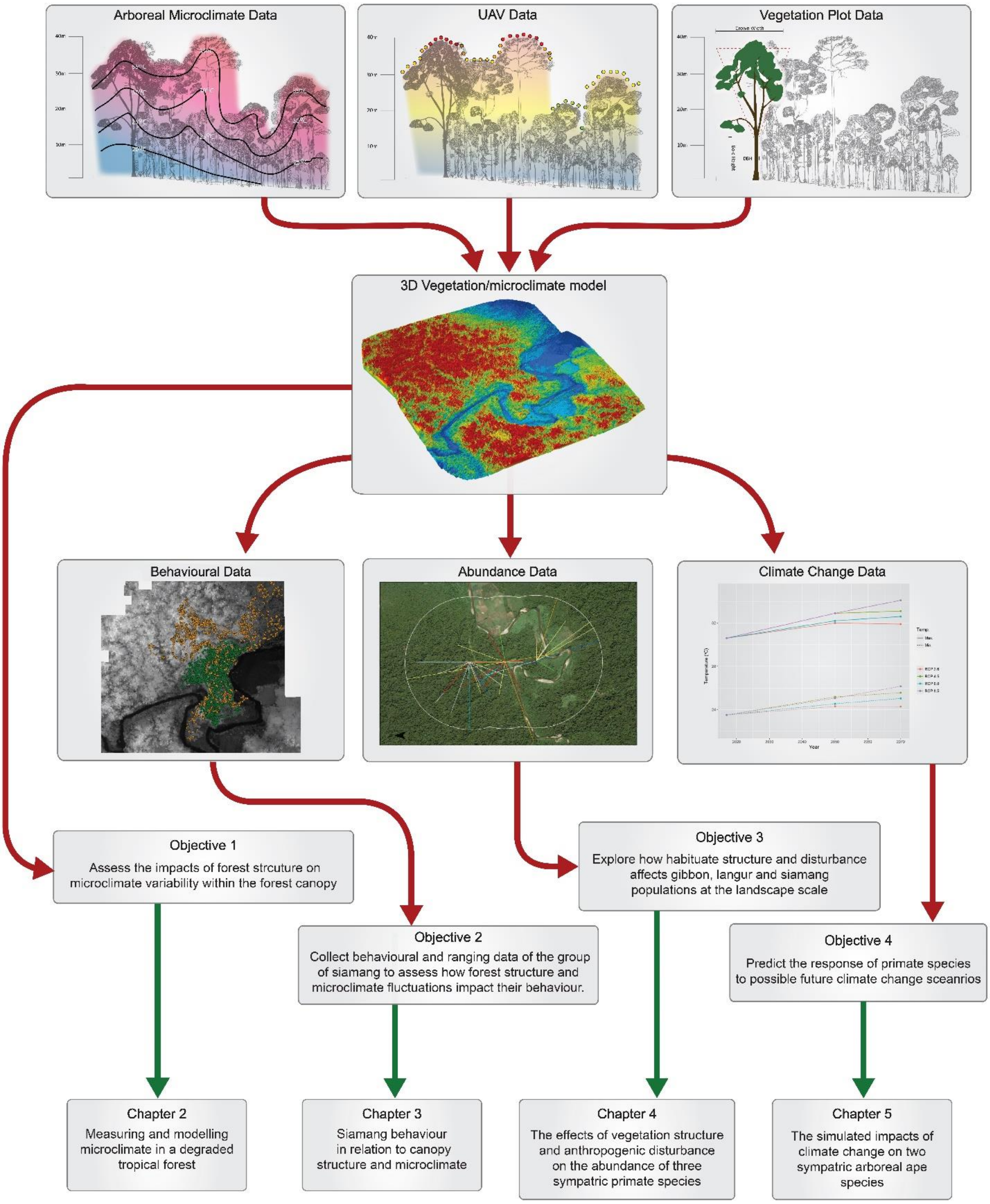


Figure 1.1 - Illustrative flow diagram of thesis structure and objectives

1.4 Primate Conservation

The world's primate populations are on the decline. It is estimated that ~60% of primate species are now threatened with extinction and ~75% have declining populations (IUCN, 2016) due to escalating anthropogenic pressures (Estrada et al., 2017). It is essential that we understand how their conservation status is affected by anthropogenic disturbance. Our closest biological relatives, primates, are an essential component of tropical biodiversity, contributing to forest regeneration and ecosystem health (Malhi et al., 2014). By identifying the major threats to primate communities, observing patterns of change, measuring primate densities and predicting how human activities might affect primates in the future, studies can assist in developing successful conservation strategies aiding in the direct protection of primate species and the indirect protection of the areas they inhabit (Grow et al., 2010). For example, a notable recent success in primate conservation, the golden lion tamarin conservation programme (GLTCP), restored a population of less than 170 individuals inhabiting the Brazilian Atlantic coast forest to a currently viable population of 1600 (Dietz et al., 1994, Kerr et al., 2016). The GLTCP conducted continuous monitoring of the remaining wild population of golden lion tamarins (*Leontopithecus rosalia*) from 1983, which allowed a set of specific conservation goals to be developed, targeted actions to be taken, the effectiveness of these actions to be evaluated and the goals and strategies to be adjusted as knowledge of the species increased (Kleiman et al., 1986, Kleiman et al., 2000, Kerr et al., 2016). The success of the GLTCP is not only measured in population numbers of golden lion tamarins, but also the effect on the preservation of their preferred habitat. 10,604 hectares of Atlantic coastal forest are now permanently protected due to conservation efforts, securing the biodiversity of all species in this area (Kleiman et al., 2000). In this way, primate species can serve as biodiversity indicators and "umbrella species". Primate species' habitat requirements are broad enough that their presence is a good indicator of biodiversity of the region (Rijksen & Meijaard, 1999). For instance, if orang-utans (*Pongo* spp.) are present at high densities in Southeast Asian forest then the area is likely also to contain at least five other species of primates, at least five species of hornbills, at least 50 different fruit-tree species, and 15 liana species (Rijksen & Meijaard, 1999). In this regard, many primate species' habitat requirements are broad enough that if they were made the focus of protective management or conservation actions, then biodiversity of species within its range would also be preserved (Lawton et al., 1998, Caro & O'Doherty, 1999, Muldoon & Goodman, 2015).

Primates as a taxonomic group vary widely. Most species have evolved in complex environments in which multiple primate species live sympatrically, with varying diet, life history, fecundity, locomotive patterns, and subsequently exhibit differing habitat requirements. Species that inhabit the same environment inevitability specialise to take advantage of distinct and relatively separate ecological niches, a process called niche differentiation (MacKinnon and MacKinnon, 1980). Varying habitat requirements across sympatric species is often apparent in a species' ability to adapt to forms of anthropogenic disturbance (Manduell et al., 2012, Hoffman and Riain, 2012, Marshall et al., 2010, Marsh et al., 2016, Wieczkowski and Kinnaird, 2008). Some primate species are behavioural and morphological generalists and have developed the behavioural plasticity that allow them to persist in anthropogenically disturbed habitats (collared lemur, *Eulemur collaris,* Donati et al., 2011; howler monkeys, *Alouatta palliata*, Cristobal-Azkarate and Arroyo-Rodríguez, 2007; diademed sifaka, *Propithecus diadema* Irwin 2008; moustached guenon *Cercopithecus*, Tutin, 1999; black and white colobus, *Colobus guereza,* Gillespie and Chapman, 2008), whilst morphological or behavioural specialists appear to be more vulnerable (bearded saki monkeys, *Chiropotes satanas chiropotes,* Boyle and Smith, 2010; red colobus, *Piliocolobus rufomitratus*, Gillespie and Chapman, 2008, Schwitzer et al., 2011). However, some primate species show an extraordinary ability to adapt to environmental change (Garber et al., 2006). In Madagascar, the diademed sifaka (*Propithecus diadema*) inhabiting in fragmented forests minimized energy expenditure by utilising fallback food sources and reduced daily path length, when high-energy fruit resources were unavailable (Irwin, 2008a, 2008b). The collared lemur (*Eulemur collaris*), also inhabiting forest fragments, increased time spent travelling and feeding, and reduced group size in response to reduce calorific intake (Donati et al., 2011). In Gabon, the moustached guenon (*Cercopithecus cephus*) increases the degree of fission-fusion group dynamics in response to forest degradation, to decreasing intraspecies feeding competition (Tutin, 1999). Given these varied adaptions to environmental change, understanding how each species within a primate community responds to ecological fluctuations is of prime importance in identifying which conservation actions may benefit specific or multiple species.

1.4.2 Primate conservation in Indonesia

Indonesia's 17,000 islands are home to a diverse collection of primate species, most of which are at risk of extinction. The IUCN/SSC Primate Specialist Group (IUCN/SCC 2008) classified over 84% of the over 40 Indonesian primate species as threatened with extinction. Due to its volcanic geology (Hall and Holloway, 1998), climatic stability (Gathorne-Hardy et al. 2002), and associated rapid speciation processes (Whitmore 1987), the Southeast Asian islands are extreme biodiverse (Myers et al. 2000), but much of their biodiversity is threatened with extinction. As well as high levels of biodiversity, Indonesia is also one of the most populated countries in the world, home to 245.45 million people in 2014 (World Bank, 2014). Human population growth, coupled with industrialization and the lack of effective governmental protection, threaten Indonesia's forests and primates (Sodhi et al., 2004). Conservation efforts are more necessary than ever before, though it is difficult to develop plans that consider both the needs of a growing human population and the habitat requirements of primate species (Sodi et al., 2010). Conservation efforts of primate species in Indonesia have repeatedly been unsuccessful. In 2007, President Susilo Bambang Yudhoyono launched Indonesia's Strategy and Action Plan for National Conservation of Orang-utans. Since the launch of this programme, there have been no land-use changes made that might safeguard orang-utan populations (Meijaard, 2014). In Sumatra, satellite imagery has shown that protected areas experienced similar levels of deforestation to areas allocated for commercial logging (Gaveau et al., 2009). Understanding the impacts of degradation within both protected and non-protected areas of orang-utan and other endangered primate species habitat is of key importance to safeguarding these populations under present conditions (Tang et al., 2010). By presenting accurate data to government agencies on the impacts of illegal logging within protected areas on "umbrella species" such as endangered primates, a potential outcome of this study is to incentivise the active protection of these areas.

For primate species, dietary and behavioural flexibility may offer some resilience to anthropogenic disturbance. The extreme adaptability of primate species may be due to their unique physiological traits. Primates display a unique brain-to-body mass ratio (Fleagle, 2013). Large brains relative to body size may provide a "cognitive buffer", allowing behavioural flexibility for species inhabiting altered environments (Sol, 2008, 2009). Large brains in primates, specifically neocortex size, has also been linked to social group complexity, termed the "social brain hypothesis" (Dunbar & Shultz, 2007). The "social brain hypothesis" claims ecological problems such as survival, foraging and rearing offspring are more effectively solved socially than by an individual's unaided efforts, and that evolution of energetically expensive large brains are only possible if species live socially (Dunbar, 1992). Indonesian primates present an obvious contradiction to these two theories, as the Sumatran orang-utan, siamang and Sumatran lar gibbon are all ape species with low group numbers. The Sumatran orang-utan, large-brained yet mostly solitary, Critically Endangered though with one of the broadest diets among extant primates is the most striking of these three examples. There must be other factors that are more influential than their recent evolutionary past that causes the currently low group numbers and low population densities in *Pongo abelii, Symphalangus syndactylus* and *Hylobates lar vestitus.* Studies of 19th Century accounts of primate encounters have concluded that orang-utans occurred at significantly higher densities than those which are currently seen (Meijaard et al., 2010). This apparent dramatic fall in population numbers was theorised to be due primarily to hunting (Meijaard et al., 2010). In Kalimantan, survey data showed that between 44,170 and 66,570 orang-utans were killed within the respondents' active hunting lifetimes (between approx. 1930 – 2010) (Davis et al., 2013). Much of our current ecological understanding of orang-utans and other Indonesian primate species may be based on field studies of animals living at lower densities than they did historically (Meijaard et al., 2010). Coupled with Indonesia's high deforestation rates (2001-2014: 18.5 millon hectares, Global Forest Watch, 2017) Southeast Asian primates, and the biodiversity of the region as a whole, have seen consistent declines (Sodhi et al., 2004).

The primate species known to inhabit Northern Sumatra and their IUCN Red List statuses are: the Sumatran orang-utan (Critically Endangered), Sumatran lar gibbon (Endangered), siamang (Endangered), Thomas's langur (*Presbytis Thomasi*, Vulnerable), Silvery lutung (*Trachypithecus cristatus,* Near Threatened*)* long-tailed macaque (*Macaca fascicularis*, Least Concern) and Sunda slow loris (*Nycticebus coucang*, Vulnerable). This study will focus on the three most threatened primate species, the Sumatran orang-utan, Sumatran lar gibbon and siamang.

1.4.3 Sumatran orang-utan (*Pongo abelii*)

Theorized to have a wide distribution during the Pleistocene (2,588,000 to 11,700 years ago) spanning Southeast Asia and mainland Asia, including areas between Vietnam, Northern India and Southern China, wild orang-utans now only inhabit Sumatra and Borneo (Goossens, et al., 2009). The islands of Borneo and Sumatra are isolated from one another by the South China Sea, a separation that has been in place for at least 8000 years (Harrison et al., 2006). Until recently, orang-utans were classified as a single species with a Bornean (*Pongo pygmaeus pygmaeus*) and Sumatran (*Pongo pygmaeus abelii*) subspecies (Delagado and van Scaik, 2000). Analysis of mitochondrial DNA (mtDNA) led to the elevation of the two subspecies to species level in 1996 (Xu and Arnason, 1996), with DNA analyses showing a high degree of genetic diversity between these two orang-utan subspecies, more so than that between African apes and humans (Fischer et al., 2006). A meta-analysis of multiple genetic studies of orang-utans supports a divergence between Bornean and Sumatran orang-utans between 2.7 and 5 million years ago (Steiper, 2006). However, the recent description of a third species, *Pongo tapanuliensis,* with fewer than 800 individuals inhabiting the Batang Toru region of Sumatra, has shed more light on the evolutionary relationship between Sumatran and Bornean populations (Nater et al., 2017). *Pongo tapanuliensis* likely represents the oldest evolutionary lineage of the genus *Pongo*, with a split from more northern Sumatra populations hypothesised to have occurred 3.38 million years ago (Nater et al., 2017). Mitochondrial DNA analysis shows *Pongo tapanuliensis* is more similar to Bornean orag-utans than *Pongo abelii,* with a split between these populations likely to have occurred ~674 thousand years ago, presenting a relatively complex picture of the *Pongo* genus' speciation and dispersal (Nater et al., 2017, Nasution et al., 2018).

Current Asian primate classification recognizes two orang-utan species inhabiting the island of Sumatra (*Pongo abelii* and *Pongo tapanuliensis*) and three subspecies inhabiting the island of Borneo, *Pongo pygmaeus pygmaeus*, in the northwest and *Pongo pygmaeus wurmbii* in the southwest and *Pongo pygameus morio* in East Kalimantan (Brandon-Jones et al., 2004). Physiologically, *Pongo abelii* have slightly narrower faces than *Pongo tapanuliensis* and Bornean orang-utans, due to mandibular variation which is itself systematic of the variation in diets between *Pongo abelii, Pongo tapanuliensis* and Bornean *Pongo pygmaeus* subspecies; *P. p. pygmaeus, P. p. wurmbii,* and *P. p. morio. Pongo abelii* is a more frugivorous species than its Bornean counterparts due to the high availability of fruit on the island of Sumatra in relation to Borneo (Wich et al., 2006), caused by the apparent higher soil fertility in Sumatra compared with Borneo. (MacKinnon et al., 1996; Rijksen and Meijaard, 1999). Volcanic eruptions that partly formed the island of Boreno took place before those in Sumatra (MacKinnon et al., 1996) and its more eroded volcanic rock reduces soil fertility, which in turn reduces forest productivity (Wich et al., 2006).

The high productivity of Sumatran forest enables orang-utans to rely on a fruit-based diet, even in times of fruit scarcity, unlike Bornean orang-utans which rely heavily on 'fallback' food sources such as unripe fruits, leaves, epiphytes, lianas and bark (Knott, 1998). Whilst there is inter-population variation in orang-utan diets (MacKinnon, 1974), fluctuations in fruit supply seem only to effect activity budgets and not the majority of food resource eaten, with populations inhabiting masting forests being less active than populations in non-masting forests (Morrogh-Bernard et al., 2009).

The orang-utan is unique among ape species, in that it has two distinct male morphs, flanged and unflanged (Fleagle, 2013). Flanged males develop broad facial flanges and grow to a body size that can be over twice that of females. Both morphs can be reproductively active, but flanged males seem to be the preferred sexual partner for fertile females (Fox, 1998, Utami et al., 2002), though this additional reproductive success may come with an additional energetic expenditure due to increased body weight (Morrogh-Bernard et al., 2009).

The availability of high-quality food items is predicted to be a governing force in orang-utan sociality, given that temporary party sizes and copulation frequency increase in Borean orang-utans during periods of high fruit availability (Knott, 1998). However, few studies have shown a statistically significant increase in party size, or sociality, during periods of fruit abundance in Sumatran orang-utans (Wich et al, 2006), suggesting that the origins of the orang-utan's current extreme version of fission-fusion social dynamics stems from a previous, more cohesive social system which has since been dispersed due to environmental change (Carne et al., 2012). The current orang-utan social system has previously been described as: an age-graded male group with adult males acting as range guardians for their reproductively active sub-adult male relatives (MacKinnon, 1979), a dispersed social system with promiscuous mating with strong male-male competition (Rodman & Mitani, 1987), and a variant of this model, with an emphasis on female choice (Schurmann & van Hooff, 1986). Given the now accepted model that female distribution and relationships are a response to the distribution of risks and resources in the environment, and male distribution and relationships are a response to the spatiotemporal distribution of mating opportunities (Davies, 1992), a highly-dispersed form of social organisation would initially suggest that a reduction in available resources has led orang-utans to their current form of social system (Harrison and Chivers, 2007).

Given that orang-utans have extremely slow life histories, with the longest inter-birth intervals, lactation periods, and juvenile dependency of any non-human primate (Galdikas and Wood, 1990, Knott, 2001, Wich et al., 2004), they are extremely sensitive to outside factors that may cause population declines (Rijksen and Meijaard, 1999). Currently listed as Critically Endangered by the International Union for the Conservation of Nature (IUCN) Red List and listed as one of the "The World's 25 Most Endangered Primates" in 2000, 2002, 2004, 2006, 2008, 2014 and 2016 (Schwitzer et al., 2015), Sumatran orang-utans are threatened primarily by habitat loss, habitat degradation and habitat fragmentation (Robertson and van Schaik., 2001). Deforestation rates in Sumatra are amongst the highest in the tropics. Accessible lowland forests, which support the highest densities of orang-utans, are particularly vulnerable to clearance and fragmentation (Cambell-Smith et al., 2011). Wich et al. (2001) reported that 49.3% of all Sumatra's forest was lost between 1985 and 2007. Given that the loss of as little as 1% of females each year can place populations on an irreversible course to extinction (Marshall et al., 2009), developing conservation plans to enable the effective protection of Sumatra's remaining lowland forests is crucial to the survival of *Pongo abelii.*

In Sikundur, the study site for this project, *Pongo abelii* have shown some resilience to the effects of anthropogenic disturbance (Knop et al., 2004) though other sites have demonstrated that recent logging activities negatively affects orang-utan densities, (Engstrom, 2000; Rao and van Schaik, 1997; Rijksen, 1978; Robertson and van Schaik, 2001; van Schaik and Azwar, 1991; van Schaik et al., 2001; Wich et al., 2003). However, orang-utan densities in Sikundur are seemingly very low (<1 ind/km^2) (Knop et al., 2004) compared with other sites (van Schaik et al., 2001; Wich et al., 2003), possibly due the low densities of large strangling figs, an important fall-back food source for orang-utans (Wich et al., 2004). This supports the theory that lowland dipterocarp forests in Sumatra have a low carrying capacity of orang-utans due to the dominant dipterocarp tree family not being important food sources for orang-utans, except in mast years. The historic selective logging of these areas may not significantly affect the availability of food sources for orang-utans but may allow other food source trees to prosper in a previously dipterocarp dominated environment, effectively leaving available food sources relatively stable, but dramatically changing the forest structure.

1.4.4 Sumatran lar gibbon (*Hylobates lar vestitus*)

The emergence of small apes in Asia was nearly simultaneous (i.e., 16–14 mya) with the split of large Asian apes from the rest of the hominoid line (Figure 1.1; Locke et al. 2011). Unlike large Asian ape species, hylobatids appear as an exclusive Asian branch of hominoid evolution, with no known representations in Europe or the Middle East (Perelman et al., 2011). The gibbon speciation is estimated to have occurred between 9 mya and 4 mya when the four major hylobatid genera *Nomascus, Hoolock, Symphalangus*, and *Hylobates* emerged over a period of 2-3 million years (Chan et al., 2010, 2012). These four phylogenetically distinct allopatric genera are hypothesised to have diversified due to geographical separation (Chan et al., 2013, Thinh et al., 2010). However, this separation was most likely followed by unidirectional gene flow between *H. lar* and *H. moloch*, between *H. agili*s and *H. muelleri*, and between *N. leucogenys* and *N. siki* (Chan et al., 2013). Subsequently, gibbons are the most diverse group of living apes. Due to a sparse fossil record, there is currently little understanding of the biogeographic history of gibbons (Chaterjee, 2001), though a number of scenarios have been proposed to describe the radiation of hylobatid species. Groves (1972) proposed lowering sea levels, due to glaciation in the Pleistocene causing eustatic sea level fall, as a contributing factor in the dispersal of the lar group of gibbons. Chivers (1977) provides a robust assessment of the chronological history of the paleoenvironment of Sundaland, the biogeographic region of Southeast Asia, including the possible migration routes for different gibbon species. More modern works using mitochondrial DNA (mtDNA) data provide a perhaps more accurate, if more complex, picture of gibbon evolutionary history, suggesting a rapid Miocene radiation or sudden variance event followed by gene flow (Roos and Geissmann, 2001; Raaum et al., 2005; Israfil et al. 2011; Matsudaira and Ishida 2010; Perelman et al., 2011; Thinh et al. 2010a; Meyer et al., 2012; Carbone et al. 2014).

As the global climate cooled and Asian forest contracted (Cannon et al. 2009), it is likely that what once may have been a vast, continuous habitable forest stretching from West Europe across Eurasia until Borneo (Morley et al., 1987, Grehan and Schwartz 2009), gradually shifted into a matrix of forest fragments and savanna (Morley, 2000), in which only isolated tropical forests preserved a stable microclimate of low fluctuating ecological conditions. It is under these conditions that the highly specialised form of locomotion of hylobatids evolved. *Hylobates* have the longest forelimbs relative to body size of any living primates, enabling their acrobatic form of richochetal brachiating travel, typically high in the canopy (Fleagle, 2013). Physiologically, Hylobates are the smallest extant apes (5-11kg), and the most primitive, retaining many monkey-like features (ischial callosities, Vilensky, 1978). The small body size of Hylobatidea has been interpreted as a derived adaptation during periods of global climate change during the Mid-Miocene that became established before hylobatids split into the four genera known today (Lewis et al. 2008).

The Sumatran lar gibbon, or Sumatran white-handed gibbon (*Hylobates lar vestitus*) is a subspecies of the wider ranging *Hylobates lar*, found only in northern Sumatra. As with other gibbon species *Hylobates lar vestitus* is primarily a frugivore, with 71% of its diet made up of fruit (45% Ficus spp.), 24% insects, 4% young leaves and 1% flowers (Brockelman et al., 1998). Earlier research on the social system and dispersal of *Hylobates lar* suggested highly territorial, monogamous pairs living in family groups, with sub-adults forced out of the family group at maturity (Ellefson, 1974). However, detailed long-term studies of multiple habituated wild gibbon groups within the same area have shown multiple male take overs of existing groups, juvenile males emigrating to neighbouring groups, and male dispersal an average of two years after reaching maturity (Brockelman et al., 1998). Genetic studies have confirmed that many gibbon offspring are the result of matings outside of the family group (Barelli et al., 2008). Like most apes, *Hylobates lar* exhibit late age at first reproduction, long interbirth intervals (Reichard & Barelli, 2008) and a long juvenile period which manifest themselves in low rates of reproduction in the wild (Yanuar, 2009). Gibbons are highly territorial and defend core home ranges with near daily calling bouts, complex duets between bonded pairs which can be heard up to 1km away (Clarke et al., 2006). As well as serving a territorial function (Geissmann, 1993) and potentially being individually recognisable (Oyakawa et al., 2007), these calls provide researchers with the benefit of non-invasive forms of data collection of non-habituated groups.

Hylobates lar verstitus’ highly arboreal specialisation, frugivorous diet, and low fecundity mean they are sensitive to anthropogenic disturbance (MacKinnon, 1986). In a comprehensive study of gibbon population densities across 53 areas in Borneo, Cheyne (et al., 2016) found gibbons present in all areas where there is forest; however, the quality of forest affected population density. Forest block size affected longevity of populations, and populations were seemingly susceptible to the ‘compression effect’, i.e. populations occupying smaller fragments were at unsustainably high densities. In Sumatra, primary tropical rain forests, especially in the lowlands, have disappeared rapidly with the majority of land being converted for commercial timber concession, crop plantations or agricultural and human settlements (Tomich et al., 2001). Forest degradation, in the form of selective logging changes canopy structure (FAO, 1981, Jepson et al., 2001) and decreases potential habitat availability for the mainly primary forest dwelling *Hylobates lar* (Johns, 1988). Subsequently, *Hylobates lar verstitus* is currently listed as Endangered by the IUCN Red List of Threatened Species. Within the Sikundur site, historical selective logging and forest loss at the borders of the Gunung Leuser National Park is likely to compress the existing population into higher population densities than are sustainable, especially given the heterogeneous nature of forest degradation in the area (see Figure 2.5).

1.4.5 Siamang (*Symphalangus syndactylus*)

The siamang (*Symphalangus syndactylus*) is a monotypic, gibbon-like ape, which is relatively under-studied; with most information from wild individuals originating from only a few groups (Chivers, 1974, Chivers, 1976, Morino, 2012, Morino, 2016, Morino, 2017, Lappan, 2007a, Lappan, 2007b, Lappan, 2008, Lappan, 2009a, Lappan, 2009b, Lappan, 2009c, Lappan, 2010, O'Brien et al., 2003). Having diverged after the smaller hoolock/crested gibbons from the stem hylobatid lineage (Figure 1.1), siamang present a secondary increase in body size after hylobatids had already undergone substantial body size reduction due to climate variability during the Mid-Miocene (Lewis et al. 2008, Jablonski and Chaplin 2009). Recent molecular phylogeny studies have confirmed this, and so initial theories that *Symphalangus* occupies a basal position in hylobatid lineage are unlikely (Figure 1.1; Roos and Geissmann, 2001).

Symphalangus syndactylus in Sumatra shares almost the entirety of its distribution with the white-handed gibbon (*Hylobates lar*) in the north, or the agile gibbon (*Hylobates agilis*), in the south (Marshall and Sugardjito, 1986). Siamangs show greater folivory than other gibbon species, their larger body size allowing for a longer intestinal tract, which allows for longer digestive periods, potentially extracting additional nutrition from leaves (Chivers and Raemaekers, 1986). However, studies of siamang and sympatric gibbon species show that both display broad diets and broad dietary overlap, especially over seasonal time periods (Lan, 1993). The siamang has almost twice the body weight of sympatric gibbon species (ca. 11-12 kg vs. 5-6 kg) (Jungers, 1984) and can exhibit larger group sizes compared to other gibbon species (mean 3.9 vs. mean 2.6 in Sumatra) (O'Brien et al., 2003) suggesting distinct differences in ecology and behaviour between the siamang and the two sympatric gibbon species; an exhibit of ecological niche differentiation (Caldecott, 1980). However, ecological niche separation seems an inadequate explanation for their body size differences (Reichard & Preuschoft, 2016). A relatively unexplored explanation for the larger body size of siamang may be its ability to adapt to montane as well as lowland tropical forest. With a relatively smaller surface area to body mass, siamang would lose less heat energy in a cooler environment than a smaller gibbon (Reichard & Preuschoft, 2016). Additionally, a more leaf-based diet would allow siamang additional nutritional options as seasonal availability of fruit becomes more pronounced and plant species diversity is reduced at higher elevations (Cannon et al. 2007a, Cannon et al. 2007b). A study using data derived from the available literature showed that siamang is better adapted to cooler climates at higher elevation (or more northern latitudes), compared with hylobatids of smaller body size (Reichard & Preuschoft, 2016).

Siamang have repeatedly been reported to show longer activity time, longer feeding time, and less travel time compared with lar gibbons (Chivers and Raemaekers, 1986, Elder, 2009). Siamang have been shown to have shorter average day ranges than smaller hylobatids (Bartlett, 2011). The behavioural ecology of siamang, consuming more leaves, higher feed/forage ratio, and smaller daily ranges than sympatric gibbon species, seems to point toward a sympatric association where each occupies relatively different ecological niches, despite their apparent similarities. Siamang have been found at higher densities at higher altitudes than sympatric gibbon species in Sumatra (Yanuar, 2009) and are seemingly sensitive to disturbance (Nowak, pers. comm., 2016). Siamang, like gibbon and orang-utan species, are threatened by deforestation and opportunist collection for the pet trade (O’Brien et al., 2004). Between 1995 and 2000, almost 40% of the habitat for this species on Sumatra was damaged or destroyed by logging, road development (which acts as physical barrier and increases hunting rate) and conversion to agriculture or plantations (O'Brien unpubl. data). The siamang is one of the most heavily traded gibbon species for illegal pet trade (V. Nijman pers. comm, 2016).

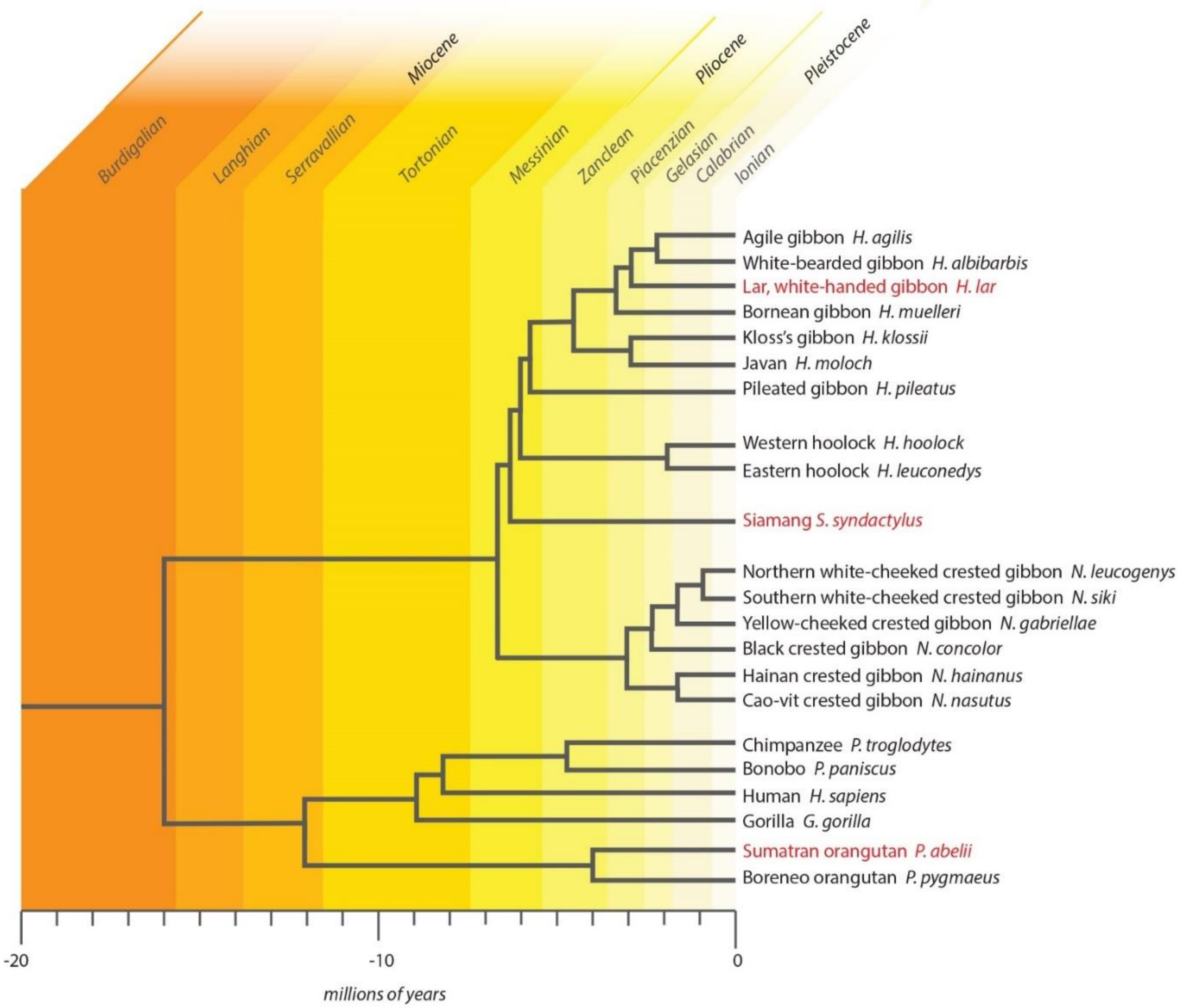


Figure 1.2 - Dated ape phylogenetic tree. Study species are highlighted in red. Adapted from; Roos and Geissmann, 2001; Raaum et al., 2005; Fischer et al., 2006; Chatterjee, 2006; Jablonski and Chaplin, 2009; Matsudaira and Ishida 2010; Thinh et al. 2010; Israfil et al. 2011; Perelman et al., 2011 and Carbone et al. 2014

1.5 Behavioural thermoregulation

The synergistic effects of forest degradation and climate change could have profound effects on organisms which have evolved within the stable climatic envelope of tropical rainforests (Ahumada et al., 2011). Mammalian tropical rainforest species typically have narrow thermal tolerances and are already living near their upper thermal limits (Corlett., 2011). Changes in climate and the creation of gaps with forest canopy can alter temperatures experienced by a number of these species, placing them under thermoregulatory stress.

In mammals, thermoregulation is the maintenance of temperature, ensuring optimal functioning of the organism. Thermoregulatory capacities are strongly related to energy balance. Energy expenditure is lowest when ambient temperature corresponds to the thermoneutral zone (temperature tolerance range) of the animal (Terrien et al., 2001). In the case of thermal changes, core temperature within the thermoneutral zone can be maintained by physiological mechanisms such as shivering, sweating and panting (Kind and Farner., 1961). These physiological changes inevitably cause increased rates of energy expenditure (Cordain et al., 1998). However, behavioural adjustments can be made by species to lower physiological responses, reducing energy costs, such as seeking locations which are within the thermoneutral zone of the individual (Pruetz, 2007, Briscoe et al., 2014).

Temperatures above the thermoneutral zone can negatively affect oestrus in females and social grouping of mammals in the long term (Anderson et al., 2006). In the short term, heat exposure induces reduced energetic costs. Caloric intake at high ambient temperature has been shown to reduce energy intake in some mammals (Zub et al., 2013). Conversely, decreased locomotor activity in response to high ambient temperature has been repeatedly observed, as locomotor activity in high ambient temperature increases energy expenditure (Shido et al., 1991). The effects of heat exposure on mammalian energetics and survival is far from linear (Levesque et al., 2016). Despite generally being regarded as strict homeotherms, mammals demonstrate a large degree of daily variability in body temperature and there is a general lack of understanding of mammalian responses to high ambient temperature, above their thermoneutral zones (Huey et al., 2012, McCain and King, 2014). While increases in body temperature at high ambient temperature have been shown to reduce the energetic costs and increase the efficiency of evaporative cooling in some small desert mammals (Degen, 1997), the relationship between water loss, body temperature and ambient temperature at the upper limits of the thermoneutral zone in mammals is largely unknown (Levesque et al., 2016). Additionally, few studies have compared upper limits of thermoneutral zones measured in the lab to conditions experienced by animals under natural conditions (but see Moyer-Horner et al., 2015). Most mammals in natural environments avoid heat during the hottest hours of the day by retreating in shaded cooler places, thus adjusting daily activity when faced with hot conditions (Gonzalez-Zamora et al., 2011). Whilst posture may allow some species to increase their surface-area ratio and promote conductive heat exchanges between skin and air (Stelzner and Hausfater, 1986), for primarily arboreal species, the selection of habitat which provides sufficient protection from solar radiation, to remain within their thermoneutral zone, is limited.

The thermoneutral zone in primate species is mostly less than 6°C in range. Below these ambient temperatures, heat production increases. Above this, heat production also increases due to physiological processes to dissipate heat, i.e. panting or sweating, (see Table 1.1).

Table 1.1 - Thermoneutral zones of primate species in the available literature (from Takemoto, 2004)

Suborder	Species	Thermoneutral zone (°C)	Literature cited
Prosimii	*Microcebus murinus*	25-28	Aujard et al., 1998
	Galago spp.	22.5-27.5, 30-32.5	Muller, 1995
	Nycticebus coucang	31.4-36.6	Whittow et al., 1977
	Tarsius syrichta	32-35	McNab and Wright, 1987
Anthropoides	*Cebulla pygmaea*	27-34	Genoud et al., 1997
	Leontopithecus rosalia	28.1	Thompson et al., 1994
	Cercopithecus mitis	24-25	Muller et al., 1983
	Homo sapiens	28-32	Davson, 1970

In primates, exposure to ambient temperatures above 36°C has led to thermal distress and hyperthermia (Stitt & Hardy, 1971). Hill's (2004, 2006) thermal stress classification system for wild baboons used the following groupings for classifying thermal stress: Below Thermoneutral (<24°C), Thermoneutral (24–30°C), Moderately Above Thermoneutral (30-38°C), Extremely Above Thermoneutral (>38°C).

Primates experiencing high ambient temperature are likely to use behavioural thermoregulation to mitigate additional energy expenditure; changing daily activities and ranging to increase protection from solar radiation and reducing locomotion. Many primate species have been observed to change activity and ranging behaviour in responses to seasonal and extreme ambient temperature change (Hanya, 2004, Poulsen et al., 2001, Vasey, 2005). Chimpanzees in tropical forest have been recorded to increase their terrestrial behaviour as temperatures rise and to increase arboreal behaviours when temperatures are low, reducing thermoregulation costs by avoiding solar radiation during periods of high ambient temperature (Takemoto, 2004). Sleeping site selection in groups of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) were at significantly lower altitudes in winter months than summer months, a thermoregulatory adaption to remain within their thermoneutral zone (Cui et al., 2006). Similarly, Baboons engage in more sedentary activities as ambient temperature rises throughout the year (Hill, 2004). With predicted anthropogenic climate change estimated to increase global temperatures by 2^{o}C by the year 2020 (the current internationally adopted climate mitigation target, Collins et al., 2013), and

62.6% of all primate species projected to experience temperature increases greater than the global mean (mean 2.2^{o}C, Graham et al., 2016) thermoregulation for many primate species, particularly those with narrow thermal thresholds and in degraded forests, may become a challenge. Climate change on the island of Sumatra is predicted to be less severe than land-locked areas due to its proximity to the sea (~1 ^{o}C per ^{o}C of global warming) and will likely see an slight increase in precipitation levels (~0 - 2.5 % increase per ^{o}C global warming) (Graham et al., 2016).

1.6 Climate change effects on primates

1.6.1 Community Changes

As sympatric primate species are affected by, and respond to, anthropogenic disturbance (forest degradation, deforestation) in different ways, the response of individual species to climate change will also alter the composition of primate communities (Root et al., 2003). In Chapman's (2010) long-term study (36 years) of forest degradation on a primate community of several sympatric species, the composition and population densities of different species changed in unexpected, unpredictable ways. In this study, a complex set of environmental and biotic factors caused changes in patterns of fruit production, altering food availability. At this study site, blue monkeys (*Cercopithecus mitis*), considered to be generalists and adaptable to changes in forest structure and fruit production, were slowly out-competed by mangabeys *(Lophocebus albigena)*, considered old-growth forest specialists, as forests regenerated (Mitani et al, 2000). However, this comes at the cost of overall health, as male mangabeys in logged forest have been found to have a lower body mass than males in unlogged forest (Olupot, 2000), perhaps due to the increased energetic demands of reduced canopy pathways (Gebo and Chapman, 1995). The population dynamics of sympatric primate species responding to the novel demands of anthropogenic disturbance may result in "boom and bust" population fluctuations, which have yet to become fully evident. The interactions between multiple species in a regenerating forest are complex, and as an environment regenerates it may favour the ecological adaptations of different primate species during different periods of degradation and regeneration.

Whilst ecological, behavioural and locomotive adaptability may govern primate species' vulnerability during times of extreme stress (i.e. logging events, hunting), the structure of primate communities can be inexorably changed due to anthropogenic activities (Peres, 1999). In the face of the seemingly exponential rise in global temperatures, the beneficial impacts of sympatric primate communities (poly-specific predator protection, location of food items) may decrease as some species decline in primate communities. Whilst this may result in a period of population boom in previously sympatric primate species (Peres and Dolman, 2000), it may cause the remaining species to become more vulnerable to other negative impacts (Buchanan-Smith, 1999).

1.6.2 Diet and dietary specialisation

Dietary specialisation will greatly affect how vulnerable a specific species is to climate and environmental change. Primates are relatively flexible in terms of diet, often eating a range of food items, which are generally categorised as; vegetative plant matter (leaves), reproductive plant parts (fruits, seeds, flowers), plant exudates (gum and sap) and insects/fauna (Altman, 1988). Many primate species consume multiple items from these four categories, but they differ significantly in the proportions in which they are consumed. Of equal importance when reviewing the impacts of climate change on primate species in terms of diet is the use of food resources of relatively poor nutritional quality (termed “fallback foods”), when preferred foods are scarce (Marshall et al., 2009).

As climate change takes effect, temperatures in tropical forest areas are predicted to rise, and as a result, reduced net rainfall will be experienced (Bonan, 2008) leading to lower digestibility, lower quality, and higher concentrations of plant secondary compounds in leaves (Rothman et al., 2015) which may impact on folivore species. In contrast, frugivorous species may benefit as temperatures increase (Soloman & Cramer, 1993). The “CO_2 fertilisation effect” (i.e. larger amounts of carbon dioxide in the atmosphere due to anthropogenic emissions increasing the rate of both photosynthesis and growth for plants) would suggest that fruit production would increase. However, in a 12-year study, Clark et al. (2013) found that aboveground net primary productivity (ANPP) was adversely affected by increasing minimum temperature and dry-season water stress. With the predicted rapid warming across tropical regions, tropical forest productivity could sharply decline through the coming decades.

Due to the diversity of fallback food items utilised by primate species, it is difficult to predict what effect climate change may have on their availability. However, given the previous examples of vegetative and reproductive plant parts, many primate species are likely to become more reliant on fallback foods. The most common applied definition of fallback foods is food items whose use is significantly negatively correlated with the abundance of preferred foods (Wrangham et al., 1998). During “ecological crunch periods”, or “bottlenecks” (i.e. periods of extreme food scarcity), the use of fallback foods becomes of prime importance (Boag and Grant, 1981). Lambert (2007) classifies fallback food items within a continuum, at one extreme are abundant, low-quality foods (such as leaves and bark, vegetative plant matter) and at the other, are less abundant high-quality fallback foods (such as fruit and seeds). Low quality fallback foods require specific anatomical adaptations (dental or digestive characteristics [thicker dental enamel, longer molar shearing crests, longer digestive retention times]) to allow the processing of these food items. Rare, high-quality fallback foods require behavioural adaptations (fission-fusion social systems, tool use) to allow species to utilise them. Neither of these strategies precludes the other, for instance orang-utans displays thick enamel (Smith et al., 2012), tool use (van Schaik et al., 1996), and extreme fission-fusion social dynamics (van Schaik, 1999). Dietary flexibility, in terms of both behavioural and morphological adaptations, as opposed to specialised dietary niche or category, may determine specific primate species' ability to survive in the face of rising global temperatures.

1.6.3 Life history and phenology

Most primate species have 'slow' life histories, i.e. small litters, slow growth rates, late sexual maturity, long gestation and long interbirth intervals (Table 1.2). Species with slow life histories are less able to compensate for increased mortality with increased fecundity and are therefore more vulnerable to population extinction (MacArthur and Wilson, 1967). Whilst some primate species show behavioural adaptions to the challenges of climate change (Chivers, 1991; Lee, 1991) their slow life histories mean the number of generations required to allow genetic adaptation to suit altered environments (for example, increased tolerance to plant secondary compounds in folivores) will not keep pace with a changing environment, as species with 'fast' life histories may be able to (Williams et al., 2008).

Phenological events, such as fruiting events leading to food abundance, are often synchronised with reproductive events (Brockman & van Schaik, 2005). Desynchronisation between fruiting and reproductive events, due to climatic changes, may result in increases in mortality in infants and mothers, as well as lower reproductive rates, higher vulnerability to disease and predation, and lower chances of offspring survival (Marshall & Wich, 2013). The size and cohesiveness of primate groups also fluctuates substantially in response to food availability (Wrangham et al., 1996) causing reduced group size/cohesion (Dunbar, 1996), which may impact on infant and mother health due to the increased energetic demands of locating food items, reduced alloparenting and decreased intraspecfic predator protection.

Table 1.2 - Northern Sumatran primate species' life history attributes and IUCN Red List status

Species (Scientific)	IUCN Red List Status	Interbirth Interval	Average number of off-spring	Average gestation period	Average weaning age	Average time to independence	Age at sexual maturity (female)
Macaca fascicularis	LC	390 days (mean)	1	162 days	14 months		4 years
Presbytis thomasi	V	1.5 to 2 years	1	165 days	13 months	15 to 18 months	4 years
Nycticebus coucang	V	1 year (mean)	1	188 days	4 months	16 to 26 months	18 to 24 months
Hylobates lar vestitus	E	3.5 years (mean)	1	217 days	20 months		6 to 9 years
Symphalangus syndactylus	E	2 to 3 years	1	232 days	21 months		6 to 7 years
Pongo abelii	CR	3 to 4 years	1	252 days	48 months	9.3 years	12.3 years

1.6.4 Time-budget models

All actions which fulfil physiological requirements need time to complete. The search and processing of food is required by all animal life, and the distribution of food resources in time and space govern the majority of how animal time is spent (Matthiopoulos et al., 2003). Whilst primate species show slow life histories and metabolic rates, and low total energy expenditure (Kuzawa et al., 2014), their generally large group sizes mean the energetic demands of maintaining a large brain and the competition for food resources are high, requiring long time periods of travel and foraging for individuals to fulfil requirements. These requirements may change with climatic and environmental variables (Figure 1.3). Low precipitation, leading to lower density and quality of food resources may lead to more time spent foraging and feeding (Donati et al., 2011), with other activities, such as moving, resting and socialising allocated less time (Tutin, 1999). Abiotic variables, such as seasonality, have been shown to impact on the distribution of food items, increasing moving time (Wallace, 2006). There is a clear feedback loop between increased moving and feeding time, as the energetic cost of moving to locate dispersed food items itself requires energetic input (Stephens & Krebs, 1986). Resting time acts as a reservoir from which all other activities are drawn, though for many species enforced resting time due to thermoregulation (Mount, 1979) or digestion (van Soest, 1982) is a necessary activity.

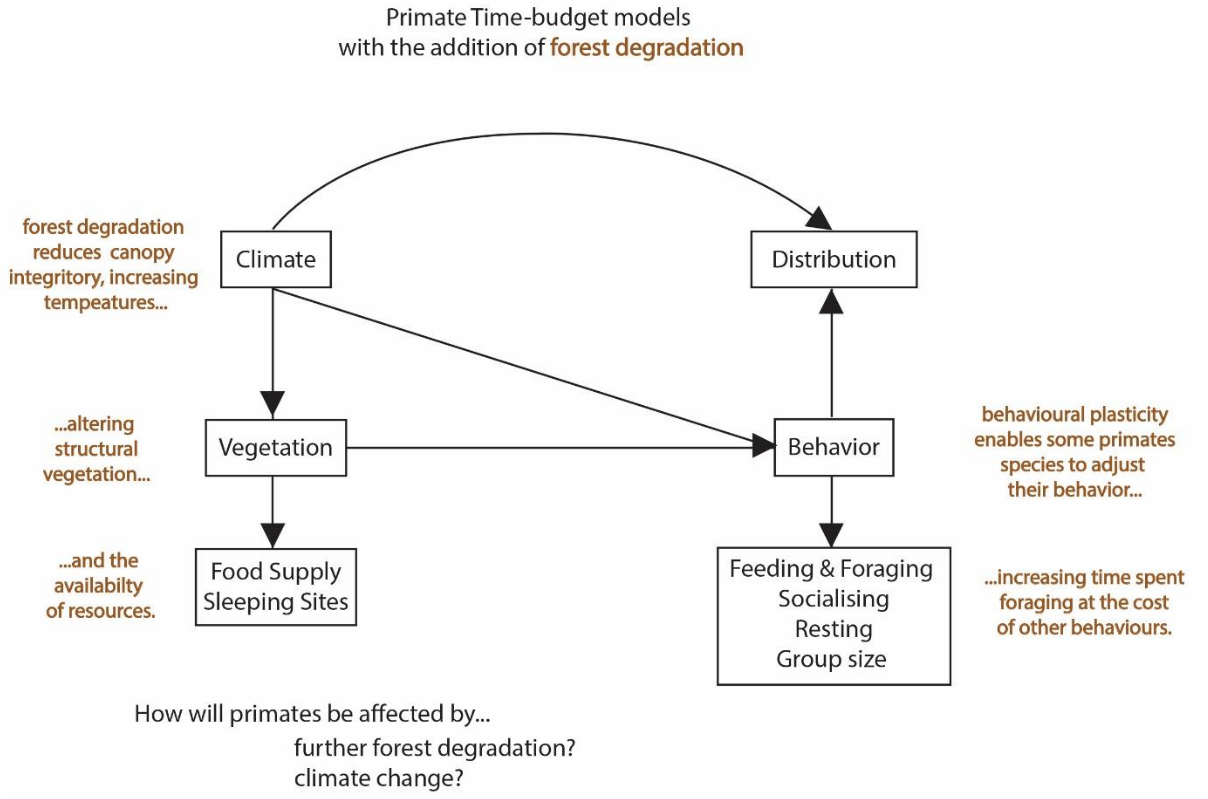


Figure 1.3 - Primate time-budget models with the addition of forest degradation, adapted from Dunbar et al., 2009

Korstjens et al. (2010) showed that across primate genera (N = 78), enforced resting time is a function of three variables: mean annual temperature, the variance in monthly mean temperature across the year (a measure of seasonality) and the percentage of leaves in the diet. These two limitations on behaviour (moving/feeding time feedback loop and enforced resting) enact to decrease the frequency and duration of social behaviour (Dunbar, 1992, Lehmann et al., 2007, Lehmann et al., 2010, Korstjens et al., 2010, Dubar et al., 2009) which may, in time, express itself as a decline in fecundity for primate species. Leaves (vegetative plant parts) are important factors influencing enforced resting time. Leaves are generally high in fibre and require long digestion times if sufficient proteins are to be extracted from them. In increased temperatures, the energetic costs of ranging for high-quality food resources increases and reliance on fallback food resources, such as leaves, may also increase. Subsequently, enforced resting time for many primate species may increase (for both thermoregulation and digestion), limiting range sizes and social interaction, subsequently expressed, possibly over generational time periods, as a lowering of population density.

1.6.6 Extreme weather and disturbances

Climate change will not just cause a rise in temperature, but also disrupt weather patterns, cloud cover and rainfall, but also is predicted to exacerbate the extremes of seasonal changes, including rainfall patterns, (Feng et al., 2013) and disturbances (fire, drought, pathogen outbreaks, hurricanes, windstorms, landslides) (Dale et al., 2001). In Japan, a typhoon impacted on the availability of fruit for Japanese macaques (*Macaca fuscata*) forcing them to feed intensively on seed and nuts that had fallen on the ground, in direct competition with sika deer (*Cervus nippon*) and field mice (*Apodemus argenteus*) (Tsuji and Takatsuki, 2008). In Belize, a hurricane had similar effects on black howler monkeys (*Alouatta pigra*) with low fruit availability forcing them to adopt a folivorous diet, resulting in less time spent travelling and reduced social interactions (Behie and Ravelka, 2015). In Madagascar, a two-year drought caused infant mortality to reach 80% in ring-tailed lemurs (*Lemur catta*) and 20.8% of all adult females died. Four years after the drought, the population had recovered to pre-drought numbers due to high birth rates, early sexual maturity and an increased range of food items (Gould et al., 1999). These examples display the adaptability of primates to disturbances caused by extreme weather, which are the products of climate change (Feng et al., 2013). Singularly, many primate species may be able to adapt to these additional stressors, but multiple factors acting in synergy, together with the additional pressures of anthropogenic disturbance, may exacerbate primate population declines (Estrada et al., 2017).

1.7 Previous work in relation to data chapters

Whilst these factors (1.6.1 – 1.6.6) may pose challenges to primate species, many species will face additional challenges when they are affected by multiple factors simultaneously. Many primate species show remarkable resilience to environmental change (Gould et al., 1999; Schaffer et al., 2012), however, no group of primate species is seemingly at more risk than the arboreal apes, due to their specialised diet, low fecundity, and high energetic requirements. Conversely, arboreal ape species show a wide range of behavioural adaptability, and often persist even in the face of anthropogenic disturbance, painting a complex picture of how they will be affected in a changing climate. Using the available literature as reviewed in this first chapter, the differing behavioural ecology, social structure and life-history traits of each species (1.4.3 – 1.4.5) will be used to assess their capacity to adjust to both climate change and anthropogenic disturbance.

Adequately understanding the possible effects of anthropogenic disturbance and climate change on arboreal primates necessitates the understanding of the impacts of canopy structure on within-canopy microclimates. Typically, the climates of study sites are characterised by the climate recordings of the nearest weather station, or rudimentary base camp measurements of temperature and rainfall (Beehner et al. 2006; De la Fuente et al., 2014). Given that arboreal microclimates differ significantly to terrestrial microclimates (Samson and Hunt, 2012), characterising the thermal environment that arboreal primates experience from these measurements may not reflect conditions that arboreal species are exposed to (Thompson et al., 2016). As on-animal measures of microclimate or temperature are not prudent for non-habituated, highly arboreal, Endangered primate species, given the health risks (Cunningham et al., 2015), within-canopy microclimate measurements coupled with detailed vegetation surveys will enable the exploration of the impacts of vegetation structure on microclimates. The study of how canopy topography influences canopy microclimate will form the basis for Chapter 2.

Understanding the effects of vegetation structure and the microclimate variability on arboreal primates' behaviour and ranging is key to understanding how they may be affected by anthropogenic disturbance and future climate change. For relatively under-studied species, such as *Symphalangus syndactylus,* siamang (see Figure 3.1), recordings of habitat preference are particularly important to ensure potential conservation actions are targeted and effective (Mittermeier and Van Roosmalen, 1981). To add to existing knowledge of this species, and to aid in the understanding of how adept they may be in adapting to anthropogenic disturbance, requires the habituation and subsequent behavioural observation of siamang in their natural habitat for an extended period. This will allow the recording of their habitat use, as well as insights into how they may be affected by future climate change. This study of siamang behaviour and ranging will be covered in Chapter 3.

Habitat structure, as it is affected by natural variation and anthropogenic disturbance, alters habitat quality for, and therefore the abundance of, different primate species within the same landscape (Marsh et al., 2016). Historic selective logging in the Sikundur area may have altered habitat quality for arboreal primates. Different species' relative abundance to sites of forest degradation may give an indication of their adaptability to further anthropogenic disturbance (Wilson and Wilson, 1975). If species show that behavioural and ecological plasticity is present across a large range of differing habitat types, then they are more likely to be able to adapt to future challenges (Crispo et al., 2010; Wong and Candolin, 2015). A wide-ranging, landscape-scale survey of the abundance and vegetation structure of the larger Sikundur region will allow a detailed understanding of how historic forest degradation impacts the abundance of three primate species, *Presbytis thomasi, Hylobates lar vertitus* and *Symphalangus syndactylus.* This study will be detailed in Chapter 4.

The factors covered in this Chapter (1.6.1 – 1.6.6) as well as within-canopy microclimate and habitat suitability in the face of future climate change will be addressed in Chapter 5. Using insights obtained from Chapters 2 and 3, the habitat suitability of the larger Sikundur area will be assessed for two primate species, *Symphalangus syndactylus* and *Pongo abelii.* Reviewing each species' habitat use and behavioural adaptability, Chapter 5 will assess each species' ability to withstand different levels of future predicted climate change.

Chapter 2. Measuring and modelling microclimate in a degraded tropical forest

2.1 Introduction

Habitat modification and climate change are among the primary threats to global biodiversity (Nowakowski et al., 2018). Land-surface temperatures in tropical rainforest regions have risen by ~0.25^{o}C per decade since the mid-1970s (Malhi and Wright, 2004) and are projected to rise by 3-8^{o}C over the 21st century (Malhi et al., 2009). Forest degradation, measured by partial canopy cover loss, affected 185 million ha between 2000 and 2012, with over 156 million ha of this within tropical forests (van Lierop et al., 2015). Although species are experiencing both habitat modification and climate change simultaneously, these threats are typically studied independently (Sirami et al., 2017, Oliver and Morecroft, 2014), despite habitat modification affecting thermal landscape variation (Todd and Andrews, 2008; Arroyo-Rodrigues et al., 2016; Tuff et al., 2016).

Ecologists aiming to understand and predict the influence of climate on species often use models based on macroclimatic variables, which are generally measured by standard meteorological stations. However, organisms experience climate at a small (micro-) scale and temperature variation is highly scale-dependent (Chen et al., 1999). Due to the influence of vegetation structure, microtopography and soil, microclimate may only be weakly correlated with macroclimate (Graae et al., 2012, WallisDeVries et al., 2011, Potter and Hargrove, 2013). Many vertebrates experience spatial variation in temperature over a range of tens to hundreds of metres per day, depending on body size and mobility (Jenkins et al., 2007). Mobile organisms can move within landscapes which incorporate a broad range of microclimates, allowing them to maintain their optimum climatic conditions (Oliver and Morecroft, 2014). Tree gaps, rocks and logs provide a spatial and temporal mosaic of temperatures, which various species may be able to exploit (depending on their size and locomotive ability) to thermoregulate and buffer against high temperatures (Scheffers et al., 2014a).

Microhabitats have been shown to buffer temperatures in a consistent manner within forest systems and can reduce extreme heat exposure by up to 10°C (Scheffers et al., 2014b). In a degraded forest the availability of microhabitats and the effectiveness of their thermal buffering are heavily influenced by varying levels of vegetation density (Pringle et al., 2003). The level of degradation, time since degradation and plant species establishment will affect forest structure (Pohlman et al., 2007; Norris et al., 2012; Harper et al., 2005; Brokaw, 1982; Mulkey and Pearcy, 1992; Laurance et al., 2006) and therefore microclimate (Figure 2.1). The availability and distribution of thermal buffering microhabitats may lead to only a fraction of available habitat being frequently utilised by certain species, depending on their exposure and sensitivity to temperature variation (Williams et al., 2008). Understanding how forest degradation affects microclimate is therefore key to understanding species behaviour in a degraded forest landscape.

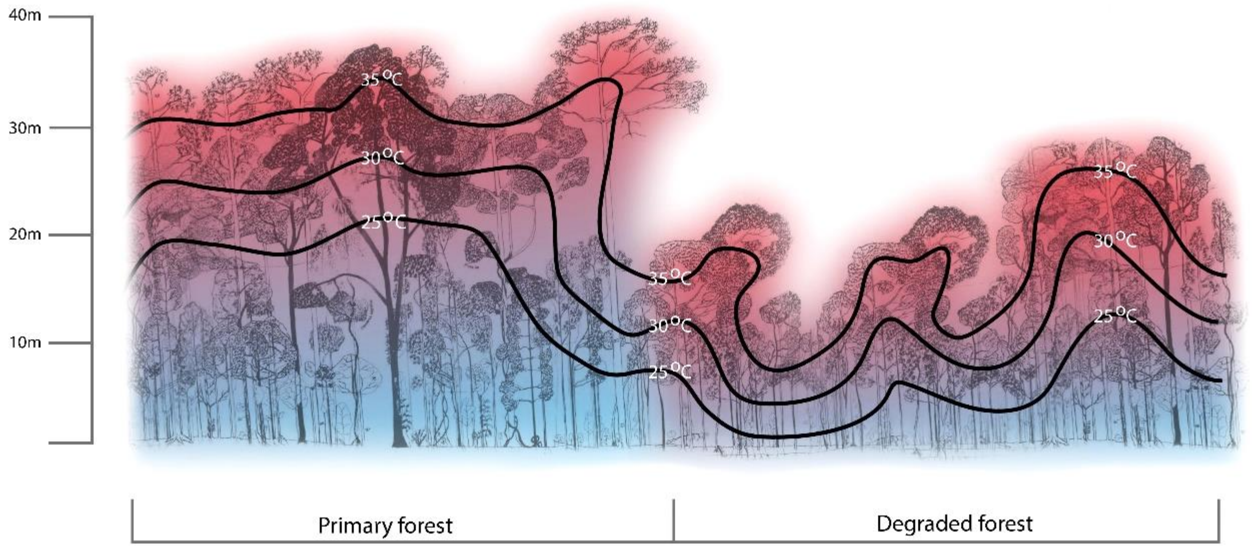


Figure 2.1. Stylised illustrative hypothesis of the effect of forest degradation on microclimate

Despite the long history of microclimatology (Potzger, 1939), it is only more recently that developments in technology and advances in computing power have made taking simultaneous measurements over large areas possible (Jones, 2013; Wang et al., 2013). However, measuring small-scale microclimate fluctuations across a large scale in structurally complex degraded forest habitats presents significant challenges, especially when selective logging has taken place at the site periodically over several decades. In Colombia, for example, thermally buffered microhabitats increased in abundance and changed in composition with forest succession, from young-secondary forest to primary forest (González del Pliego et al., 2016). Thermal variation is not restricted to horizontal variation in vegetation composition, but also occurs vertically among canopy strata. Thermal variation along the vertical strata of habitats provides thermoregulatory opportunities for arboreal species that can climb or descend to track preferred temperatures (Scheffers et al., 2017). In a degraded forest, changes in vegetation structure due to selective logging will greatly alter the microclimate environment across relatively small distances, vertically and horizontally. This creates a dynamic, three-dimensional thermal landscape in which temperature varies on diurnal and seasonal cycles. However, to measure microclimate accurately across a degraded forest landscape, at the small scales that most species experience, requires new and innovative methods.

Detailed three-dimensional vegetation surveys over large areas have previously been prohibitively expensive for most researchers (Hummel et al., 2011), with light detection and ranging (LiDAR) from small aircraft and time-consuming terrestrial surveys being the only options to obtain these data (Hill and Hinsley, 2015). With the advent of unmanned aerial vehicles (UAVs) used in an ecological context (Koh and Wich, 2012, Anderson and Gaston, 2013, Zahawi et al., 2015) and Structure from Motion software (SfM), measurements of canopy topography are now accessible and cost effective (Alexander et al., 2017, Lisein et al., 2013, Wich, 2015). Similarly, it is only recently that 'data logging' hardware, measurement systems which independently record data points at set times, have been available at lost cost, and therefore usable in large quantities (Hubbart et al., 2005). Combining these technologies enables the development and testing of a three-dimensional microclimate model that incorporates vegetation structure across a wide landscape (Chabot et al., 2014; Goetz et al., 2007).

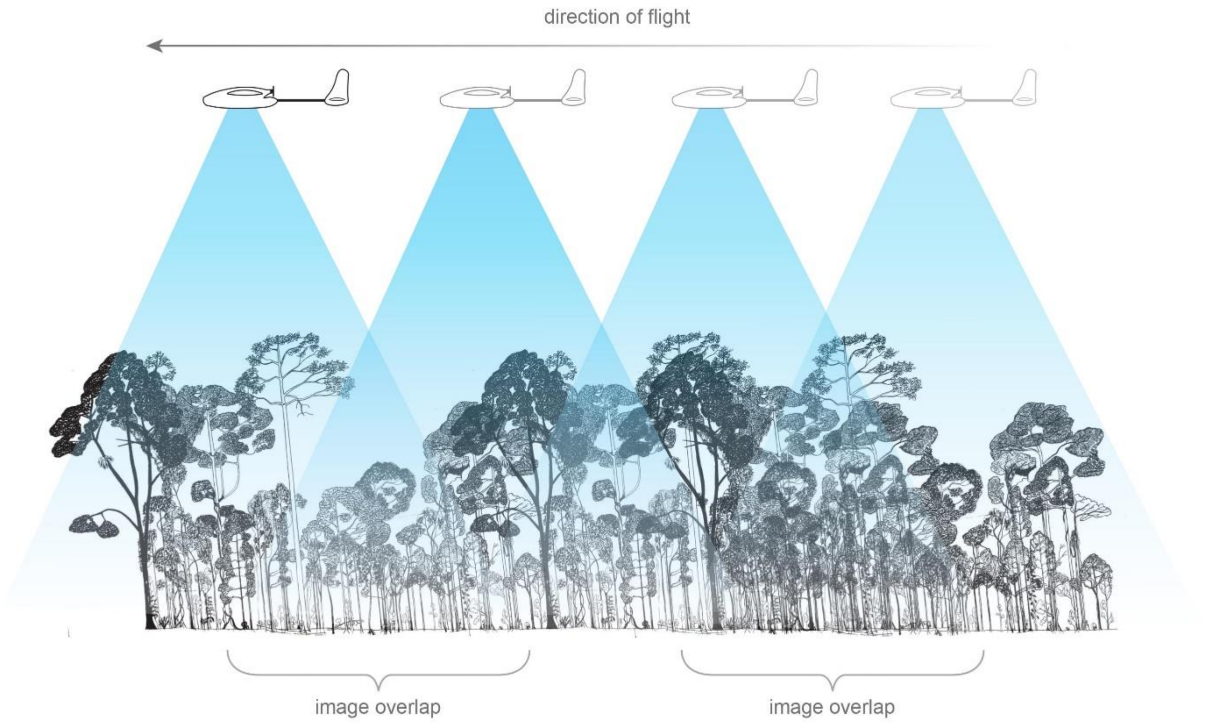


Figure 2.2. Illustrative diagram of UAV data collection protocol showing image capture overlap

Unmanned Aerial vehicles (UAVs) are an emergent remote sensing technology that employ self-navigating 'drones' to collect photographic aerial imagery of a given area. UAVs are capable of surveying forests at fine scales (Getzin et al., 2012). The use of UAVs in geomorphological mapping is often facilitated by the application of photogrammetric techniques such as Structure from Motion (Harwin and Lucieer, 2012; Westoby et al., 2012; Micheletti et al. 2015). SfM utilises overlapping imagery acquired from multiple viewpoints to reconstruct the camera position and camera geometry (Figure 2.2). From these reconstructed camera locations, two-dimensional imagery collected using UAVs can be translated into three-dimensional structural models, given sufficient image overlap. (Westoby et al., 2012; Fonstad et al. 2013; Micheletti et al. 2015).

Given correct deployment and attainment of accurate ground control data, the horizontal accuracy and precision of resultant aerial imagery and digital surface models (DSMs) generated through SfM can be better than satellite imagery and aerial LIDAR (±0.2 m; Fonstad et al., 2013; Hugenholtz et al., 2013). Using these data, wide-ranging three-dimensional models of tropical forests can be acquired using low-cost methods producing canopy topography data. d'Oleire-Oltmanns et al. (2012) deployed a small fixed-wing platform to monitor rates of soil erosion over a 6km^2 area in Morocco, showing how small UAVs may be used to bridge the gap between field scale and satellite imagery. Szantoi et al. (2017) used a combination of UAV technology and LANDSAT 5, 7 and 8 satellite imagery for image classification to detect small-scale deforestation and degradation. However, three-dimensional structural data from drones does have some limitations. Mlambo et al., (2017) found that a poor correlation was observed between SfM tree heights and ground measured heights ($R^2 = 0.19$) due to a closed canopy structure, such that SfM failed to generate enough below-canopy ground points, presenting a challenge for detailed data acquisition by UAVs in dense tropical forests. Given these limitations, it is necessary to ground truth data acquired through UAVs in tropical forest environments.

This study aims to explore the effects of vegetation structure on microclimates within a degraded tropical forest and enable the landscape-wide prediction of microclimate within forest canopies. This required detailed and wide-ranging vegetation surveys (both field- and UAV-based) combined with *in-situ* microclimate measurements at the microhabitat scale, enabling the construction of a microclimate model that allows predictions of temperature at the scale of tens of metres. This will enable the modelling of temperature horizontally, vertically and temporally across the field site for subsequent work and provide a detailed understanding of how vegetation structure affects microclimate fluctuations.

2.2 Materials and Methods

2.2.1 Study Site

The Sikundur site, within the Gunung Leuser Ecosystem conservation area (Lat: 3.95, Long: 98.07 decimal degrees), Northern Sumatra, has been the focus of previous conservation research projects (Knop et al., 2004, Askew et al., 2016), but remains a relatively unstudied area and one of the last remaining sections of lowland forests in Sumatra.

The Gunung Leuser Ecosystem conservation area is considered one of the most important bastions of tropical biodiversity, being the only remaining area where Sumatran orang-utans (*Pongo abelli*), elephants (*Elephas maximus sumatranus*), tigers (*Panthera tigris sumatrae*), rhinos (*Dicerorhinus sumatrensis*) and sun bears (*Helarctos malayanus*) still co-exist (Hitchcock and Meyers, 2006). The Gunung Leuser Ecosystem conservation area is a significant part of the 'Tropical Rainforest Heritage of Sumatra' (TRHS), a UNESCO World Heritage site and a stronghold for Sumatran orang-utans.

The Sikundur study site itself covers ca. 15 x 7 km of the Gunung Leuser Ecosystem (Figure 2.3). The Sumatran Orang-utan Conservation Programme (SOCP) started orang-utan and habitat monitoring at Sikundur in 2012. The Sikundur area was previously known as the Sikundur Reserve (est. 1938) prior to the formation of the Taman Nasional Gunung Leuser (TNGL, est. 1980), the administrative section of the Department of Agriculture that oversees the Gunung Leuser Ecosystem. This area was selectively logged from the late 1960s, which continued and progressively intensified in some areas until the 1980s (Cribb, 1988; Wind, 1996). During the logging operations from the late 1960s until 1982, an average of 11 large trees per hectare were felled (Knop et al., 2004). Five years after the end of the logging operation, Abdulhadi et al. (1987) found that 54% of the remaining trees still showed some damage caused by the logging. Following the establishment of the TNGL, logging in the Sikundur area continued primarily at the park border. Currently, illegal logging and complete land clearing are still present near the south-eastern boundary of the Sikundur Monitoring Post at the TNGL border (Figure 2.4), in addition to more generalized illegal human extractive activities (e.g., bird trapping, damar resin extraction, hunting and fishing).

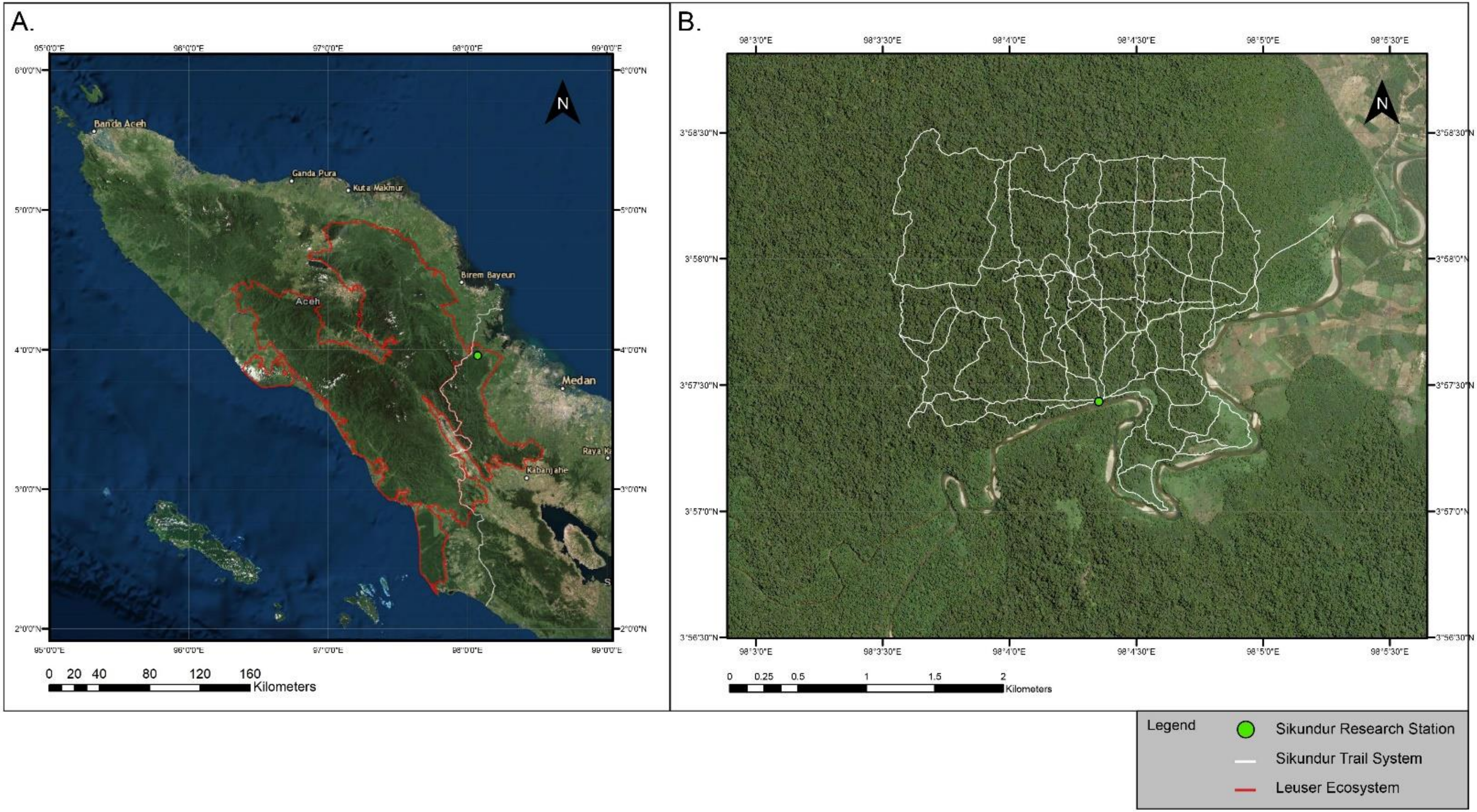


Figure 2.3 – **A**. Northern Sumatra, showing the Sikundur Research Station within the Leuser Ecosystem **B**. Sikundur Research Station and trail system

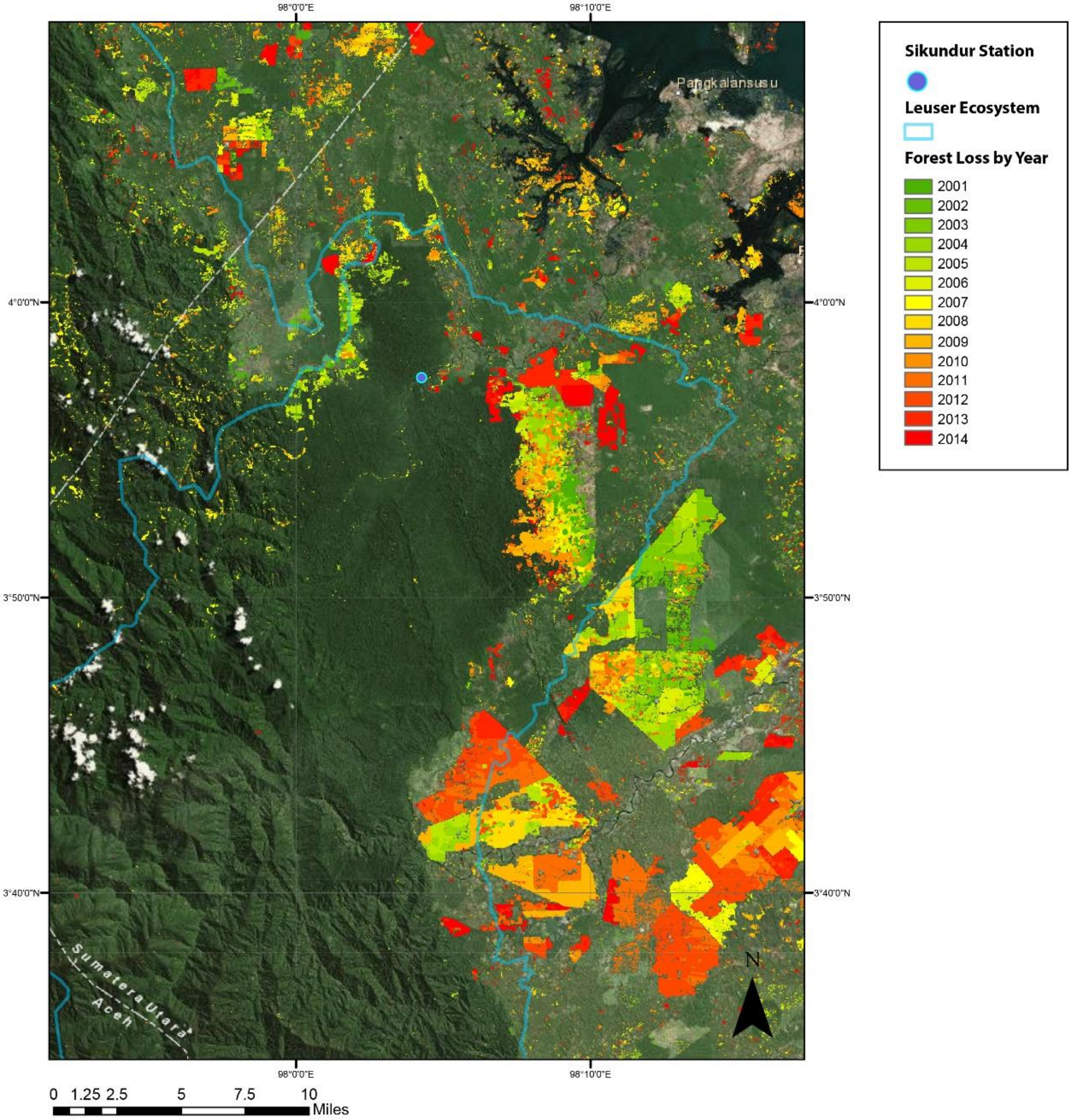


Figure 2.4. Satellite imagery of the larger Sikundur area showing the Leuser Ecosystem border and forest loss by year since 2001, adapted from Hansen et al., 2013

Climatological and phenological data collected between 2013 and 2015 by SOCP staff show average monthly temperatures at the field station as 27.4° C, with a monthly range of 26.1-29.7° C (Figure 2.5). During the observation period, temperature highs were recorded for the months of February-July, whereas temperature lows were recorded for the months of January and August-December. The average monthly rainfall was 251.7 mm, with a monthly range of 12.4 to 535.4 mm

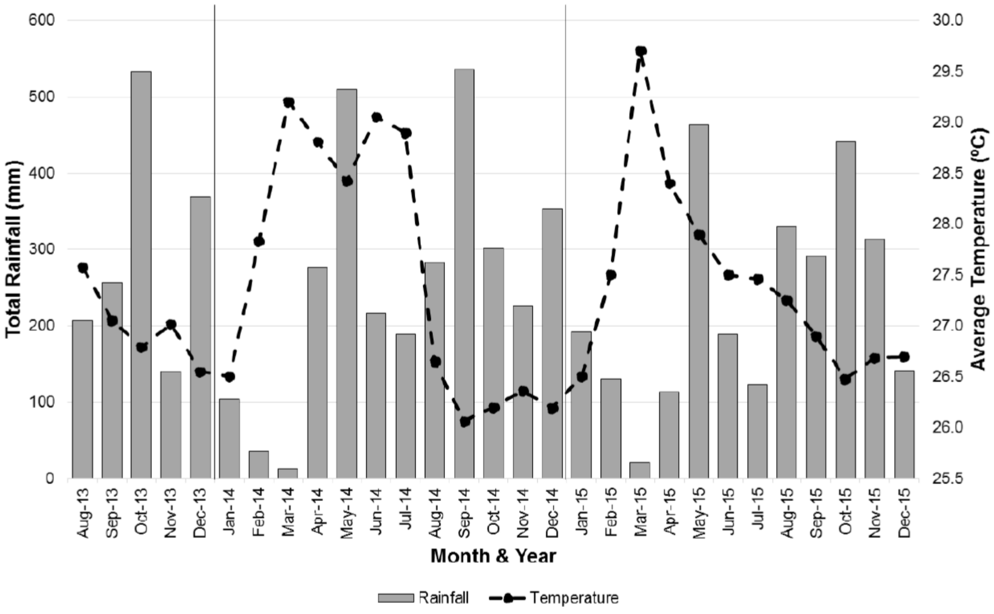


Figure 2.5. Monthly rainfall and temperature for the Sikundur Monitoring Post from August 2013 – December 2015, from Sikundur Monitoring Post Annual Report 2015 (Sumatran Orang-utan Conservation Programme, 2016).

The average percentage of liana and tree stems (>10 cm diameter at breast height) that were bearing fruit in 20 phenological plots was 2.8% for the period of June 2013 – December 2015, with a range of 0.3-13.0% (Figure 2.6). High fruiting values were generally observed during May-October; however, consistent levels of high fruit productivity were during August and September. Low fruit levels were present during January-April and November-December (Figure 2.6)

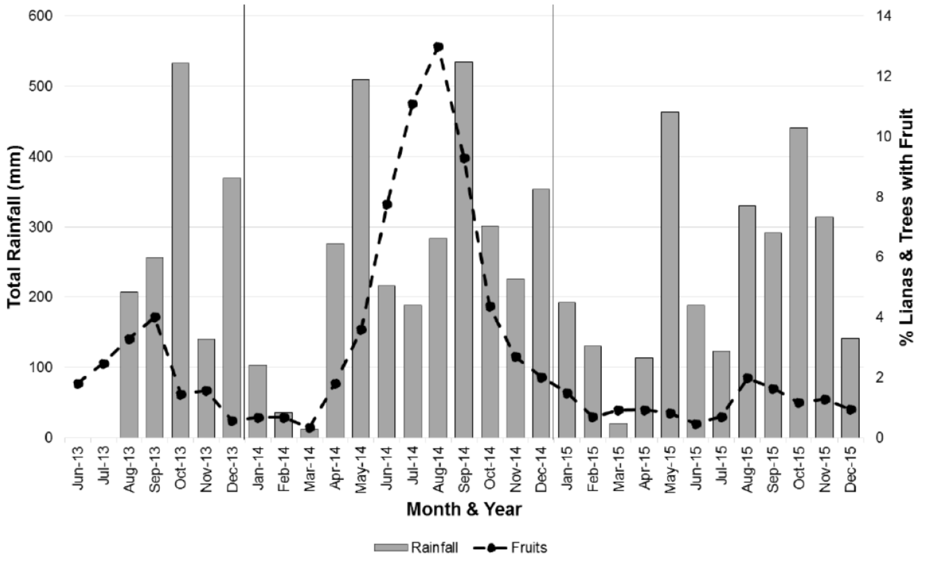


Figure 2.6. Monthly percentage of fruit availability and rainfall for the Sikundur Monitoring Post from August 2013 – December 2015, from Sikundur Monitoring Post Annual Report 2015 (Sumatran Orang-utan Conservation Programme, 2016).

The average fruiting level for Sikundur (i.e., 2.8%) falls close to the percent fruiting score range of a number of Bornean field sites (3.0-6.8%), but well below the published range of percent fruiting scores (6.9-30.57%) of two Sumatran sites, Ketambe and Suaq Balimbing (Wich et al. 2011b). The Sikundur site has lower fruit productivity than that of previously studied Sumatran orang-utan field sites, indicating either Sumatran forests are less homogenous than previously thought, or historic selective logging has had a dramatic effect on the fruit production of Sikundur.

The Sikundur area, 30–100 m above sea level, consists of diverse mixed dipterocarp lowland forests with rich alluvial forest along the rivers (de Wilde and Duyfjes, 1996). The study site covers both pristine forest and forest that was mechanically logged and then left untouched to recover. This area was included in extensive vegetation and physiography surveys by Laumonier (1997), who identified multiple forest types within the area with limited topographical variation. Further study in this diverse area presents a unique opportunity to examine the responses of multiple primate species to the effects of a gradient of anthropogenic disturbance over multiple forest types.

2.2.2 Vegetation Plots

Classifying and enumerating vegetation across large areas is prohibitively expensive for most research projects (Hummel et al., 2011). To overcome this, ecologists use more cost-effective sampling methods that can provide accurate information over large areas, such as, plots (Stohlgren and Chong, 1997, Schwarzkopf and Rylands, 1989, Ganzhorn, 1989, Southwood and Henderson, 2009), transects (Whitten, 1982, Loya, 1978), point-quarter sampling (Ganzhorn et al., 2011, Marsh et al., 2016), and line-intercept sampling (Messmer et al., 2000). In this project, given that vegetation will be compared to results derived from UAV data, randomly placed quadrats/fixed-sized plots were used (Figure 2.7). This allows for small scale, detailed vegetation data that can be extrapolated to larger scale vegetation classification by comparing variables derived from UAV data to direct measurements taken from plots of a fixed size. To explore the relationship between vegetation structure and microclimate recordings, vegetation structure was recorded in vegetation plots, following methods used by Manduell et al. (2012). Within the Sikundur study area, nine 25m x 25m plots were used to record vegetation variables across the area. Their location was randomly chosen using ArcMap (version 10.4) ('Create Random Points' function), located at least 500m apart (Figure 2.8). Multiple variables from each tree within the plot larger than 10cm in diameter as measured at breast height (1.3 metres above ground, Ganzhorn et al., 2011) were recorded. The variables measured for each tree within the plot were; diameter at breast height (DBH), tree height and height at bole (measured using a ‘Nikon Forestry Pro’ laser range finder/hypsometer using the ‘three point measurement’ mode), canopy width (measured as the distance at the cardinal compass points from the trunk which the canopy reached in metres), canopy connectivity with surrounding trees (measured as a percentage), crown shape (classified as; cone, inverted cone, spherical, elongated spherical, bent), and a branch count of the tree (classified as; number of branches >20cm, 10-20cm, 10-4cm, 2-4cm, 0-2cm in diameter). From these variables, plot level variables were derived; mean tree height, tree height range, mean bole height, mean DBH, mean crown area, mean connectivity and mean branch counts of each category.

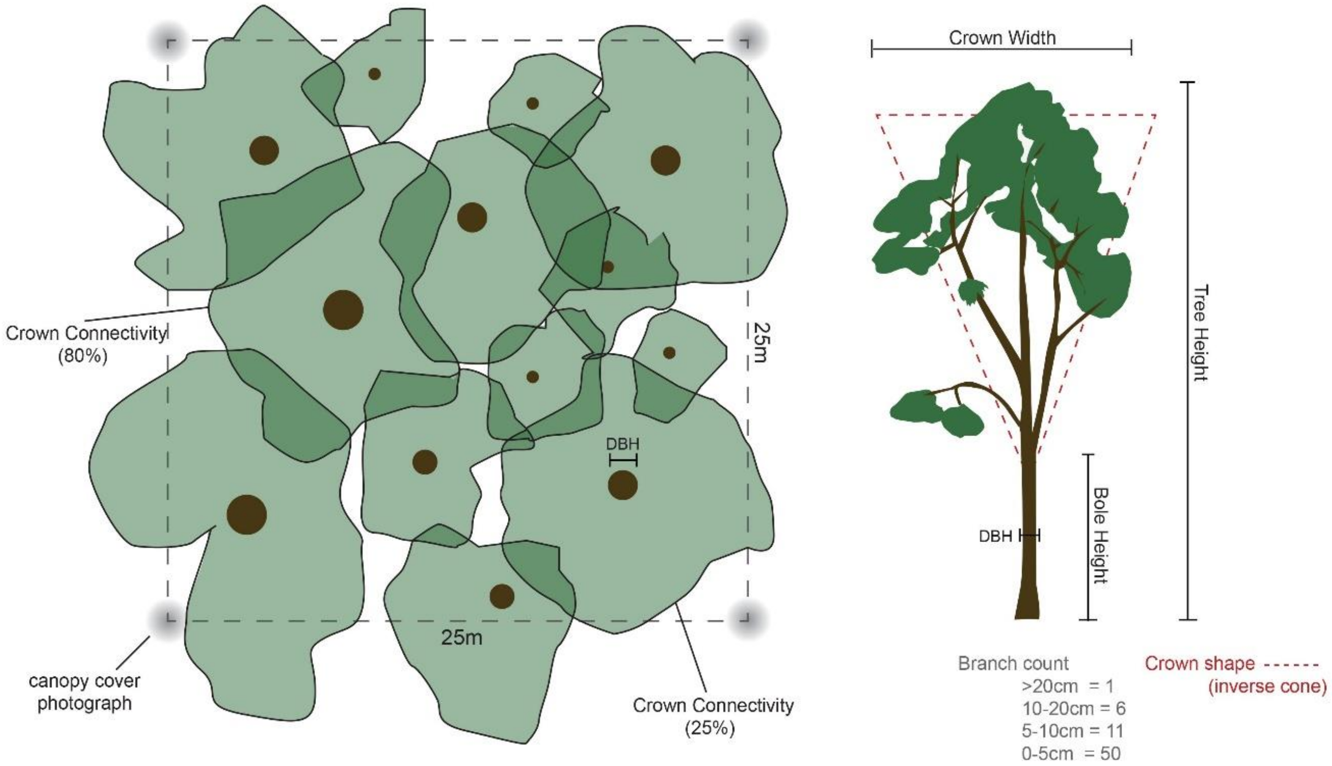


Figure 2.7. Illustrative diagram of vegetation plot variables measured

Additionally, at each corner of the vegetation plot, an indicative measure of canopy cover was acquired using a digital camera to record upwards pointing photographs, with imagery subsequently processed using CanopyDigi software (Goodenough and Goodenough, 2011) to measure canopy cover. CanopyDigi (version 1.0) assesses canopy density percentage via estimation of light penetration. This involves flexible digital image analysis of standard canopy photographs taken with a digital camera with a user-selected threshold between dark (canopy) and light (sky) areas (Figure 2.9). The threshold is selected manually due to the inability of automated algorithms to successfully determine an appropriate threshold, especially when the relative contrast between vegetation and sky changes across an image (e.g., sun-illuminated vegetation against white cloud, etc.). For a full description of the functions of CanopyDigi see Goodenough and Goodenough (2011). Digital photographs of canopy cover were processed from full colour JPEG format to the required 640x480 pixel, monochrome BMP format using ReaCovertor Pro (version 1.67), using the ‘maximum entropy’ algorithm as suggested by the program designers. Image files were processed in CanopyDigi and the resulting canopy density percentages and Morisita’s index values, a statistical measure of dispersion in which high values indicate the ‘clumpedness’ of gaps, were calculated to the mean of each plot (Figure 2.9).

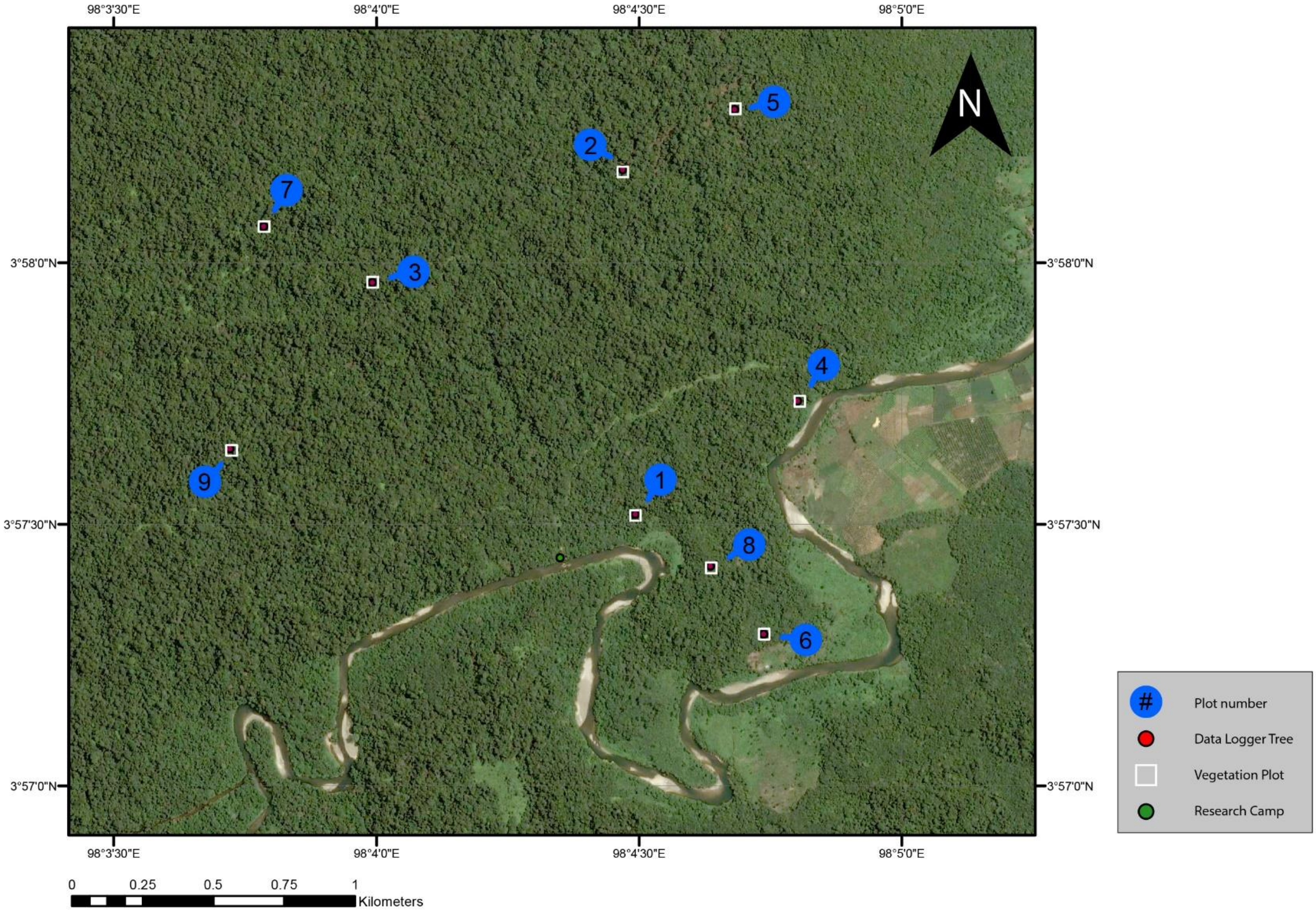


Figure 2.8 - Data logger and vegetation plot locations within Sikundur

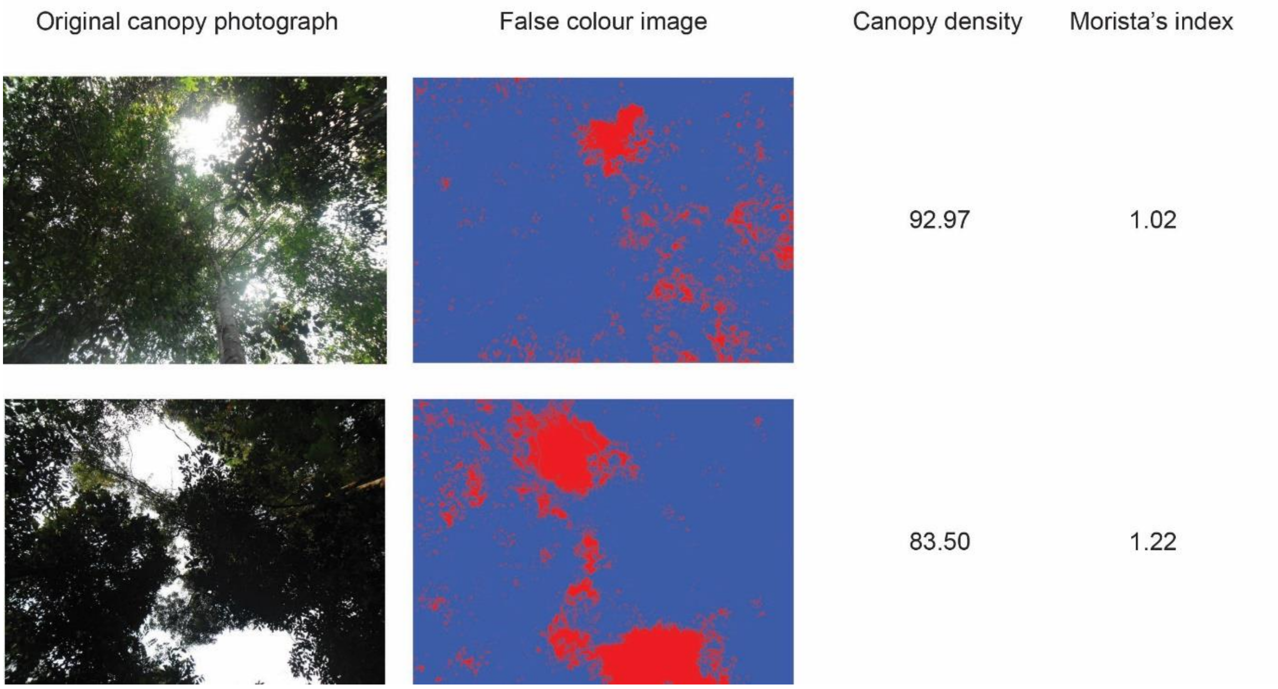


Figure 2.9 - Canopy photographs and respective false colour images and CanopyDigi analysis

2.2.3 Microclimate data loggers

To record fluctuations in microclimate and how these are affected by vegetation structure, 22 data loggers (HOBO UA-002-08 8K Pendant Temp/Light Logger), that measure temperature and luminosity at set time intervals, were placed at various tree heights within the vegetation plots to measure changes in temperature and luminosity over the study period of 6 months (Figure 2.10). These data loggers were used without solar shields and their accuracy is given by the manufacturer as ± 0.53°C within the range 0° to 50°C. The deployment of these data loggers at various heights and within areas of differing vegetation structure enabled the statistical modelling of microclimate data in relation to three-dimensional position within the forest canopy. Using this dataset of fluctuating temperatures recorded at various known positions within and below the canopy, data logger results were used to develop a model that, with sufficiently detailed and wide-ranging vegetation structure data and local weather data, allows microclimate modelling across the study site, creating an microclimate model for the entire area.

Twenty-two microclimate data loggers were placed within 9 trees, with 2-3 data loggers per tree, and one tree located in each of the nine field plots (Figure 2.8). Data loggers were placed in randomly determined trees per plot. The data loggers were placed as high as possible in each tree with another data logger placed ~1.5m from ground level. In trees with three data loggers (n=4), a second data logger was placed 7-10 vertical metres (as measured in rope length) from the topmost logger. Data loggers were programmed to record a data point (Temp/LUX) at 60-minute intervals over the study period. In total, these data loggers recorded 48,695 data points between June – November 2017.

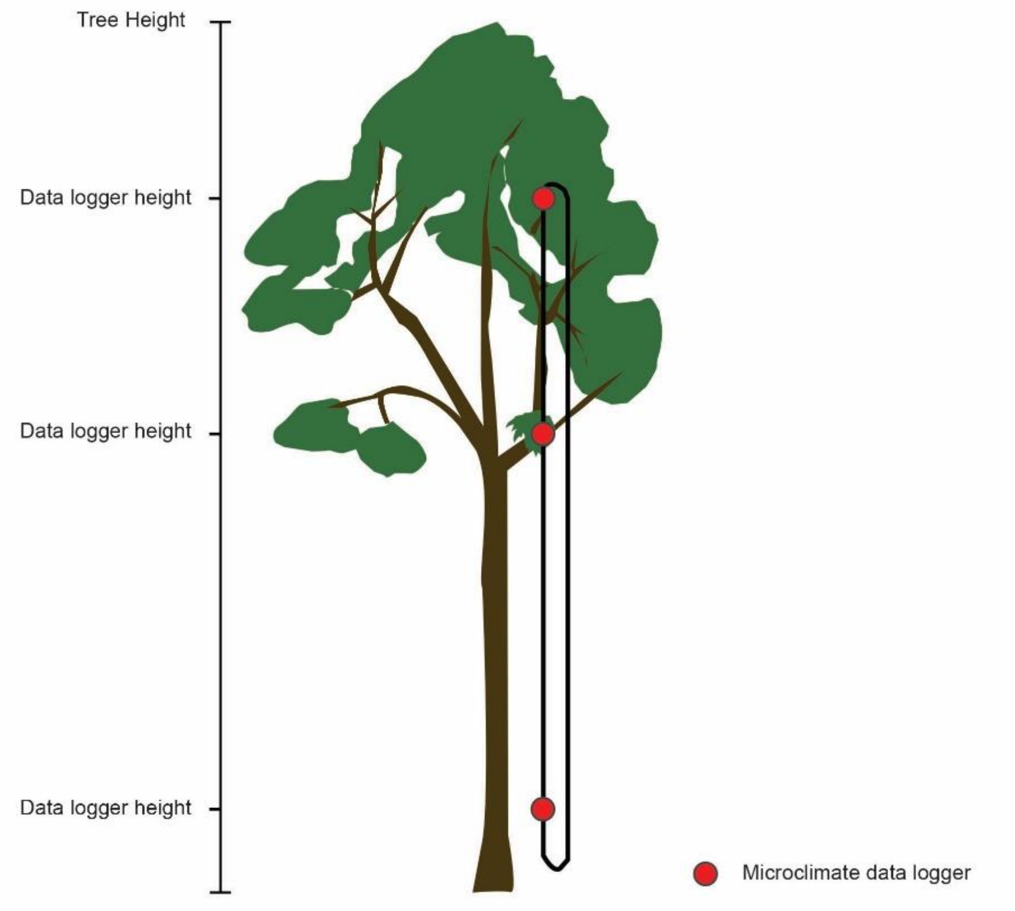


Figure 2.10 - Illustrative diagram of vertical microclimate data logger placement within trees

Additional recordings were made manually at the Sikundur research station, measuring temperature and rainfall at 6am, 1pm and 6pm using a thermometer and a rain gauge. A data logging weather station was also used at the Sikundur research station recording; temperature (°C), wind chill (°C), dew point (°C), humidity (%), relative pressure (hpa), absolute pressure (hpa), wind speed (km/h), gust speed (km/h), wind direction, rain fall (mm/hr) every hour and daily rainfall (mm/24hr) measured between 12:01am and 11:59pm.

Daylight cloud cover for each hour of data logger recording time was determined by calculating the mean LUX readings of all data loggers for each hour of each day and dividing this by the maximum of the same variable, or:

$$\text{daylight cloud cover} = 1 - \left(\frac{\text{Mean of data loggers LUX hourly recording (single day)}}{\text{Max of mean data logger LUX hourly recording (total)}}\right)$$

For example;

$$1 - \left(\frac{\text{8,688.5 (1pm 1st of August 2017 mean LUX}}{\text{31,614 (1pm max of mean LUX)}}\right) = 59\%\ \text{cloud cover}$$

2.2.4 Unmanned Aerial Vehicles

To record aerial imagery of the study site, a fixed-wing Unmanned Aerial Vehicle (UAV) was used. The modified “Skywalker” UAV (see Figure 2.11), was controlled manually (i.e. radio controlled) for take-off and landings and switched to autopilot to fly along pre-set “lawnmower” routes programmed using Mission Planner software (see Figure 2.12). To enable the capture of imagery, a digital camera (SONY RX100 mk4) took RGB photographs at GPS locations controlled by the autopilot and a Seagull #MAP 2 switch, programmed via MissonPlanner software (version 1.3.58), ensuring 80% overlap of each photograph, both in the direction of drone travel and between flight paths (known as ‘sidelap’). To ensure the accuracy of these photograph locations, the photographs taken by the UAV were time-matched with the GPS locations of the UAV during flight, downloaded from the autopilot log file, and ‘geotagged’ using ExifToolGui software (version 5.14), pairing GPS locations with individual photographs, refining the preset locations of image capture set using MissonPlanner software. Eleven mapping flights over the Sikundur area were flown between June 13th – 16th 2017 covering a total area of ~26km^2. In total, 4811 geotagged images were then processed in Agisoft Photoscan software (version 1.2.0.2152) using ‘Structure-from-Motion’ (SfM) (Cunliffe et al., 2016).

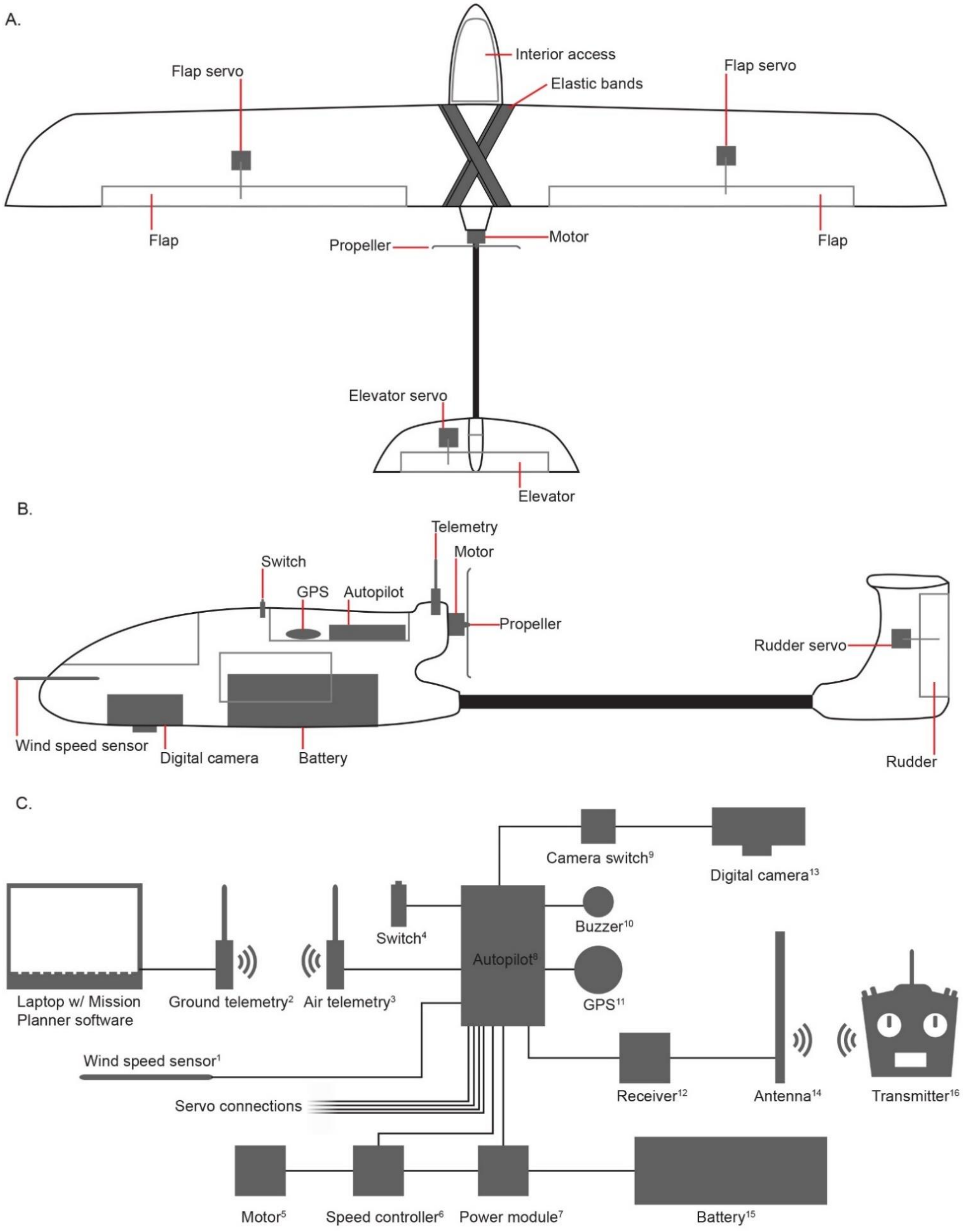


Figure 2.11. **A.** Top down view of modified the “Skywalker” fixed-wing UAV used with major parts labelled **B.** Side view of the UAV with major parts labelled **C.** Illustrative wiring diagram of components [1] HK Pilot Analog Air Speed Sensor And Pitot Tube Set [2] RFD 800 - 900mhz Ultra long-range radio modem [3] Micro HKPilot Telemetry with Integrated PCB Antenna 915Mhz [4] E-Switch safety switch button (inc. w/Fixhawk) [5] SunnySky 2820 800 kv [6] TURNIGY Plush 60amp Speed Controller [8] Fixhawk autopilot [9] Seagull #MAP 2 [10] 30mm Buzzer (inc. w/Fixhawk) [11] UBLOX Micro M8N GPS Compass Module [12] RFDANT 900 receiver[13] Sony RX100 mk4 [14] Flex1 902-928 MHz ISM Band Antenna [15] Multistar High Capacity 10000mAh 4S 12C LipPo Pack [16] Futaba T8J 8 Channel Digital Proportional Radio Control System

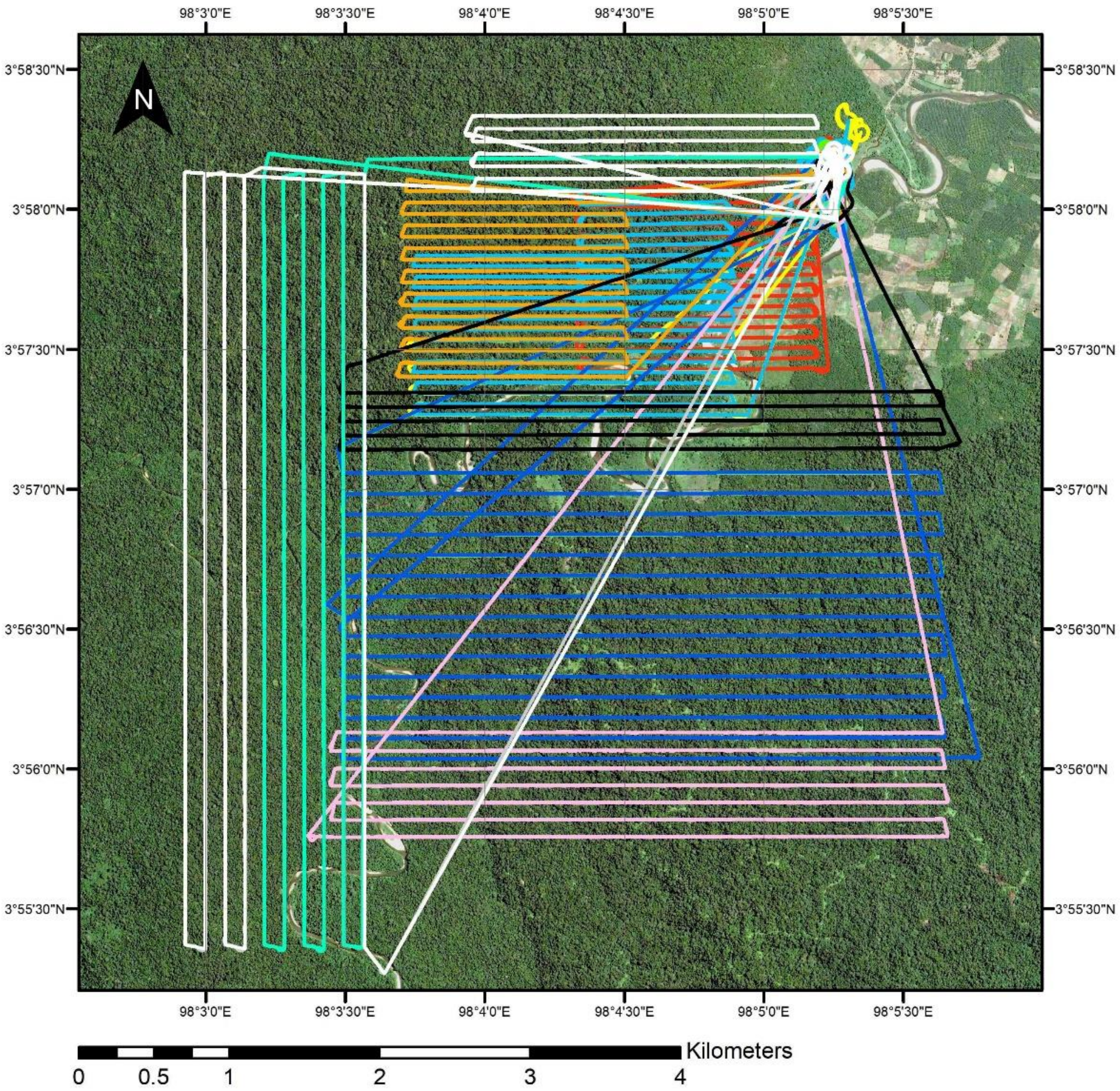


Figure 2.12 - UAV flight paths over the Sikundur area flown between June 13th – 16th with each flight shown in a separate colour

Due to the large size of the area and high tree coverage, ground control points (GCPs) were not used during flights or processing. Instead, camera position and scene geometry were reconstructed simultaneously by Agisoft Photoscan software through the automatic identification of matching features in multiple images. These tie points (n = 1,631,784), such as corner points (edges with gradients in multiple directions), were tracked from image to image, enabling initial estimates of camera positions and object coordinates, which were then refined iteratively using non-linear least-squares minimisation (Snavely, 2008) producing a 'dense' point cloud (Turner et al., 2012). The resulting point cloud had an average of 15.2 points per metre squared or a total of 879,189,006 points. From the dense point cloud a mesh was created, a featureless three-dimensional polygonal model, onto which textures are then reprocessed, reforming the original photographs onto the three-dimensional model. Only one of the products of this process is used in further analysis; a Digital Surface Model (DSM) giving surface elevation (i.e. elevation above sea level of the tallest surface features, such as tree crowns, as opposed to a Digital Terrain Model [DTM] giving ground elevation). The resulting DSM had a resolution of 25.7 cm^2 per cell, resulting in a GeoTiff DSM 24,525 x 25,576 cells in size. Total processing time was 211 hours.

Using the resulting DSM, incoming solar radiation was estimated across the forested study site using the Potential Incoming Solar Radiation tool in System for Automated Geoscientific Analyses (SAGA) software (version 2.3.2) (Conrad et al., 2015). This allowed for the estimation of incoming solar radiation, measured in kWH/m^2, hitting the site with hourly increments to match the data recording regime of the microclimate data loggers. These hourly increments of solar radiation (from 6am – 7pm) were then calculated for a single day each month (the 16th) for June – November 2017, adjusting monthly values as the sun's zenith changed though the months.

To allow direct comparison to vegetation plots and to account for inaccuracies in GPS locations of data logger sites and XYZ error in the DSM, both the DSM and the Potential Incoming Solar Radiation layers were aggregated to a spatial resolution of 25m before data were extracted for use in microclimate modelling. The DSM was aggregated to produce eight separate variables, namely: 'max' (maximum elevation within the aggregated 25m spatial resolution), 'min' (minimum elevation within the aggregated 25m spatial resolution), 'median' (median elevation within the aggregated 25m spatial resolution), 'mean' (mean elevation within the aggregated 25m spatial resolution), 'range' (range of elevations within the aggregated 25m spatial resolution), 'standard deviation' (standard deviation of elevations within the aggregated 25m spatial resolution), 'mean 3x3' (mean elevation within an aggregated 75m spatial resolution) and 'relative height' (mean elevation within an aggregated 75m spatial resolution minus the mean elevation within 25m spatial resolution).

These values were then extracted from the aggregated grids at the locations of each data logger using ArcGIS (version 10.4).

Similarly, results of the Potential Incoming Solar Radiation analyses were aggregated to a spatial resolution of 25m and extracted, with separate layers created for each hour of the day (7am-7pm) and each month (June – November 2017) for a total of 72 layers, with only the pertinent layer matched to the data logger data point and extracted (i.e. a data logger reading at 3pm in August was matched with the same Potential Incoming Solar Radiation layer and the aggregate value extracted).

2.2.5 Statistical analyses

Multiple linear regressions were used to predict vertical temperature gradients within the forest canopy by comparing the difference between top-most and bottom-most data logger recorded temperatures with plot level vegetation variables (mean DBH, mean tree height, mean bole height, mean number of branches >20cm in diameter, mean number of branches between >20-10cm in diameter, mean number of branches >10-4cm in diameter, mean number of branches >4-2cm in diameter, mean number of branches >2-0cm in diameter, mean connectivity, and canopy density and Morisita’s index) (Blok et al., 2011. Multiple linear regressions were also used to predict temperature using plot level vegetation variables (as listed above), as well as canopy structure variables derived from UAV surveys (‘max’, ‘min’, ‘median’, ‘mean’, ‘range’, ‘standard deviation’, ‘mean 3x3’ and ‘relative height’), the product of potential incoming solar radiation analysis (kWH/m^2), local weather variables collected at the site using a weather station (minimum temperature, daily rainfall, cloud cover), and LUX measurements from data loggers (Bottyan and Unger, 2003). The best predictors were selected based on their significance (p-value) and effect on model power when removed (adjusted R^2 of model).

Before the models were run, plot level vegetation variables, UAV derived canopy structure variables, potential incoming solar radiation and local weather variables were checked for multicollinearity using Pearson’s correlation. Variables found to be significantly correlated ($p < 0.05$, R^2 =>0.35) were removed from the analysis. Residual errors of this analysis were tested for normality using the Kolmogorov-Smirnov test in order to check the assumptions of general linear models, and the residual errors were found to be normally distributed. Vegetation structure differences between plots were tested using a Kruskal-Wallis test. All statistical analyses were performed with R (version 3.4.1) using R studio (version 1.0.153).

2.3 Results

2.3.1 Vegetation plots

A total of 249 trees were measured over 9 vegetation plots. DBH ranged from 10 to 110cm, tree height from 5-38m, bole height from 0.5-31m and crown area between 1.9-212.5m^2 (Figures 2.13a-2.13b). Variables associated with high plot level biomass, and therefore the presence of old-growth forest, (DBH, Tree height, Crown area, Frey et al., 2016) showed a strong relationship (DBH ~ Tree Height, $\beta = 1.85$, $R^2 = 0.517$, $p=<0.005$, DBH ~ Crown area, $\beta = 0.37524$, $R^2 = 0.518$, $p=<0.005$, Tree Height ~ Crown area, $\beta = 0.12237$, $R^2 = 0.361$, $p=<0.005$ area, Figure 2.14). Nearly all structural vegetation variables were significantly different between vegetation plots (Tree Height, K-W: χ 2 = 29.178, df = 9, p = < 0.001, Crown Area, K-W: χ 2 = 20.678, df = 9, p = 0.008, Connectivity K-W: χ^2 =45.07, df = 9, p < 0.001, Branches >Diam.20cm , K-W: χ^2 = 15.497, df = 9, p = 0.050, Branches Diam.2-4cm , K-W: χ^2 = 16.557, df = 9, p = 0.035, Branches Diam.2-0cm , K-W: χ^2 = 29.481, df = 9, p <0.001, see Figure 2.13a, 1.13b). DBH measurements were found to be statistically similar across vegetation plots (K-W: χ^2 = 5.739, df = 9, p = 0.67). Some sites had signs of historic logging (i.e. tree stumps, cut sections of tree), but these were unquantifiable, as leaf litter decomposition made the assessment of their abundance within a given area unreliable.

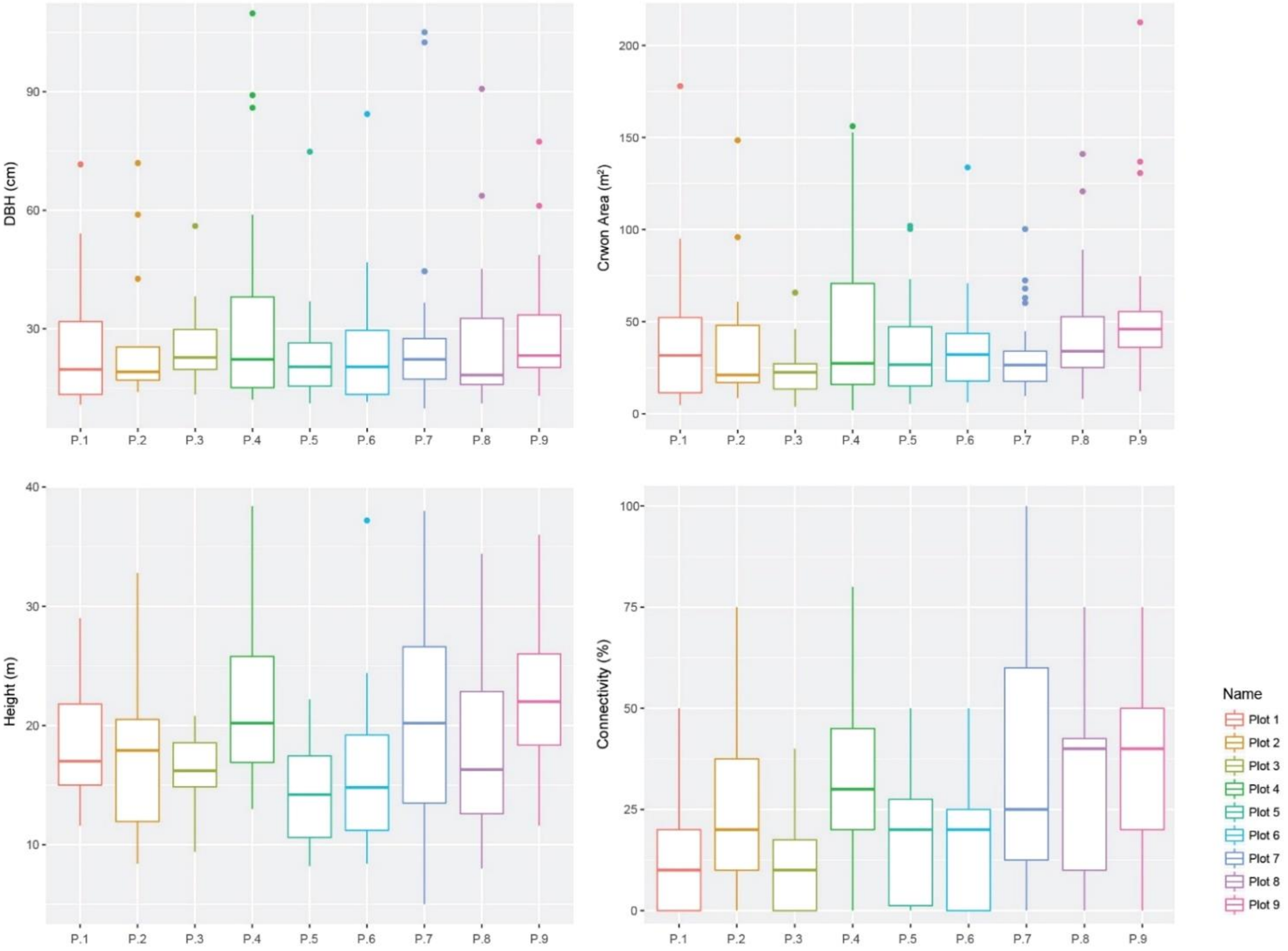


Figure 2.13a - Vegetation plot measurements

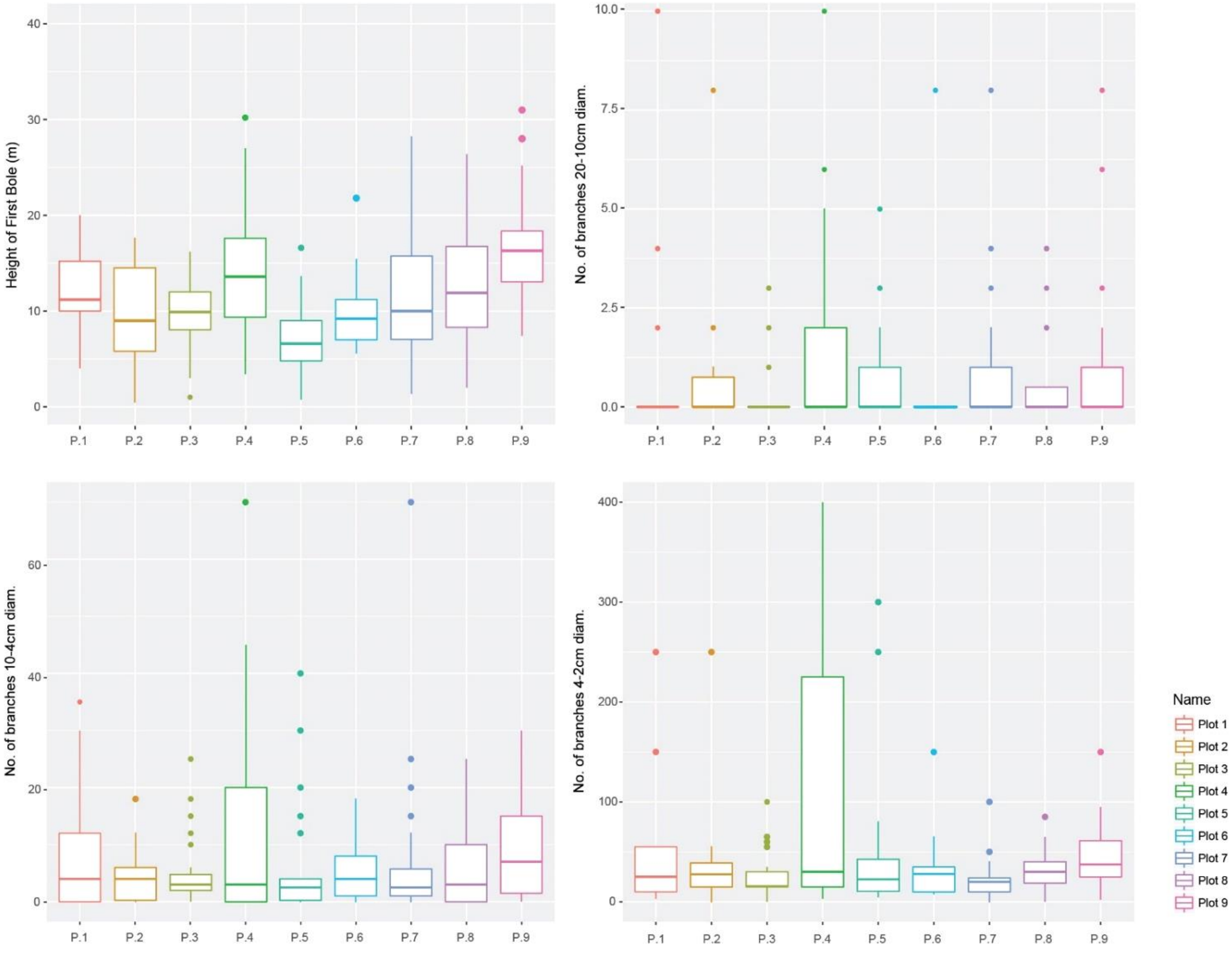


Figure 2.13b - Vegetation plot measurements

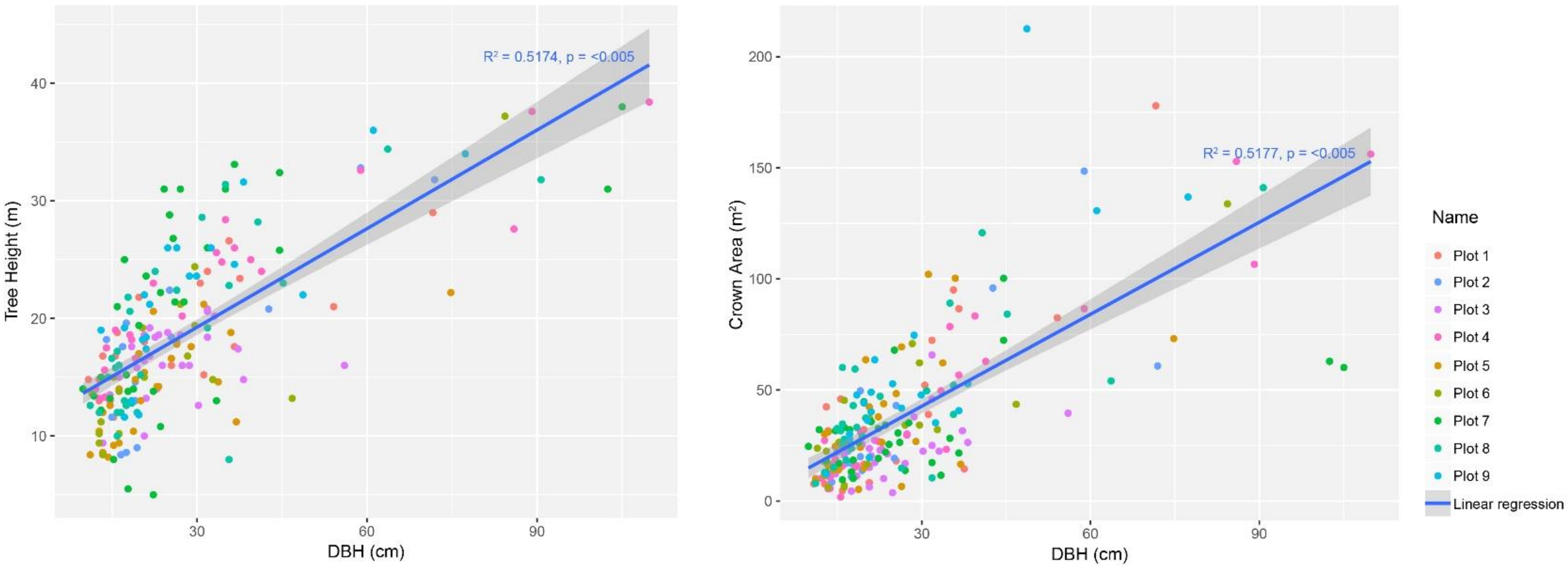


Figure 2.14 - The relationships between DBH and tree height (m) and DBH and crown area(m^2) vegetation variables measured in plots

2.3.2 Microclimate recordings

Temperatures recorded by microclimate data loggers (n = 20, n = 2 failed) ranged from 21.28°C to 43.11°C, with the mean temperature across all time periods being 26.20°C, based on 48,695 data points recorded between June to November 2017 (Figure 2.15).

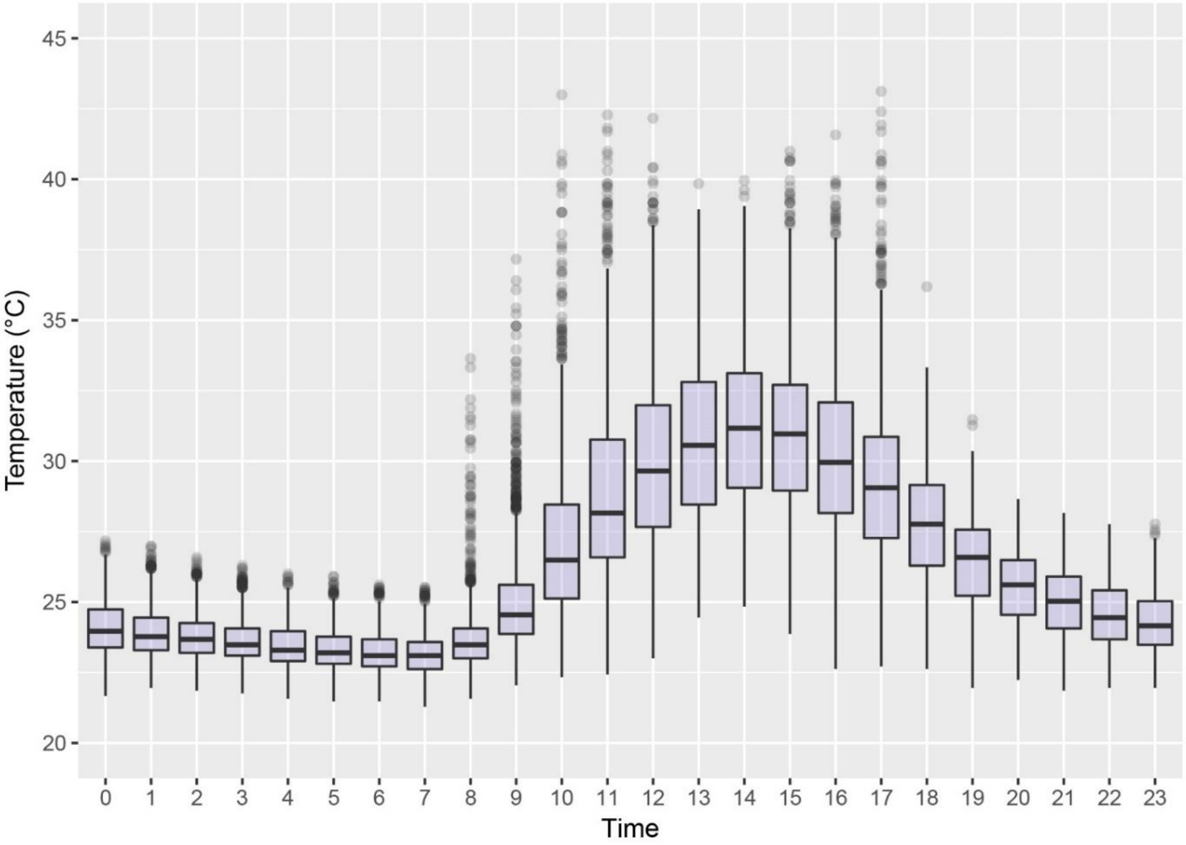


Figure 2.15 – Temperatures recorded by microclimate data loggers from June to November 2017 by hour

Data loggers were placed at various heights within trees, from 1 to 31m above the ground; logger height was to be significantly correlated to the mean temperature recorded by the data logger (Logger Height, $\beta = 0.064$, $p = 0.0026$, $r = 0.61$, $df = 20$), showing a vertical temperature gradient with height. Data loggers recorded a wide range of temperatures simultaneously, with recordings at the same hour of the day varying by as much as 15.2°C between data loggers recording at different locations (e.g. 21/06/2017, 11:00am, data logger "1a": 42.3°C, data logger "8c": 27.1°C). Across all data loggers the hottest part of the day on average was 2pm, (range of means from 33.8°C [data logger "1a"] to 27.5°C [data logger "8c"]) although temperature peaks on individual days ranged from 9am to 5pm (see Figure 2.16a, 2.16b), suggesting that the degraded Sikundur forest is a climatically dynamic environment.

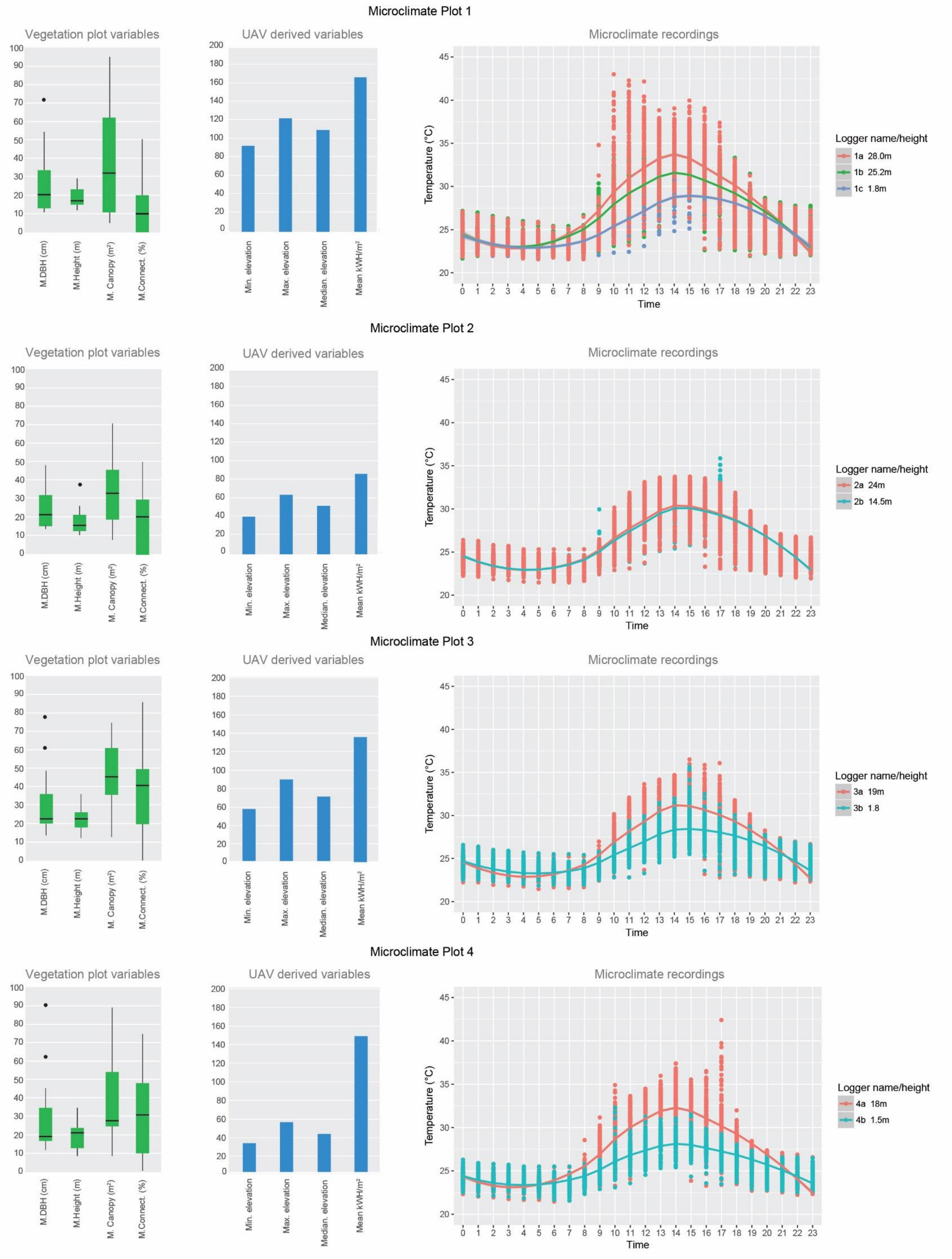


Figure 2.16a – Details of each microclimate plot variables recorded, including data from vegetation plots, UAV surveys and microclimate measurements

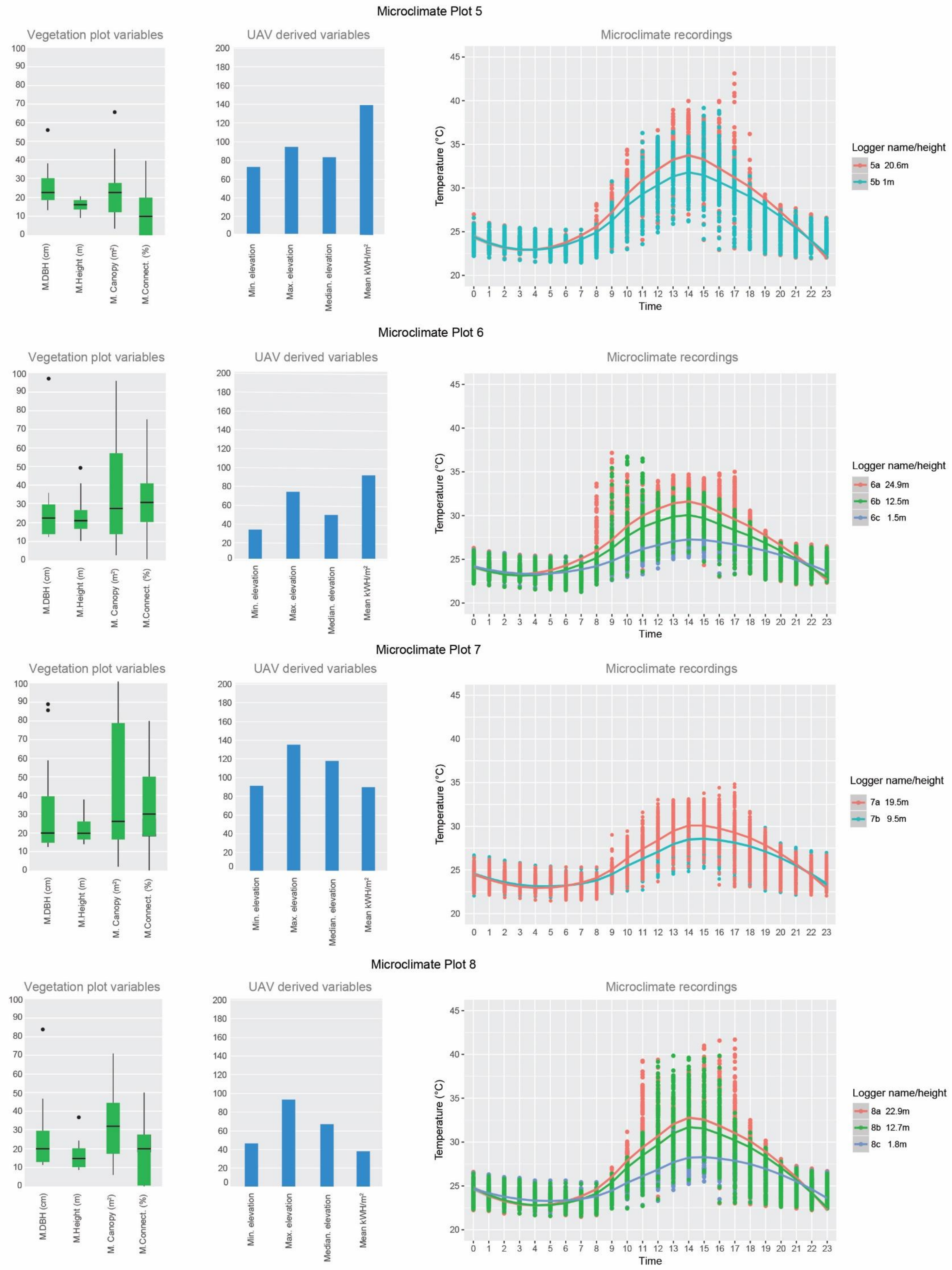


Figure 2.16b – Details of each microclimate plot variables recorded, including data from vegetation plots, UAV surveys and microclimate measurements (Plot 9 not shown as 2nd logger failed)

2.3.3 Vegetation structure effect on temperature gradients

To establish whether a relationship existed between vegetation plot variables and vertical temperature gradients (i.e. the difference between simultaneously recorded temperatures from the top-most data logger and the bottom-most data logger), multiple linear regressions were performed. Vertical temperature gradients had a significant relationship (at $p < 0.05$) to plot level vegetation structure (Table 2.1). Mean bole height, mean canopy area and ‘mean number of branches >10cm in diameter’ (summarised from ‘mean number of branches >20cm in diameter’ and ‘mean number of branches 10-20cm in diameter to avoid multicollinearity) were all significantly related to temperature gradients. However, the time of day and weather conditions affected how vegetation plot structure impacted upon vertical temperature gradients. During hours with large ranges of temperature gradients (11am – 1pm), vegetation structure had a strong impact, as shown in large r-squared values. In hours with low variation in vertical temperature gradients (7- 8am, 4-7pm) plot-level vegetation structure had less impact, as shown by low r-squared values (Table 2.1, Figures 2.17 and 2.18).

To explore the effects of local weather conditions on vertical temperature gradients, data logger recordings were separated into temperatures recorded in high cloud cover (≥75% cloud cover) and low cloud cover (≤25% cloud cover) (see section 1.2.3). Vertical temperature gradients were greater in low cloud cover, and resulted in higher r-squared values (for example; at 12pm R^2= 0.265 in high cloud cover, R^2 = 0.604 in low cloud cover, Table 2.1, Figure 2.18), suggesting vegetation structure has a larger impact on temperature gradients when solar radiation is not blocked by cloud cover. Data logger recordings in high (≥75%) cloud cover showed a reduced impact of vertical temperature gradients, although the effects of vegetation structure were still significant (Table 2.1, Figure 1.17). Additionally, in low cloud cover, vertical temperatures reached their maximum gradient earlier in the day than in cloudy conditions (12 noon as opposed to 1pm).

Table 2.1 - Results of multiple linear regressions detailing the best fit models of the effects of vegetation variables on vertical temperature gradient in high and low cloud cover by hour, using non-correlated variables (grey highlighted lines for readability only)

The effect of vegetation structure on temperature gradient with high cloud cover ($\geq 75\%$)

	7am			8am			9am			10am			11am			12pm			1pm		
Variable	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p
Intercept	-1.069	-5.701	<0.001	0.206	2.922	0.004	1.815	6.606	<0.001	4.522	7.025	<0.001	5.610	6.948	<0.001	5.769	6.758	<0.001	8.555	7.155	<0.001
Mean Bole Height	0.116	8.324	<0.001				-0.169	-6.438	<0.001	-0.366	-6.009	<0.001	-0.466	-6.440	<0.001	-0.489	-6.400	<0.001	-0.808	-5.632	<0.001
Mean Canopy Area	-0.008	-3.400	<0.001	0.006	-3.938	0.000							0.016	2.328	0.021	0.035	4.706	<0.001	0.045	6.749	<0.001
Mean no. branch >10cm				0.133	3.042	0.003	0.646	7.121	<0.001	0.815	3.804	<0.001	1.116	4.144	<0.001	1.572	5.555	<0.001	1.914	6.598	<0.001
Mean Connectivity	-0.009	-3.086	0.002	-0.009	-4.627	<0.001													0.034	1.996	0.0472
Res. Stand. Error.	0.239			0.235			0.413			0.935			1.079			1.150			1.092		
Adjusted R^2	0.264			0.167			0.234			0.159			0.205			0.265			0.3673		
degrees of freedom	215			219			219			207			196			200			213		
p-value	<0.001			<0.001			<0.001			<0.001			<0.001			<0.001			<0.001		

	2pm			3pm			4pm			5pm			6pm			7pm		
Variable	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p
Intercept	9.311	9.198	<0.001	4.806	3.816	<0.001	4.515	4.058	<0.001	2.253	2.986	0.003	0.036	0.281	0.779	0.022	0.223	0.824
Mean Bole Height	-0.889	-7.291	<0.001	-0.468	-3.121	0.002	-0.445	-3.306	0.001	-0.213	-2.697	0.008						
Mean Canopy Area	0.042	6.541	<0.001	0.054	6.886	<0.001	0.025	3.567	<0.001	0.012	2.303	0.022						
Mean no. branch >10cm	1.602	5.701	<0.001	4.446	4.324	<0.001	0.630	2.003	0.046							-0.333	-3.270	0.001
Mean Connectivity	0.054	3.657	0.003	0.039	2.154	0.032	0.044	2.716	0.007	0.031	3.079	0.002	0.021	3.911	<0.001	0.018	5.008	<0.001
Res. Stand. Error.	1.077			1.260			1.123			0.902			0.736			0.496		
Adjusted R^2	0.333			0.206			0.084			0.056			0.060			0.119		
degrees of freedom	218			215			221			215			223			248		
p-value	<0.001			<0.001			<0.001			<0.001			<0.001			<0.001		

The effect of vegetation structure on temperature gradient with low cloud cover ($\leq 25\%$)

	7am			8am			9am			10am			11am			12pm			1pm		
Variable	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p
Intercept	-0.413	-2.213	0.2795	4.961	4.679	<0.001	8.867	6.866	<0.001	8.862	7.102	<0.001	14.309	10.740	<0.001	13.606	10.460	<0.001	10.220	12.69	<0.001
Mean Bole Height	0.061	3.074	0.002	-0.457	-4.890	<0.001	-1.001	-6.285	<0.001	-0.900	-5.705	<0.001	-1.747	-10.300	<0.001	-1.613	-9.843	<0.001	-0.826	-10.685	<0.001
Mean Canopy Area	-0.004	-3.167	0.002	0.050	5.401	<0.001	0.049	5.011	<0.001	0.025	2.629	0.009	0.129	12.480	<0.001	0.128	12.929	<0.001	0.040	6.328	<0.001
Mean no. branch >10cm							3.469	7.361	0.010	3.634	8.008	<0.001	5.161	10.830	<0.001	5.026	10.687	<0.001	2.613	11.65	<0.001
Mean Connectivity	-0.012	-4.987	<0.001				0.051	2.616	<0.001	0.057	3.000	0.003	0.120	5.800	<0.001	0.104	5.230	<0.001			
Res. Stand. Error.	0.201			1.642			1.594			1.467			1.522			1.471			1.043		
Adjusted R^2	0.158			0.185			0.298			0.278			0.587			0.604			0.5075		
degrees of freedom	215			217			216			205			202			199			211		
p-value	<0.001			<0.001			<0.001			<0.001			<0.001			<0.001			<0.001		

	2pm			3pm			4pm			5pm			6pm			7pm		
Variable	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p	β	t	p
Intercept	13.034	14.395	<0.001	10.042	8.324	<0.001	13.852	9.607	<0.001	19.830	11.165	<0.001	0.910	2.015	0.045	0.167	1.281	0.202
Mean Bole Height	-0.981	-11.315	<0.001	-0.956	-6.301	<0.001	-1.201	-6.695	<0.001	-1.980	-8.984	<0.001						
Mean Canopy Area	1.017	2.581	0.011	0.048	5.183	<0.001	0.031	2.889	0.004	0.055	4.025	<0.001	0.030	3.502	<0.001	0.012	3.766	<0.001
Mean no. branch >10cm	2.312	9.337	<0.001	2.900	6.187	<0.001	2.464	4.567	<0.001	4.128	6.426	<0.001	0.544	2.130	0.034			
Mean Connectivity				0.053	2.889	0.004	0.054	2.478	0.014	0.123	4.590	<0.001	0.030	2.368	0.019	0.022	5.004	<0.001
Res. Stand. Error.	1.153			1.412			1.722			2.210			1.474			0.566		
Adjusted R^2	0.401			0.256			0.200			0.282			0.061			0.123		
degrees of freedom	217			224			218			214			213			214		
p-value	<0.001			<0.001			<0.001			<0.001			<0.001			<0.001		

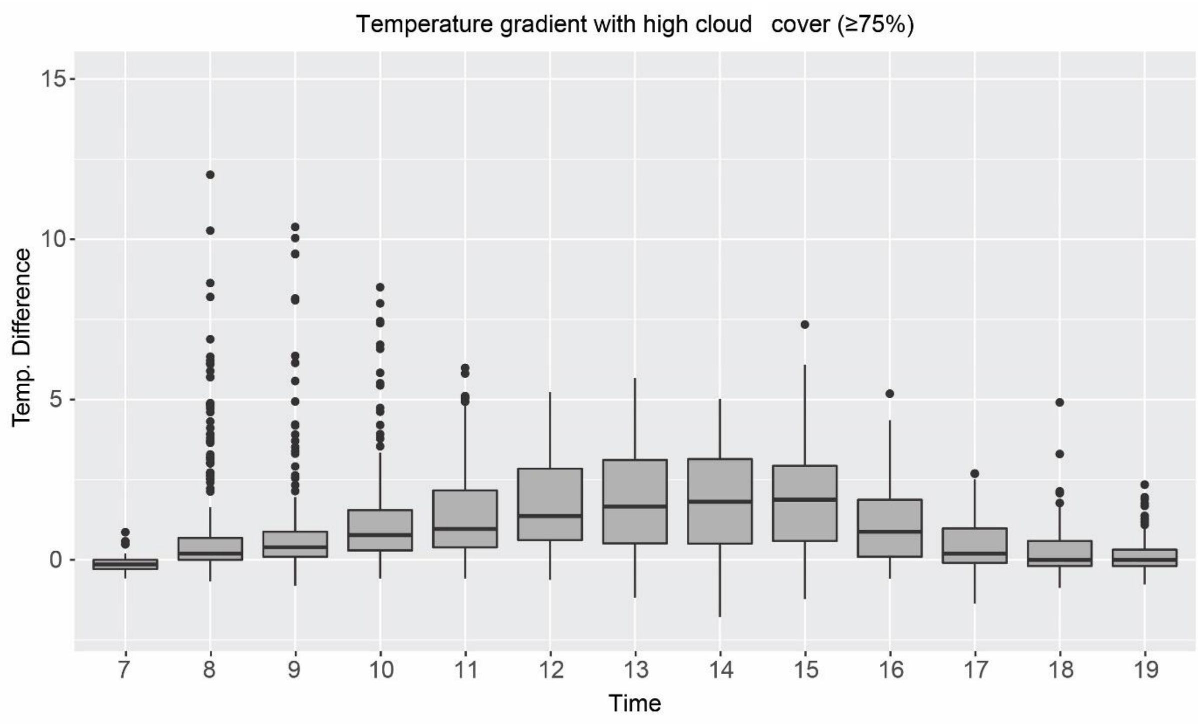


Figure 2.17 - Temperature difference (°C) between top-most and bottom-most data loggers in same trees under high cloud cover

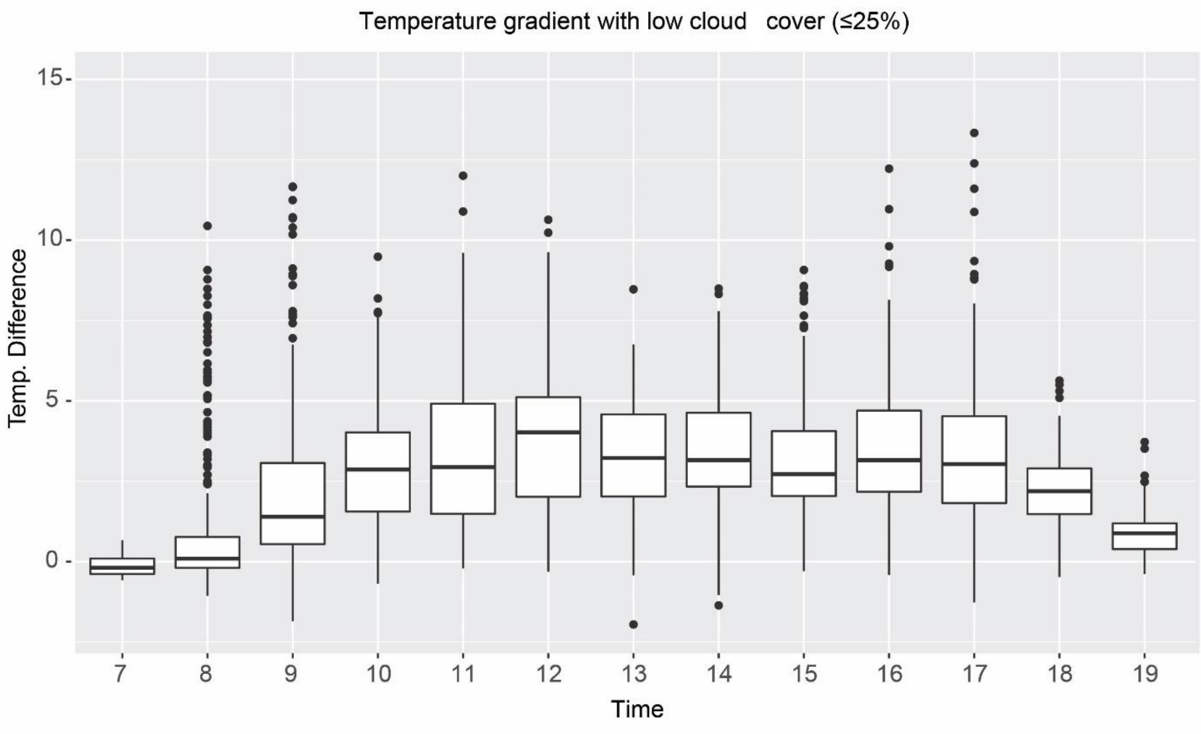


Figure 2.18 - Temperature difference (°C) between top-most and bottom-most data loggers in the same tree in low cloud cover

Mean values for vertical temperature gradient are related, but not significantly, with the height difference between high and low data loggers per tree (Figure 2.19). This suggests that vegetation structure variables (in addition to vertical distance) govern temperature gradients. Temperature gradients are altered across weather conditions and between day and night, with temperature gradients at their most extreme in low cloud cover, and most similar at night with some inverse temperature gradients, meaning the top-most data logger records lower temperatures than the bottom-most logger, suggesting some temperature retention occurs closer to the ground at night.

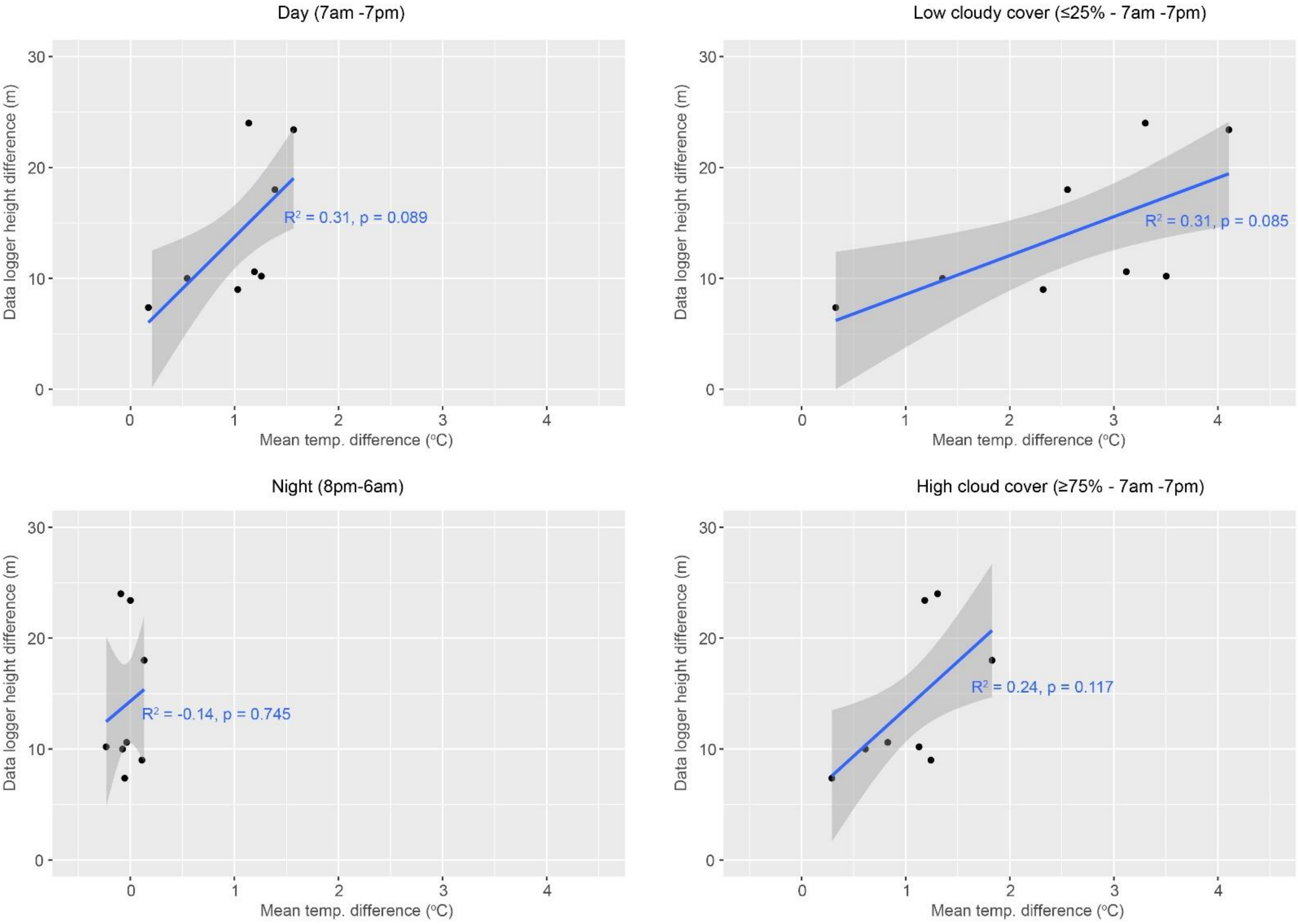
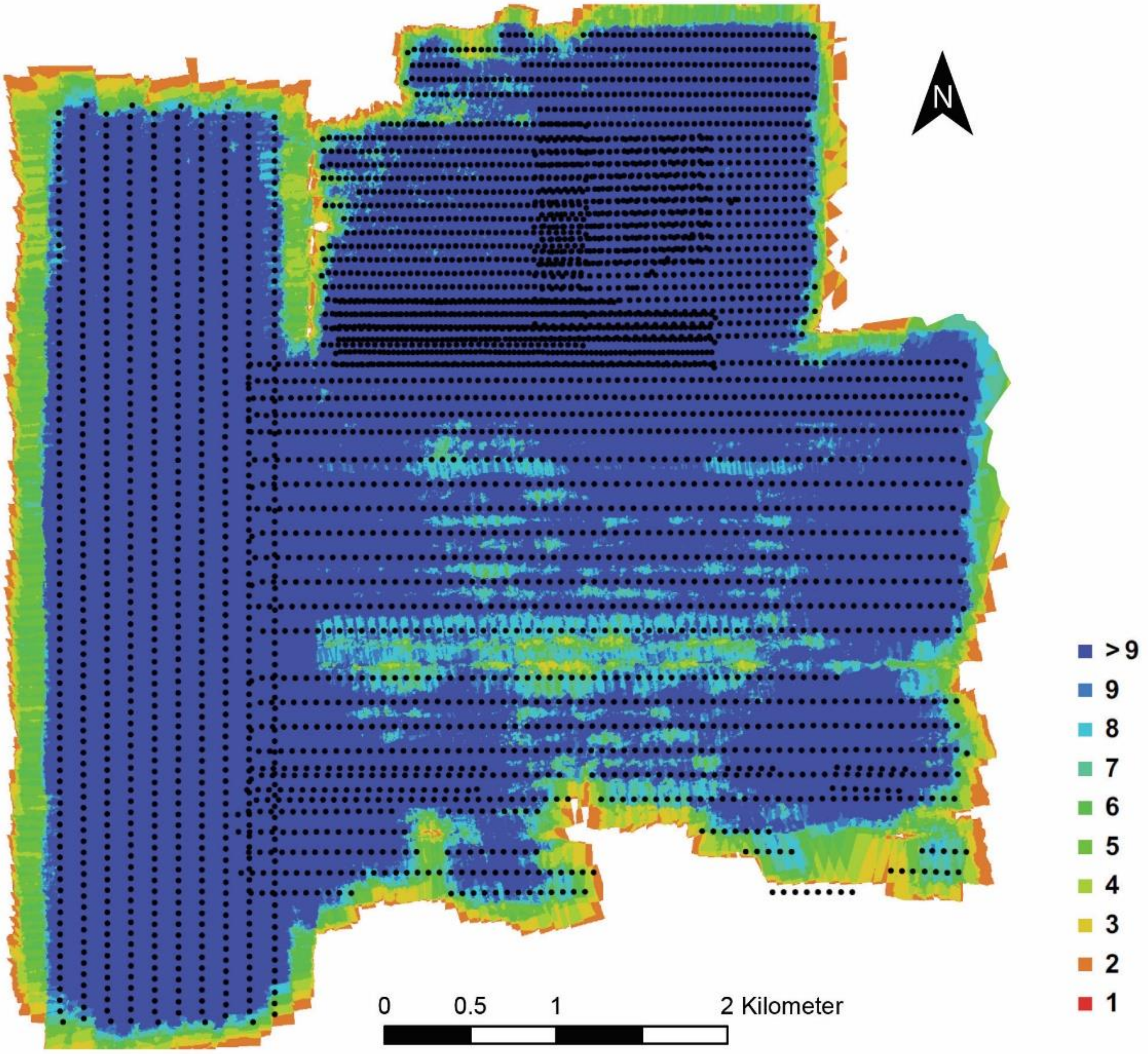


Figure 2.19 - Data logger height difference compared to mean temperature gradients in different weather and light conditions

2.3.3 UAV surveys

The initial processing of 4811 UAV acquired images (ground resolution of 0.064 m/pixel at ~250 m flying height) through the feature-matching procedure implemented in the SfM algorithm, produced a point cloud consisting of 1,816,102 features over an area of 26.8 km^2 (Figure 2.20). Due to a high degree of image overlap, initial average camera location error was below 4m (mean XY error = 3.22m, mean Z error = 1.23m, mean total error = 3.83m). A large amount of this error was concentrated in the southern portion of the flight path area and this area was removed in the final DSM (Figure 2.21). UAV derived variables, extracted from the aggregated DSM, were related with vegetation plot variables associated with old-growth forests, such as canopy heterogeneity (Figure 2.22) (Frey et al., 2016): ‘Tree height range’ of vegetation plots ~ ‘Range of elevations’ from the DSM (R^2 = 0.53, p = 0.018), ‘Mean number of branches >20cm in diameter’ ~ ‘Mean kilowatts per metre squared’ (R^2 = 0.59, p = 0.009), ‘Mean number of branches 0 – 2cm in diameter’ ~ ‘Mean kilowatts per metre squared’ (R^2 = 0.55, p = 0.014), ‘Canopy density’ ~ ‘Range of elevations’ (R^2 = -0.44, p = 0.23), ‘Canopy density’ ~ ‘Relative height ‘ (R^2 = 0.46, p = 0.032), ‘Morisita’s index’ ~ ‘Range of elevations’ (R^2 = 0.49, p = 0.23), ‘Morisita’s index’ ~ ‘Standard deviation of elevations’ (R^2 = 0.42, p = 0.036) were all significant.

Figure 2.20 – Camera locations and image overlap from UAV flights



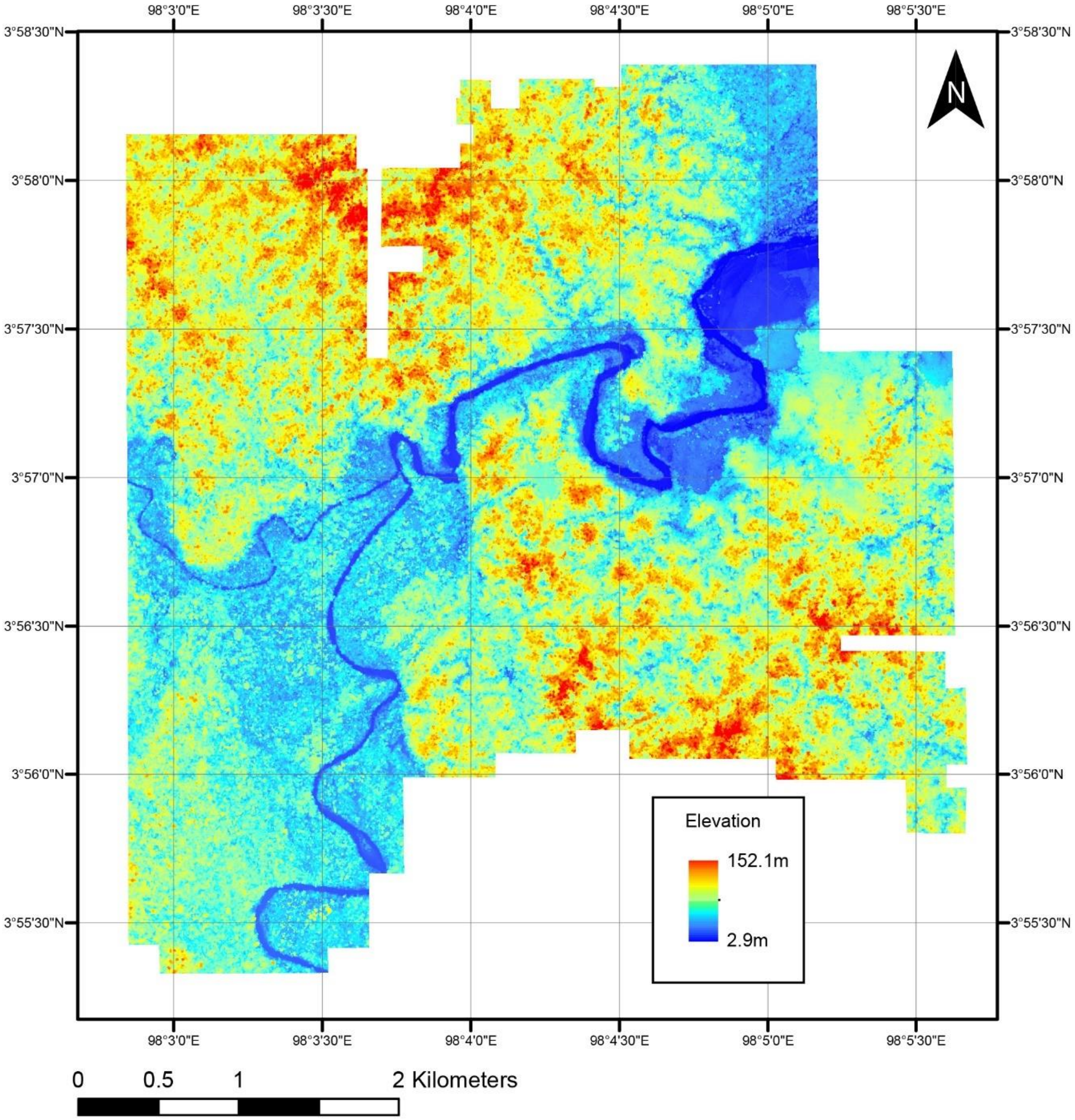
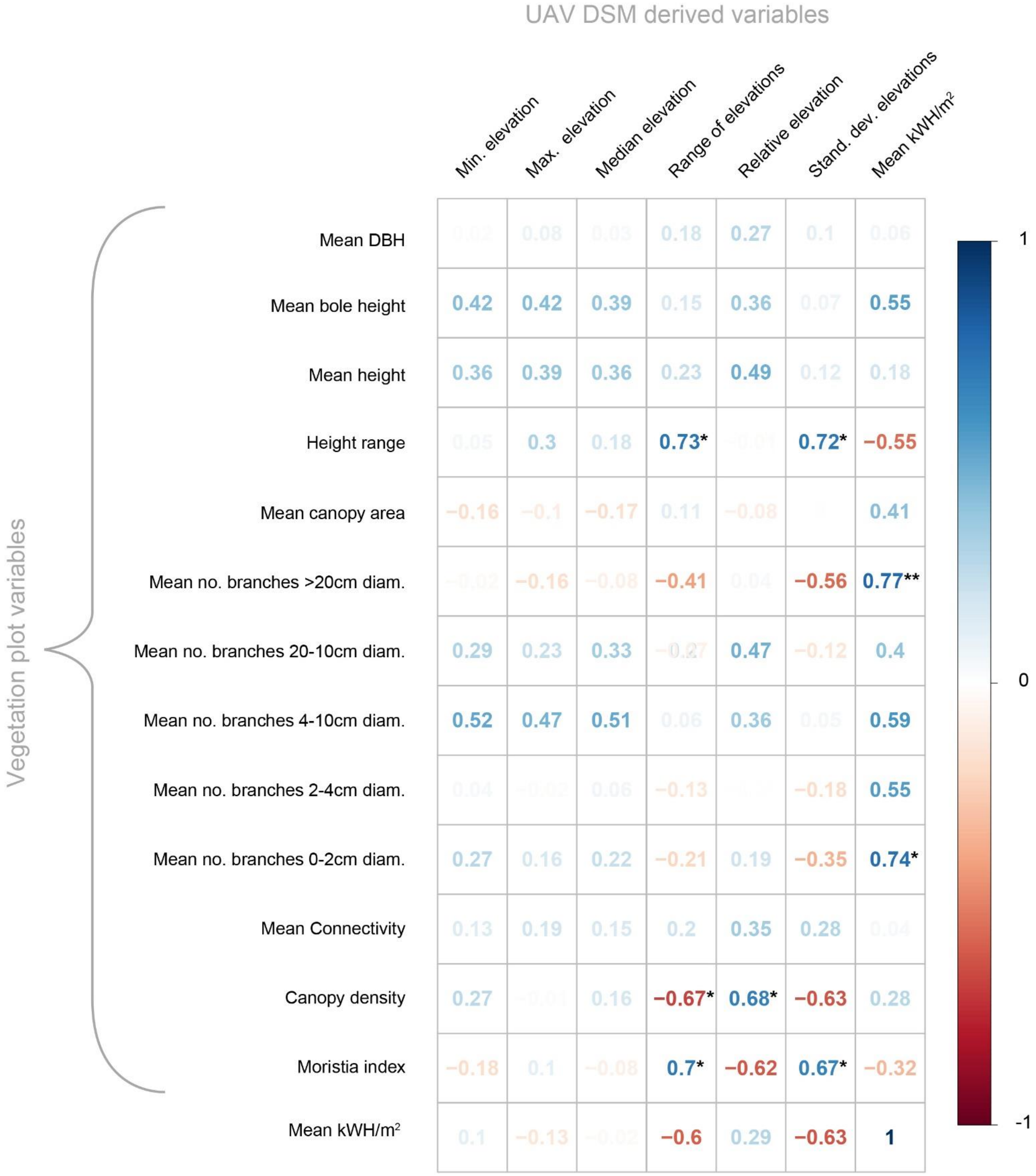
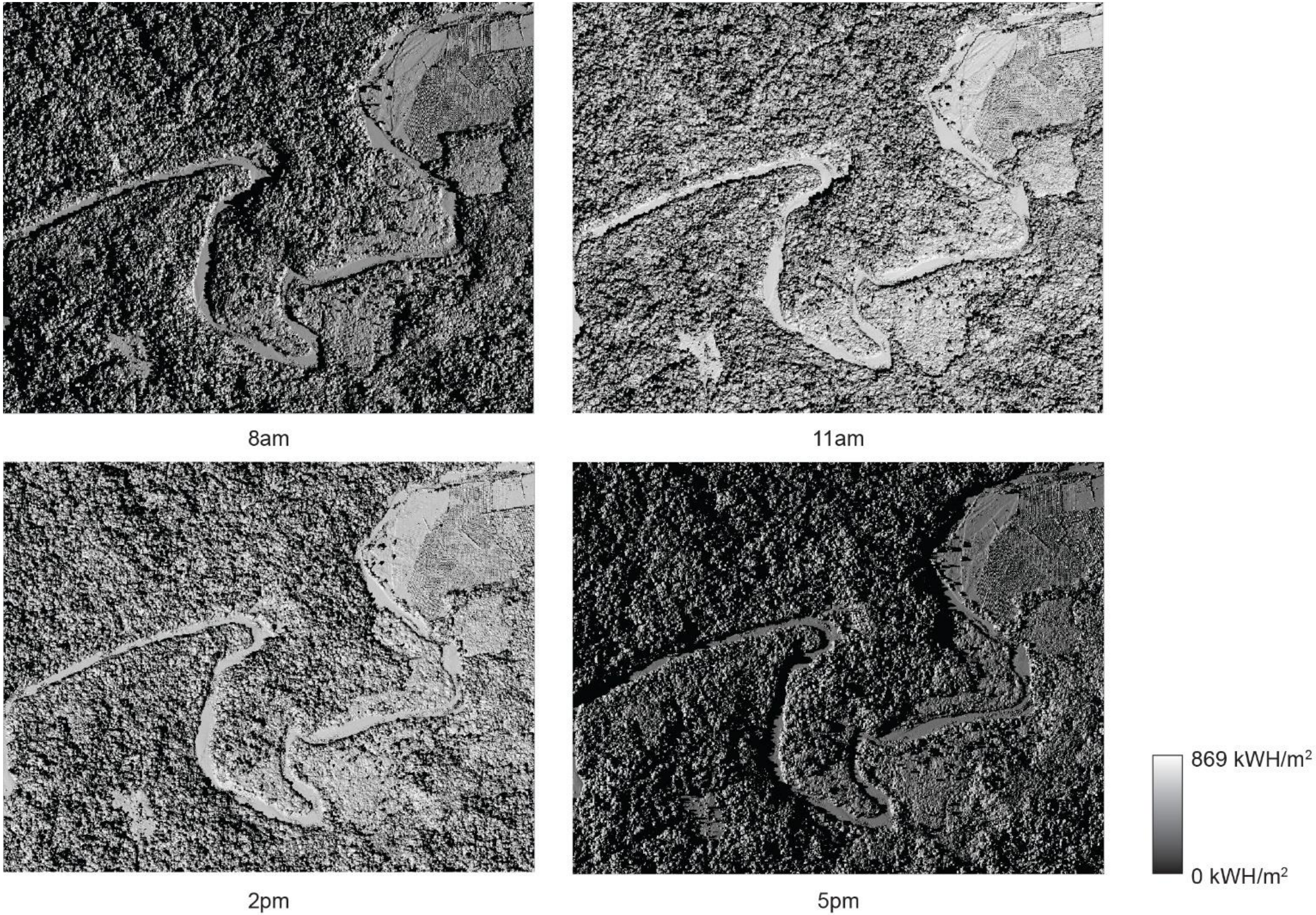


Figure 2.21 – Resulting Digital Surface Model with areas of low accuracy removed



	Min. elevation	Max. elevation	Median elevation	Range of elevations	Relative elevation	Stand. dev. elevations	Mean kWH/m²
Mean DBH	0.02	0.08	0.03	0.18	0.27	0.1	0.06
Mean bole height	0.42	0.42	0.39	0.15	0.36	0.07	0.55
Mean height	0.36	0.39	0.36	0.23	0.49	0.12	0.18
Height range	0.05	0.3	0.18	0.73*	−0.01	0.72*	−0.55
Mean canopy area	−0.16	−0.1	−0.17	0.11	−0.08	0	0.41
Mean no. branches >20cm diam.	−0.02	−0.16	−0.08	−0.41	0.04	−0.56	0.77**
Mean no. branches 20-10cm diam.	0.29	0.23	0.33	−0.27	0.47	−0.12	0.4
Mean no. branches 4-10cm diam.	0.52	0.47	0.51	0.06	0.36	0.05	0.59
Mean no. branches 2-4cm diam.	0.04	−0.02	0.06	−0.13	[illegible]	−0.18	0.55
Mean no. branches 0-2cm diam.	0.27	0.16	0.22	−0.21	0.19	−0.35	0.74*
Mean Connectivity	0.13	0.19	0.15	0.2	0.35	0.28	0.04
Canopy density	0.27	−0.01	0.16	−0.67*	0.68*	−0.63	0.28
Moristia index	−0.18	0.1	−0.08	0.7*	−0.62	0.67*	−0.32
Mean kWH/m²	0.1	−0.13	−0.02	−0.6	0.29	−0.63	1

Figure 2.22 - Pearson's correlation matrix of UAV and vegetation plot (n = 9) derived variables with mean kWH/m^2 for reference, r values shown. ' * ' denotes a significant correlation (p=<0.05), ' ** ' denotes a highly significant correlation (p=<0.01)



8am

11am

2pm

5pm

Figure 2.23 - Subsection of the Potential Incoming Solar Radiation analysis of a section of the Sikundur DSM, shown by hour in July 2017

2.3.4 Modelling Microclimate

To establish whether a relationship existed between vegetation variables and mean temperature, multiple linear regressions were used to compare plot level and UAV vegetation measurements to mean temperatures recorded by data loggers (n = 20), collected over a 6-month period. No vegetation variables, with the exception of logger height (Logger Height, $\beta = 0.064$, $p = 0.0026$, $r = 0.565$, df = 28), were significantly related with mean logger temperature. To enable the determination of which independent variables best explain the relationship between hourly temperature recordings by data loggers and environmental variables, multiple linear regression was used to compare plot level and UAV vegetation measurements to these recordings (n = 48630). Time and basic weather data collected by weather stations accounted for 14% of the variation in microclimate data logger recordings (Model 1, Table 2.2). This rose to 15% with the inclusion of logger height as a variable (Model 2, Table 2.2). With the addition of plot scale vegetation variables, only a marginal increase to 15.3% was seen in the model's predictive power (Model 3, Table 2.2). This is comparable to a similar model using canopy structure variables extracted from the UAV derived DSM (Model 4, Table 2.2). The addition of a variable to calculate daylight cloud cover (see section 1.3.3) to the variables used in Model 3 (i.e. weather, data logger height, vegetation plot variables and cloud cover) accounted for 70% of the variation in temperature recordings (Model 5, table 1.2). Using solely the aggregated Potential Incoming Solar Radiation layer, together with time, weather and data logger height variables accounted for 43% of the variation in microclimate data logger recordings (Model 6, table 1.2), suggesting that a model using the overall 3-dimensional structure of the forest and how its surfaces are hit by incoming solar radiation is a more accurate predictor of microclimate than either UAV or vegetation plot measurements (Models 3 and 4). By both including cloud cover and potential incoming solar radiation, 70% of the variation in microclimate measurements can be accounted for (Model 7).

A final model was made by replacing the 'Time' variable with an mean of the LUX readings across all loggers at that hour and included the UAV canopy structure variables, 72% of the variation in temperature could be accounted for (Model 8, Table 2.2, Figure 2.24).

To explore how canopy structure affected temperature throughout the hours of the day, the data set was separated into recordings made each hour and multiple linear regressions were used to explore which variables influenced temperature on an hourly basis. All the variables mentioned above were used, with those not significantly correlated removed from the analysis (see Table 2.3). Divided by time, the effect of vegetation variables can be seen to be more influential in predicting microclimate as the sun rises (i.e., 10am 11am), suggesting these variables are important in buffering incoming solar radiation. However, as temperatures plateau (see Figure 2.15) during the hottest part of the day (2pm) some vegetation variables (max – mean elevation) are no longer significant, suggesting that ambient temperature rise negates some of the effects of vegetation structure at these times. Collectively, these models had a mean residual standard error of 1.28ºC.

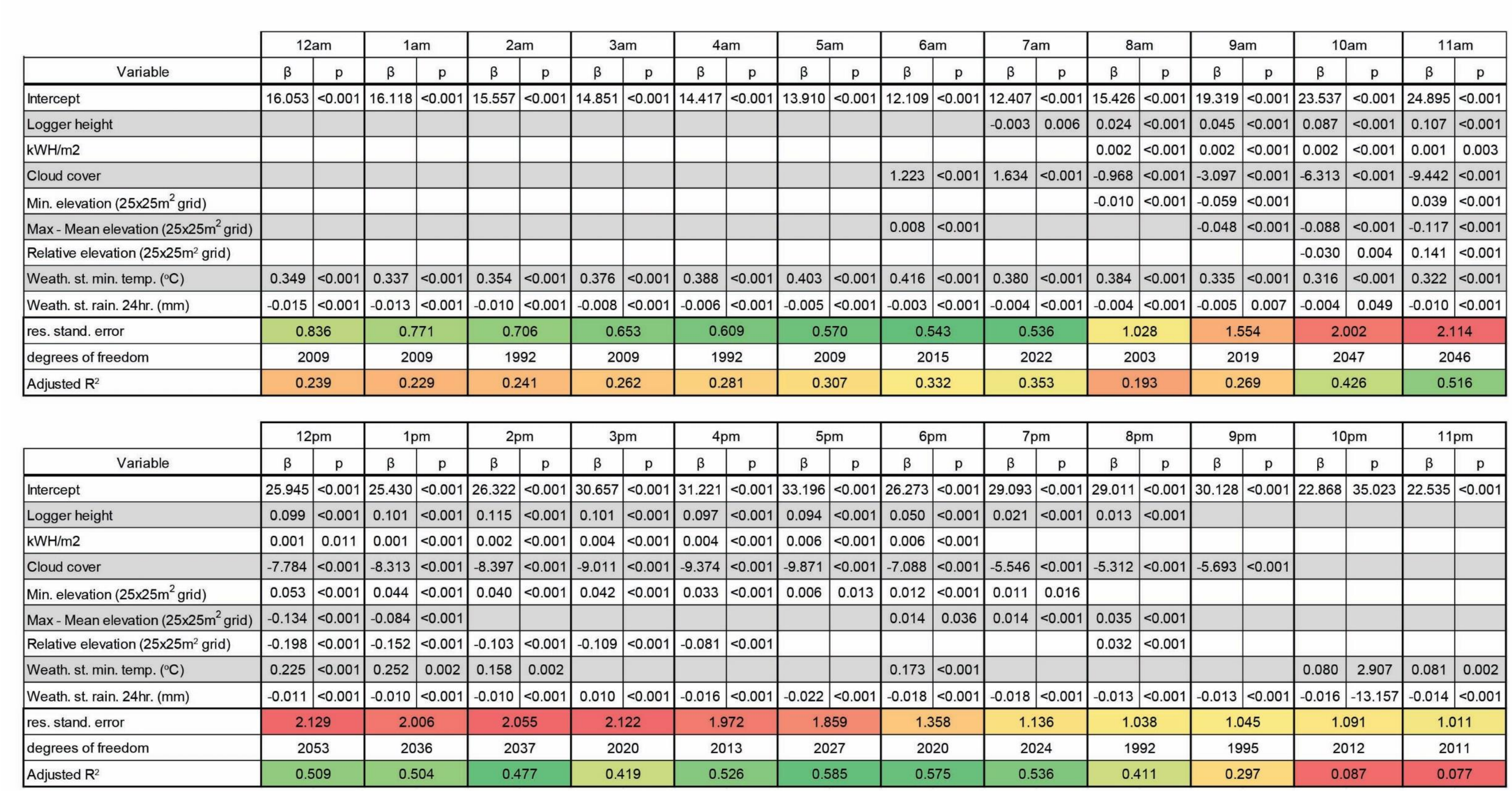
An adult male siamang emerging from the canopy

Table 2.2 - Results of multiple linear regressions detailing the best fit models of the effects of vegetation variables on temperature recordings, using non-correlated variables (grey highlights for readability only)

	Model 1			Model 2			Model 3			Model 4		
Variable	β	t	p	β	t	p	β	t	p	β	t	p
Intercept	20.2629	-9.007	<0.001	19.7804	51.370	<0.001	20.4205	51.722	<0.001	19.5703	49.818	<0.001
Time	0.1737	83.440	<0.001	4.1689	84.140	<0.001	0.1737	84.194	<0.001	0.1737	84.241	<0.001
Mean LUX at hour												
Logger height				0.0409	28.800	<0.001	0.0379	25.452	<0.001	0.0360	21.863	<0.001
Mean tree height (m)							-0.0181	-3.995	<0.001			
Mean canopy area (m^2)							-0.0263	-4.649	<0.001			
kWH/m^2												
Cloud cover												
Min. elevation (25x25m^2 grid)										0.0121	10.562	<0.001
Max - Mean elevation (25x25m^2 grid)										-0.0264	-5.316	<0.001
Relative elevation (25x25m^2 grid)										-0.0368	-7.043	<0.001
Weath. st. min. temp. (^{o}C)	0.1771	10.800	<0.001	0.1746	10.740	<0.001	0.1757	10.813	<0.001	0.1755	10.808	<0.001
Weath. st. rain. 24hr. (mm)	-0.0173	-24.410	<0.001	-0.0174	-24.810	<0.001	-0.0173	-24.627	<0.001	-0.0175	-24.968	<0.001
res. stand. error		3.167			3.140			3.138			3.136	
degrees of freedom		48560			48559			48557			48556	
Adjusted R^2		0.138			0.152			0.153			0.154	

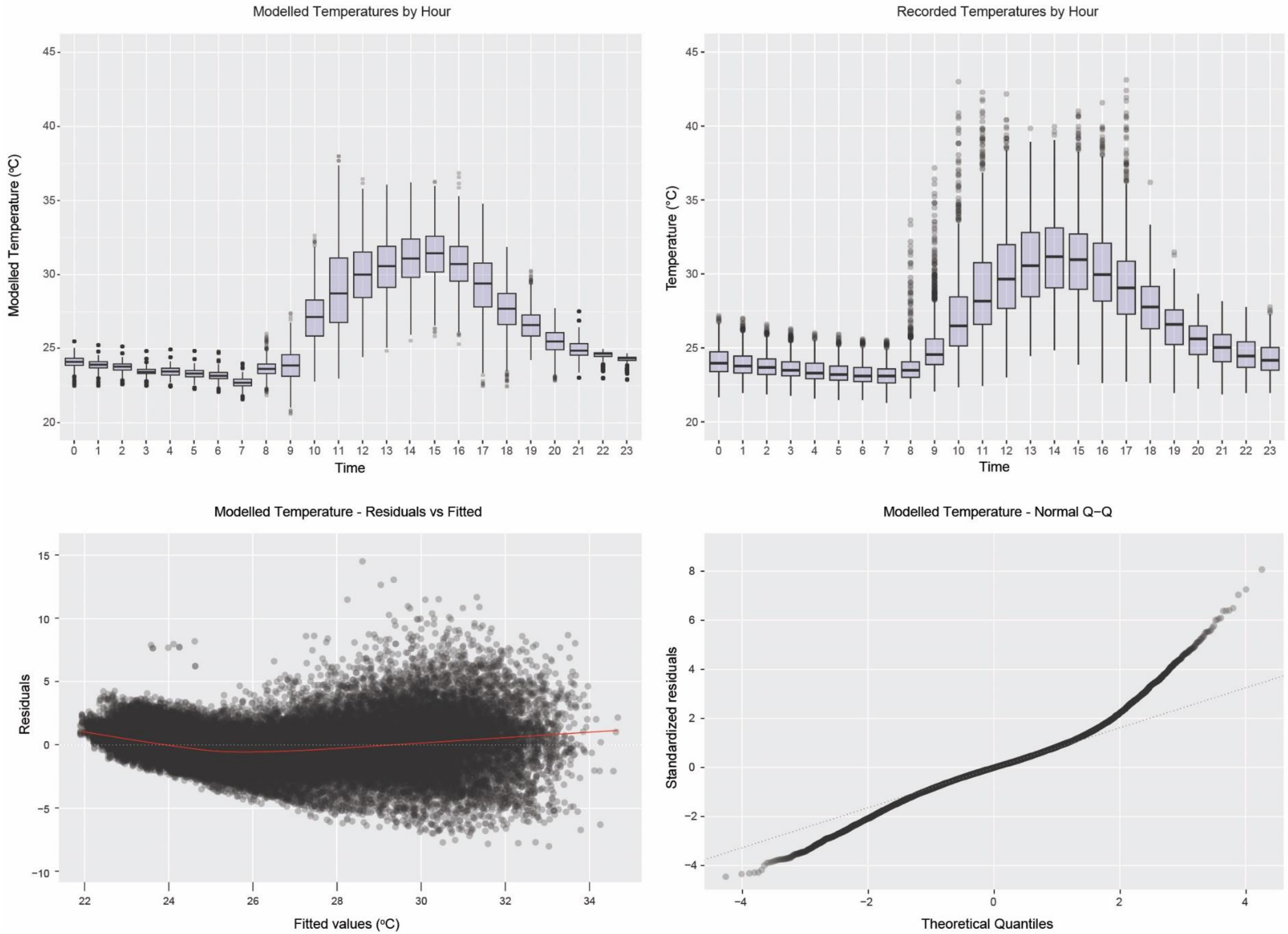
	Model 5			Model 6			Model 7			Model 8		
Variable	β	t	p	β	t	p	β	t	p	β	t	p
Intercept	27.1470	114.407	<0.001	19.3095	61.050	<0.001	26.0244	113.040	<0.001	25.2552	111.166	<0.001
Time	0.0339	25.6250	<0.001	0.1603	94.410	<0.001	0.0434	32.300	<0.001			
Mean LUX at hour										0.0002	62.997	<0.001
Logger height	0.0403	45.260	<0.001	0.0450	38.560	<0.001	0.4300	51.070	<0.001	0.0363	38.241	<0.001
Mean tree height (m)	-0.0105	-3.8710	<0.001									
Mean canopy area (m^2)	-0.2068	-6.106	<0.001									
kWH/m^2				0.0116	153.100	<0.001	0.0023	32.080	<0.001	-0.0018	-20.108	<0.001
Cloud cover	-10.402	-295.172	<0.001				-9.5018	-211.790	<0.001	-8.4406	-177.223	<0.001
Min. elevation (25x25m^2 grid)										0.0119	18.023	<0.001
Max - Mean elevation (25x25m^2 grid)										-0.0243	-8.495	<0.001
Relative elevation (25x25m^2 grid)										-0.0285	-9.473	<0.001
Weath. st. min. temp. (^{o}C)	0.2778	28.5690	<0.001	0.1450	10.860	<0.001	0.2625	27.220	<0.001	0.2590	27.753	<0.001
Weath. st. rain. 24hr. (mm)	-0.0070	-16.7360	<0.001	-0.0114	-19.670	<0.001	-0.0068	-16.430	<0.001	-0.0100	-24.591	<0.001
res. stand. error		1.877			2.579			1.859			1.800	
degrees of freedom		48556			48558			48557			48554	
Adjusted R^2		0.697			0.428			0.703			0.722	

Table 2.3 - Results of multiple linear regressions detailing the best fit models of the effects of vegetation variables on hourly temperature recordings, using non-correlated variables, with RSE and adjusted R^2 values given with conditional formatting (green [best] – red [worst]) to denote their accuracy (grey highlights for readability only)



	12am		1am		2am		3am		4am		5am		6am		7am		8am		9am		10am		11am	
Variable	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p
Intercept	16.053	<0.001	16.118	<0.001	15.557	<0.001	14.851	<0.001	14.417	<0.001	13.910	<0.001	12.109	<0.001	12.407	<0.001	15.426	<0.001	19.319	<0.001	23.537	<0.001	24.895	<0.001
Logger height															-0.003	0.006	0.024	<0.001	0.045	<0.001	0.087	<0.001	0.107	<0.001
kWH/m2																	0.002	<0.001	0.002	<0.001	0.002	<0.001	0.001	0.003
Cloud cover													1.223	<0.001	1.634	<0.001	-0.968	<0.001	-3.097	<0.001	-6.313	<0.001	-9.442	<0.001
Min. elevation (25x25m^2 grid)																	-0.010	<0.001	-0.059	<0.001			0.039	<0.001
Max - Mean elevation (25x25m^2 grid)													0.008	<0.001					-0.048	<0.001	-0.088	<0.001	-0.117	<0.001
Relative elevation (25x25m^2 grid)																					-0.030	0.004	0.141	<0.001
Weath. st. min. temp. (°C)	0.349	<0.001	0.337	<0.001	0.354	<0.001	0.376	<0.001	0.388	<0.001	0.403	<0.001	0.416	<0.001	0.380	<0.001	0.384	<0.001	0.335	<0.001	0.316	<0.001	0.322	<0.001
Weath. st. rain. 24hr. (mm)	-0.015	<0.001	-0.013	<0.001	-0.010	<0.001	-0.008	<0.001	-0.006	<0.001	-0.005	<0.001	-0.003	<0.001	-0.004	<0.001	-0.004	<0.001	-0.005	0.007	-0.004	0.049	-0.010	<0.001
res. stand. error	0.836		0.771		0.706		0.653		0.609		0.570		0.543		0.536		1.028		1.554		2.002		2.114	
degrees of freedom	2009		2009		1992		2009		1992		2009		2015		2022		2003		2019		2047		2046	
Adjusted R^2	0.239		0.229		0.241		0.262		0.281		0.307		0.332		0.353		0.193		0.269		0.426		0.516	

	12pm		1pm		2pm		3pm		4pm		5pm		6pm		7pm		8pm		9pm		10pm		11pm	
Variable	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p	β	p
Intercept	25.945	<0.001	25.430	<0.001	26.322	<0.001	30.657	<0.001	31.221	<0.001	33.196	<0.001	26.273	<0.001	29.093	<0.001	29.011	<0.001	30.128	<0.001	22.868	35.023	22.535	<0.001
Logger height	0.099	<0.001	0.101	<0.001	0.115	<0.001	0.101	<0.001	0.097	<0.001	0.094	<0.001	0.050	<0.001	0.021	<0.001	0.013	<0.001						
kWH/m2	0.001	0.011	0.001	<0.001	0.002	<0.001	0.004	<0.001	0.004	<0.001	0.006	<0.001	0.006	<0.001										
Cloud cover	-7.784	<0.001	-8.313	<0.001	-8.397	<0.001	-9.011	<0.001	-9.374	<0.001	-9.871	<0.001	-7.088	<0.001	-5.546	<0.001	-5.312	<0.001	-5.693	<0.001				
Min. elevation (25x25m^2 grid)	0.053	<0.001	0.044	<0.001	0.040	<0.001	0.042	<0.001	0.033	<0.001	0.006	0.013	0.012	<0.001	0.011	0.016								
Max - Mean elevation (25x25m^2 grid)	-0.134	<0.001	-0.084	<0.001									0.014	0.036	0.014	<0.001	0.035	<0.001						
Relative elevation (25x25m^2 grid)	-0.198	<0.001	-0.152	<0.001	-0.103	<0.001	-0.109	<0.001	-0.081	<0.001							0.032	<0.001						
Weath. st. min. temp. (°C)	0.225	<0.001	0.252	0.002	0.158	0.002							0.173	<0.001							0.080	2.907	0.081	0.002
Weath. st. rain. 24hr. (mm)	-0.011	<0.001	-0.010	<0.001	-0.010	<0.001	0.010	<0.001	-0.016	<0.001	-0.022	<0.001	-0.018	<0.001	-0.018	<0.001	-0.013	<0.001	-0.013	<0.001	-0.016	-13.157	-0.014	<0.001
res. stand. error	2.129		2.006		2.055		2.122		1.972		1.859		1.358		1.136		1.038		1.045		1.091		1.011	
degrees of freedom	2053		2036		2037		2020		2013		2027		2020		2024		1992		1995		2012		2011	
Adjusted R^2	0.509		0.504		0.477		0.419		0.526		0.585		0.575		0.536		0.411		0.297		0.087		0.077	



Modelled Temperatures by Hour

Recorded Temperatures by Hour

Modelled Temperature - Residuals vs Fitted

Modelled Temperature - Normal Q−Q

Figure 2.24 –Results of the best model for hourly temperature, including modelled temperature (top left) for comparison to recorded temperature (top right), the model's residuals plotted against fitted values (bottom left) and the model's standardised residuals plotted against theoretical quantiles (bottom right). See Table 2.3

2.4. Discussion

The aim of this study was to explore the effect of vegetation structure on microclimate within the canopy of a historically degraded tropical forest, whilst developing a cost-effective method for wide-ranging habitat assessment that enables microclimate modelling within forest canopies at the scale of tens of metres. This was largely achieved despite a highly dynamic climatic environment in the Sikundur forest, with large differences in simultaneous measurements between loggers (15.2ºC difference between simultaneous data logger readings), expanding the previously assessed ability of microhabitats to buffer against heat exposure (Scheffers et al., 2014b). Temperature peaks were also highly changeable between microclimate readers depending on their location (Figure 2.16a and Figure 2.16b), suggesting that the degraded forest at Sikundur is climatically variable, with vegetation density and topographic location altering the effectiveness of thermal buffering temporally (Pringle et al., 2003). This thermal dynamism can also be seen in the vertical temperature gradients, with higher mean temperatures recorded by data loggers placed higher into the canopy, as seen in other studies (Scheffers et al., 2017). The temperature gradient between high and low data logger recordings was clearly affected by plot level vegetation structure, with the effects becoming more pronounced with low cloud cover. In the exploration of vertical temperature gradients, high mean bole height was seen to reduce the difference between high and low data logger recordings, 'flattening' temperature variation, creating more uniform plot wide temperatures. High values in mean bole height are associated with old-growth forest (Franklin and Van Pelt, 2004) and may regulate incoming solar radiation within the vegetation plot. Low values in mean bole height are associated with regenerating or degraded forests (Rutishauser et al., 2016; Pereira et al., 2002). Less substantial vegetation structure may allow solar radiation to penetrate the canopy, uniformly warming data loggers within the plot. Other vegetation variables associated with old-growth forest, such as high values in counts of large branches (e.g. 'mean number of branches >10cm in diameter') are associated with increased temperature gradients, providing greater shade for the lower data loggers whilst those higher in the canopy were subjected to solar radiation. The interplay of these variables changes throughout the day, as the sun's relative zenith alters the relationship between temperature and vegetation variables (Table 2.1). In sunny conditions, with low cloud cover, vertical temperature gradients decreased after 1pm, suggesting that after this time, temperatures lower down in the canopy were warming to levels more comparable with loggers high in the canopy. The finding that sunlight and shade have had the biggest influence on microclimate within a given forest site (apart from baseline climate and weather effects) also highlights that more homogenous canopy structures are capable of maintaining stable microclimates, and heterogenous canopy structures produce a more dynamic thermal environment. This suggests that forest degradation alters microclimate spatially and temporally and may dramatically alter the habitats of arboreal mammals.

There were no clear relationships between plot level vegetation structure, as measured using traditional forest survey methods, and mean microclimate measurements, possibly due to the influence of numerous factors such as canopy structure, the plot's placement in relation to surrounding canopy and vegetation, and the temporal influence of sunlight and shade on each area. These effects are not measured using traditional vegetation plots but can be identified using UAV derived canopy models. Traditional measures of vegetation structure, such as mean DBH, may not be the most influential factors in governing forest microclimate, but rather the placement of a given site in relation to sunlight and shade.

UAV derived measurement of canopy structure had few strong relationships with traditional measurements of vegetation structure, although canopy height range and canopy connectivity measured in plots had strong relationships to the range of elevations and relative elevations as measured by UAV. This suggests that whilst both are accurate measurement of vegetation structure, ground-based measurements may only be weakly related to canopy structure measurements overall. Given the stronger influence of UAV derived variables on microclimate, ground-based measurements may be a poor indicator of microclimate within forested areas.

The highly dynamic climatic variation in Sikundur renders accurate microclimate modelling in this environment difficult. Despite a large amount of the variance being accounted for in the modelled temperature ($R^2 = 0.72$), the best fitting model is accurate only to 1.8^{o}C in real terms. However, given that the HOBO data loggers used in this study are accurate to ± 0.53°C, it is possible that the model is accurate to ca. 1.2^{o}C in relative terms, seemingly accurate enough for most biological questions related to mammalian species. A number of factors could explain this lack of accuracy. Measuring additional variables may have improved the models presented here, for instance humidity and soil moisture. Data logger installation may also be a factor in model inaccuracy. The lack of sunshades used to protect data loggers from direct sunlight may account for some higher temperature recordings and decrease the accuracy of the model. Direct sunlight may have also produced a 'greenhouse effect' within the data logger units themselves, in which the logger unit is temporarily heated by direct sunlight and recorded temperatures are unusually high for following data points. Whilst some of this error could have been corrected by removing data points in which LUX levels (or lagged LUX levels) reached values associated with direct sunlight (LUX ~=>32,000), due to the data loggers' programmed recording schedule (1 data point recorded each hour), loggers could have been subjected to direct sunlight between the recorded data points, making this adjustment imperfect, so it was not used.

Despite these pitfalls, this study shows that the combination of microclimate data loggers and the highly detailed Digital Surface Models produced by Unmanned Aerial Vehicle surveys to model microclimate produces robust, accurate models that can be extrapolated over wide areas. Similar studies that have utilised LiDAR and advanced statistical techniques have achieved similar results in predicting microclimate as the current study ($r = 0.87$, Frey et al., 2016). However, the methods utilised in the current study have the distinct benefit of being low-cost. All the variables used in the final model can be recorded using only microclimate data loggers, a weather station at a given study site and the appropriate UAV surveys over the area across which microclimate results are to be extrapolated.

The application of Potential Incoming Solar Radiation analysis using highly accurate DSMs generated from UAV surveys increases the accuracy of predicted microclimate models, effectively being a coarse-grain abstraction for many variables usually measured in microclimate studies (slope, aspect, relative topographic position, vegetation, wind exposure) (Dobrowski et al., 2011). Whilst this may not account for finer-grain fluctuations in microtopography, and other influences on microclimate (presence of streams or pools, soil moisture), it does allow for rapid assessment of these combined effects on microclimate. Also, the generation of a microclimate model which includes minimum and maximum daily temperatures as well as rainfall allows the direct adjustment of the model to future levels of predicted climate change (in HADGEM2 for example, Collins et al., 2008; Brands et al., 2013; Moss et al., 2008).

Due to the abstraction of topographical and vegetation variables produced by Potential Incoming Solar Radiation analysis and the nature of data collection by UAV, directly detecting areas in which historical forest degradation has taken place using the methods in this study is difficult. This study has shown that below canopy vegetation structure impacts microclimates, yet UAV surveys as yet have failed to identify direct relationships between features detectable using UAV and plot level vegetation characteristics in areas of high topographic relief or microtopography. This lack of strong correlations between vegetation plot and UAV variables make direct comparisons between these variables problematic (see Figure 2.22), as seen in previous studies (Mlambo et al., 2017). However, the strong relations between the range of tree heights as measured in vegetation plots and by UAV suggests that each method is an accurate recording of a form of vegetation structure, but given their different perspectives, each method records variables that have few strong relationships to one another. Whilst simple analysis of DSMs, such as classifying areas of low range as devoid of vegetation and thus deforested, is possible, historical forest degradation remains difficult to quantify. As stated in other studies, historically degraded forest can appear to be structurally similar to old-growth forest (Brearley et al., 2004; DeWalt et al., 2003). However, microclimate modelling may provide a proxy for quantifying degradation level in anthropogenically disturbed forests. Given that the thermal buffering effects of old-growth forest are well known (Frey et al., 2016; Parker et al., 2004; De Frenne et al., 2013), areas in which temperatures are above mean modelled temperatures are likely to be historically degraded. Whilst multiple previous studies have been able to quantify tree crown size from LiDAR derived data sets (Alexander et al., 2017; Alexander et al., 2018, La et al., 2015) and detection of individual trees has been achieved using solely UAV derived data (Kattenborn et al., 2014; Fitz et al., 2013) and very high resolution satellite imagery (Wagner et al., 2018), measurements of tree crown size have yet to be achieved across heterogenous landscapes using UAV derived datasets. Whilst direct measurements of biomass are currently out of the scope of this study, given the level of detail that is achievable through the use of UAV at the landscape scale, basic measurements may be possible.

2.4.1 Future recommendations

With further analysis, using Empirical Bayesian Kriging 3D regression and/or Boosted Regression Trees, the potentially imperfect microclimate recording taken in this study (due to sunshades not being used) may improve the microclimate model accuracy. Future studies utilising similar methods could be greatly enhanced if GPS coordinates and height measurements of data logger placement were more accurate. Using handheld GPS units under dense canopy meant that GPS readings were accurate to approx. ±10m, rendering the precise location of data loggers uncertain, and therefore the attributed UAV/PICSR values to these areas. The inclusion of additional variables such as humidity and soil moisture would also greatly increase model accuracy. Additionally, placing microclimate data loggers in ‘open’ areas (e.g. at forest edges and areas cleared for agriculture), would allow direct comparison between different landscape types, broadening the potential application of this combination of technologies, allowing the impact of future potential climate change to be modelled on agriculture, for example.

2.5 Conclusions

Coupling detailed plot level vegetation surveys and microclimate data loggers within the tree canopy has clearly shown a relationship between vegetation structure and vertical temperature gradients, which may be of great importance to arboreal mammals. Large bodied, highly arboreal mammals are likely to favour areas with pronounced vertical temperature gradients during the hottest parts of the day, especially in low cloud cover. Within a degraded tropical forest such as Sikundur, this may limit their available habitat and reduce overall habitat suitability. This may be exacerbated in the face of future predicted climate change. Using wide ranging UAV canopy surveys and microclimate data loggers to model microclimate over large areas, it may be possible to explore the effects of future climate change within canopies over large areas, and in turn, the effects of these changes on highly arboreal mammals, such as siamang and orang-utan.

Chapter 3. Siamang behaviour in relation to canopy structure and microclimate

3.1 Introduction

Understanding the impacts of degradation within both protected and non-protected areas of high biodiversity is of key importance to safeguarding arboreal primate populations under present conditions (Tang et al., 2010). The effects of selective logging on the ecology of tropical forests are still poorly understood, as most studies lack comparable pre- and post-logging data (Laufer et al., 2013). Quantitative measures of selective logging are challenging to assess, as the uneven distribution of valuable tree species makes areas of forest degradation difficult to assess using satellite imagery (Struebig et al., 2013). Due to the dispersed nature of selective logging, and the subsequent regrowth of understory tree species, historically logged forest cannot easily be classified as logged and non-logged, but rather exhibits heterogenous gradients of degradation (Struebig et al., 2013). This form of logging can have a relatively low impact compared with other forms of anthropogenic disturbance, such as fragmentation and fire, in terms of reduced habitat (Chaves et al., 2012, Barlow et al., 2006), with most logged forests containing at least 50% of the biomass and more than 75% of the species compared to undisturbed forest (Berry et al., 2010, Putz, 2012). However, for long lived species there may be a delayed negative effect caused by this discrete form of habitat disturbance, the full ecological consequences of which have not yet become apparent (Tilman et al., 1994, Vellend, 2006).

The advent of selective logging of tropical forests, prominent in lowland forests of Northern Sumatra between 1976-1988 and then again intermittently in the 1990s, (Sumatran Orang-utan Conservation Program, 2015), changes canopy structure, altering the growth of plant species, and disturbs or displaces fauna (Chapman et al., 2007). Whilst the direct effect of historical forest degradation may be marginal in terms of reduced habitat, changes in forest structure due to selective logging alter the behaviour and densities of primates foraging for dispersed food resources (Marshall et al., 2009; Chaves et al., 2012). Microclimate changes in degraded areas also drastically alter how and when primates use disturbed areas of forest (Takemoto, 2004; Suggitt et al., 2011). Coupled with the additional structural complexity exhibited in selectively logged forests, these effects can have a substantial impact on the well-being of primates inhabiting these areas, which may be exacerbated by future predicted climate change.

Primate species are particularly susceptible to forest degradation (Arroyo-Rodríguez et al., 2013; Benchimol and Peres, 2014). Due to their low birth rates and slow life histories, any species that cannot quickly adapt their behaviour to emerging changes are ultimately faced with extinction (Chapman and Peres, 2001). Highly arboreal primate species, such as

Hylobatidae, which rely on continuous forest canopy to locomote efficiently, are especially affected by habitat degradation as reduced canopy integrity places them under additional energetic demands (Takemoto, 2004, Marsh et al., 2016). Despite numerous studies on the effects of habitat degradation and anthropogenic disturbance on primate populations (Marsh and Chapman, 2013), new findings frequently arise with each additional study (Benchimol and Peres, 2014). Given primates' behavioural flexibility within and across species, and their largely threatened status, further investigation into the effects of habitat degradation on individual primate species is necessary (Ewers and Didham, 2006). Understanding the impacts of degradation on endangered primate species' habitat is of key importance to safeguarding these populations under present conditions (Tang et al., 2010).

The lesser apes are generally described as largely monogamous, territorial and frugivorous (Leighton, 1987; Bartlett, 2007). They are highly arboreal, with long forelimbs and a reduced thumb appendage to aid in brachiation (Van Horn, 1972). Siamang movements typically follow patterns of brachiation along large boughs during locomotion (travel), quadrupedal clambering and suspensory postures during feeding among small branches, and seated postures on large supports during resting (Fleagle, 1976). Siamang groups are larger than those of the smaller, mostly sympatric, gibbon species (mean 3.9 vs. mean 2.6 in Sumatra) (O'Brien et al., 2003) and they are roughly twice the body weight at adulthood (siamang: 11-12 kg, other gibbon spp.: 5-6 kg) (Jungers, 1984). They are therefore, seemingly, more dependent on large trees than either of their sympatric ape species; the lighter, more agile lar gibbon (*Hylobates lar*) or the larger, mostly solitary orang-utan (*Pongo abelii*) (Wich et al., 1999), that utilise orthograde suspension and “tree-swaying” strategies to locomote efficiently through areas with small, flexible substrates (Thorpe and Crompton, 2005; Thorpe et al., 2007; Thorpe et al., 2009).

Siamang also differentiate themselves from sympatric gibbon species by their large gular sac, found in both males and female, allowing siamang to make loud, resonating territorial calls or songs, typically in the morning or in response to other nearby siamang groups (Chivers, 1976; Hewitt et al., 2002; McAngus et al., 2004). However, much of the reported siamang behaviour differs between studies. Multiple studies have reported differing levels of frugivory, ranging from as low as 20% (Chivers, 1974; Chivers et al., 1975) to as high as 61% (Palombit, 1996). Group size seems to fluctuate from male-female pairs (Aldrich-Blake and Chivers, 1973) to habituated groups containing six individuals (Lappan, 2007). Home range size ranges from 15 hectares (Chivers, 1974) to 47 hectares (Raemaekers, 1977). This is relatively unsurprising given the behavioural flexibility of primate species (Van Schaik, 2013, Chapman and Rothman, 2009) and the ability of groups and individuals to adapt to their environment, showing markedly divergent behaviour from those of the same species, even within close proximity to each other (Chapman et al., 2002). However, there are limits to primate species adaptability, especially in response to rapid changes caused by anthropogenic disturbance (Arroyo-Rodríguez et al., 2013; Benchimol and Peres, 2014; Marsh et al., 2016). To enable the effective conservation of primate species, these limits should be ascertained. For siamang, these limits are not known due to the low number of studies on the species.

Studies which focus on siamang are relatively rare in comparison to those on other ape species, accounting for 0.59% of the available literature on ape species published since 1970 (from Web of Science search, on April 12th 2019, using genus name as search term; *Symphalangus* = 90 of 15,364 returns from searches using ape genus names, Figure 3.1). Of these studies (n = 90), less than a third (n = 21) involve direct observations of wild siamang behaviour.

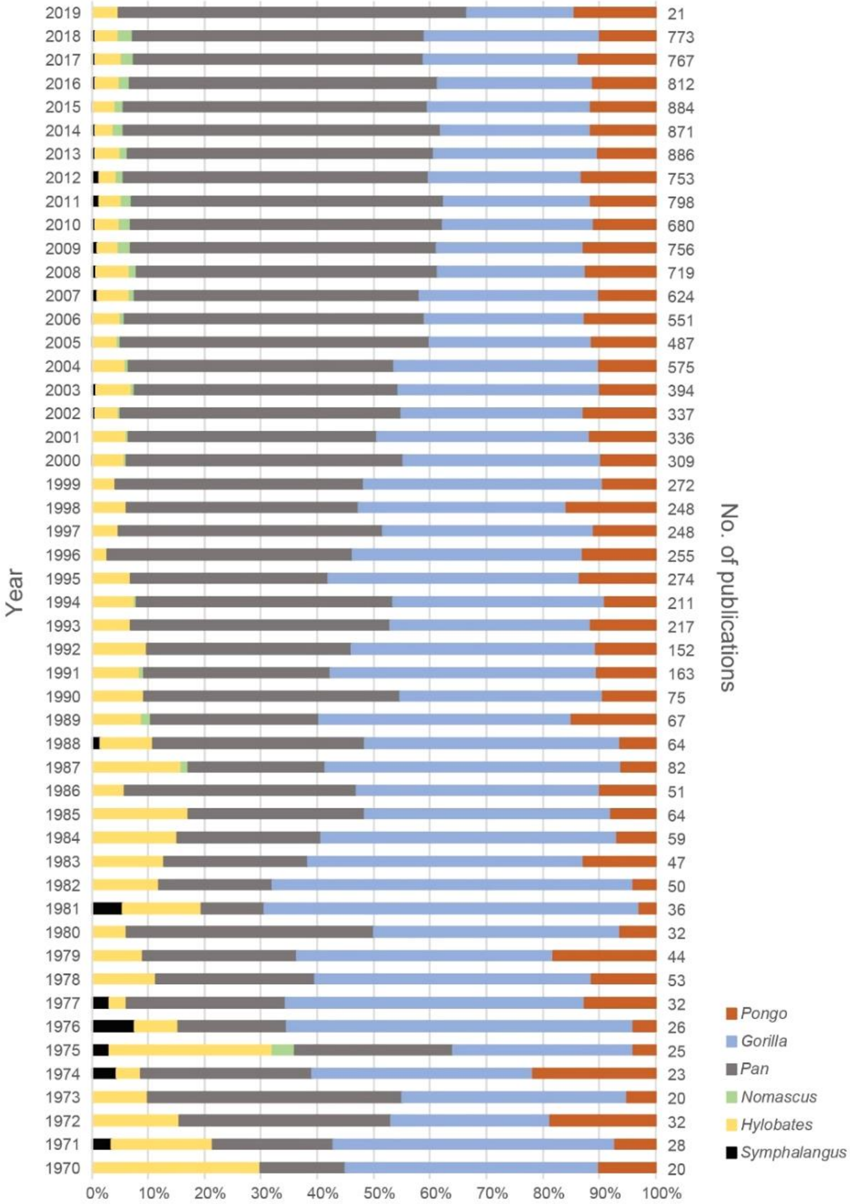


Figure 3.1 - Publications on non-human ape species by genus from Web of Science search conducted conducted on April 12th, 2019

The bulk of this literature is from four regions, the Way Canguk Research Area within the Bukit Barisan Selatan National Park in the extreme southwest of Sumatra (O'Brien et al., 2003; O'Brien et al., 2004; Lappan; 2007a; Lappan; 2007b; Lappan; 2009; Lappan and Morino, 2014; Morino, 2015), Ketambe in the southern area of the Aceh province in north Sumatra (Palombit, 1992; Palombit, 1995a; Palombit, 1995b; Palombit, 1996), and three sites in peninsula Malaysia; Ulu Gombak, Ulu Sempam and Kuala Lompat (Chivers, 1974, Chivers 1975, Chivers, 1976).

Although the Sikundur study site is only 50km north-east of Ketambe, it is a vastly different habitat. Ketambe lies within a rich, fruit abundant riverine valley, with the Mount Leuser range to the east and the Mount Bandahard range to the west. In contrast, Sikundur, to the east of the Mount Bandahard range, is a lowland forest with low fruit abundance (SOCP, 2016, see Figure 2.5). Furthermore, due to a suspected disease outbreak, *Hylobates* and *Symphalangus* numbers in Ketambe fell dramatically in between late 1987 and early 1998 (Palombit, 1992), with now only a few individuals remaining (D'Agostino, personal communication). This may be the same skin disease that affected the siamang population in Way Canguk Research Area, killing approximately 50% of the population between 2011 and 2016 (Lappan et al., 2017). As such, observations of siamang within Sikundur not only allows the investigation of a previously unstudied population of siamang, but a population inhabiting an ecologically different habitat which has undergone significant anthropogenic disturbance in the past (Abdulhandi et al., 1987; Knop et al., 2004; SOCP, 2015) but which has seemingly been untouched by a lethal skin disease that has dramatically affected other studied populations.

This study aims to document the behaviour and ranging of siamang inhabiting the Sikundur area, a historically selectively logged, lowland dipterocarp forest on the edge of the Gunung Leuser National Park, Northern Sumatra (see section 1.2.1). This study aims to investigate the relationship between siamang behaviour, canopy structure and microclimate, to see if inhabiting a degraded forest places additional demands on siamang groups. The variation in the location and abundance of food resources has previously been shown as the primary driver of spatial preference by tropical forest frugivores (Garber, 1987; van Schaik et al., 1993; Saracco et al., 2004). Vegetation structure, independent of food resources, has also been shown to be a key determinant of the presence and population density of frugivores, especially those animals that are predominately arboreal (Matthiopoulos, 2003, Marsh et al., 2016). The three-dimensional spatial configuration of forest habitat may affect: the capacity of arboreal vertebrates to move through their habitat (Emmons & Gentry, 1983), access food resources (Hill et al., 2004), sleeping and resting sites (Pruetz et al., 2008). The effects of forest structure on microclimates have long been studied in tropical forests (Sheeny, 1977; Chen et al., 1999, Pringle et al., 2003), but how the synergistic relationship between canopy structure and microclimate affects topical forest frugivores, in terms of habitat preference, ranging and behaviour, has yet to be addressed.

As a large arboreal mammal, canopy structure is of primary importance to siamang survival (Hardus et al., 2012), and enables them to locomote to obtain food resources, reach sleep sites, and avoid predation (Thorpe and Crompton, 2006). Similarly, as relatively large bodied mammals, siamang are sensitive to fluctuations in temperature. Travel in high temperatures and direct sunlight increases energetic expenditure (Gonzalez-Zamora et al., 2011) and increases the secretion of sweat (Hiley, 1976), increasing the need for moisture. These limitations may govern when and where travel for siamang is appropriate, thereby determining which areas of forest siamang utilise at the hottest part of the day. This may effectively reduce daily range size in the long term for siamang, reducing social interactions and ultimately limiting gene flow.

This study uses data collected and models produced in chapter one to measure the synergistic effects of canopy structure on climate and its impacts on siamang behaviour and ranging, combining 3-dimensional canopy structure analysis and microclimate modelling with long-term behavioural recordings of siamang. Siamang are expected to attempt to mitigate high temperatures by altering their height and location within the canopy, seeking areas which may buffer against solar radiation. However, in a degraded forest, the opportunities to mitigate high temperatures are likely to be reduced, resulting in siamang experiencing high temperatures. To investigate the ability of UAV data and microclimate data loggers to measure the synergistic effects of canopy structure on climate and its impact on arboreal wildlife, these technologies were used in conjunction with long-term behavioural recordings of siamang.

3.2 Methods

3.2.1 Habituation

Before detailed behavioural observations of primates can take place, they must be habituated to the presence of human researchers. The goal of habituation is to reduce the initial fear shown by primate species to human presence and ultimately, for them to ignore the observer (Williamson and Feistner, 2003). Unhabituated primates are difficult to observe at close range, making individual identification problematic, and their behaviour difficult to record. Primates disturbed by the presence of observers show altered patterns of behaviour and ranging and introduce bias into data collection. Historically, the techniques involved in primate habituation were not described in detail as they were seen as a means to an end (Tutin and Fernandez, 1991). Whilst more recent literature has sought to amend this (Ando et al., 2008; Bertolnai and Boesch 2008) and look more deeply into the effectiveness (Crofoot et al., 2010) and consequences (Goldsmith, 2005) of habituation, there is still a lack of species-specific literature on the topic (but see Jack et al., 2008). Before habituation of siamang at Sikundur was attempted, advice was sought from experienced gibbon researchers that had habituated groups in other areas (Nowak, personal communication; Cheyne personal communication; Chivers personal communication). Largely, their advice followed the available literature on the habituation process (Williamson and Feistner, 2003) with some minor differences. Because gibbon species are highly arboreal and 'skittish', they are likely to flee upon their first sighting of human observers, especially in areas in which hunting has occurred. Therefore, repeated neutral contact would not be established, as groups fleeing on initial contact repeatedly would result in a reinforcement of fleeing behaviour. Given this, general advice was, after initial contact had been establish for some days, to follow the group when they fled, for increasing periods of time, until neutral interactions were established. The location of siamang groups were estimated by their territorial call early in the mornings as the research team walked the Sikundur trail system. The group's initial estimated locations were roughly mapped (Figure 3.2). Four group locations were estimated, with a known individual female north of the research station, which seemed unafraid of observers. Camp manager Pak Suprayudi believed this siamang had previously been a pet and was released, hence its tendency to favour an area close to the research station.

One group of siamang, to the east of the research station, were well known to the staff at the Sikundur field station, as the seven members of staff had been conducting all-day follows of orang-utans within the area since the research stations was established in 2013 (SOCP, 2015) and occasionally saw the group. Field staff members Supri and Loga had also previously been conducting observations on orang-utan where both siamang and orang-utan had utilised the same feeding tree. Habituation on this group was attempted from the 26th of June 2017, with the first all-day follow (from sleeping to sleeping tree) completed on the 11th of July. However, hours of observation after this period were somewhat unreliable, frequently losing the group for large periods of the day, or unable to collect reliable data. From the 26th of July onwards, 10+ hours of observation daily were possible, with occasional lapses in this data collection regime due to losing the group for multiple days, heavy rain, time off, or other work (see Figure 3.3). We also tried to conduct behavioural follows of the single female north of the research station from the 4th of July 2017. The single female seemed unafraid of observers initially, but through the course of the first day of observations, the female fell some 10m whilst brachiating. Though seemingly uninjured, she continued for another 10 minutes or so before falling again from ~15m of height.

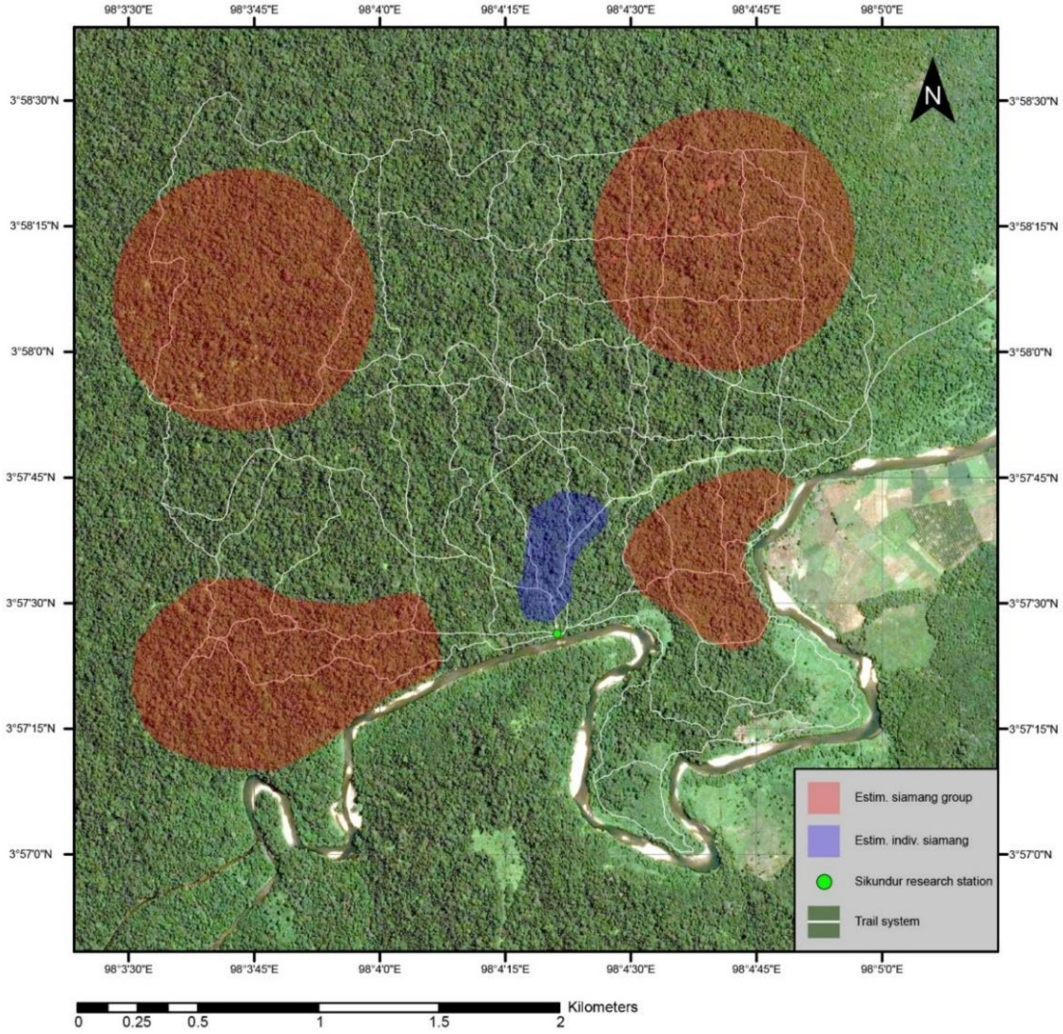


Figure 3.2 - Initial estimation of siamang group locations from ad hoc observations

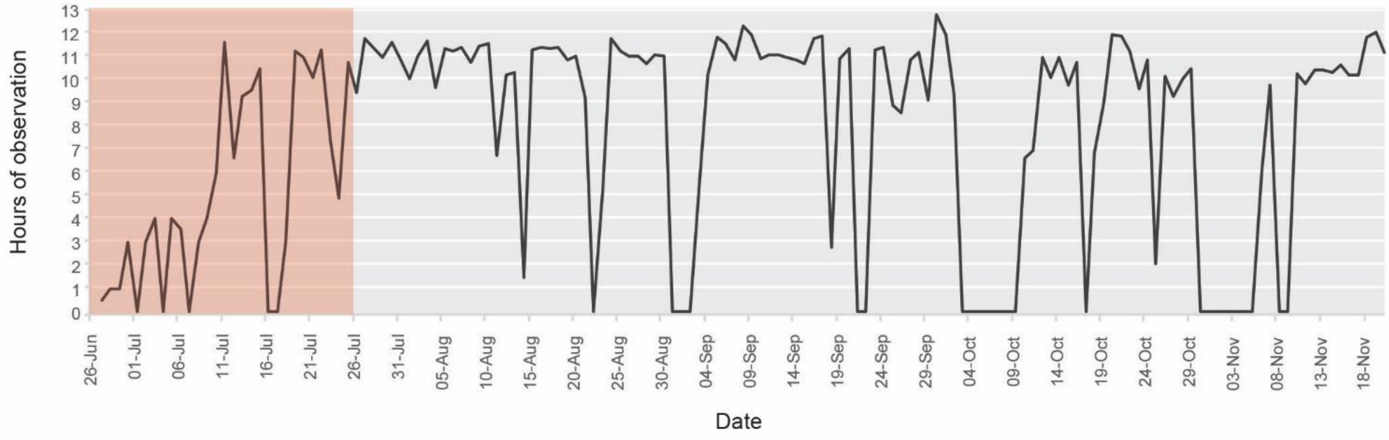


Figure 3.3 - Timeline of hours of observation of Group 1, with the habituation process highlighted in red. Total observation hours = 1,258

We could not tell if the fall was a result of our presence, if the single female was fleeing and panicked, or this was a natural occurrence. After some discussion with Pak Suprayudi, it was thought this confirmed his belief the single female had previously been a pet and was relatively unskilled in arboreal locomotion. She had been seen close to the research station frequently for at least a year. It was thought any behavioural observations of this individual would provide data that was questionable in terms of its pertinence to the main research question, i.e. her ranging seemed to be biased towards the location of the Sikundur research camp and use of canopy structure was possibly not a good representation of the species. Follows of this individual were abandoned.

Behavioral observations were also attempted on a group of siamang to the north east (known as Group 2). Attempts were made from mid-September, with little success. Trying to locate the group from territorial calls proved difficult, as they seemed to range between a hilly region in the centre of the Sikundur trail system and a boggy, partially flooded area to the north east. They repeatedly fled at the sight of researchers, and as terrain was difficult, following them for more than a few hours was problematic. After almost a month of trying to follow the group, habituation attempts were abandoned, as the allotted time for field work was coming to an end and there was little improvement in the habituation process (Figure 3.4).

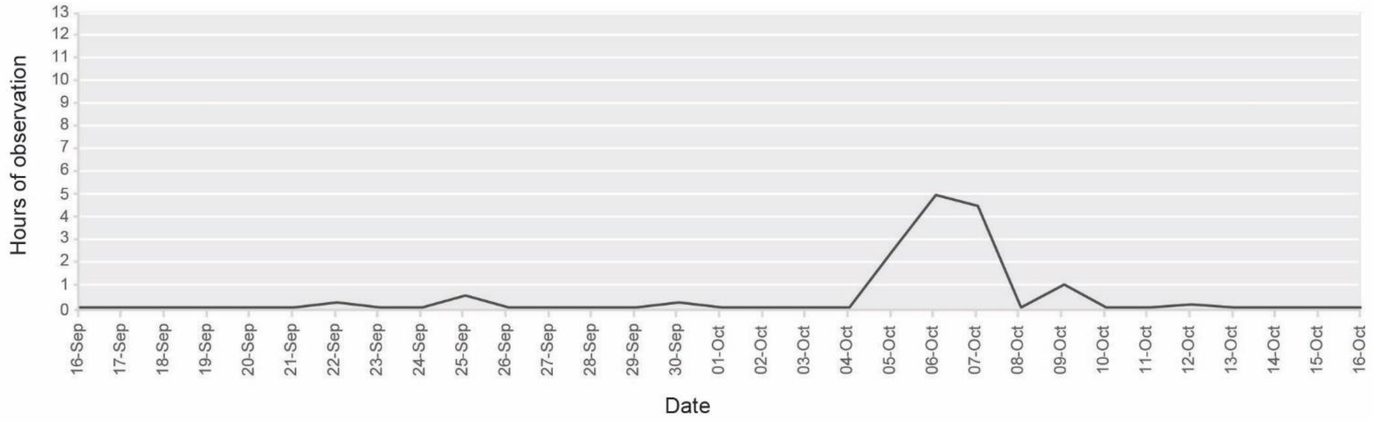


Figure 3.4 - Timeline of hours of observation of Group 2. Total observation hours = 14

3.2.2 Behavioural observations

Behavioural observations were made by three field assistants (Ucok, Dian and Yansa) and myself during all-day follows, using established methods (Altman, 1974). During observations, the activities of the siamang group were recorded at 10-minute intervals, referred to as scan sampling (Altman, 1974). Activities were classified as; resting, feeding/foraging (reaching for, handling, chewing, or swallowing food and drinking), travel, or ‘other’ which included social activities (e.g., vocalization, social grooming, social play, copulation) (Lappan, 2010). These behaviour states formed the basis for behavioural data collection. In addition to the behavioural state of the group, GPS points were taken from the approximate centre of the group every 10 minutes to record their location, and the approximate height of the group from the ground was recorded within 2 metres with the use of a Nikon Forestry Pro laser rangefinder. Within these 10-minute periods, a focal animal was chosen (rotating among members every 10 minutes) and their behaviour recorded in detail, utilising sub-categories and further details if possible (Table 3.1). Additionally, during these recordings, the approximate spread of the group from the focal individual was estimated (distance of other individuals from the focal animal), all animals' heights from the ground and any social interactions and the direction of the social interaction (who it was directed towards, received from, or if it was mutually performed) were recorded (Figures 3.5 and 3.6).

The one habituated group of siamang was made up of 3 individuals; an adult male (AM), an adult female (AF) and a sub-adult male (SAM). We initiated behavioural data collection upon the departure of the first animal from the sleeping site (or upon the first encounter of an animal in the group if sleeping site departure was not observed) and collected data until the focal adult entered the subsequent sleeping site. Behavioural data were collected from the single habituated group from the 18th of July until the 22nd of November 2017.

Behavioural data were collected using the AnimalObserver iPad application, with all data fields customised to follow Table 3.1, allowing detailed behavioural observations to be made with high inter-observer reliability (>95%).

Table 3.1 Categories of behaviour used in data collection

Category	Sub-category	Detail
Travel		
Rest		
Feed/forage	Leaf	Young Old Stem
	Fruit	All Pith Seed Flesh Skin
	Vine	
	Drink	
Other	Groom	direct to… received from… mutual with…
	Play	direct to… received from… mutual with…
	Long call	
	Copulate	with…

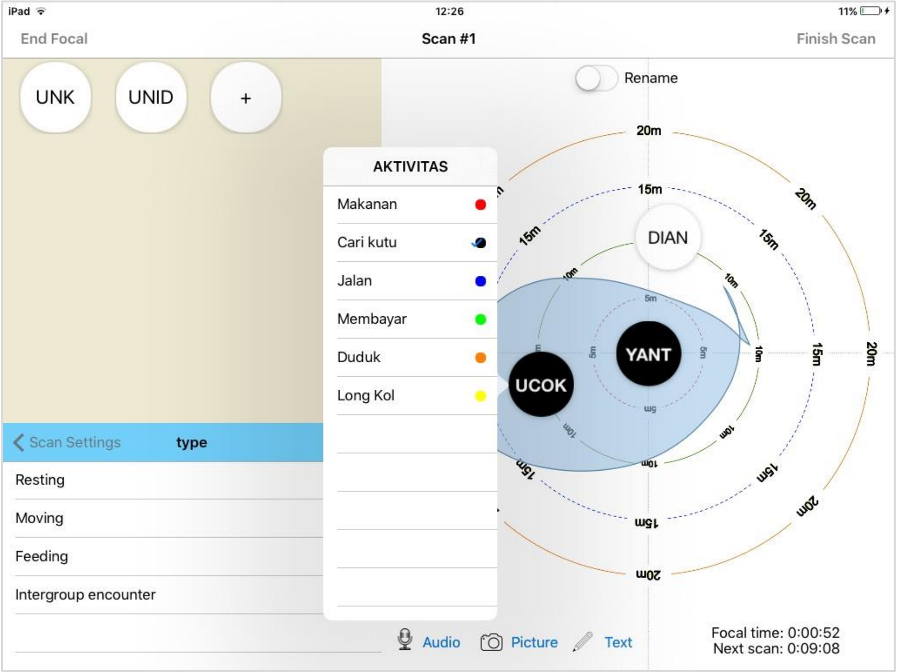


Figure 3.5 – screen shot of AnimalObserver iPad application in use, showing a group behavioural scan sample taking place

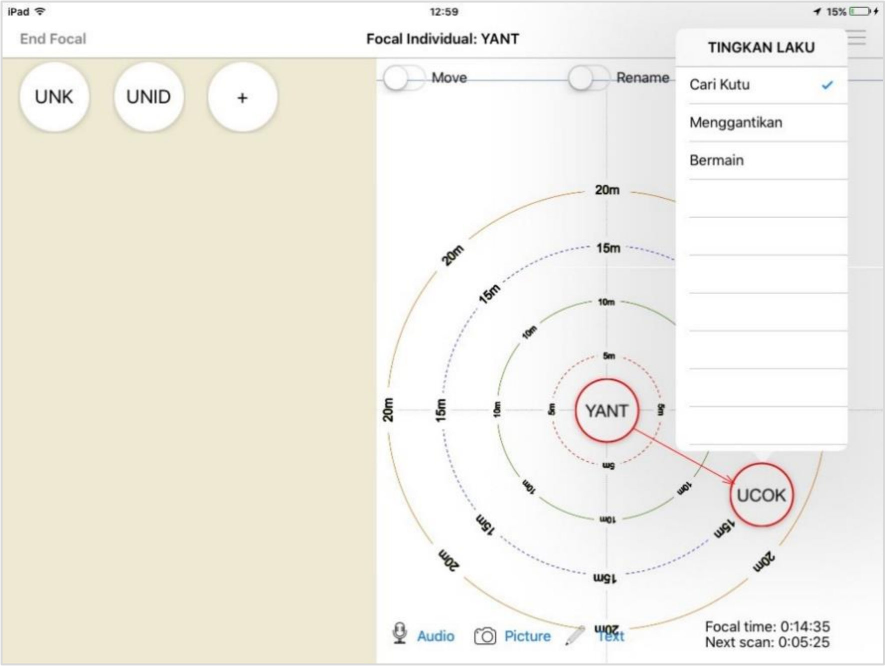


Figure 3.6 – screen shot of AnimalObserver iPad application in use, showing a behavioural interaction between two individuals

3.2.3 Canopy structure and microclimate

To assess the canopy structure of areas used by the group of siamang, the GPS points taken at the group's centre were imported into ArcGIS (version 10.4). Using the "Extract values to points" function, aggregated values from the 25x25m cells of the Digital Surface Model (created in Chapter 2, see sections 2.2.4, 2.3.3 and Figures 2.22 and 2.24) were extracted at these locations (Figure 3.7). Similarly, potential incoming solar radiation values were extracted for the GPS points from the layer calculated in Chapter 2, with the date and time of each GPS point determining which PISR layer was used. The variables extracted from the Digital Surface Model were: 'max minus mean' (mean elevation within the aggregated 25m spatial resolution subtracted from the maximum elevation within the aggregated 25m spatial resolution), 'min' (minimum elevation within the aggregated 25m spatial resolution), 'range' (range of elevations within the aggregated 25m spatial resolution), and 'relative height' (mean elevation within an aggregated 75m spatial resolution minus the mean elevation within 25m spatial resolution). To allow for the comparison of these values to a random selection, random points were generated (n = 10,000) using the "Create random points" function in ArcMap, constrained within a polygon shape of the siamang home range (see Figure 3.11). From these points the same elevation variables were extracted using the same methods as for the siamang's actual locations. For incoming solar radiation values to be randomised, random month and times values were created, within the range of values recorded in the siamang dataset, using the 'RANDBETWEEN' function in MS Excel (version 1902). These values were then matched to the times and months of incoming solar radiation values and the corresponding values extracted.

To estimate the microclimate that siamangs were experiencing, values from time dependent models (see Section 2.3.4, Table 2.3) were extracted from the siamang group's location. Aggregated DSM values based on univariate statistics of elevation within a 25x25m grid and potential incoming solar radiation values with the same grid were extracted from the respective layers, as well as weather condition values at the time the GPS points were recorded. The siamang group's mean height at the time of the GPS point was also used. These values (Aggregated DSM and potential incoming solar radiation) replaced variables in the hourly microclimate model generated in Chapter 2 (see Table 2.3, Section 2.3.4) giving an estimation of the microclimate conditions the siamang were experiencing at any given time. To enable the comparison of the modelled microclimate that the siamang were experiencing and a randomised sample, random locations were generated (n = 20,000) using the "Create random points" function in ArcMap, constrained within a polygon shape of the siamang home range (see Figure 3.9). For these random points, random times, months and heights were generated, within the range of values recorded in the siamang dataset, generated using the 'RANDBETWEEN' function in MS Excel (version 1902).

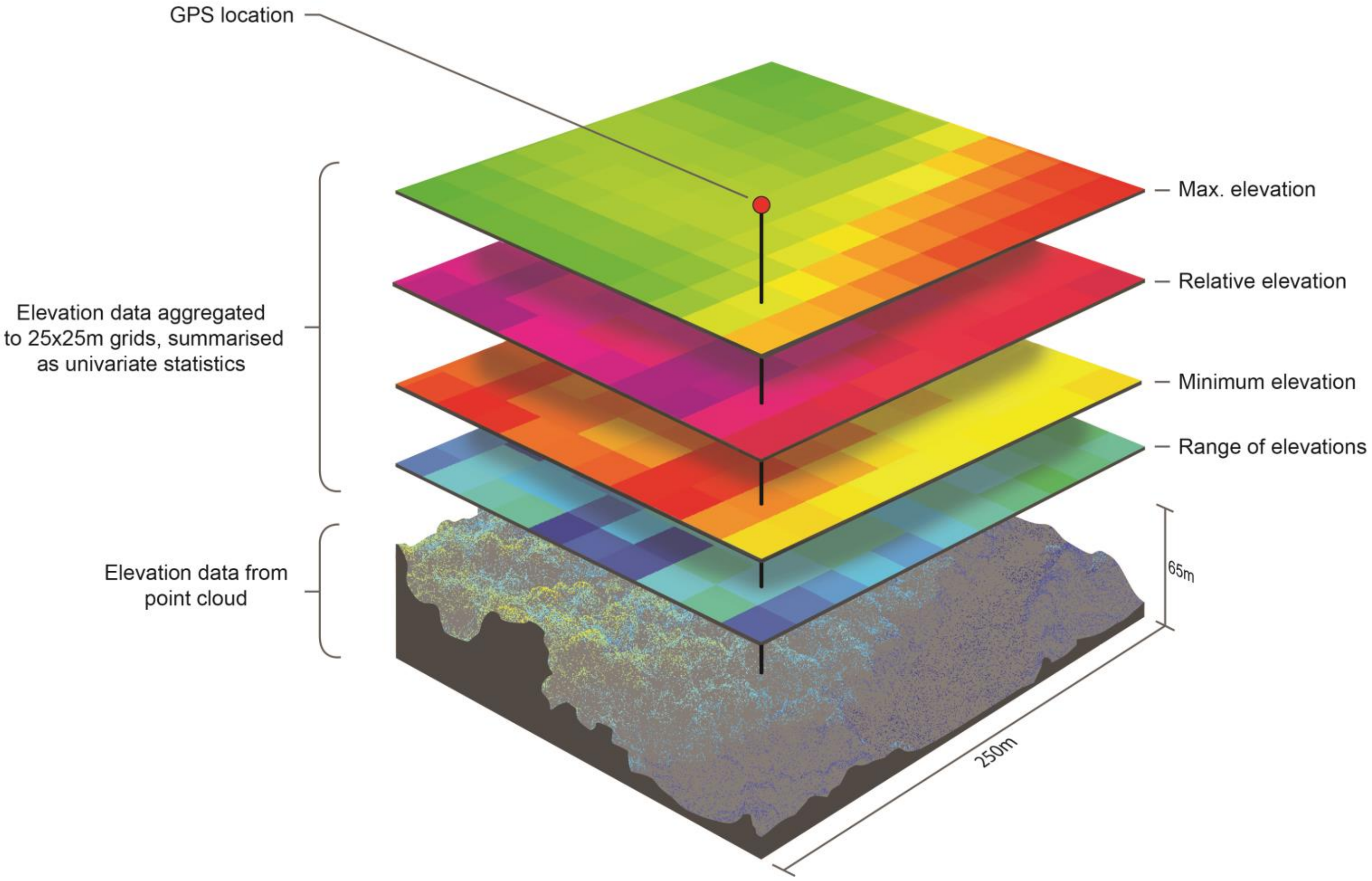


Figure 3.7 – Illustrative data extraction method for siamang canopy use

Data points were sub-sectioned for analysis into those recorded in high, low and moderate cloud cover. Each hour was divided on the basis of cloud cover, with the lower 25th percentile or below (<25%) being low cloud cover, between the 25th and 75th percentile (>25%, <75%) moderate cloud cover and above the 75th percentile (>75%) high cloud cover (see Section 2.2.3).

3.2.4 Ranging and activity budgets

Activity budgets were assessed as a percentage, with the time spent engaged in each activity divided by the total time of observation, either during the whole observation period or observation day (Altman, 1974). Home range analysis was performed using the adehabitatHR package (Calenge, 2006), in R (version 3.4.1) using kernel utilisation distribution estimation; a bivariate probability density function which gives the probability density of the animal being located at any position according to the xy coordinates.

3.2.5 Sleep sites

To assess the canopy structure of sites used by the group of siamang for sleeping, GPS points taken at sleeping trees were imported into ArcGIS (10.4). Using the “Extract values to points” function, aggregated values from the Digital Surface Model (created in Chapter 2, see sections 2.2.4, 2.3.3) measuring canopy topography in a 25x25m grid, were extracted at these locations, using the same method described above, in section 3.2.3 (see Figure 3.13). To allow the comparison of chosen sleeping sites and other available locations, a randomised selection of sites (n = 100) was created using ‘Random points’ function in ArcMap, constrained by the siamang group’s home range (Figure 3.12) with a minimum of 25m distance between each point. Variables extracted from the aggregated DSM, for both the siamang sleeping sites and the randomised selection of sites, were; ‘max minus mean’ (mean elevation within the aggregated 25m spatial resolution subtracted from the maximum elevation within the aggregated 25m spatial resolution), ‘max’ (maximum elevation within the aggregated 25m spatial resolution), ‘min’ (minimum elevation within the aggregated 25m spatial resolution), ‘median’ (median elevation within the aggregated 25m spatial resolution), ‘mean’ (mean elevation within the aggregated 25m spatial resolution), ‘range’ (range of elevations within the aggregated 25m spatial resolution), ‘standard deviation’ (standard deviation of elevations within the aggregated 25m spatial resolution), ‘mean 3x3’ (mean elevation within an aggregated 75m spatial resolution) and ‘relative height’ (mean elevation within an aggregated 75m spatial resolution minus the mean elevation within 25m spatial resolution). To enable a sleep site suitability map to be created, values from the above variables were extracted at siamang sleep sites and were compared to values extracted from random locations using Wilcoxon-Mann-Whitney rank sum tests. Variables that were found to be significantly different ($p < 0.05$) to the canopy variables from a random selection were selected, with the lower 10th percentile of each of these canopy variables was used as a threshold. A binary classification was then used for each of these variables, above (1/yes) or below (0/no) the lower 10th percentile threshold to establish preferred canopy structure of sleep sites over the entire study site. This was achieved using the ‘raster calculator’ function in ArcMap (version 10.4), using a binary selection for each variable (e.g. > threshold = binary zero/no, one/yes output). The resulting layers of each canopy structure variable were then added to each other to produce a habitat suitability index from zero to three with an index of zero describing areas in which no habitat structure variable met siamang sleep site suitability and an index of three describing areas in which all sleep site structure variable preferences were met.

3.2.6 Statistical analyses

Linear regressions were used to explore relationships between hours spent in activities and experienced levels of potential incoming solar radiation (measured in kilowatt hours per metre squared, kWH/m^2) (Basner et al., 2007). The non-parametric Kruskal-Wallis test for equality of populations, or one-way ANOVA on ranks, were used to compare canopy variables and potential incoming solar radiation (kWH/m^2), and temperature for the group sub-sectioned by cloud cover conditions and random selections (Hoffman and O'Riain, 2011). Results of Kruskal-Wallis tests were further explored using the Wilcoxon rank sum test, a paired difference test for non-normally distributed populations. All statistical analyses were performed with R (version 3.4.1) using R studio (version 1.0.153).

3.3 Results

3.3.1. Activity budget

From a total of 1257 observation hours, 1017 hours were used to assess the overall activity budget of the siamang group, with 240 hours recorded during the habituation process removed from analysis. Siamang as a collective group spent 552 hours, or 54.8% of observation hours, foraging or feeding, 30.75% of which was spent feeding or foraging on fruit; 167 hours (16.64%), were spent resting, 254 hours (25.24%), were spent travelling and 26 hours (3.31%) were spent in other activities, such as grooming, playing or territorial calling (Figure 3.8). By time of day, activity budgets were relatively stable from 7am-4pm, with more time spent resting in the early morning (having awoken but yet to leave the sleep site) and more time travelling at 5pm and 6pm (to reach a sleep site) (Figure 3.9).

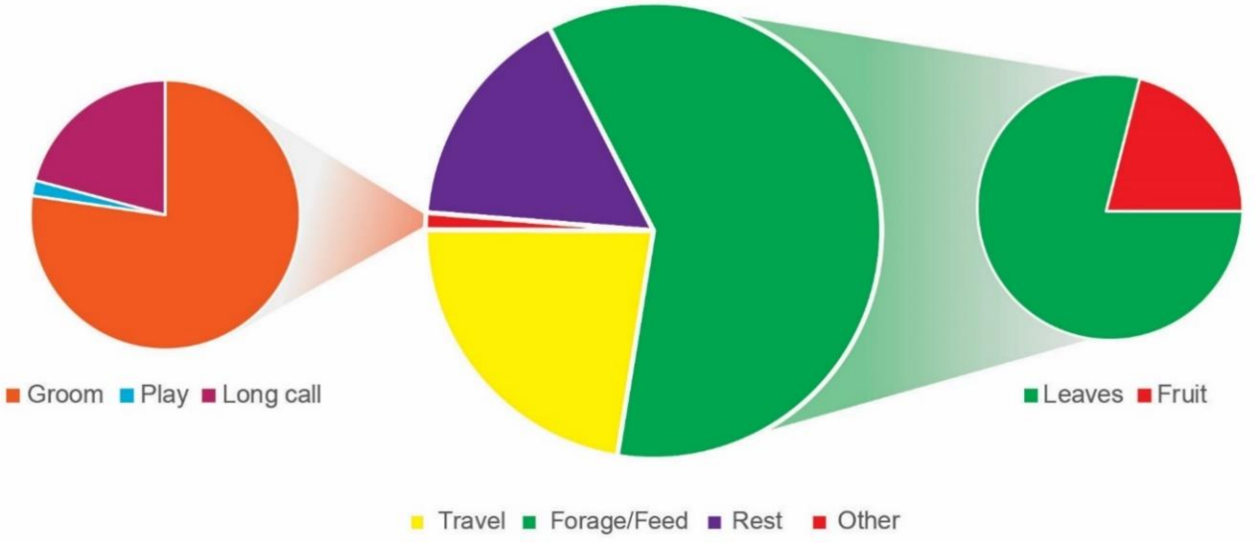


Figure 3.8 - Percentages of total siamang activity time-budgets

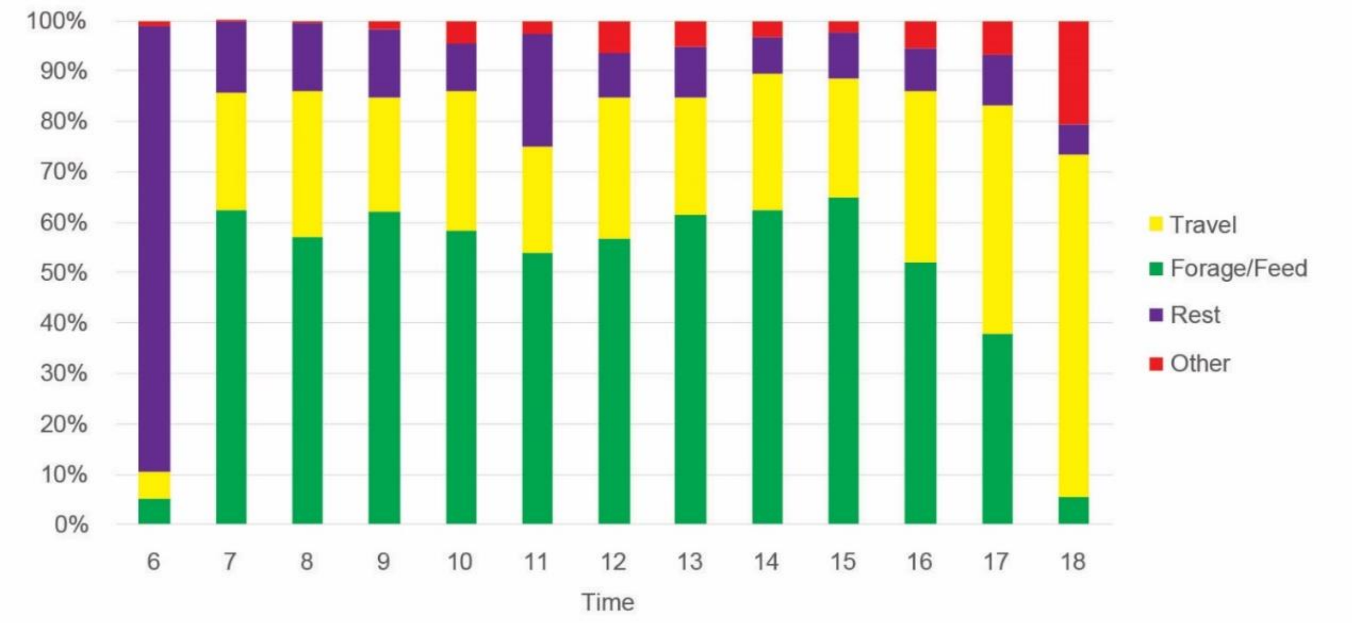


Figure 3.9 – Mean activity budget of siamang by hour

Figure 3.10 – Daily activity budget of siamang by date over the study period

3.3.2 Home range

Home range estimates were made using the 4396 GPS points recorded during behavioural follows, not including follows during the habituation period. The 95% home range size is estimated to be 64.63 hectares, or 0.64km^2 (Figure 3.11). The home range was bordered by the Besitang river to the south, east, and west and an old logging road to the north/north-west.

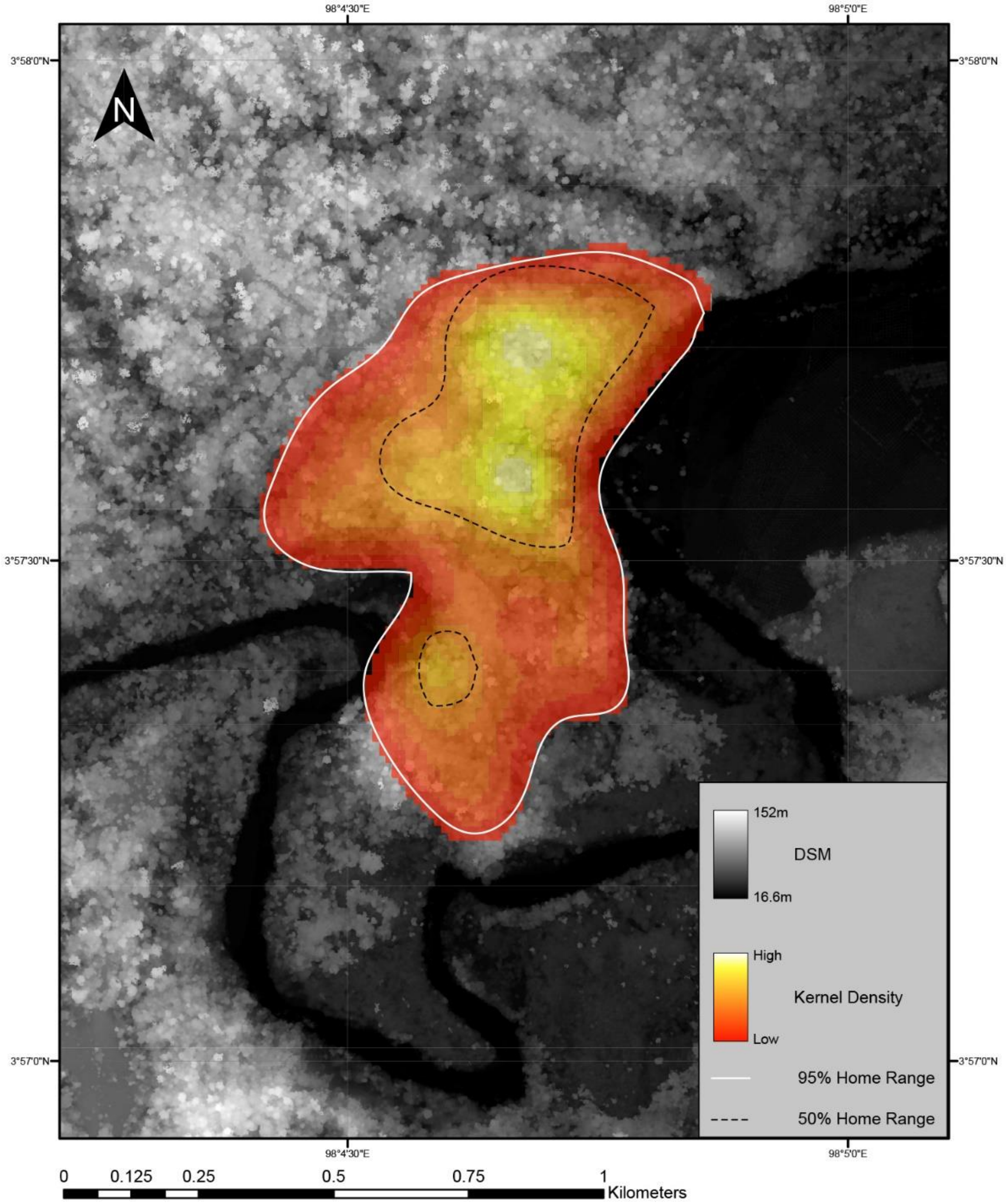


Figure 3.11 – Estimated 95% and 50% Home Range of siamang group with kernel density of use of area shown in relation to Digital Surface Model

3.3.3 Sleep sites

The siamang group used a total of 7 sleep trees during the study period, which were entered at the end of the day between 3:06pm - 6:24pm, with an average time of 4:56pm. On only one occasion was the group known to have left a sleeping tree after observations had been terminated for the day (August 29th, 2017). Typically, sleeping trees were above 30m in height, and their tree crowns relatively isolated from the surrounding canopy, often only being accessible by one neighbouring branch or by lianas.

Canopy variables extracted from DSM data (aggregated to 25x25m cells) at the location of sleeping sites were significantly different from randomised locations. Sleeping sites were significantly higher (Max elevation K-W: $X^2 = 5.423$, $p = 0.020$) and their relative elevation was higher than the canopy in the surrounding area (K-W: $X^2 = 4.722$, $p = 0.030$). Grid cells which contained sleeping sites had a higher range of elevations within the 625m^2 area of their grid (K-W: $X^2 = 4.779$, $p = 0.029$) and the standard deviation of these heights was significantly higher (K-W: $X^2 = 10.562$, $p = 0.001$) suggesting canopy gaps were present around sleeping sites. Mean elevations were also significantly higher from other areas (Mean elevation: K-W: $X^2 = 4.3359$, $p = 0.037$. However, minimum, median and max – mean elevations were not significantly different (median elevations: K-W: $X^2 = 2.8665$, $p = 0.090$, minimum elevation: K-W: $X^2 = 1.0372$, $p = 0.309$, max – mean elevation: K-W: $X^2 = 1.838$, $p = 0.175$) (Figure 3.12).

Use of each sleeping tree ranged from 1 to 35 times, although three sites were favoured, being used more than 20 times each (Figure 3.13). Frequency of use was not found to be significantly correlated with any aggregated DSM derived variable.

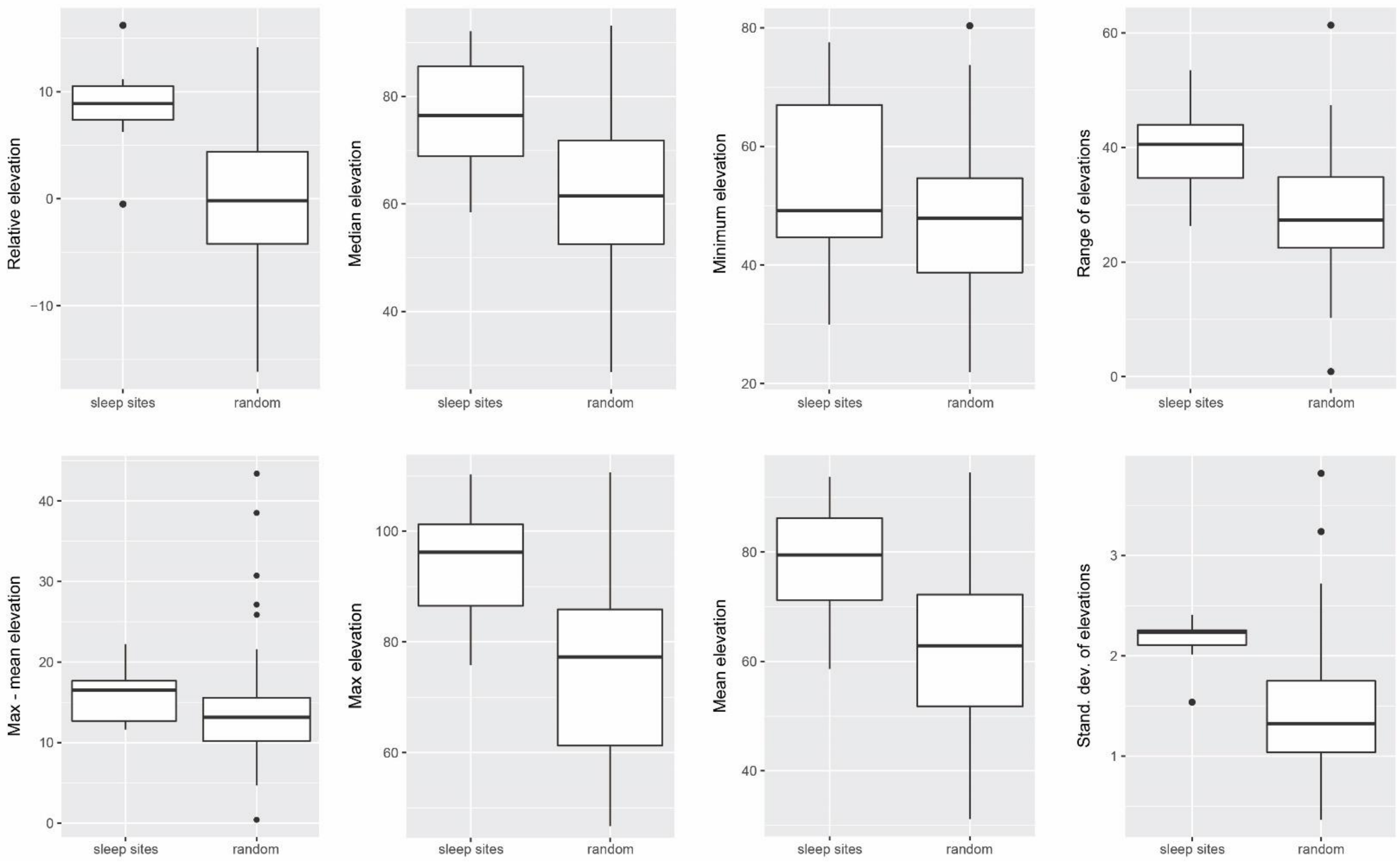


Figure 3.12 – Aggregated DSM values at sleeping sites compared with a random selection of non-sleep sites within the siamang group’s home range

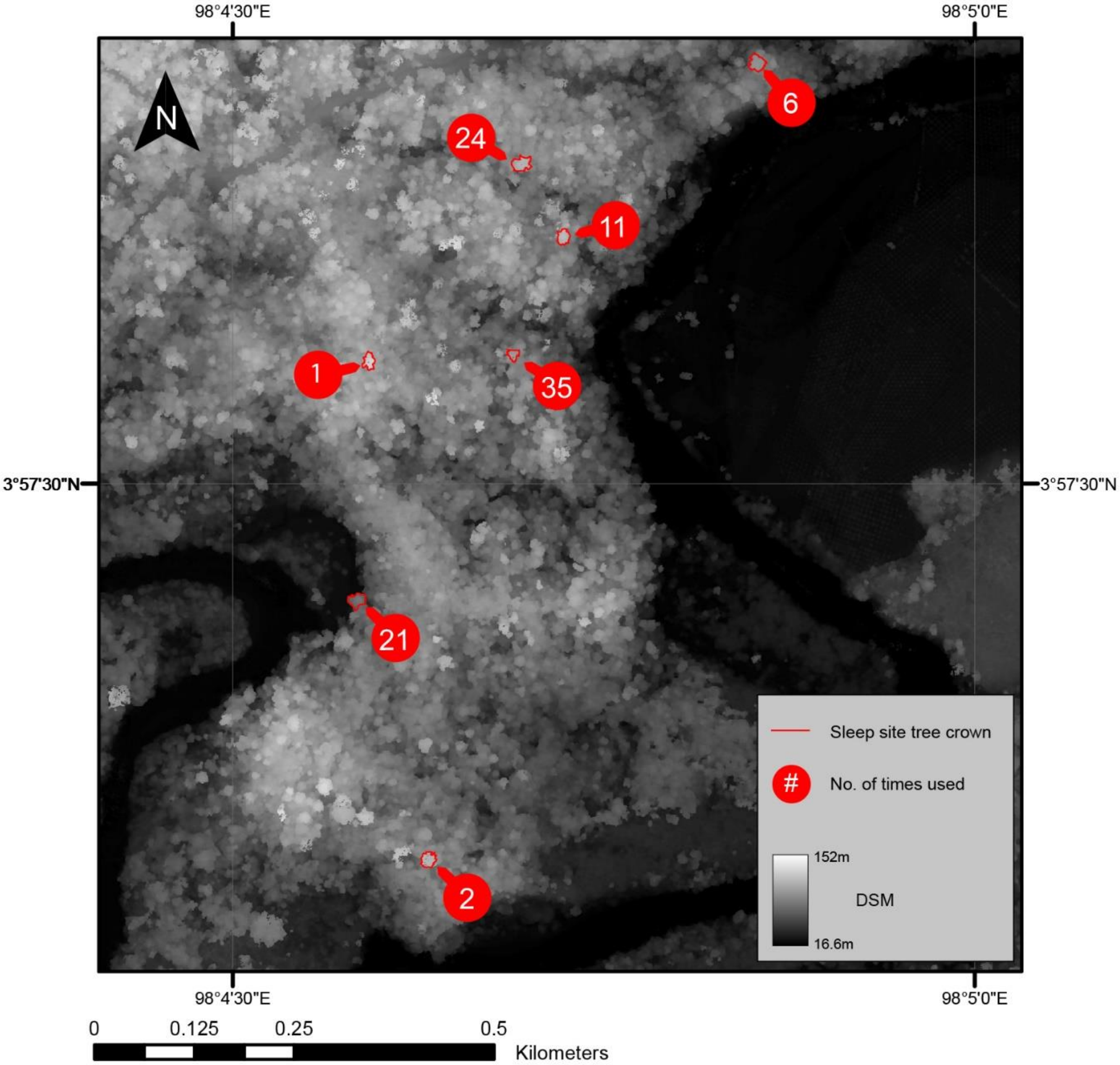


Figure 3.13 – Locations and frequency of use of siamang sleep sites plotted on the DSM map

By extracting variables from sleep sites that were statistically different from a random selection (range, standard deviation and relative elevation), and projecting these values across the entire site covered by UAV canopy surveys (see Section 2.3.3 and Figure 2.21) a simple suitability index for each 25x25m grid cell across of the entire site was produced, identifying possible siamang sleep sites throughout the larger Sikundur area (Figure 3.12).

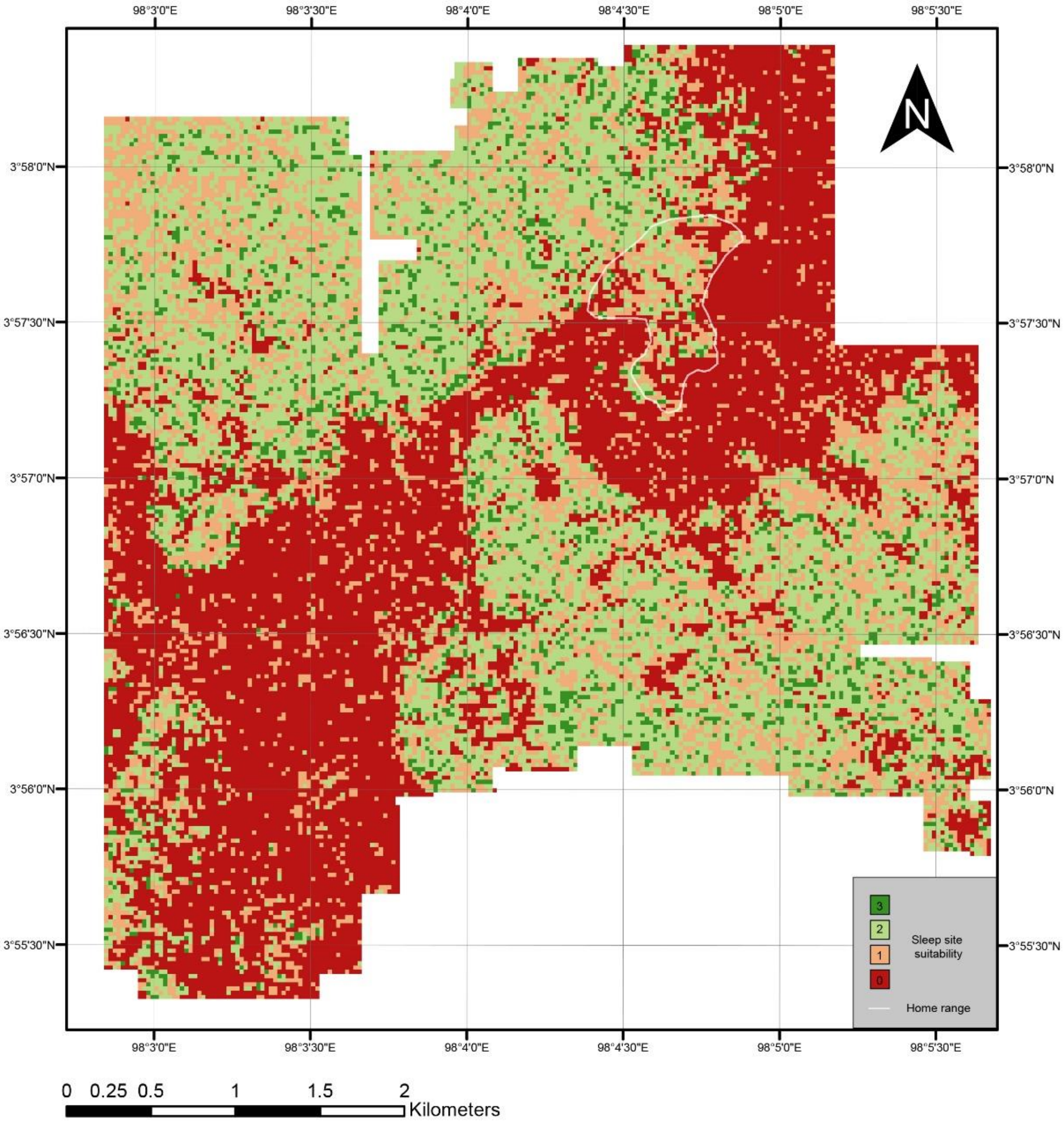


Figure 3.14 – Estimated index of siamang sleep site suitability across the larger Sikundur area, from low suitability (0) to the most suitable (3) of each 25x25m grid cell

3.3.4 Group spread and height

Group spread (distance between group members) was relatively small with the group's mean spread at 4.7m (±2.1m) from the focal individual. The maximum mean group spread (i.e. the maximum of the average distance of two other individuals from the focal individual) was recorded as 21m and the maximum total distance of an individual from the focal individual at the time of a scan sample was estimated at 32m. Mean distance of each individual from the focal individuals did not differ much among the groups' members: Adult Male: 7.6m ± 4.3m, Adult Female: 6.9m ± 3.9m, Sub-Adult Male: 6.7m ± 3.4m. Group spread fluctuations were not found to be correlated to any canopy structure, weather variable or time of day variable (at $p < 0.05$).

Mean height of the group above ground level ranged from 0-30m, with a single instance of an individual (Adult Male) coming to the ground, to consume soil. Mean group heights were significantly variable across hours of the day (K-W: $X^2 = 377.08$, df = 12, p = < 0.001), although to a lesser extent between 7am-5pm (K-W: $X^2 = 52.32$, df = 9, p = < 0.001) (Figure 3.15).

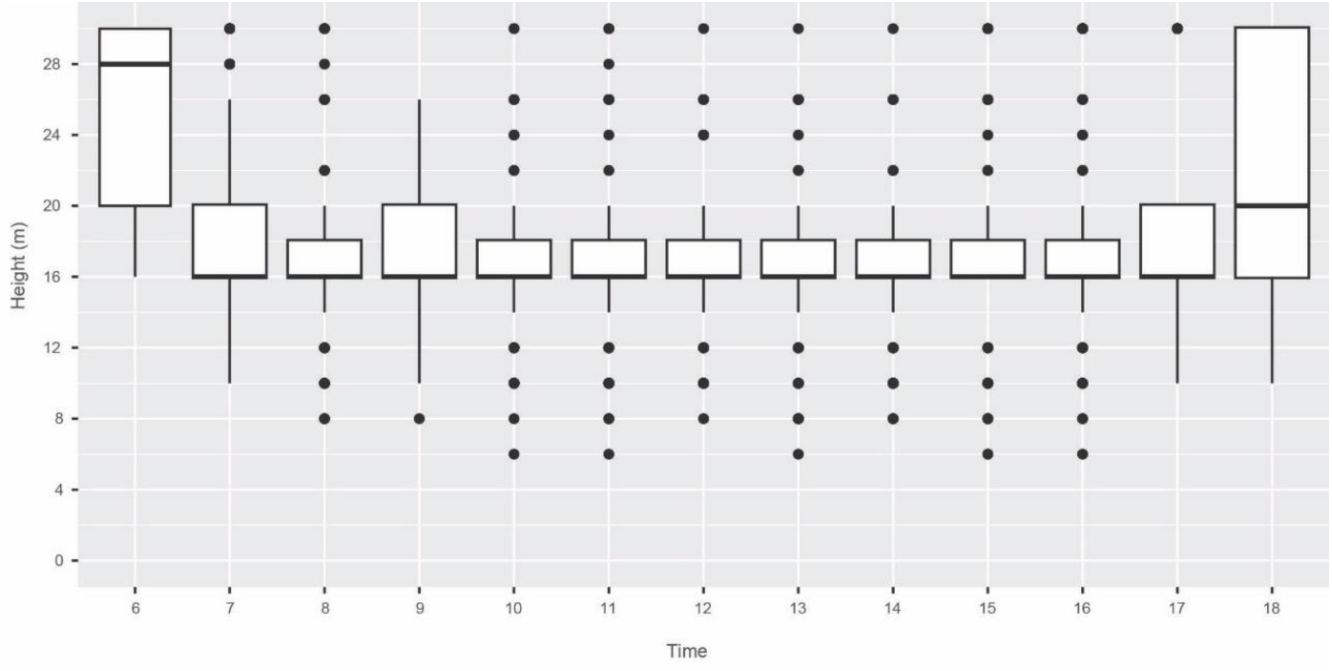
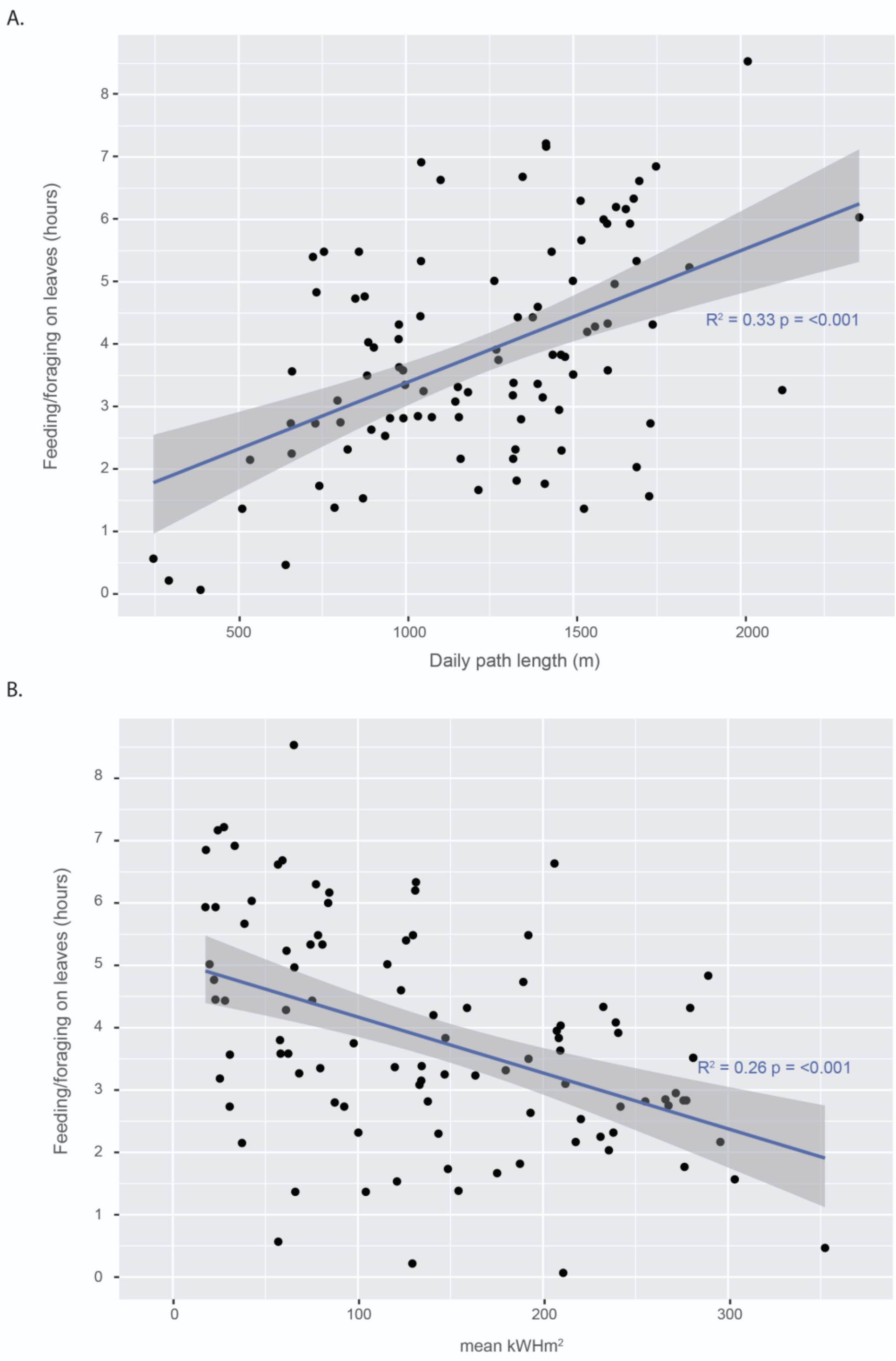


Figure 3.15 – Mean siamang group height (m) shown by time of day

To see daily behavioural patterns developed in response to environmental factors or behavioural limits, daily sums of behavioural classifications were compared to each other (from days with >8 hours of observation) and to environmental measurements. Time spent feeding/foraging on leaves was related to daily path length (Time feeding on leaves ~ daily path length, β = 0.0001, $R^2 = 0.329$, p=<0.001) and negatively related with the mean levels of solar radiation that the siamang group experienced (measured as mean kWHm^2; daily mean height ~ mean kWHm^2, β = -0.010, $R^2 = 0.255$ p=<0.001). There was a negative trend between time spent feeding or foraging for leaves and time spent feeding or foraging on fruit (Time feeding on leaves ~ Time feeding on fruit, β = -0.25373, $R^2 = 0.156$, p=<0.001). Mean solar radiation experienced by the siamang group was also negatively related to the mean height that the siamang were recorded at that day (β = -0.01003, $R^2 = 0.263$, p=<0.001). There was also a positive trend between mean solar radiation experienced and time spent resting (β = 0.0002, R^2 = 0.141, p=<0.001) and time spent resting and the mean temperature recorded by data logger that day (β = 0.0155, R^2 = 0.182, p=<0.001).

Figure 3.16 –Daily totals of time spent feeding and foraging for leaves in relation to; A. Daily path length B. potential incoming solar radiation (measured in mean kWHm^2)



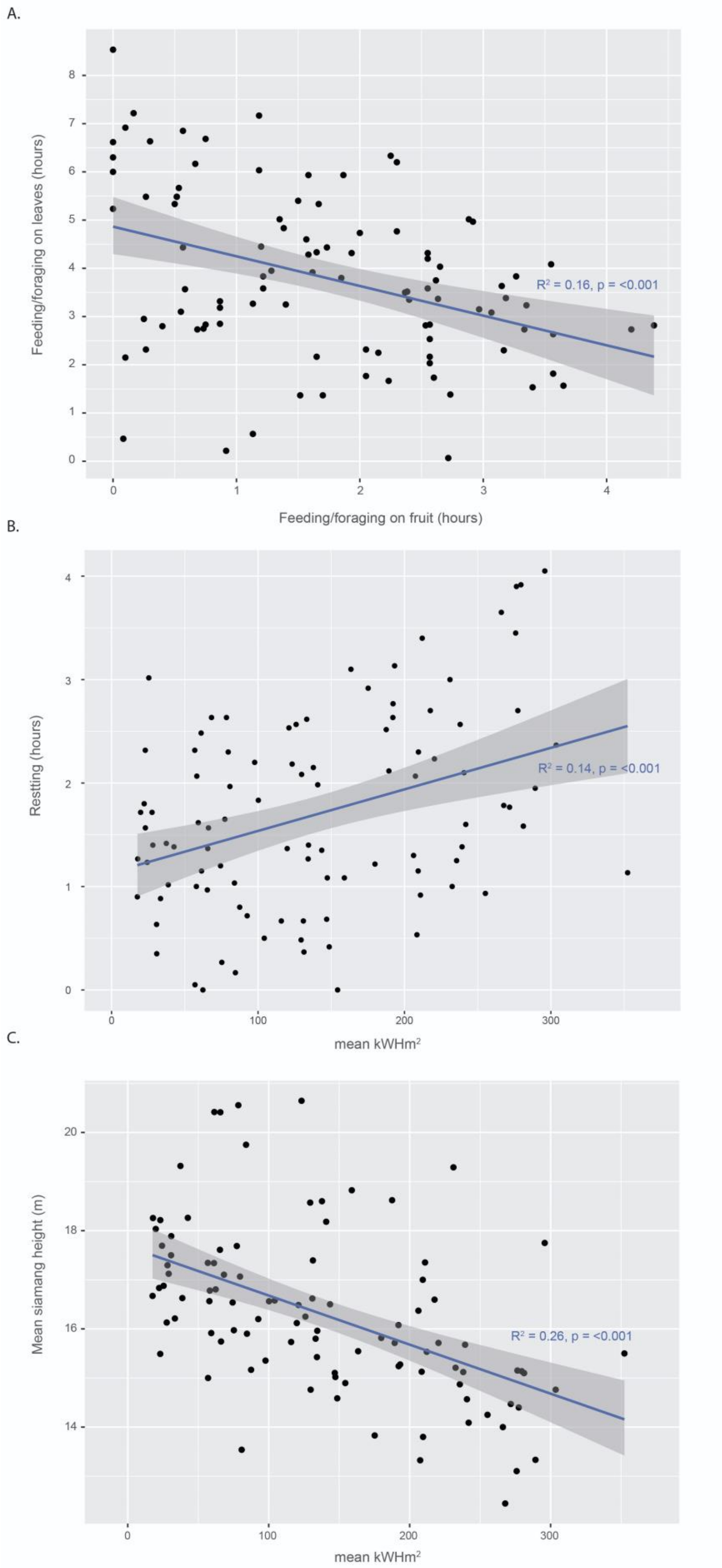


Figure 3.17 – linear regression results of **A.** time spent feeding on leaves compared to fruit **B.** Time spent resting compared to mean solar radiation **C.** Mean height compared to mean solar radiation (kWH/m^2)

3.3.5 Canopy structure

The siamang group's use of areas with different canopy structures varied throughout the day. Canopy structure variables associated with microclimate (see Table 2.2 and 2.3) extracted from siamang locations were significantly variable across the time of day (Minimum elevation, K-W: X^2 = 78.98, df = 12, p = 0.008, Relative elevation, K-W: X^2 = 75.623, df = 12, p = < 0.001, Maximum minus mean elevations, K-W: X^2 = 30.929, df = 12, p = 0.002, Range of elevations, K-W: X^2 = 23.73, df = 12, p = 0.02213, Figure 3.18).

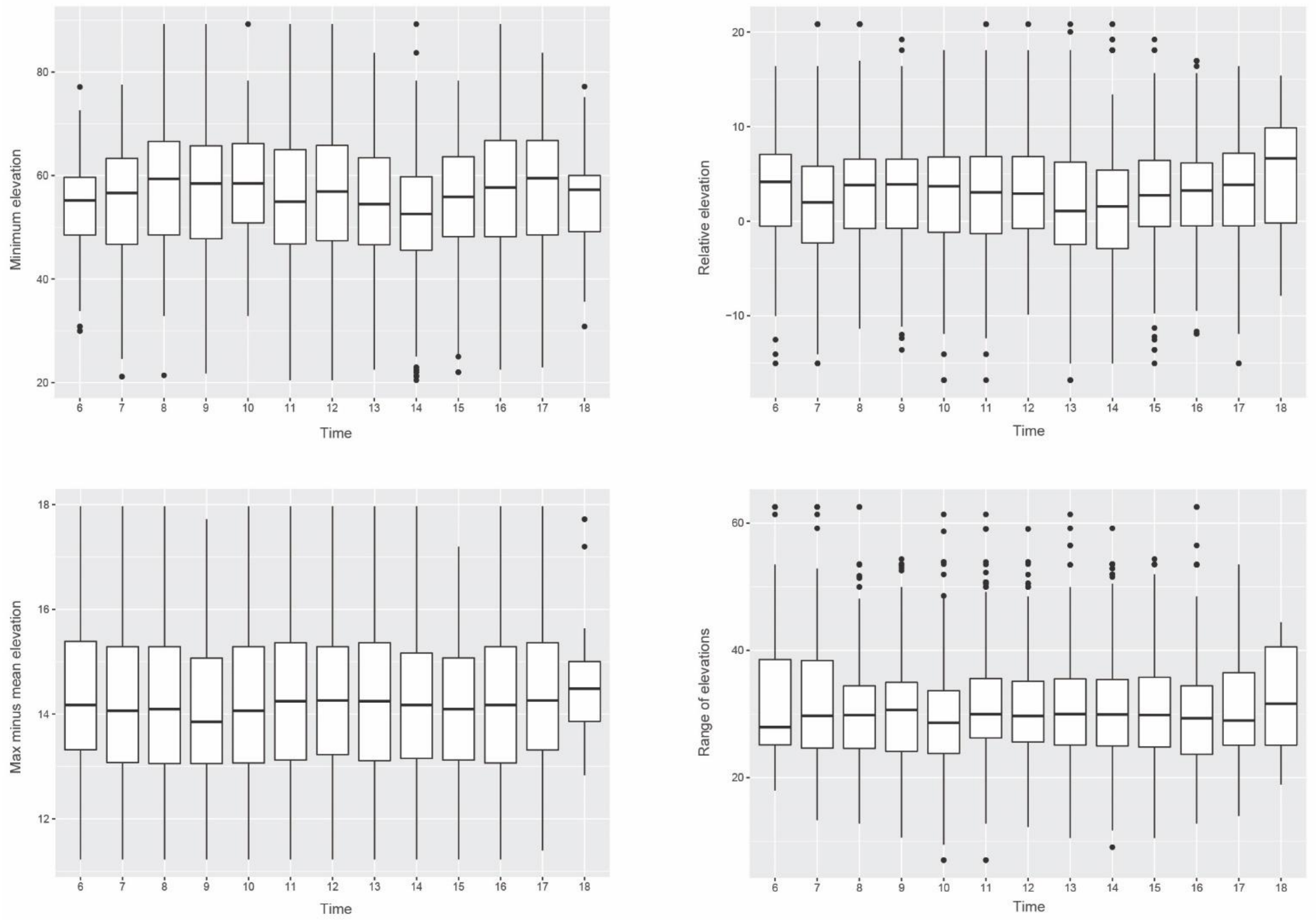


Figure 3.18 – Canopy variables associated with microclimate extracted from siamang locations, shown by hour

To see if particular canopy structures were required, or preferred, by the siamang group for different activity states to take place in, extracted canopy variables were grouped by the activity that was recorded taking place. No significant difference was found between canopy structures chosen for different activities (Minimum elevation, K-W: X^2 = 0.70458, p = 0.872, Max minus mean elevation, K-W: X^2 = 1.7345, p = 0.629, Range of elevations, K-W: X^2 = 0.76917, p = 0.856) with the exception of Relative height (K-W: X^2 = 28.247, p = <0.001). Relative height was found to be significantly variable between all activity states (Pairwise comparisons using Wilcoxon rank sum test: feed/forage ~ other; p = 0.0024, rest ~ other ; p = 0.010, travel ~ other; p = <0.001, travel ~ feed/forage, p = 0.002, rest ~ travel, p = 0.022) with the exception of 'rest' and 'feed/forage' activities (Figure 3.19).

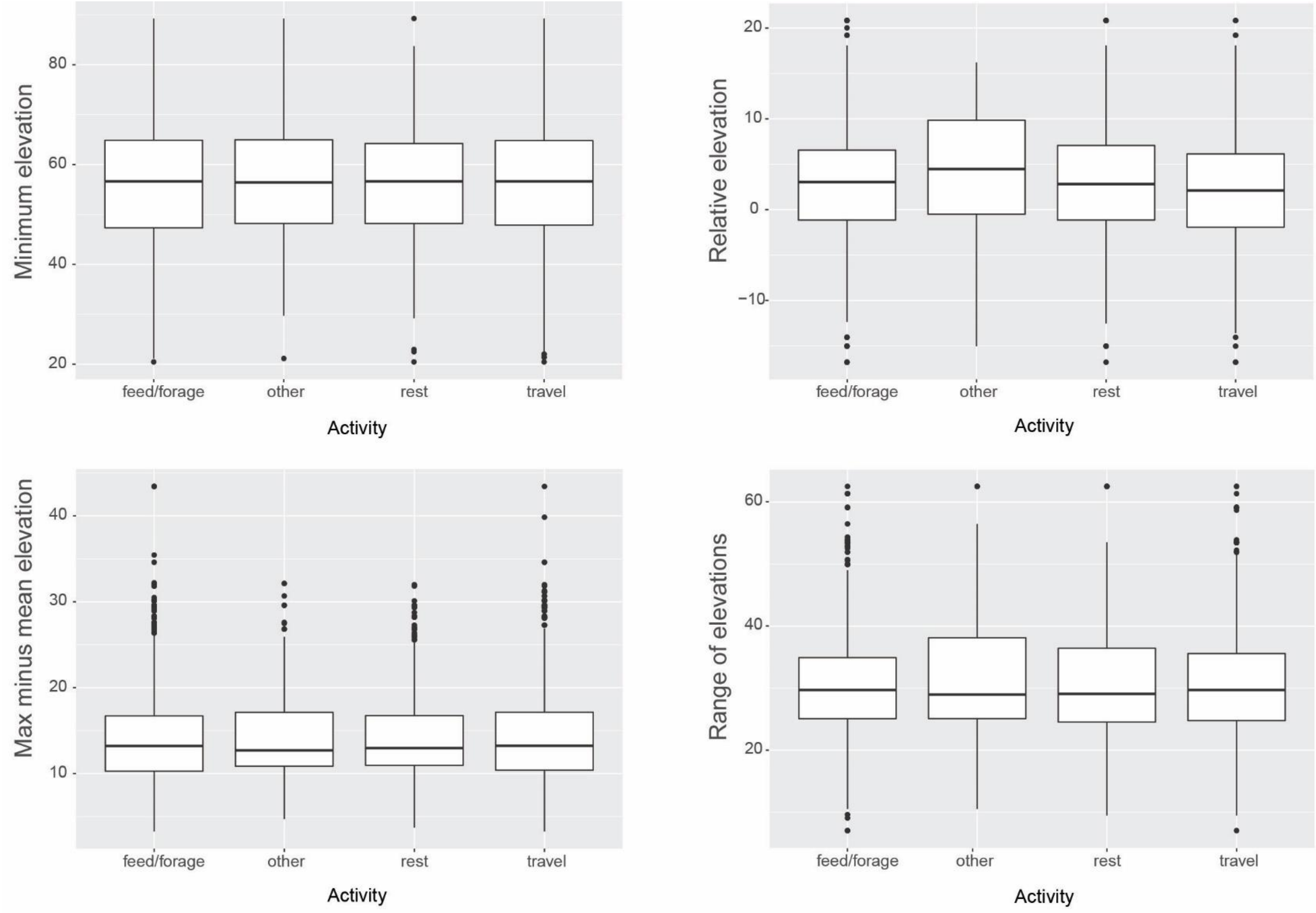
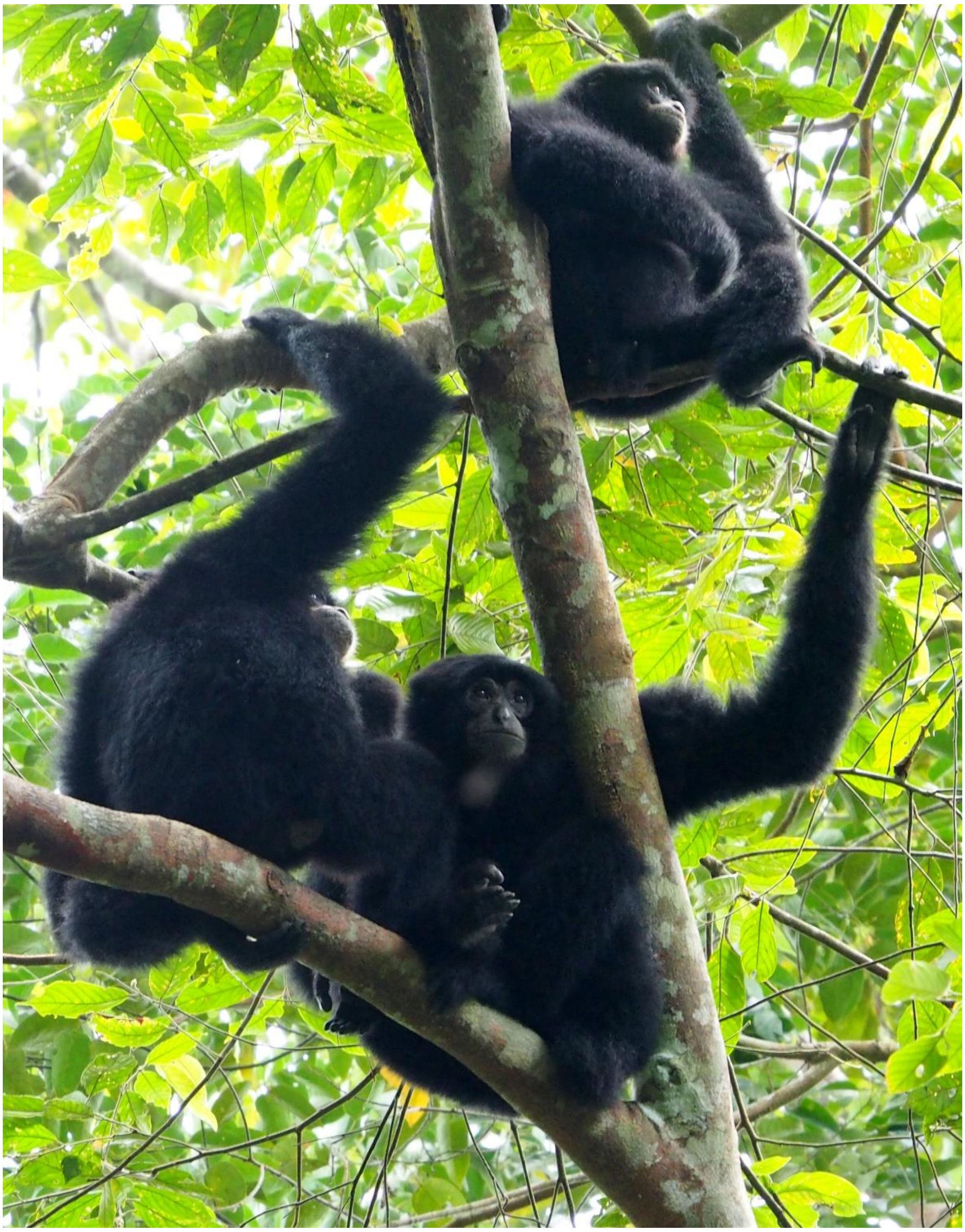


Figure 3.19 – Siamang use of areas with different canopy structures by grouped by activity state

To see whether canopy structure use was selective, and possibly increasingly selective with changing weather conditions, siamang use of canopy structure was divided into three categories, those recorded in high cloud cover (>75%), low cloud cover (<25%) and moderate cloud cover (>25%, <75%). For comparison, a fourth category was produced using a random selection of locations from within the siamang's home range and canopy structure variables extracted from these locations. Canopy structure values differed significantly between these four categories (Minimum elevation, X^2 = 250.48, df = 3, p = <0.001, Relative elevation, X^2 = 116.54, df = 3, p = <0.001, Range of elevations, X^2 = 27.034, df = 3, p = <0.001) with the exception of 'Max – Mean' elevations (X^2 = 3.026, df = 3, p = 0.3876). Dividing these categories by time of day allowed a more detailed examination of canopy structure used by the siamang, relative to the four categories; high, low and moderate cloud cover and a random selection. Typically, canopy variables extracted from siamang locations were significantly different from a random selection (Table 3.2a and Table 3.2b). Variables extracted from siamang locations in high and low cloud cover also showed some significant variation from random locations and siamang locations recorded in more temperate conditions, mainly in Minimum and Relative elevations (Figures 3.20a and3.20b and Table 3.2). In general, variations in high and low cloud cover followed predicted values from all siamang canopy values, following relationships between these values and microclimate models. For instance, relative elevation, which is negatively correlated with microclimate temperatures, is found to be consistently higher in periods of low cloud cover than in periods of either moderate of high cloud cover (Figure 3.20a, Table 3.2a).



The habituated group of siamang

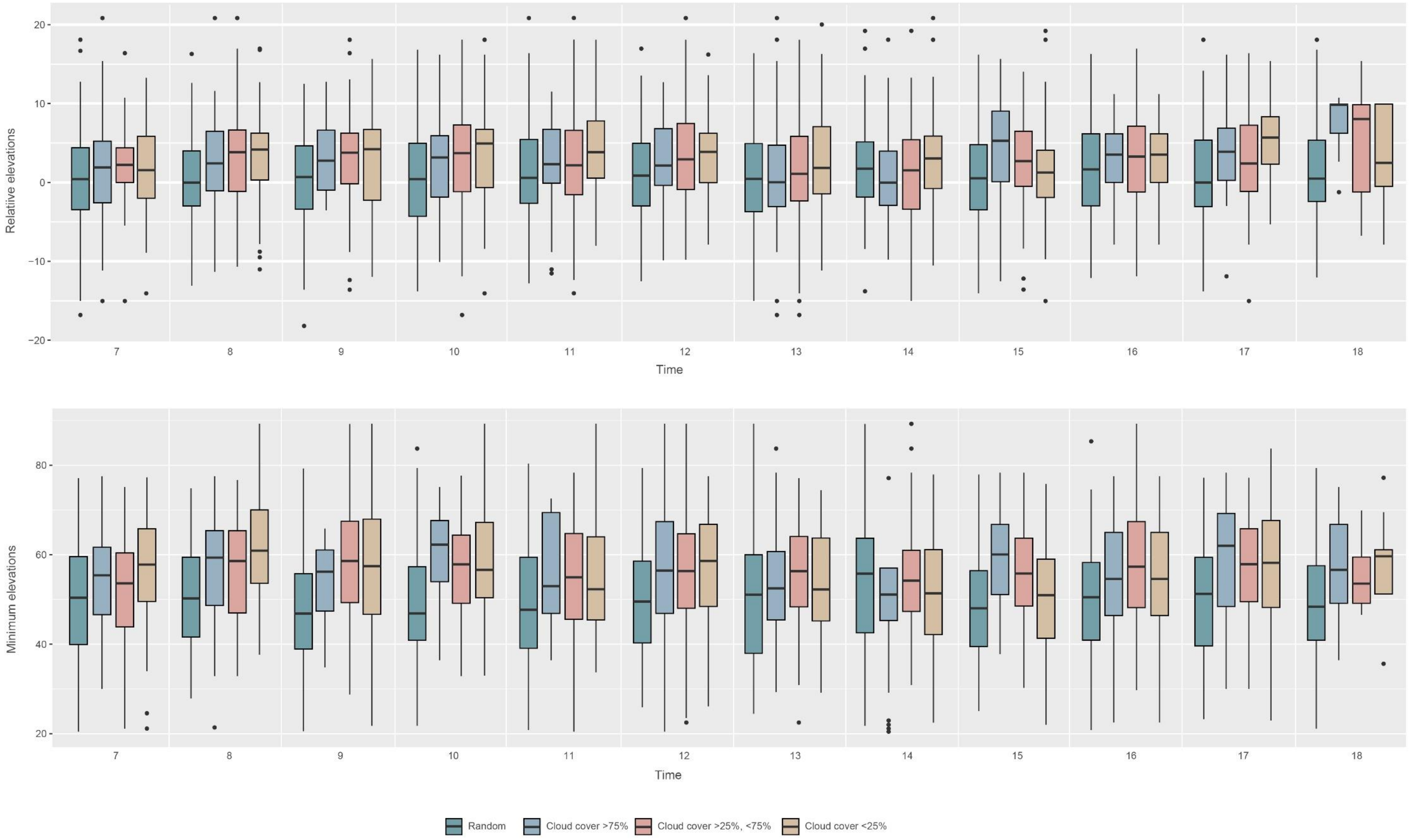
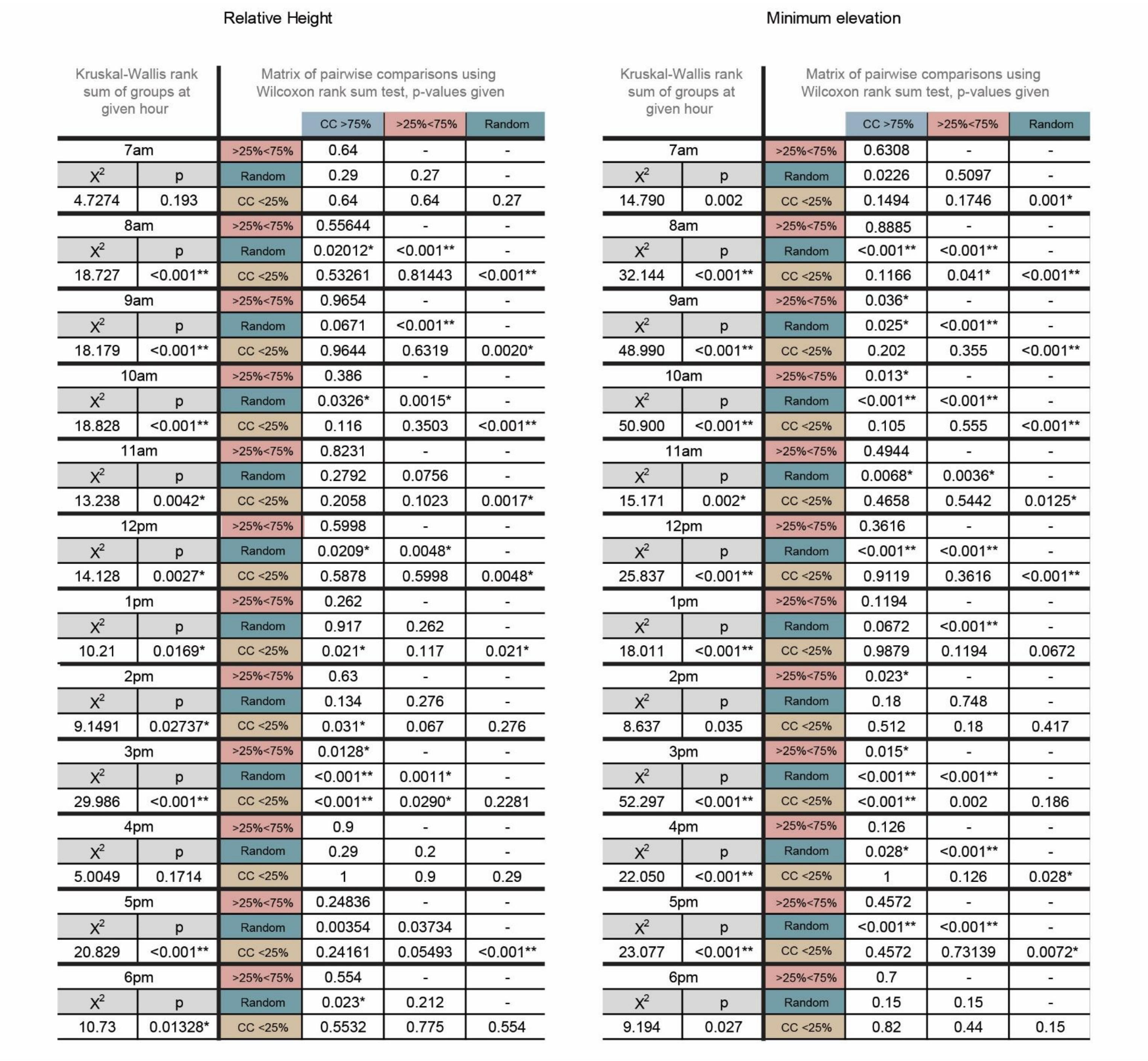


Figure 3.20a – Siamang canopy use in high, moderate and low cloud cover by hour of the day, shown with a random selection

Table 3.2a – Results of Kruskal Wallace rank sum tests between canopy variables extracted under differing conditions; siamang locations in moderate conditions (>25% - <75% cloud cover), those in high (>75%) or low (<25%) cloud cover and a random selection, given together with a matrix of relevant pairwise comparison using Wilcoxon rank sum test



Relative Height

Kruskal-Wallis rank sum of groups at given hour		Matrix of pairwise comparisons using Wilcoxon rank sum test, p-values given			
			CC >75%	>25%<75%	Random
7am		>25%<75%	0.64	-	-
X^2	p	Random	0.29	0.27	-
4.7274	0.193	CC <25%	0.64	0.64	0.27
8am		>25%<75%	0.55644	-	-
X^2	p	Random	0.02012*	<0.001**	-
18.727	<0.001**	CC <25%	0.53261	0.81443	<0.001**
9am		>25%<75%	0.9654	-	-
X^2	p	Random	0.0671	<0.001**	-
18.179	<0.001**	CC <25%	0.9644	0.6319	0.0020*
10am		>25%<75%	0.386	-	-
X^2	p	Random	0.0326*	0.0015*	-
18.828	<0.001**	CC <25%	0.116	0.3503	<0.001**
11am		>25%<75%	0.8231	-	-
X^2	p	Random	0.2792	0.0756	-
13.238	0.0042*	CC <25%	0.2058	0.1023	0.0017*
12pm		>25%<75%	0.5998	-	-
X^2	p	Random	0.0209*	0.0048*	-
14.128	0.0027*	CC <25%	0.5878	0.5998	0.0048*
1pm		>25%<75%	0.262	-	-
X^2	p	Random	0.917	0.262	-
10.21	0.0169*	CC <25%	0.021*	0.117	0.021*
2pm		>25%<75%	0.63	-	-
X^2	p	Random	0.134	0.276	-
9.1491	0.02737*	CC <25%	0.031*	0.067	0.276
3pm		>25%<75%	0.0128*	-	-
X^2	p	Random	<0.001**	0.0011*	-
29.986	<0.001**	CC <25%	<0.001**	0.0290*	0.2281
4pm		>25%<75%	0.9	-	-
X^2	p	Random	0.29	0.2	-
5.0049	0.1714	CC <25%	1	0.9	0.29
5pm		>25%<75%	0.24836	-	-
X^2	p	Random	0.00354	0.03734	-
20.829	<0.001**	CC <25%	0.24161	0.05493	<0.001**
6pm		>25%<75%	0.554	-	-
X^2	p	Random	0.023*	0.212	-
10.73	0.01328*	CC <25%	0.5532	0.775	0.554

Minimum elevation

Kruskal-Wallis rank sum of groups at given hour		Matrix of pairwise comparisons using Wilcoxon rank sum test, p-values given			
			CC >75%	>25%<75%	Random
7am		>25%<75%	0.6308	-	-
X^2	p	Random	0.0226	0.5097	-
14.790	0.002	CC <25%	0.1494	0.1746	0.001*
8am		>25%<75%	0.8885	-	-
X^2	p	Random	<0.001**	<0.001**	-
32.144	<0.001**	CC <25%	0.1166	0.041*	<0.001**
9am		>25%<75%	0.036*	-	-
X^2	p	Random	0.025*	<0.001**	-
48.990	<0.001**	CC <25%	0.202	0.355	<0.001**
10am		>25%<75%	0.013*	-	-
X^2	p	Random	<0.001**	<0.001**	-
50.900	<0.001**	CC <25%	0.105	0.555	<0.001**
11am		>25%<75%	0.4944	-	-
X^2	p	Random	0.0068*	0.0036*	-
15.171	0.002*	CC <25%	0.4658	0.5442	0.0125*
12pm		>25%<75%	0.3616	-	-
X^2	p	Random	<0.001**	<0.001**	-
25.837	<0.001**	CC <25%	0.9119	0.3616	<0.001**
1pm		>25%<75%	0.1194	-	-
X^2	p	Random	0.0672	<0.001**	-
18.011	<0.001**	CC <25%	0.9879	0.1194	0.0672
2pm		>25%<75%	0.023*	-	-
X^2	p	Random	0.18	0.748	-
8.637	0.035	CC <25%	0.512	0.18	0.417
3pm		>25%<75%	0.015*	-	-
X^2	p	Random	<0.001**	<0.001**	-
52.297	<0.001**	CC <25%	<0.001**	0.002	0.186
4pm		>25%<75%	0.126	-	-
X^2	p	Random	0.028*	<0.001**	-
22.050	<0.001**	CC <25%	1	0.126	0.028*
5pm		>25%<75%	0.4572	-	-
X^2	p	Random	<0.001**	<0.001**	-
23.077	<0.001**	CC <25%	0.4572	0.73139	0.0072*
6pm		>25%<75%	0.7	-	-
X^2	p	Random	0.15	0.15	-
9.194	0.027	CC <25%	0.82	0.44	0.15

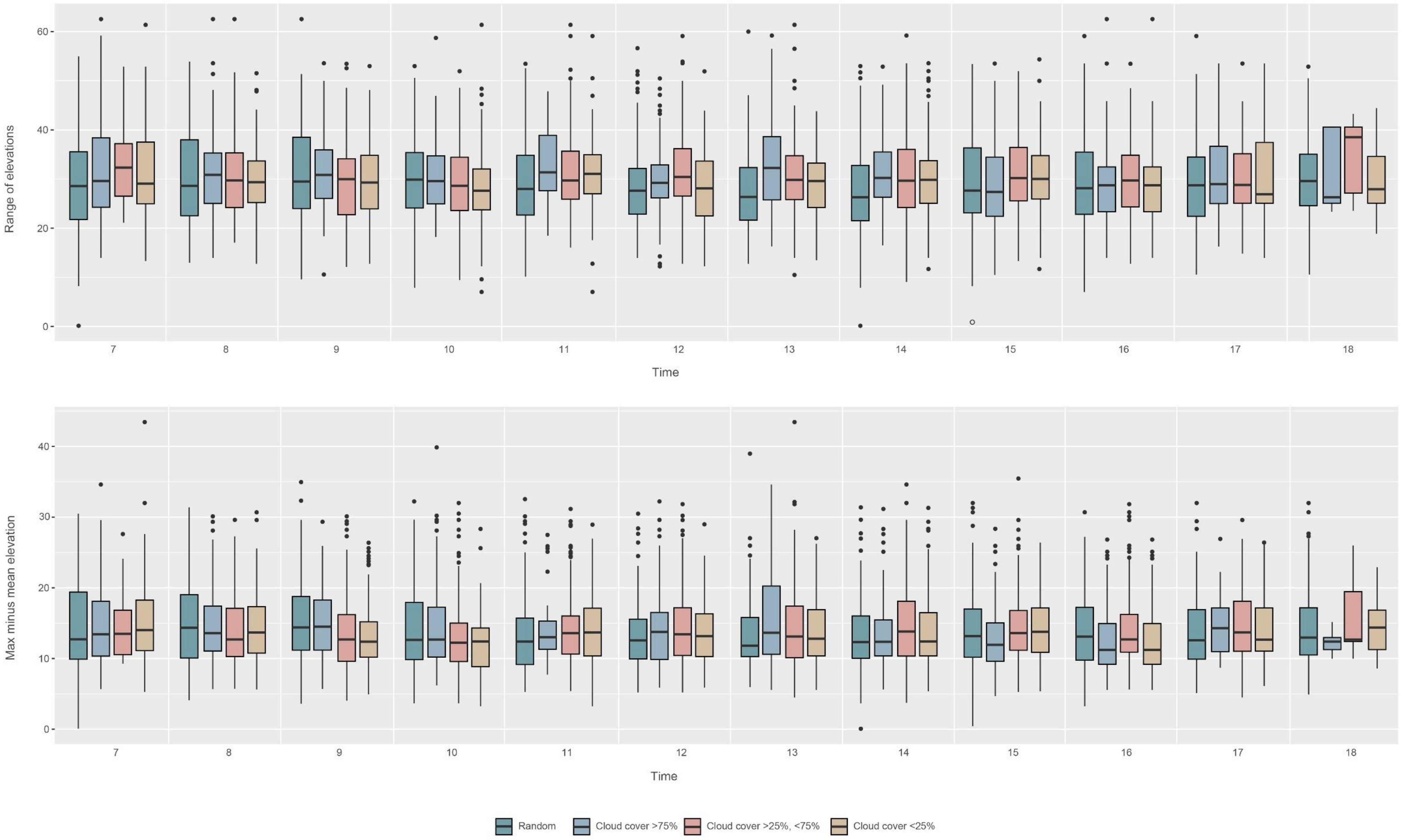
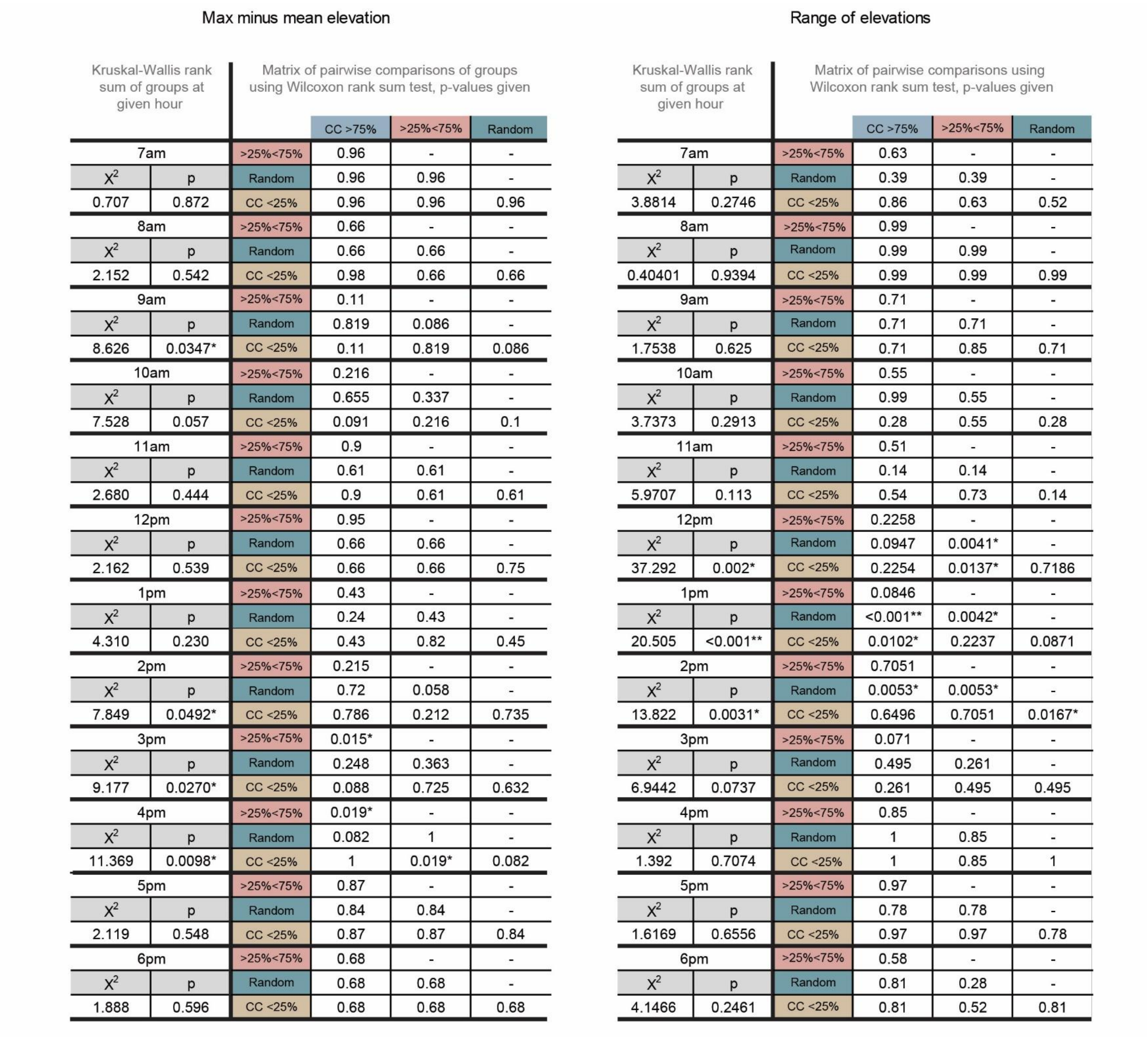


Figure 3.20b - Siamang canopy use in high, moderate and low cloud cover, by hour of the day, shown with a random selection

Table 3.2b – Results of Kruskal Wallace rank sum tests between canopy variables extracted under differing conditions; siamang locations in moderate conditions (>25%, <75% cloud cover), those in high (>75%) and low (<25%) cloud cover and a random selection, given together with a matrix of relevant pairwise comparison using Wilcoxon rank sum test



Max minus mean elevation

Kruskal-Wallis rank sum of groups at given hour		Matrix of pairwise comparisons of groups using Wilcoxon rank sum test, p-values given			
			CC >75%	>25%<75%	Random
7am		>25%<75%	0.96	-	-
X^2	p	Random	0.96	0.96	-
0.707	0.872	CC <25%	0.96	0.96	0.96
8am		>25%<75%	0.66	-	-
X^2	p	Random	0.66	0.66	-
2.152	0.542	CC <25%	0.98	0.66	0.66
9am		>25%<75%	0.11	-	-
X^2	p	Random	0.819	0.086	-
8.626	0.0347*	CC <25%	0.11	0.819	0.086
10am		>25%<75%	0.216	-	-
X^2	p	Random	0.655	0.337	-
7.528	0.057	CC <25%	0.091	0.216	0.1
11am		>25%<75%	0.9	-	-
X^2	p	Random	0.61	0.61	-
2.680	0.444	CC <25%	0.9	0.61	0.61
12pm		>25%<75%	0.95	-	-
X^2	p	Random	0.66	0.66	-
2.162	0.539	CC <25%	0.66	0.66	0.75
1pm		>25%<75%	0.43	-	-
X^2	p	Random	0.24	0.43	-
4.310	0.230	CC <25%	0.43	0.82	0.45
2pm		>25%<75%	0.215	-	-
X^2	p	Random	0.72	0.058	-
7.849	0.0492*	CC <25%	0.786	0.212	0.735
3pm		>25%<75%	0.015*	-	-
X^2	p	Random	0.248	0.363	-
9.177	0.0270*	CC <25%	0.088	0.725	0.632
4pm		>25%<75%	0.019*	-	-
X^2	p	Random	0.082	1	-
11.369	0.0098*	CC <25%	1	0.019*	0.082
5pm		>25%<75%	0.87	-	-
X^2	p	Random	0.84	0.84	-
2.119	0.548	CC <25%	0.87	0.87	0.84
6pm		>25%<75%	0.68	-	-
X^2	p	Random	0.68	0.68	-
1.888	0.596	CC <25%	0.68	0.68	0.68

Range of elevations

Kruskal-Wallis rank sum of groups at given hour		Matrix of pairwise comparisons using Wilcoxon rank sum test, p-values given			
			CC >75%	>25%<75%	Random
7am		>25%<75%	0.63	-	-
X^2	p	Random	0.39	0.39	-
3.8814	0.2746	CC <25%	0.86	0.63	0.52
8am		>25%<75%	0.99	-	-
X^2	p	Random	0.99	0.99	-
0.40401	0.9394	CC <25%	0.99	0.99	0.99
9am		>25%<75%	0.71	-	-
X^2	p	Random	0.71	0.71	-
1.7538	0.625	CC <25%	0.71	0.85	0.71
10am		>25%<75%	0.55	-	-
X^2	p	Random	0.99	0.55	-
3.7373	0.2913	CC <25%	0.28	0.55	0.28
11am		>25%<75%	0.51	-	-
X^2	p	Random	0.14	0.14	-
5.9707	0.113	CC <25%	0.54	0.73	0.14
12pm		>25%<75%	0.2258	-	-
X^2	p	Random	0.0947	0.0041*	-
37.292	0.002*	CC <25%	0.2254	0.0137*	0.7186
1pm		>25%<75%	0.0846	-	-
X^2	p	Random	<0.001**	0.0042*	-
20.505	<0.001**	CC <25%	0.0102*	0.2237	0.0871
2pm		>25%<75%	0.7051	-	-
X^2	p	Random	0.0053*	0.0053*	-
13.822	0.0031*	CC <25%	0.6496	0.7051	0.0167*
3pm		>25%<75%	0.071	-	-
X^2	p	Random	0.495	0.261	-
6.9442	0.0737	CC <25%	0.261	0.495	0.495
4pm		>25%<75%	0.85	-	-
X^2	p	Random	1	0.85	-
1.392	0.7074	CC <25%	1	0.85	1
5pm		>25%<75%	0.97	-	-
X^2	p	Random	0.78	0.78	-
1.6169	0.6556	CC <25%	0.97	0.97	0.78
6pm		>25%<75%	0.58	-	-
X^2	p	Random	0.81	0.28	-
4.1466	0.2461	CC <25%	0.81	0.52	0.81

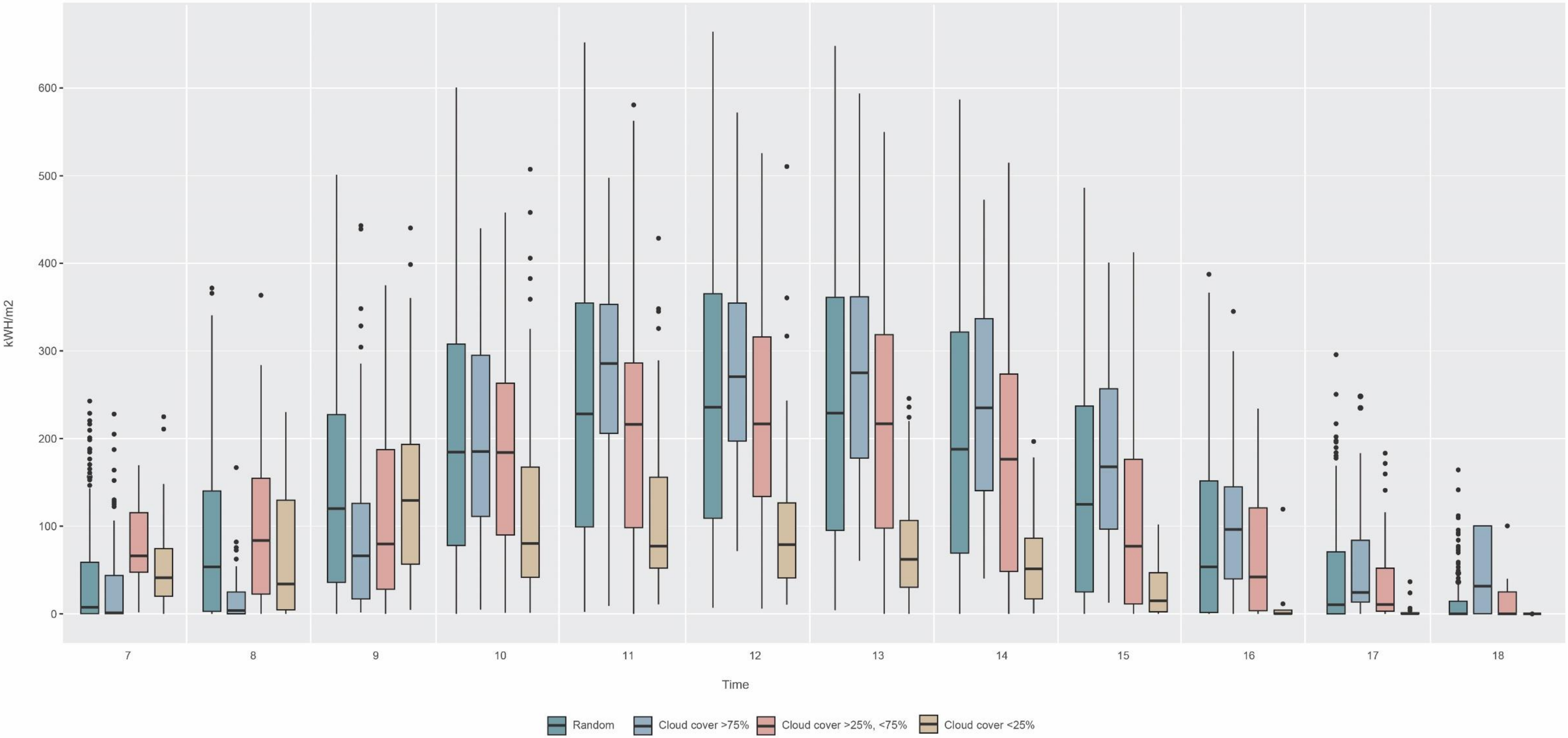


Figure 3.21 – Modelled solar radiation (measured as kWH/m^2) calculated at siamang locations in high, moderate and low cloud cover, by hour of the day, shown with a random selection

Table 3.2c – Results of Kruskal Wallace rank sum tests between potential incoming solar radiation values (measured in mean kWH/m^2) extracted under differing conditions; siamang locations in moderate conditions (>25% - <75% cloud cover), those in high (>75%) and low (<25%) cloud cover and a random selection, given together with a matrix of relevant pairwise comparison using Wilcoxon rank sum test

kWH/m^2

Kruskal-Wallis rank sum of groups at given hour		Matrix of pairwise comparisons using Wilcoxon rank sum test, p-values given			
			CC >75%	>25%<75%	Random
7am		>25%<75%	<0.001**	-	-
X^2	p	Random	0.015*	<0.001**	-
37.212	<0.001**	CC <25%	<0.001**	0.064	<0.001**
8am		>25%<75%	<0.001**	-	-
X^2	p	Random	<0.001**	0.016*	-
62.909	<0.001**	CC <25%	<0.001**	0.012*	0.375
9am		>25%<75%	0.1991	-	-
X^2	p	Random	0.0080*	0.0389*	-
10.133	0.0063*	CC <25%	0.0032*	0.0324*	0.6995
10am		>25%<75%	0.53	-	-
X^2	p	Random	0.95	0.53	-
30.803	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
11am		>25%<75%	<0.001**	-	-
X^2	p	Random	<0.001**	0.1001	-
107.1	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
12pm		>25%<75%	<0.001**	-	-
X^2	p	Random	0.01*	0.21	-
135.43	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
1pm		>25%<75%	<0.001**	-	-
X^2	p	Random	0.01*	0.21	-
145.32	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
2pm		>25%<75%	<0.001**	-	-
X^2	p	Random	0.0146*	0.05763	-
122.31	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
3pm		>25%<75%	<0.001**	-	-
X^2	p	Random	<0.001**	<0.001**	-
127.63	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
4pm		>25%<75%	<0.001**	-	-
X^2	p	Random	0.003*	0.461	-
118.11	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
5pm		>25%<75%	0.0075*	-	-
X^2	p	Random	<0.001**	0.7632	-
35.749	<0.001**	CC <25%	<0.001**	<0.001**	0.01357
6pm		>25%<75%	0.163	-	-
X^2	p	Random	0.035*	0.638	-
13.56	0.001*	CC <25%	0.014*	0.036*	0.015*

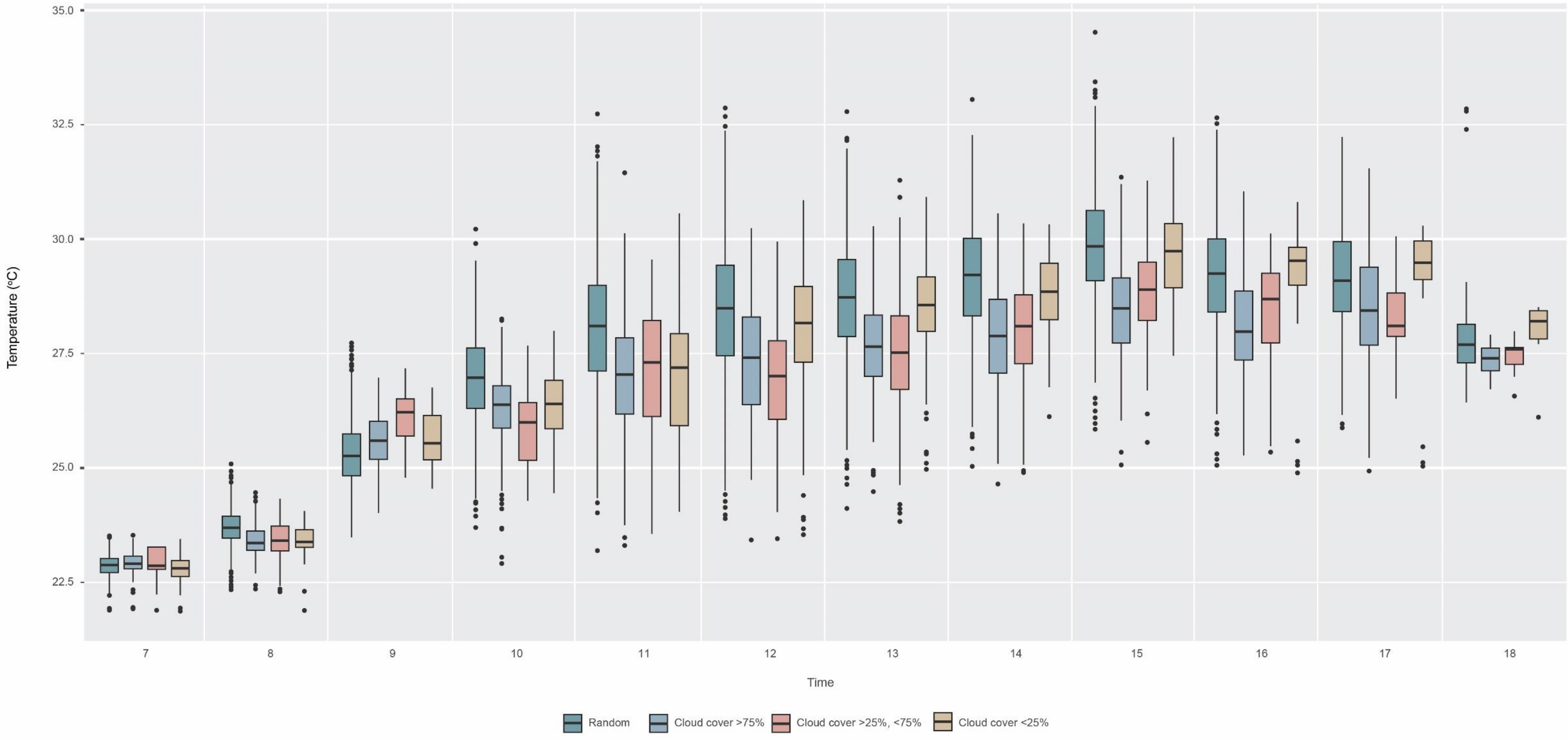


Figure 3.22 – Modelled temperatures calculated at random locations with the siamang home range compared with siamang locations in moderate conditions and high and low cloud cover

Table 3.3 – Results of Kruskal Wallace rank sum tests between modelled microclimate temperatures under differing conditions; siamang locations in moderate conditions (>25% - <75% cloud cover), those in high (>75%) and low (<25%) cloud cover and a random selection, given together with a matrix of relevant pairwise comparison using Wilcoxon rank sum test

Temperature

Kruskal-Wallis rank sum of groups at given hour		Matrix of pairwise comparisons of groups using Wilcoxon rank sum test, p-values given			
			CC >75%	>25%<75%	Random
7am		>25%<75%	0.095	-	-
X^2	p	Random	0.033*	0.562	-
13.747	0.003*	CC <25%	0.003*	0.095	0.031*
8am		>25%<75%	0.889	-	-
X^2	p	Random	<0.001**	<0.001**	-
144.35	<0.001**	CC <25%	0.889	0.889	<0.001**
9am		>25%<75%	<0.001**	-	-
X^2	p	Random	<0.001**	<0.001**	-
89.09	<0.001**	CC <25%	0.861	0.001*	0.002*
10am		>25%<75%	0.105	-	-
X^2	p	Random	<0.001**	<0.001**	-
135.23	<0.001**	CC <25%	0.184	0.010*	<0.001**
11am		>25%<75%	0.521	-	-
X^2	p	Random	<0.001**	<0.001**	-
196.18	<0.001**	CC <25%	0.810	0.800	<0.001**
12pm		>25%<75%	0.018*	-	-
X^2	p	Random	<0.001**	<0.001**	-
160.31	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
1pm		>25%<75%	0.26	-	-
X^2	p	Random	<0.001**	<0.001**	-
177.93	<0.001**	CC <25%	<0.001**	<0.001**	0.22
2pm		>25%<75%	0.37	-	-
X^2	p	Random	<0.001**	<0.001**	-
228.77	<0.001**	CC <25%	<0.001**	<0.001**	<0.001**
3pm		>25%<75%	0.002*	-	-
X^2	p	Random	<0.001**	<0.001**	-
248.04	<0.001**	CC <25%	<0.001**	<0.001**	0.046*
4pm		>25%<75%	0.006*	-	-
X^2	p	Random	<0.001**	<0.001**	-
184.08	<0.001**	CC <25%	<0.001**	<0.001**	0.390
5pm		>25%<75%	0.181	-	-
X^2	p	Random	<0.001**	<0.001**	-
69.67	<0.001**	CC <25%	0.021*	<0.001**	0.378
6pm		>25%<75%	0.657	-	-
X^2	p	Random	0.028*	0.232	-
11.57	0.009*	CC <25%	0.028*	0.106	0.232

The same method of categorising the canopy structures used by siamang by the cloud cover conditions in which they were recorded (high, low or moderate cloud cover), was used when extracting potential incoming solar radiation. Potential incoming solar radiation, a variable aggregated at the same 25x25m grid resolution, is based on the sun's location at a given time in relation to 3-dimensional canopy and is therefore time dependant (see Figure 2.23). For comparison to potential incoming solar radiation extracted from siamang locations, a random selection of locations were generated within the siamang home range, with randomised time variables, and potential incoming solar radiation values extract from these locations. Between these four categories, a significant degree of variability can be seen between conditions across hours (Table 3.2a). From 10am – 6pm, potential incoming solar radiation (measured as kWH/m^2) values are significantly lower in moderate and high cloud cover than a randomised selection. Potential incoming solar radiation at locations recorded in high cloud cover is higher than in moderate or low cloud cover (Figure 3.21), suggesting that sunlight is sought in cloudy conditions and shade preferred in strong sunlight.

To estimate the microclimate that the siamang were experiencing during behavioural observations, the time, height, and location of the siamang group, together with the derived canopy structure and incoming solar radiation variables from those locations, were combined with weather variables recorded at the time of siamang behavioural recordings. These variables were used as in the hourly microclimate equations produced in Chapter 2 (Table 2.3). Using these hourly microclimate equations, the temperatures experienced by siamang were modelled under; low, moderate and high cloud cover. A randomised selection of microclimates was also produced using random locations and times. Temperatures estimated to be experienced by the siamang were largely significantly different from a random selection of locations at the same time periods (Figure 3.22, Table 3.3). In moderate conditions and high cloud cover, temperatures that siamang experiences were significantly lower than a random selection. In low cloud cover, temperatures experienced by siamang were generally also significantly lower than a random selection, but to a lesser degree, suggesting that during periods of low cloud cover, siamang were less able to buffer against high temperatures, despite apparent changes in canopy structures use.

3.4 Discussion

Results from this study indicate that siamang inhabiting a historically degraded lowland dipterocarp forest, had a lower quality diet and larger home range than siamang inhabiting other areas (Chivers, 1974; Raemaekers, 1978; Reamaekers, 1979; Palombit, 1996), and were estimated to frequently experience temperatures at the edge of their thermal neutral zone (based on Riek and Geiser, 2013), potentially impacting on the long term welfare of the group. This study aimed to examine the relationship between siamang behaviour, canopy structure and microclimate, to see if inhabiting the degraded forest of Sikundur placed the siamang under additional demands. Whilst there was little apparent difference in the canopy structure used for separate behaviours, time of day and weather conditions influenced the siamang group's use of different canopy structures. Across nearly all time periods, siamang sought areas with more robust canopy structures when there was little cloud cover, measured as areas of forest with higher minimum elevations and higher relative elevations than those areas around it. However, canopy structure as measured here included microtopography, as UAV surveys cannot penetrate the canopy, but rather record elevation at its highest point. There is evidence to suggest that siamang use these fluctuations in canopy structure and shade to shield themselves from incoming solar radiation, seeking shade in times of low cloud cover and seeking sunlight in times of high cloud cover, showing clear signs of behavioural thermoregulation (Duncan and Pillay., 2013). Differences in canopy structure use, whilst statistically significant, were not as apparent as the fluctuation in potential incoming solar radiation levels at the siamang's locations, which showed clear divergence depending on weather conditions. This suggests that the siamang at Sikundur alter their location in relation to sunlight and shade whilst consistently using canopy structures that are sufficient for their needs. Seemingly, simang change their position within the forest canopy temporarily and geographical to enable behavioural thermoregulation, whilst using a limited range of canopy structure. Given their strict home range and limited use of degraded forest, this may reduce the amount of suitable habitat in extended periods of low cloud cover.

There is evidence that the siamang at Sikundur have limited diets. The siamang at Sikundur are at the extreme low end of frugivory compared to those recorded in other studies (this study; 20.8%, versus Chivers, 1974; 20%, Reamaekers, 1979; 34% and Palombit, 1996; 61%). There was also a recorded increase in daily path length with time spent feeding on leaves ($R^2 = 0.33$) the opposite of previous studies (Reamaekers, 1980). Together with a negative trend between time spent feeding on leaves and time spent feeding on fruit ($R^2 = 0.16$), this suggests that fruit is a preferred food source, and is sought, but is rarely found. There are low levels of fruit availability within Sikundur (SOCP, 2016, Figure 2.6), but whether is due to the natural low fruit abundance of lowland dipterocarp forest outside of 'mast' years (Sakai et al., 1999) or the direct impact of selective logging, during which large trees and large fruit trees, especially *ficus* spp., are often targeted [Chapman et al., 1992, Felton et al., 2006), is difficult to assess. The impact of potential incoming solar radiation can be seen on feeding behaviours. A negative relationship between time spent feeding on leaves and potential incoming solar radiation suggests that exposure to direct sunlight limits the time spent on foraging on low-quality foods. That no such relationship was found between incoming solar radiation and time spent feeding on fruit suggests that direct sunlight, and increased temperatures, may be tolerated for preferred food items.

Siamang seemed to reduce their height in the canopy slightly in response to direct sunlight, taking advantage of vertical temperature gradients to enable thermoregulation (see Section 1.3.3, Pringle et al., 2003), a behaviour also seen in chimpanzees (Takemoto., 2004). Given that siamang are almost exclusively arboreal, this limits their ability to fully utilise vertical temperature gradients in the same way as the semi-terrestrial *Pan* species, limiting their ability to take advantage of temperature fluctuations within the forest canopy. Additionally, as siamang are large (11-12 kg) they require canopy structures that can support their weight. These limiting factors may be shown in the relative invariant canopy structure used in different activity states (Figure 3.19) and across times (Figure 3.20b), requiring them to utilise both vertical temperature gradients and 'horizontal' changes in canopy structure between areas to behavioural thermoregulate.

Generally, resting time in primates increases with overall higher temperatures in an environment (Korstjens et al. 2009). This effect was recorded with the siamang at Sikundur, with a trend for an increased amount of time spent resting in response to incoming solar radiation (R^2 = 0.14), and mean daily temperature (R^2 = 0.18) a response seen in other studies (Poulsen et al., 2001; Cui et al., 2006; Hanya, 2004; Takemoto, 2004; Vasey, 2005, Kosheleff and Anderson., 2009,). That this effect on resting time is a relatively minor influence may suggest that due to the low-quality diet available to the siamang at Sikundur, they cannot energetically 'afford' to rest frequently during the day. However, it should be noted that the siamang entered sleeping trees relatively early in the day (between 3:06pm - 6:24pm, with an average time of 4:56pm), during which times they were seen resting and grooming, but accurate behavioural observations at this time were difficult as the siamang were in the canopy frequently >30m in height.

Sleeping trees seemed to be selected on the basis of height and a limited number of entry routes into the tree crown (though further data collection is required to quantify this). Areas in which sleeping trees were situated were significantly different from a random selection across almost all measured variables (Figure 3.12) and their presence may be key to defining siamang home ranges (Reichard, 1998; Anderson, 2000). Using projections of suitable sleeping tree sites (Figure 3.13) potential sleeping sites are relatively infrequent in the siamang home range compared to other areas, suggesting that home range of this siamang group is of relatively low quality compared with the surrounding area. However, with so few sleeping trees recorded over a large area, it is currently unsound to statistically test if sleep site projections are correct, and other factors not recorded here may influence sleep site choice.

The home range reported here was greater than those previously recorded elsewhere (this study: 64ha, Chivers, 1974: 15ha, Raemaekers, 1978: 47ha), suggesting that inhabiting a historically degraded forest places siamang under increased energetic demands, with low quality food dispersed throughout a large area and requiring a large home perimeter to be defended from neighbouring groups (Lowen and Dunbar, 1994). However, the relatively isolated home range of the siamang studied at Sikundur, bordered by historical logging roads and river on all sides, may also have led to the relatively large home range size, although further research into home ranges of other groups with the Sikundur area is required to substantiate this.

3.5 Conclusion

As a large-bodied, group-living, exclusively arboreal primate inhabiting a degraded forest, balancing energetic demands whilst remaining within a thermoneutral zone presents some challenges to the siamang at Sikundur. Their relationship between behaviour, canopy structure and microclimate presented a complex picture. As previously explored, vegetation structure has a significant impact on vertical temperature gradients within the canopy (Section 2.3.3, Takemoto, 2004). For more terrestrial primate species, changing height and coming to the ground offers a simple solution to avoiding higher temperatures higher in the canopy (Takemoto, 2004). For the exclusively arboreal siamang, this is not an option. Siamang were expected to attempt to mitigate high temperatures by altering their height and location within the canopy, seeking areas which may buffer against solar radiation. Siamang at Sikundur achieved behavioural thermoregulation through a marginal reduction their height within the canopy (Section 3.3.4, Figure 3.12), their location in respect to canopy structure (Figure 3.18a, Figure 3.12b, Table 3.1a, Table 2.1b) and by avoiding areas in strong sunlight (Figure 3.19, Table 3.2). However, in the degraded forest of Sikundur the opportunities to mitigate high temperatures are likely reduced, resulting in siamang experiencing high temperatures in low cloud cover (Figure 3.22) despite apparent attempts to mitigate incoming solar radiation (Figure 3.21).

Although no studies have ascertained the thermoneutral zone of siamang, the thermoneutral zone of primates is expected to range from 24-32°C in the lower critical temperature and 25-35°C in the upper critical temperature (Riel and Geiser, 2013). In some primate species, temperatures above 36°C have led to thermal distress and hyperthermia (Stitt & Hardy, 1971). Whilst siamang in this study seem unlikely to have experienced these extremes, due to their ability to behaviourally thermoregulate, these temperatures have been recorded at Sikundur by microclimate data loggers (see Section 2.3.2). At current levels, small increases in local temperature, either through additional habitat disturbance or climate change, could push arboreal primates such as siamang to the very edge of their thermal limits. With predicted anthropogenic climate change estimated to increase global temperatures by 2^{o}C by the year 2020 (the current internationally adopted climate mitigation target, Collins et al., 2013), and 62.6% of all primate species projected to experience temperature increases greater than the global mean (mean 2.2^{o}C, Graham et al., 2016) thermoregulation for many primate species, particularly those who are exclusively arboreal, with narrow thermal thresholds and which inhabit degraded forests, may become a challenge.

Chapter 4. The effects of vegetation structure and anthropogenic disturbance on the abundance of three sympatric primate species

4.1 Introduction

Anthropogenic effects, including habitat loss, habitat degradation and fragmentation, are leading causes of the pervasive loss of global biodiversity (Chapman and Peres, 2001; Michalski and Peres, 2005, Golberg et al., 2008). In Southeast Asia, the clear-cutting of existing forest, primarily to make land available for agricultural plantations, has been the primary concern of conservationists, as large mammals are threatened by a subsequent increase in illegal hunting, habitat loss and fragmentation (Goossens et al., 2006). In Sumatra, satellite imagery has shown that protected areas have experienced similar levels of deforestation to areas allocated for commercial logging (Gaveau et al., 2012). However, some areas that have previously been commercially logged are now within protected areas (SOCP, 2015). Understanding the impacts of historical degradation of tropical forest within both protected and non-protected areas of endangered species' habitat is of key importance to safeguarding these populations under present conditions (Tang et al., 2010). As most studies are relatively short term, the effects of selective logging on the ecology of tropical forests is still poorly understood, as data enabling the comparison of before and after logging events is rare (Laufer et al., 2013). As selective logging often targets the most valuable trees, which are unevenly distributed (Draper et al., 2019), quantitive measurements of the effects of selective logging are challenging to assess with satellite imagery (Margono et al., 2012). After selective logging events, the subsequent regrowth of understory tree species is often rapid, if not hampered by invasive species (Galán et al., 2018). This renders classifying forest areas as either 'logged' or 'intact' challenging, as they exhibit heterogenous gradients of degradation (Struebig et al., 2013). This form of logging can have a relatively low impact in terms of reduced habitat compared with other forms of anthropogenic disturbance, such as fragmentation and burning (Barlow et al., 2006; Chaves et al., 2012), with most logged forests containing at least 50% of the biomass and more than 75% of the species compared to undisturbed forest (Berry et al., 2010, Putz, 2012). However, for long-lived species such as primates, the full ecological effects of anthropogenic disturbance on population health may have not yet become apparent (Tilman et al., 1994, Vellend, 2006).

Primate species, in particular, are affected by forest degradation (Arroyo-Rodríguez et al., 2013; Benchimol and Peres, 2014). Due to their low birth rates and slow life histories, any species that cannot quickly adapt their behaviour to these emerging changes are ultimately faced with extinction (Chapman and Peres, 2001). Primates are of central importance to tropical biodiversity and to many ecosystem functions, processes, and services (Estrada et al., 2017). The evolution, feeding ecology, and geographic distribution of primates are closely linked to the diversification of flowering plants, a principal source of food (pollen, nectar, fruits, and seeds) (Sussman et al., 2013) for many animals and humans (Kone et al., 2008, Heymann et al., 2011). Given this, primate species' habitat requirements are broad enough that their abundance is a good indicator of biodiversity of the region (Rijksen & Meijaard, 1999). However, while some primate species exhibit morphological adaptations and behavioural plasticity that allow them to subsist in degraded habitats (howler monkeys, *Alouatta palliata* (Cristobal-Azkarate and Arroyo-Rodríguez, 2007); collared lemur, *Eulemur collari*s (Donati et al., 2011); diademed sifaka, *Propithecus diadema* (Irwin 2008a, b); black and white colobus, *Colobus guereza* (Gillespie and Chapman, 2008); moustached guenon, *Cercopithecus* (Tutin, 1999)), others appear to be more vulnerable due to greater specialisation both morphologically and behaviourally (red colobus, *Procolobus rufomitratus* (Gillespie and Chapman, 2008); bearded saki monkeys, *Chiropotes satanas chiropotes* (Boyle and Smith, 2010; Schwitzer et al., 2011). Highly arboreal primate species, which rely on continuous forest canopy to locomote efficiently, are especially affected by habitat degradation as reduced canopy integrity places them under additional energetic demands (Takemoto, 2004, Marsh et al., 2016). Despite numerous studies on the effects of habitat degradation and anthropogenic disturbance on primate populations (Marsh and Chapman, 2013), new findings frequently arise with each additional study (Benchimol and Peres, 2014). The growing understanding of primates' flexibility within and across species necessitates further investigation of the effects of habitat degradation on individual primate species and the impacts on tropical forests (Ewers and Didham, 2006). However, anthropogenic disturbance is far from uniform across landscapes and may affect differing land types within a single landscape in differing ways. These landscape-scale responses to anthropogenic disturbance present different threats to primate species depending on species' life history strategy, dietary requirements and habitat preference. Factors that enable some species to persist in degraded forests include a small home range, broad-ranged diet and small group size (Purvis et al., 2000) (e.g. howler monkeys, genus *Alouatta* (Bicca-Marques, 2003); mantled howler monkeys, *Alouatta palliata* (Estrada, 1999); white-faced capuchins, *Cebus capucinus* (Panger et al., 2002)), whereas primate species with large home ranges, specialist diets and large group sizes can be more severely and immediately affected by forest degradation (Andrén, 1994) (e.g. southern gentle lemurs, *Hapalemur meridionalis* (Eppley et al., 2011); brown spider monkeys, *Ateles hybridus* (Link et al., 2012); spider monkeys, family *Atelidae* (Rimbach et al., 2012)).

This study tests the hypothesis that historical disturbance in the form of selective logging and forest clearance affects ecological variables such as tree size, canopy homogeneity, and vegetation structure, which in turn affect primate population abundance. Sites of discreet anthropogenic disturbance, such as historic logging roads, selective logging and recent slash and burn agriculture on small scales, are difficult to detect with satellite imagery, but can be identified using an emergent technology, Unmanned Aerial vehicles (UAVs), allowing the effects of discrete forest degradation on vegetation structure and primate populations to be assessed. By quantifying levels of disturbance through UAVs and traditional vegetation surveys and assessing multiple primate species' abundance, the potential effects of historical forest degradation can be assessed. This study assesses the effects of historic logging events on the abundance of two diurnal sympatric ape species: lar gibbons (*Hylobates lar vertitus*) and siamang (*Symphalangus syndactylus*), and the sympatric Thomas' leaf monkey (*Presbytis thomasi)* in a continuous area of lowland forest with various levels of degradation, within Sikundur, part of the Gunung Leuser Ecosystem, Northern Sumatra. This area was selectively logged from the late 1960s, which continued and progressively intensified in some areas until the 1980s (Cribb, 1988; Wind, 1996). During the logging operations from the late 1960s until 1982, an average of 11 large trees per hectare were felled (Knop et al., 2004). Five years after the logging operations ceased, Abdulhadi et al. (1987) found that 54% of the remaining trees still showed some sort of damage caused by the logging. Following the establishment of the TNGL, large-scale logging operations within the area ceased, although small-scale land clearance has taken place within the border of the National Park, with a loss estimated at 25,722 ha per year (from Hansen et al., 2013, see Figure 2.4). Currently, illegal logging and complete land clearing are still present near the south-eastern boundary of the Sikundur Monitoring Post at the TNGL border, in addition to more generalized illegal human extractive activities (e.g., bird trapping, damar resin extraction, and fishing). We analysed the influence of habitat quality, measured using terrestrial and aerial surveys, on the abundance of these three primate species. Given that high-quality habitat has been empirically linked to high fruit production (Chapman et al., 1992), we hypothesize that the ripe-fruit specialist *H. lar vertitus* would be less abundant in areas of forest with low habitat quality and the more folivious *S. syndactylus and P. thomasi* would be more resilient to habitat degradation.

4.2 Methods

4.2.1 Study site

The study site, Sikundur, covers 75km^2 of rare lowland dipterocarp forest at the border of the Gunung Leuser Ecosystem National Park (03^{o}59 N, 98^{o}00E – 03^{o}52N, 98^{o}06E). The Sikundur area was previously known as the Sikundur Reserve (est. 1938) prior to the formation of the Taman Nasional Gunung Leuser (TNGL, est. 1980), the administrative section of the Department of Agriculture that oversees the Gunung Leuser Ecosystem. The

Sumatran Orang-utan Conservation Programme (SOCP) started orang-utan and habitat monitoring at Sikundur in 2012, and their research station at Sikundur was used throughout this study. See section 2.2.2 for more information.

4.2.2 Primate abundance estimation

Typically, line transect surveys are used to calculate the abundance of primate species (Buckland et al., 2010, Nijman and Menken., 2005, Sorsen and Fedigan, 2000, Cramer et al., 2007, Marsh et al., 2016). However, line transect surveys were conducted in 2015 at the site (Slater, 2016; Consiglio, 2016) with few primate sightings. Given the difficulty of obtaining reliable data using line transects at this site, passive auditory surveys were chosen as a method to conduct abundance surveys, a common practice for vocalising primate species (Cheyne et al., 2008; Hamard et al., 2010). Long, loud vocalisations made by individuals or entire groups are produced by many species and are among the most distinctive sounds in each species' vocal repertoire. These are typically species-specific and used to communicate between and within groups over long distances (Mitani & Stuht, 1998). Loud calls may be used to communicate within a group to maintain proxemics (Mitani and Nishida, 1993) or as territorial defence (Raemakekers and Raemaekers, 1985; Hill, 1994), and to regulate distance between groups without costly physical conflicts (Whitehead, 1989). This putative function is supported by the observation that loud calls are frequently 'contagious', in that one individual or group call stimulates others to counter-call (Steenbeck et al., 1999). Within Sikundur, the Thomas langur, the lar gibbon and siamang all initiate and respond to loud calls on an almost daily basis (Gittins and Raemaekers, 1980). In the lesser apes (lar gibbon and siamang), pairs or small groups 'duet' in their loud calls or songs (Geissmann, 1999). In most gibbon species, mates combine their call repertoire in relatively rigid, precisely timed and complex vocalisations to produce patterned duet songs (Haimoff, 1984; Geissmann, 1995). Largely monogamous, gibbons' combined songs are suggested not only to serve as territorial defence, but also for strengthening group or pair bonds (Chivers, 1976; Brockelman and Srikosamatara, 1984) and as an advertisement of those bonds to neighbouring groups (Geissman, 1999). The lar gibbon is small compared to other members of the *Hominoidea*, more comparable to that of a large monkey (5 to 11 kg). This is likely to make them vulnerable to predation from large cats, snakes and birds of prey and, perhaps because of this, gibbons almost exclusively reside in the upper forest canopy (van Schaik and van Hooff., 1983; Leighton, 1987; Reichard, 1998). The siamang, the largest of the lesser apes, exhibits a particularly complex vocal structure (Haimoff, 1981). Siamang songs can last up to 20 minutes, with rhythmic high pitch "yells" and characteristic "booms" produced by their large inflated throat sacs often accompanied by acrobatic swinging between branches and lunges within tree canopies (personal observation). In the Thomas' langur, a group's single alpha male regularly calls in the early morning as a territorial identifier, a short, characteristic "shriek" preceded by a series of "coughs" (Wich et al, 2003).

Given the difficulty in accurately identifying a single primate's calling location over multiple days or identifying individual primate groups by their call, encounter rates of each species from vocalisations was used as an estimate of abundance. Vocal encounter rate sampling was carried out throughout the Sikundur study site, covering as much area as possible. As estimated detection distances of primate vocalisations from a vocal sampling post is approximately 1km (Brockelman and Srikosamatara, 1984), each post was placed approximately 1km apart to sample each area, with minimal overlap between areas (Figure 4.1). Two sampling posts were located at each of 11 areas (labelled as Sites A-K), for a total of 22 posts. Vocal encounters were recorded at each site from 5am – 10am for 4 days in succession, unless heavy rainfall in the early morning prevented surveys (mean sampling days = 3.72). In total, there were 410 sampling hours, between May and July 2016. During the sampling period, calls in differing directions and distances were noted, along with the species emitting the call, with the total number of separate groups of each species identified by the researcher. The encounter rate for each species at each sample point was calculated as the total number of groups of each species detected divided by the total sampling effort (Marsh et al., 2016, Plumptre and Cox, 2006; Fewster et al., 2009). In this study, sampling effort was measured as the hours in which vocal sampling took place at a given location, e.g. if ten groups of langurs were heard vocalising at a vocal sampling point over the total sampling period of 20 hours, the encounter rate of langurs at that location would equal 0.5.

4.2.3 Vegetation plots

Four vegetation plots were carried out at each of the 11 sites of vocal samples, to provide an estimate of the surrounding vegetation. In the 25 x 25m plots, each tree with a diameter more than 10cm was measured, recording its diameter at breast height (DBH), tree height and height at bole, canopy area (with radius calculated by the mean of the measured distance, in metres, at the cardinal compass points from the trunk to the outside edge of the canopy in the equation $A = \pi r^2$) and canopy connectivity with surrounding trees (estimated as a percentage) (Figure 2.7). Additionally, at each corner of the vegetation plot, an indicative measure of canopy cover was determined using a digital camera, with imagery subsequently processed using CanopyDigi software (Goodenough and Goodenough, 2011) to derive canopy cover. Based on these measurements, mean values of vegetation plot variables were produced to characterise vegetation structure in each area (n = 11). Additionally, univariate statistics were generated from tree height measurements to produce two additional variables; range of tree heights and standard deviation of tree heights for each area. In summary, nine variables for each area were produced by vegetation plots that were used in analysis; mean DBH, mean tree height, mean bole height, mean crown area, mean connectivity, tree height range, standard deviation of tree height, mean canopy density and Morista’s index of canopy dispersion. See section 2.2.2 for more information.

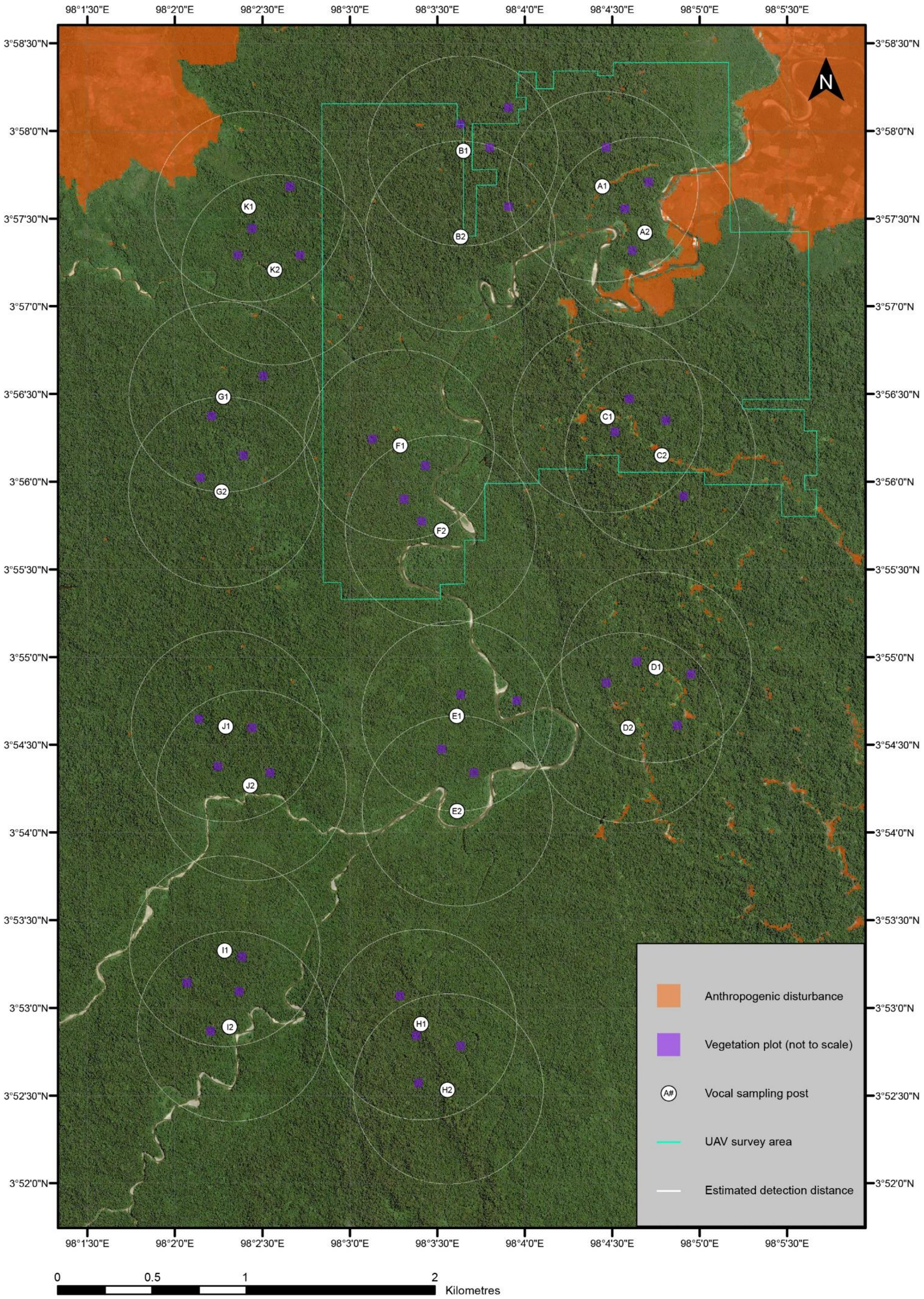
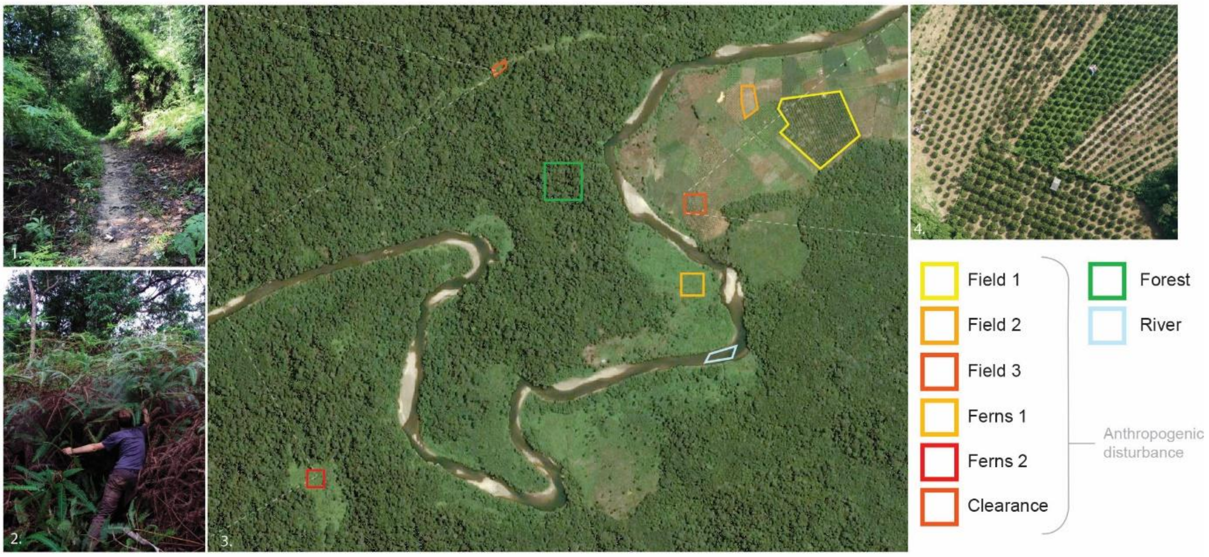


Figure 4.1 – Sikundur area with data collection site and areas of anthropogenic disturbance as determined by interactive supervised classification of the underlying Landsat 8 OLI image

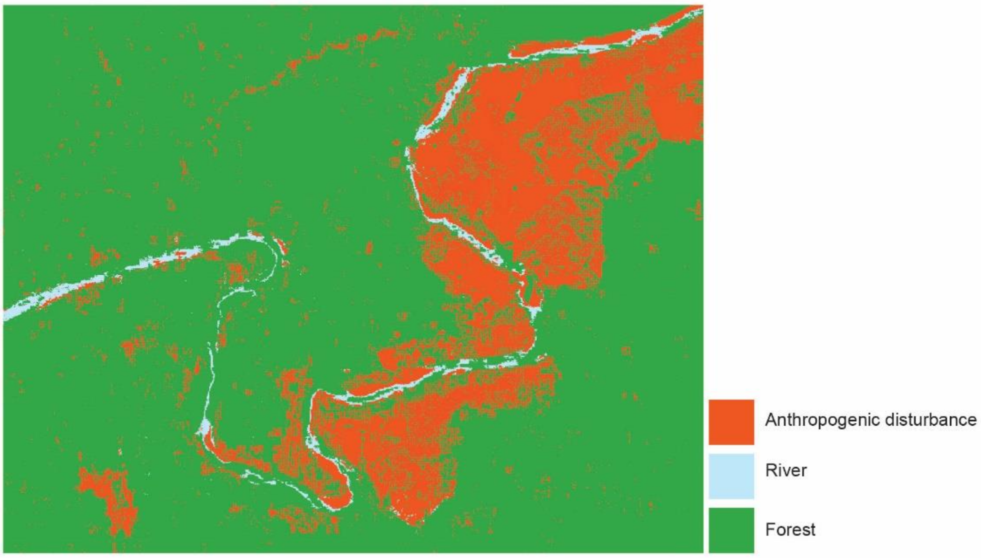
4.2.4 Determining areas of anthropogenic disturbance

To enable the identification of areas of both current and historic anthropogenic disturbance, interactive supervised classification was carried out on Landsat-8 RGB composite imagery (Lung and Schaab, 2006, Szantoi et al., 2017) using GIS software (Arcmap 10.4) with ground-truth areas of degradation selected for polygon training (Figure 4.1). Current anthropogenic disturbance, in the form of agricultural plantations, are easily identifiable from satellite imagery given the regular patterns of vegative growth (Figure 4.2, 1.A). Historic logging roads throughout the Sikundur area leave wide, clear cut trails. These deforested areas are then repopulated by ferns (*Pteridophyta spp*.), inhibiting the regrowth of tree species (Figure 4.2, A.1 and A.2); a well identified characteristic of degraded forest (Walker et al., 2010; Felton et al., 2006; Slocum et al., 2006; Lynch et al., 2009). These relatively small areas of degradation can be difficult to identify, but their characteristic light green colour in a Landsat-8 RGB composite can be identified once areas of their occurrence has been ‘ground-truthed’. Areas of both current and historic degradation were ‘ground-truthed’ in a section of the site and used as the basis for polygon training. The entire Sikundur area was included in interactive supervised classification. Polygon training using known areas of forest, river and stones (adjacent to rivers), were individually classified and then grouped as natural habitat (Figure 4.2.A). Areas containing *Pteridophyta spp*. including historical logging roads, cleared land and agricultural plantations were individually classified and then grouped as areas of anthropogenic disturbance (Figure 4.2, A.1, A.2, A.3, A.4). The resulting vector shapes, after some manual editing of vectors, were then divided by landcover type (Figure 3.2, B) and the anthropogenic disturbance vector extracted. The anthropogenic disturbance vector was then converted into a raster image (rasterization) with the minimum cell size of 25x25m (Figure 4.2, C). The resulting raster layer can be seen in Figure 4.1. A simple count of the number of these cells within a 250m, 500m, 750m and 1000m radius of each vocal sampling point was used to evaluate the quantity of anthropogenic disturbance within each area.

A. Interactive supervied classification - polygon training sample



B. Vector data from polygon training



C. Rasterised vector with 25x25m cell size

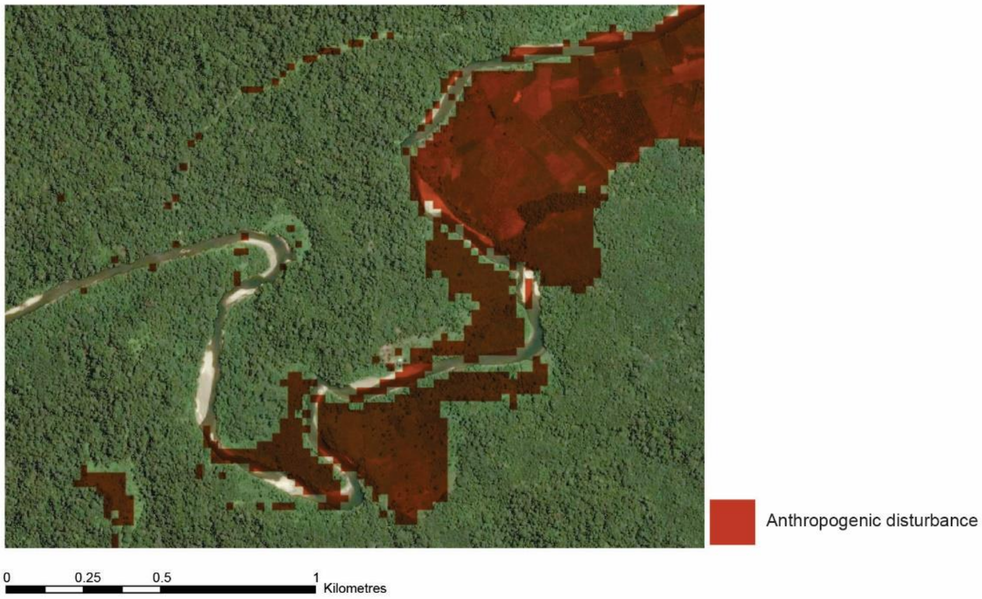


Figure 4.2 – A. Sample of polygon training locations for interactive supervised classification of LANDSAT 8 OLI imagery showing 1. and 2. historic logging roads dominated by *Pteridophyta spp*., B. Results of interactive supervised classification with three land units. C. Rasterised layer used in analysis overlay on LANDSAT 8 OLI imagery

4.2.5 Unmanned aerial vehicles

To record detailed aerial imagery of the study site, a fixed-wing Unmanned Aerial vehicle (UAV) was used. The modified “Skywalker” UAV (see Figure 2.11), was controlled manually (i.e. radio controlled) for take-off and landings and switched to autopilot to fly along “lawnmower” routes programmed using Mission Planner software (see Figure 2.12). To enable the capture of imagery, a digital camera (SONY RX100 mk4) took RGB photographs at GPS locations controlled by the autopilot and a Seagull #MAP 2 switch, programmed via MissonPlanner software (version 1.3.58), ensuring 80% overlap of each photograph, both in the direction of drone travel and between flight paths (known as ‘sidelap’).

Eleven mapping flights over the Sikundur area were flown between June 13th and 16th 2017, covering a total area of ~26km^2. In total, 4811 geotagged images were then processed in Agisoft Photoscan software (version 1.2.0.2152) using ‘Structure-from-Motion’ (SfM). The resulting Digital Surface Model (DSM), which was used in analysis, had a spatial resolution of 25.7 cm^2 per cell, resulting in a GeoTiff DSM that was 24,525 x 25,576 cells in size.

See section 2.2.4 for more information

Variables were extracted from the DSM at 250m, 500m, 750m and 1000m radius of each vocal sampling point using the ‘v.rast.stats’ function in GRASS GIS (version 7.4.1), which calculates basic univariate statistics within a specified vector. The univariate statistics calculated were the minimum, maximum, range and standard deviations of elevations, as well as the variety and variance of elevations within each sampling radius, where variety is the number of unique values in a sample and variance is defined by:

$$Variance = \frac{\sum(x_i - \bar{x})^2}{n-1}$$

where x_i equals each elevation value within the sample (with each value being $x_1, x_2 x_3 \ldots$etc) , $\bar{x}$ equals the mean elevation value in the sample and n equals the quantity of numbers in the sample (Rust, 1985).

Despite being wide ranging, some areas within the radii of vocal sampling points were not covered by UAV surveys. In these circumstances, ‘no data’ returns were treated as ‘no data’, with no replacement of variables, or ‘dummy’ numbers returned in place of ‘no data’ within univariate statistics.

4.2.6 Statistical analysis

Linear regressions were used to assess population abundance of each primate species using plot level vegetation variables (diameter at breast height, tree height and bole height, canopy width, canopy connectivity, canopy density) and a count of anthropogenic disturbance cells separately. The best predictors were selected based on their significance (p-value) and effect on model power (adjusted R^2 of model) if removed. Linear regressions were also used to predict population abundance of each primate species using UAV derived vegetation variables. Since the area of vocal sampling was used as the unit of analysis two separate models were run due to sample size limitations. One model compared primate species abundance to mean vegetation plot variables in each area of vocal sampling ($n = 22$) and one compared primate species abundance to vegetation variables derived from UAV surveys ($n = 8$). Additionally, linear regressions were used to compare plot level vegetation variables to UAV derived vegetation variables and to compare plot level vegetation variables to one another, to see if such variables predicted one another and assess co-linearity. Levels of anthropogenic disturbance were also compared with vegetation plot and UAV vegetation variables, to see if anthropogenic disturbance effected vegetation characteristics. Residual errors of these analyses were tested for normality using the Kolmogorov-Smirnov test in order to check the assumptions of linear models, and the residual errors were found to be normally distributed. Vegetation structure differences between the eleven sampling areas were tested using a Kruskal-Wallis test. Linear regression was used to compare vegetation plot characteristics to one another, as well as to compare primate species encounter rates to one another. All statistical analyses were performed with R (version 3.4.1) using R studio (version 1.0.153)., with alpha set to 0.05.

4.3 Results

4.3.1 Plot-level vegetation structure

In total, 1313 trees, in 44 plots, across 11 vocal sampling areas were measured to assess plot-level vegetation structure. Diameter at breast height (DBH) was highly variable between areas (K-W: $X^2 = 36.423$, df = 10, $p = <0.001$). Tree height was also highly variable (K-W: $X^2 = 272.55$, df = 10, $p = <0.001$), as well as crown area (K-W: $X^2 = 88.149$, df = 10, $p = <0.001$) and crown connectivity (K-W: $X^2 = 114.58$, df = 10, $p = <0.001$) (Figure 4.3a). Tree height and diameter at breast height were related ($\beta = 1.89779$, $R^2 = 0.508$, $p = <0.001$). Similarly, DBH and crown area were weakly related ($\beta = 0.92169$, $R^2 = 0.2405$, $p = <0.001$), as were crown area and tree height ($\beta = 6.835$, $R^2 = 0.233$, $p = <0.001$) (Figure 4.3b). No other vegetation plot variables had a significant relationship.

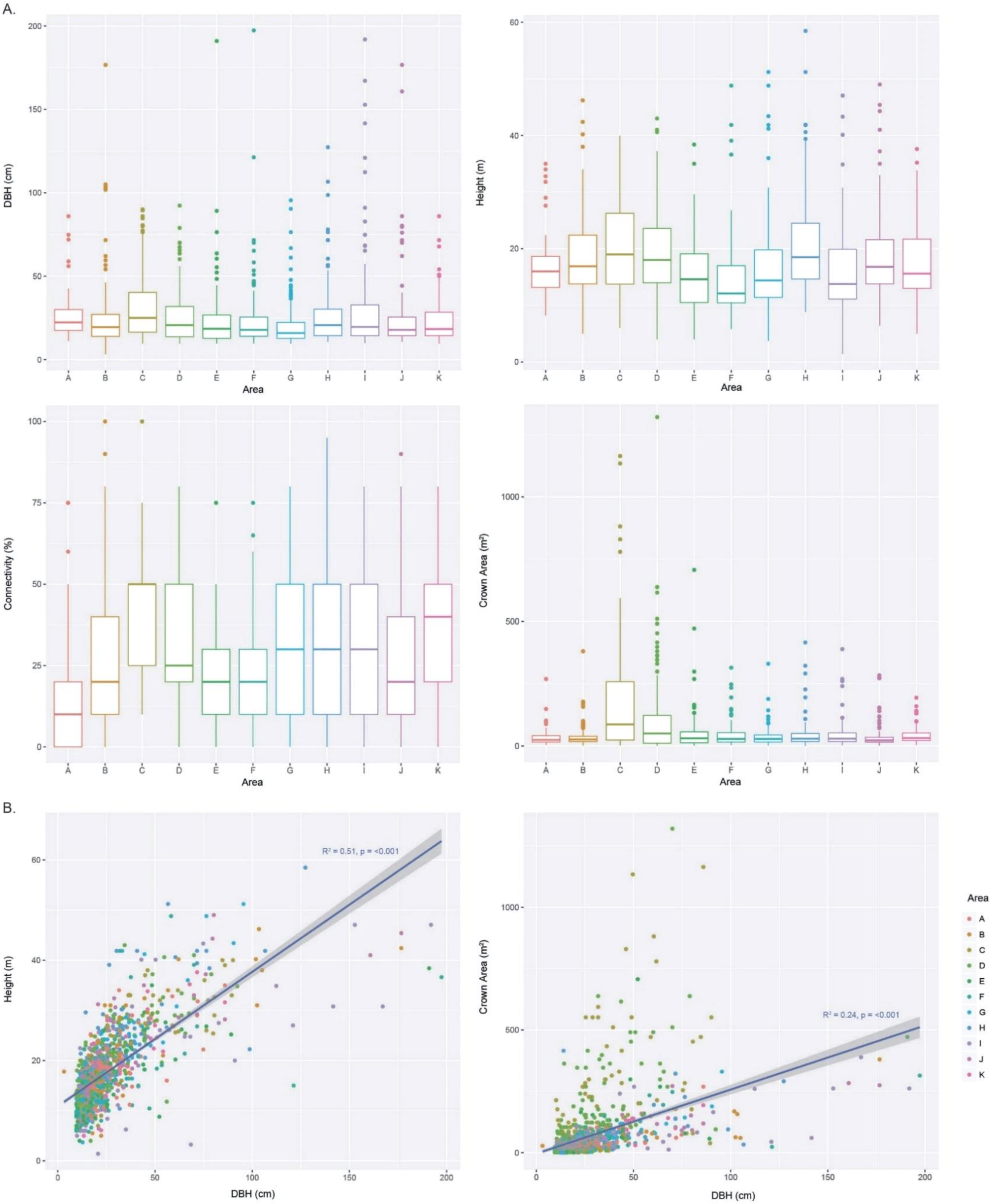


Figure 4.3 – **A**. Comparison of individual tree vegetation variables by sampling area **B**. Results of linear regression between height and DBH (left) and crown area and DBH (right)

4.3.2 Plot-level vegetation structure in relation to anthropogenic disturbance

Mean range of tree heights measured in each vocal sampling area were negatively related to the number of grid cells containing anthropogenic disturbance, with the effect growing in strength as the sampling radius taken into consideration was enlarged. (Tree height range ~ Anthropogenic disturbance within 500m, $\beta = -4.16$, $R^2 = 0.181$, $p = 0.043$, Tree height range ~ Anthropogenic disturbance within 750m, $\beta = -14.50$, $R^2 = 0.189$, $p = 0.038$, Tree height range ~ Anthropogenic disturbance within 1000m, $\beta = -26.31$, $R^2 = 0.309$, $p = 0.006$). No other plot-level vegetation variables were significantly related to anthropogenic disturbance.

4.3.3 Primate encounter rates in relation to plot-level vegetation structure

In total, 1059 encounters of primate vocalisations were recorded. *Presbytis thomasi* were heard vocalising the most (n = 555), followed by *Hylobates lar* (n = 346) and *Symphalangus syndactylus* (n = 157). *Presbytis thomasi* were encountered in all areas, with encounter rates ranging from 0.05 encounters (Area A, post 2) to 1.25 (Area D, post 2). In relation to vegetation characteristics, as measured by vegetation plots within the areas of vocal sampling posts, *Presbytis thomasi* encounter rates were positively related to the range of tree heights within a vocal sampling area (Langur ER ~ Tree height range, $\beta = 0.036$, $R^2 = 0.56$, $p = <0.001$) and negatively related to anthropogenic disturbance at 1000 m radius (Langur ER ~ Anthropogenic disturbance within 1000m, $\beta = -6.568_{-4}$, $R^2 = 0.24$, $p = 0.018$). *Hylobates lar* were also encountered in all areas, with encounter rates ranging from 0.05 encounters (Area E, post 1) to 0.87 encounters per hour (Area J, post 2). *Hylobates lar* encounter rates were positively related to a number of variables consistent with large trees; mean tree diameter at breast height (Gibbon ER ~ Mean tree DBH, $\beta = 0.046$, $R^2 = 0.36$, $p = 0.002$, Gibbon ER ~ Mean tree height, $\beta = 0.061$, $R^2 = 0.28$, $p = 0.009$, Gibbon ER ~ Mean bole height, $\beta = 0.079$, $R^2 = 0.38$, $p = 0.0017$, Gibbon ER ~ Mean crown area, $\beta = 0.0027$, $R^2 = 0.278$, $p = 0.0097$). *Symphalangus syndactylus* were encountered in all but one area (Area K), but most frequently in Area J post 2, at a rate of 0.40. *Symphalangus syndactylus* encounter rates were positively related with the standard deviation of tree heights within a vocal sampling area (Siamang ER ~ Tree height standard deviation, $\beta = 0.049$, $R^2 = 0.22$, $p = 0.023$). No other plot-level vegetation variables were significantly related with primate encounter rates of any species.

4.3.4 Plot-level vegetation structure in relation to UAV vegetation structure

Vegetation structure variables, as measured by mean values of vegetation plots at each sampling area, were compared with UAV-derived vegetation variables measuring three-dimensional canopy structure in a radius at each vocal sampling point. UAV surveys covered 8 of the 22 vocal sampling posts, a potentially confounding factor in statistical analysis due to a low sample size, but some highly correlated values suggest that UAV-derived measurements of vegetation are strongly linked to mean area-wide recordings of vegetation structure measured at the plot level. Ranges of elevations, over a 500 m radius, were highly related to mean tree height (Range of elevations at 500m radius of vocal sampling post ~ Mean tree height, $\beta = 7.415$, $R^2 = 0.975$, $p = <0.001$). This relationship retained a similar strength at larger radius sample areas (Range of elevations at 750m radius of vocal sampling post ~ Mean tree height, $\beta = 6.7519$, $R^2 = 0.931$, $p = <0.001$, Range of elevations at 1000m radius of vocal sampling post ~ Mean area tree height, $\beta = 7.467$, $R^2 = 0.902$, $p = <0.001$).

Table 4.1 – Summary of primate species encounter rates, mean vegetation variables and estimates of anthropogenic disturbance at differing radii around the 22 vocal sampling points

Area	Post	Gibbon ER	Siamang ER	Langur ER	Mean DBH (cm)	Mean Bole Height (m)	Mean Tree Height (m)	Mean Crown Area (m^2)	Mean Connectivity (%)	Tree Height Range (m)	Stdev. Of Tree Height in Area	Mean Canopy Density	Morista's Index of Canopy	Anthro. Disturb. within 250m	Anthro. Disturb. within 500m	Anthro. Disturb. within 750m	Anthro. Disturb. within 1000m
A	1	0.45	0.3	0.15	25.51	9.92	16.49	34.51	17.22	26.80	5.62	77.22	1.09	8	22	65	327
A	2	0.6	0.1	0.05	25.51	9.92	16.49	34.51	17.22	26.80	5.62	77.22	1.09	3	248	853	1166
B	1	0.5	0.1	0.5	26.37	12.46	19.03	37.70	26.03	41.20	7.83	76.11	1.08	2	3	7	9
B	2	0.35	0.15	0.55	26.37	12.46	19.03	37.70	26.03	41.20	7.83	76.11	1.08	0	0	1	8
C	1	0.65	0.1	0.45	31.28	14.70	20.59	188.32	40.63	34.00	8.27	75.92	1.10	13	33	54	73
C	2	0.9	0.2	0.8	31.28	14.70	20.59	188.32	40.63	34.00	8.27	75.92	1.10	18	36	55	96
D	1	0.5	0.3	0.8	25.68	13.26	19.52	111.43	33.17	43.00	7.29	68.48	1.12	4	13	35	62
D	2	0.55	0.2	1.25	25.68	13.26	19.52	111.43	33.17	43.00	7.29	68.48	1.12	9	17	39	59
E	1	0.05	0.05	0.3	23.85	8.66	15.28	51.42	22.82	34.40	6.15	67.44	1.18	0	0	0	0
E	2	0.35	0.05	0.3	23.85	8.66	15.28	51.42	22.82	34.40	6.15	67.44	1.18	0	0	0	0
F	1	0.15	0.05	0.65	24.72	9.12	14.52	44.67	20.13	43.01	7.23	72.74	1.14	1	1	2	3
F	2	0.15	0.15	0.7	24.72	9.12	14.52	44.67	20.13	43.01	7.23	72.74	1.14	0	0	0	0.09
G	1	0.3	0.1	0.85	21.31	10.95	16.62	43.68	33.26	47.51	7.79	66.76	1.15	0	1	1	4
G	2	0.25	0.25	0.75	21.31	10.95	16.62	43.68	33.26	47.51	7.79	66.76	1.15	0	1	3	3
H	1	0.15	0.25	0.9	26.25	12.81	20.50	44.55	30.91	49.66	8.86	74.40	1.08	0	0	0	0
H	2	0.45	0.2	1.4	26.25	12.81	20.50	44.55	30.91	49.66	8.86	74.40	1.08	0	0	0	0
I	1	0.55	0.25	0.6	31.74	10.85	16.52	48.50	31.79	45.64	8.96	74.82	1.09	0	0	0	0
I	2	0.4	0.2	0.85	31.74	10.85	16.52	48.50	31.79	45.64	8.96	74.82	1.09	0	0	0	0
J	1	0.47	0.27	0.40	26.47	11.65	18.99	39.59	24.78	42.60	8.20	74.14	1.09	0	0	1	3
J	2	0.87	0.40	1.07	26.47	11.65	18.99	39.59	24.78	42.60	8.20	74.14	1.09	0	0	0	0
K	1	0.13	0	0.27	23.85	10.28	17.55	43.65	34.80	32.60	6.49	85.11	1.03	0	0	14	290
K	2	0.20	0	0.40	23.85	10.28	17.55	43.65	34.80	32.60	6.49	85.11	1.03	0	0	3	7

Area A

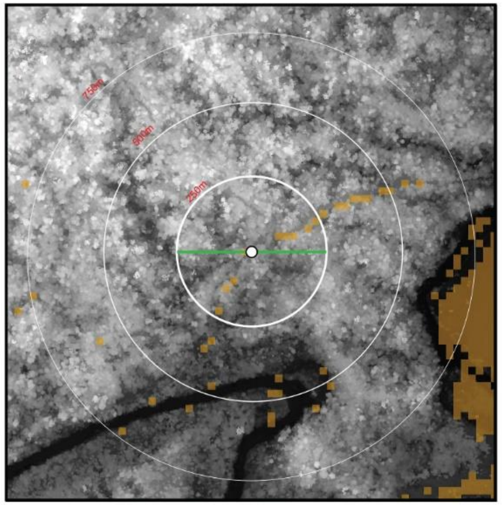
Post 1

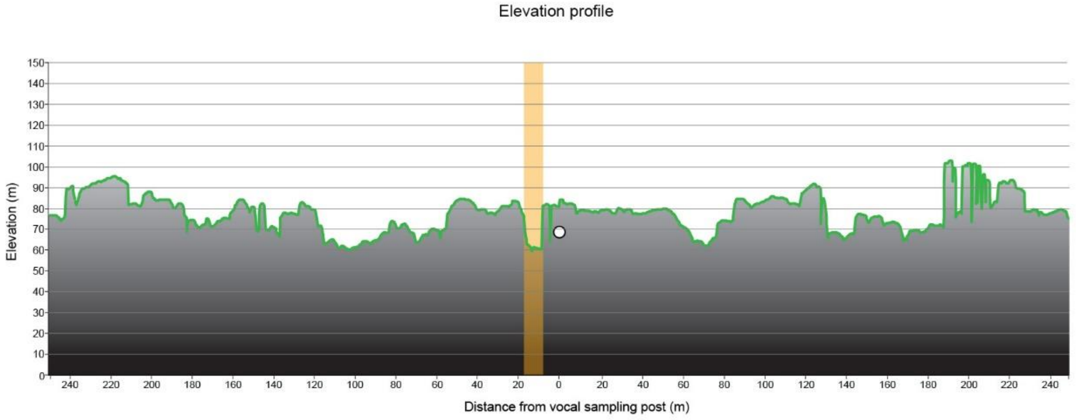
mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
75.43	34.23	115.56	81.32	2.39E+06	180.14	8

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
72.64	20.16	120.80	100.64	3.30E+06	330.05	22

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
71.28	18.63	131.45	112.82	1.14E+07	427.76	65

Gibbon ER	Siamang ER	Langur ER
0.45	0.3	0.15





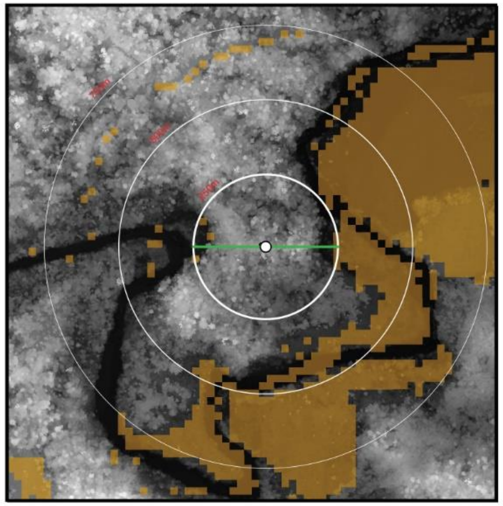
Post 2

mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
59.79	20.79	101.25	80.46	2.53E+06	231.09	3

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
50.93	10.49	114.24	103.74	8.32E+06	409.42	248

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
49.31	2.92	114.24	111.32	1.34E+07	370.21	853

Gibbon ER	Siamang ER	Langur ER
0.6	0.1	0.05



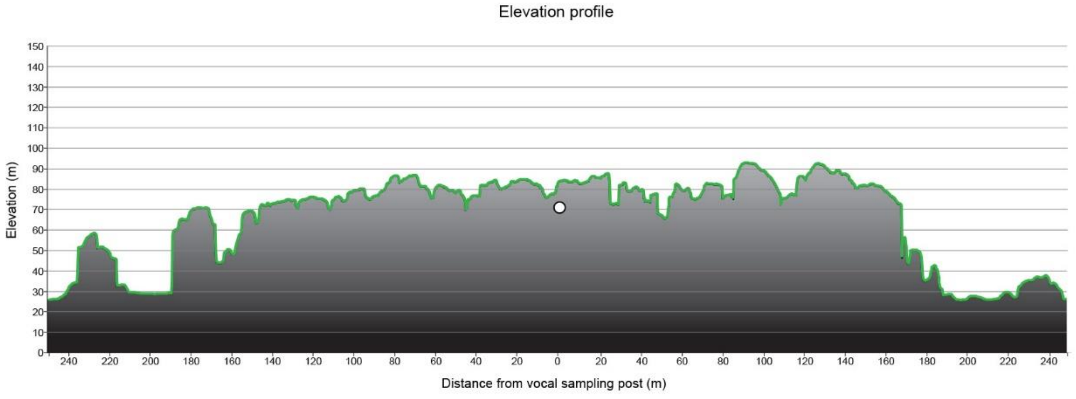


Figure 4.4a – UAV vegetation surveys and univariate statistics for Area A

Area B

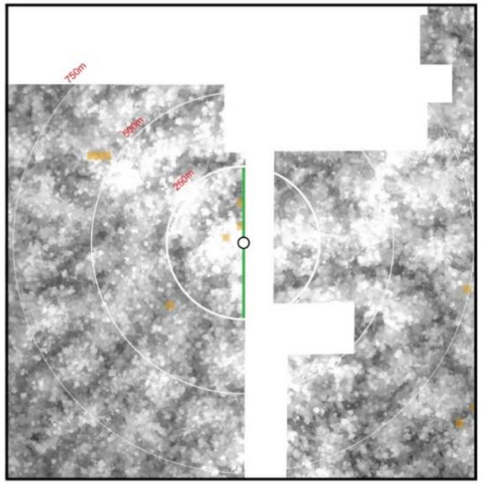
Post 1

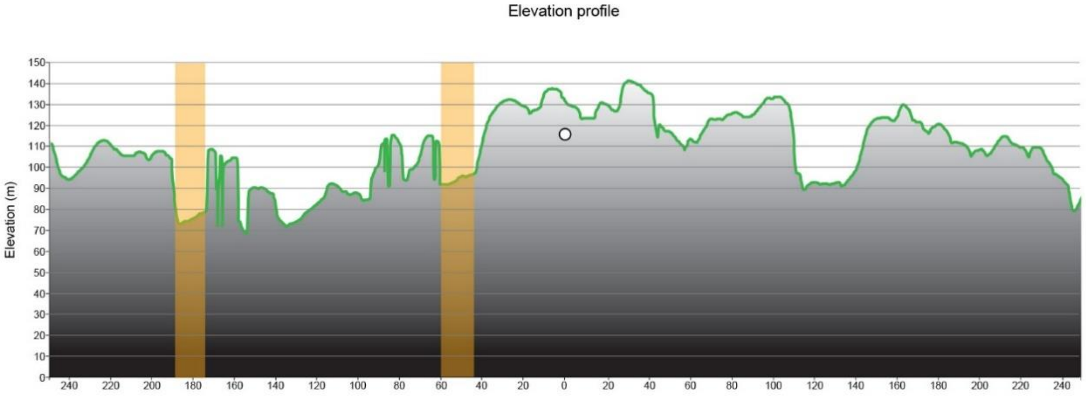
mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
93.72	50.26	136.94	86.68	1.76E+06	232.39	3

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
90.12	39.69	149.90	110.21	5.53E+06	239.87	4

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
89.18	31.56	150.24	118.67	8.66E+06	292.85	7

Gibbon ER	Siamang ER	Langur ER
0.5	0.1	0.5





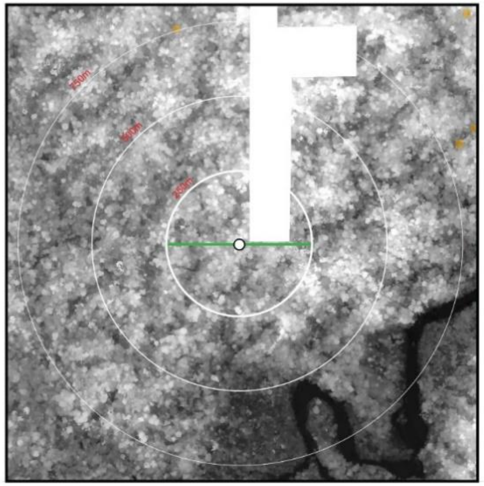
Post 2

mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
89.59	45.38	130.75	85.37	2.07E+06	191.21	0

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
84.46	30.37	136.94	106.56	6.20E+06	281.55	0

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
78.86	14.69	137.51	122.82	1.04E+07	400.94	1

Gibbon ER	Siamang ER	Langur ER
0.35	0.15	0.55



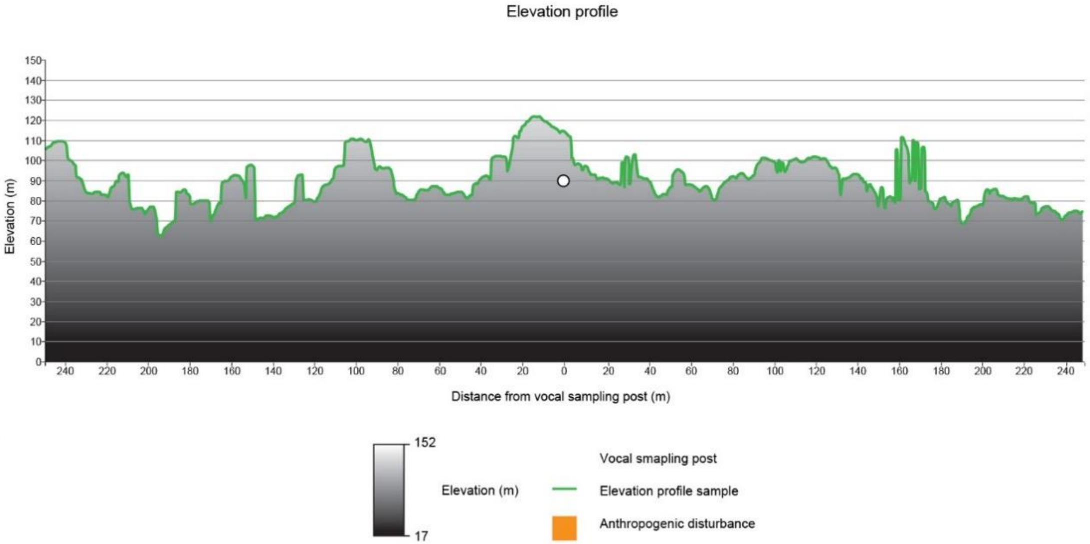


Figure 4.4b – UAV vegetation surveys and univariate statistics for Area B

Area C

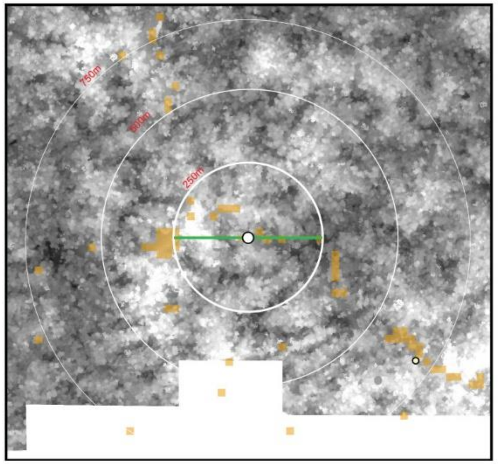
Post 1

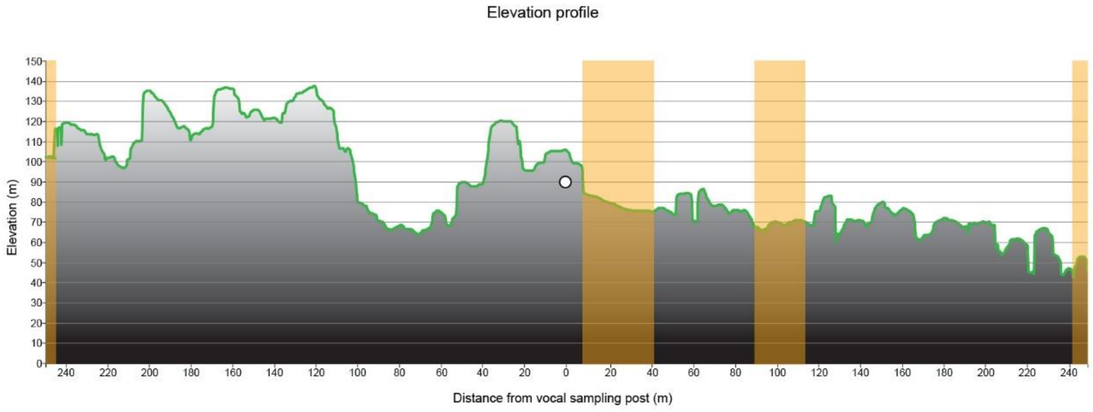
mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
79.44	36.80	125.85	89.06	2.44E+06	241.52	13

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
86.56	34.37	143.04	108.68	6.11E+06	301.73	33

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
86.94	34.37	149.70	115.34	8.43E+06	305.01	54

Gibbon ER	Siamang ER	Langur ER
0.65	0.1	0.45





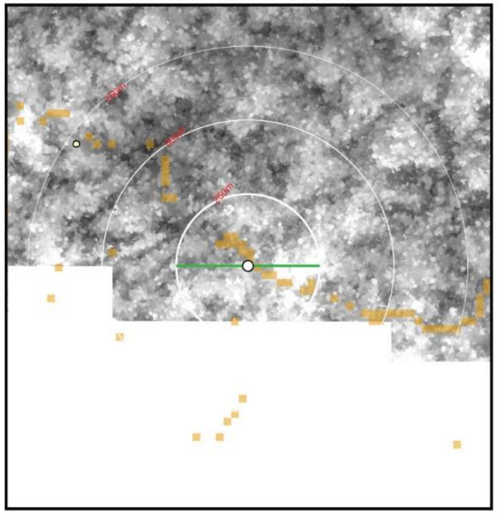
Post 2

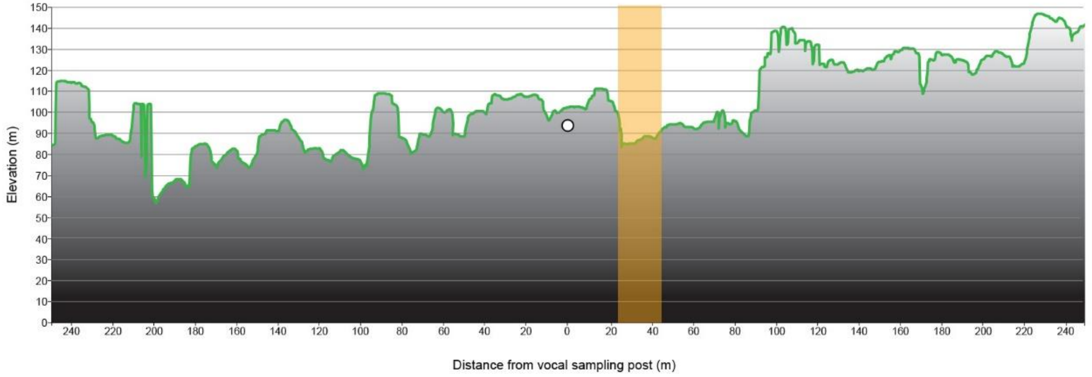
mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
87.16	34.37	139.85	105.48	2.47E+06	308.58	18

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
85.16	34.37	146.50	112.14	6.45E+06	300.93	36

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
82.78	31.14	146.50	115.36	8.92E+06	289.35	55

Gibbon ER	Siamang ER	Langur ER
0.9	0.2	0.8





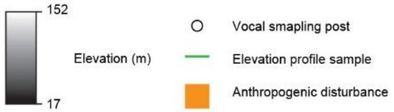


Figure 4.4c – UAV vegetation surveys and univariate statistics for Area C

Area F

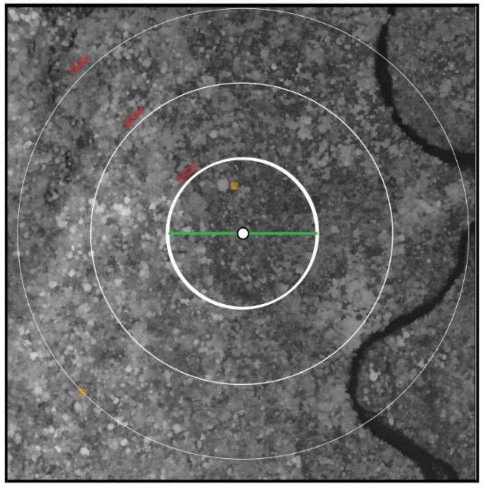
Post 1

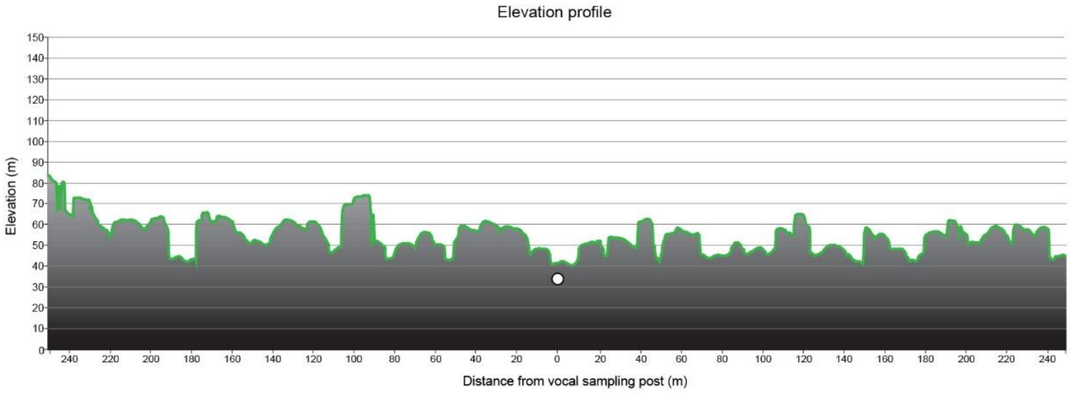
mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
55.09	37.35	91.65	54.30	2.41E+06	77.69	1

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
59.09	36.03	107.89	71.86	6.23E+06	105.77	1

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
58.81	22.98	107.89	84.90	8.97E+06	125.65	2

Gibbon ER	Siamang ER	Langur ER
0.15	0.05	0.65





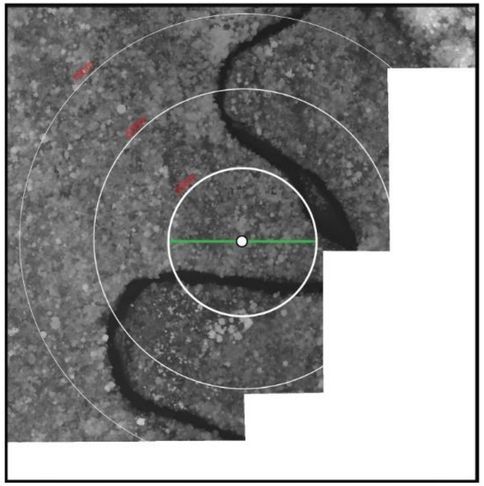
Post 2

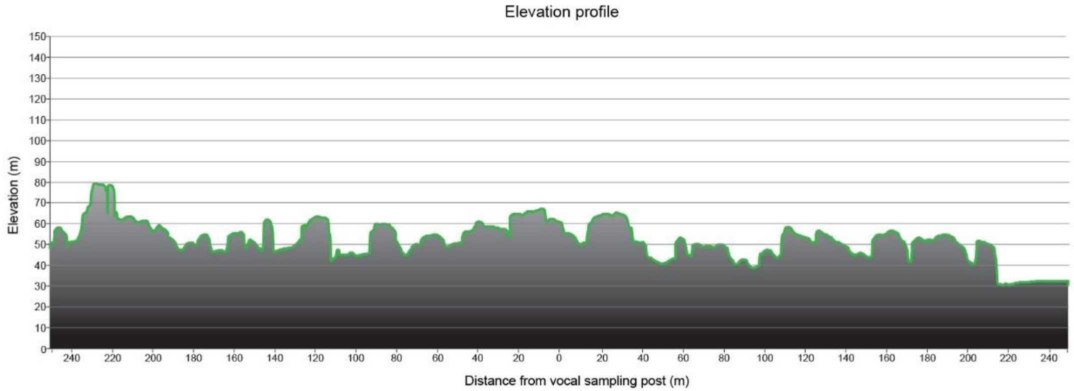
mean ele. 250m radius	min. ele. 250m radius	max ele. 250m radius	range ele. 250m radius	variety of ele. 250m radius	variance ele. 250m radius	Anthro. Disturb. 250m radius
52.95	25.87	85.09	59.22	2.43E+06	99.32	0

mean ele. 500m radius	min. ele. 500m radius	max ele. 500m radius	range ele. 500m radius	variety of ele. 500m radius	variance ele. 500m radius	Anthro. Disturb. 500m radius
54.31	25.87	92.05	66.18	6.22E+06	109.31	0

mean ele. 750m radius	min. ele. 750m radius	max ele. 750m radius	range ele. 750m radius	variety of ele. 750m radius	variance ele. 750m radius	Anthro. Disturb. 750m radius
56.14	25.87	102.80	76.93	8.25E+06	114.95	0

Gibbon ER	Siamang ER	Langur ER
0.15	0.15	0.7





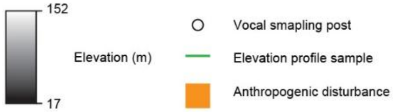


Figure 4.4d – UAV vegetation surveys and univariate statistics for Area F

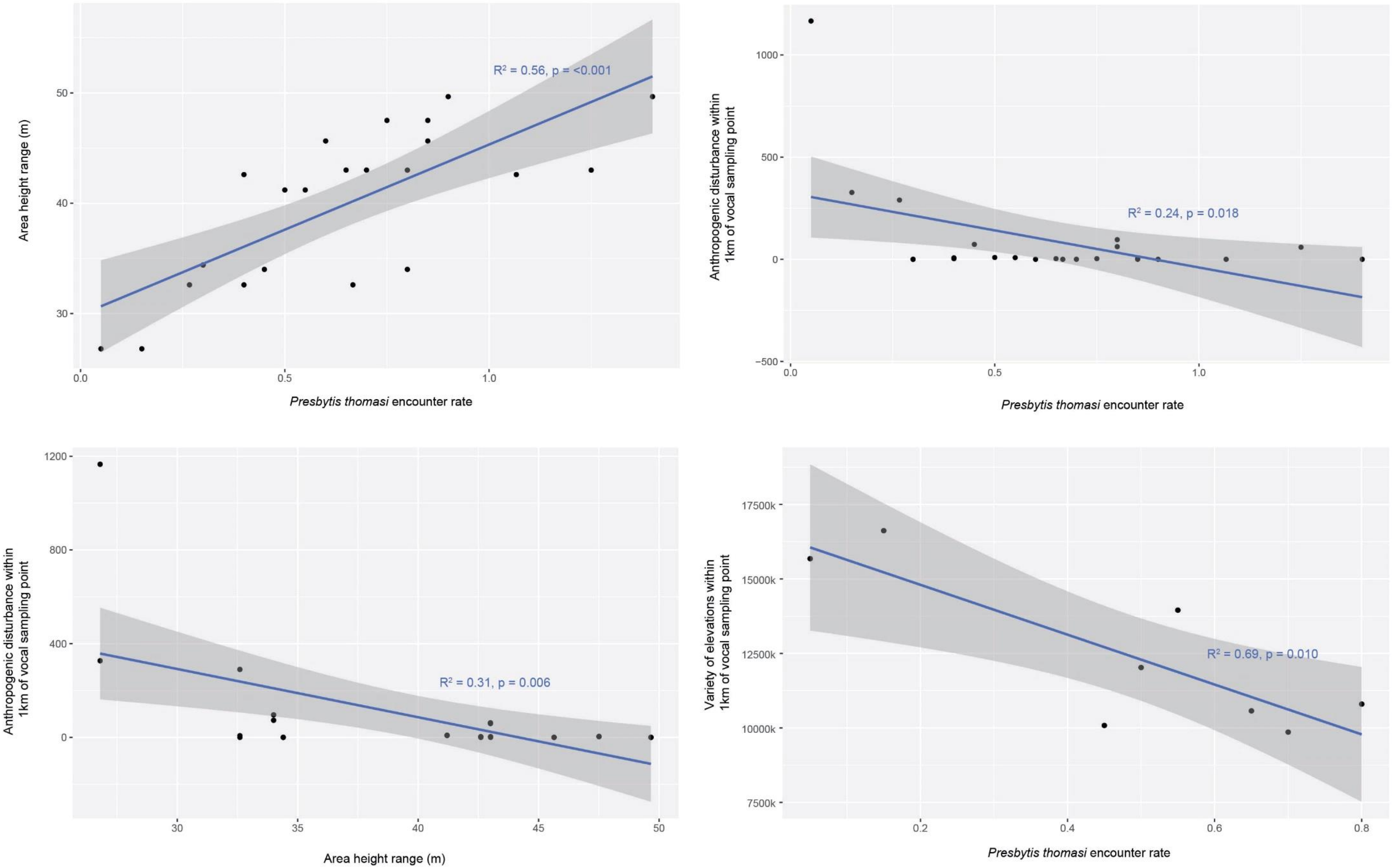
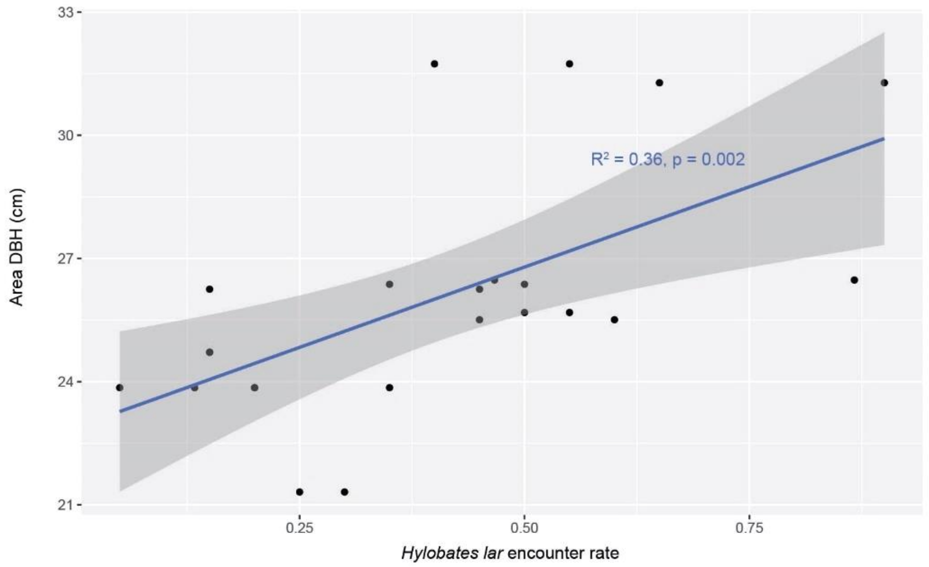
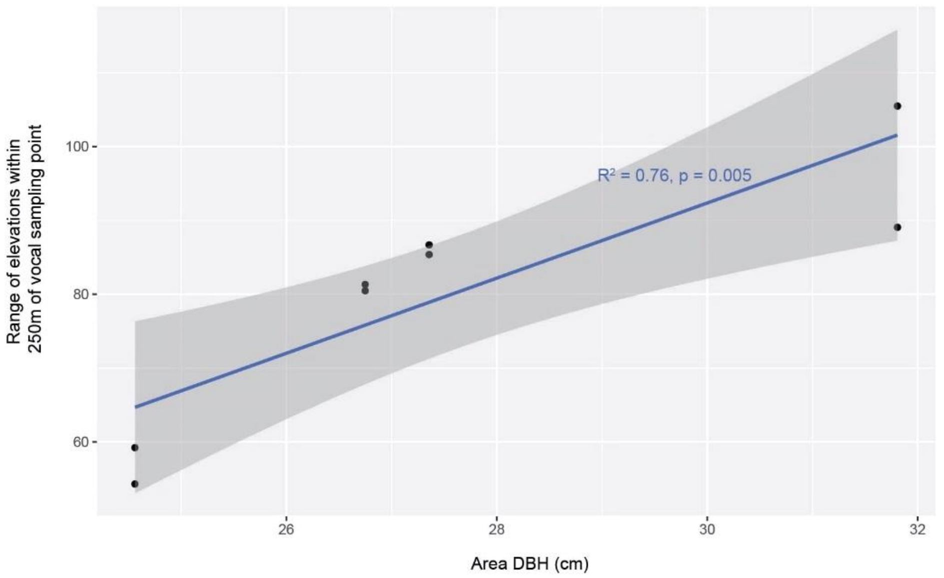
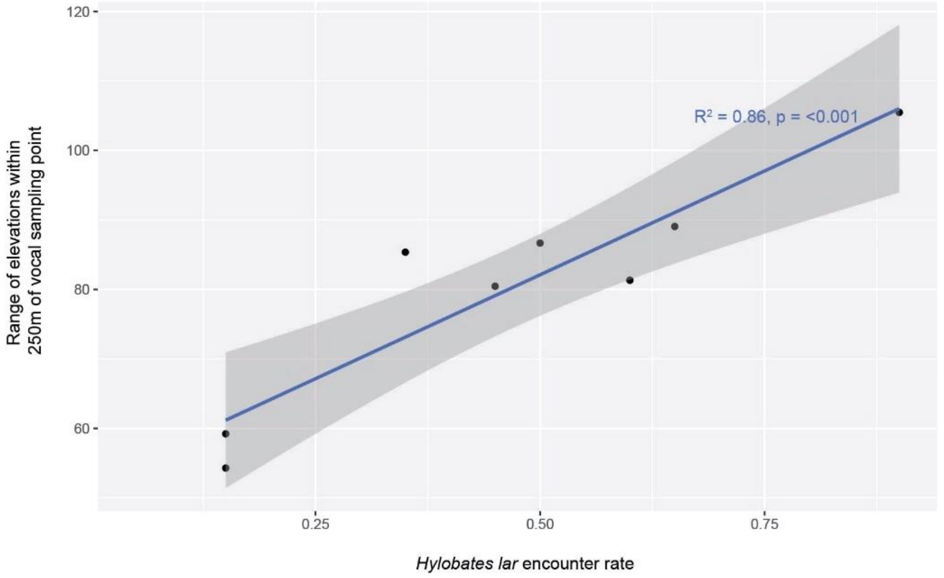
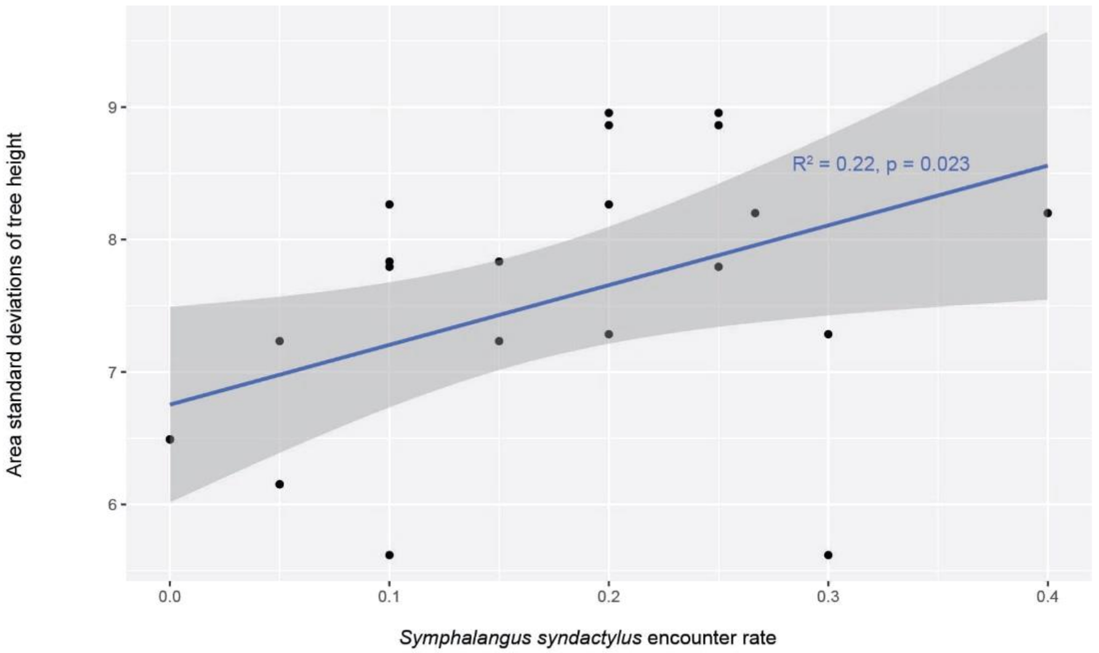


Figure 4.5 - Statistical relationships between ecological variables and *Presbytis thomasi* encounter rates


Area DBH (cm)
33
30
27
24
21
R² = 0.36, p = 0.002
0.25
0.50
0.75
Hylobates lar encounter rate


Range of elevations within 250m of vocal sampling point
100
80
60
R² = 0.76, p = 0.005
26
28
30
32
Area DBH (cm)


Range of elevations within 250m of vocal sampling point
120
100
80
60
R² = 0.86, p = <0.001
0.25
0.50
0.75
Hylobates lar encounter rate



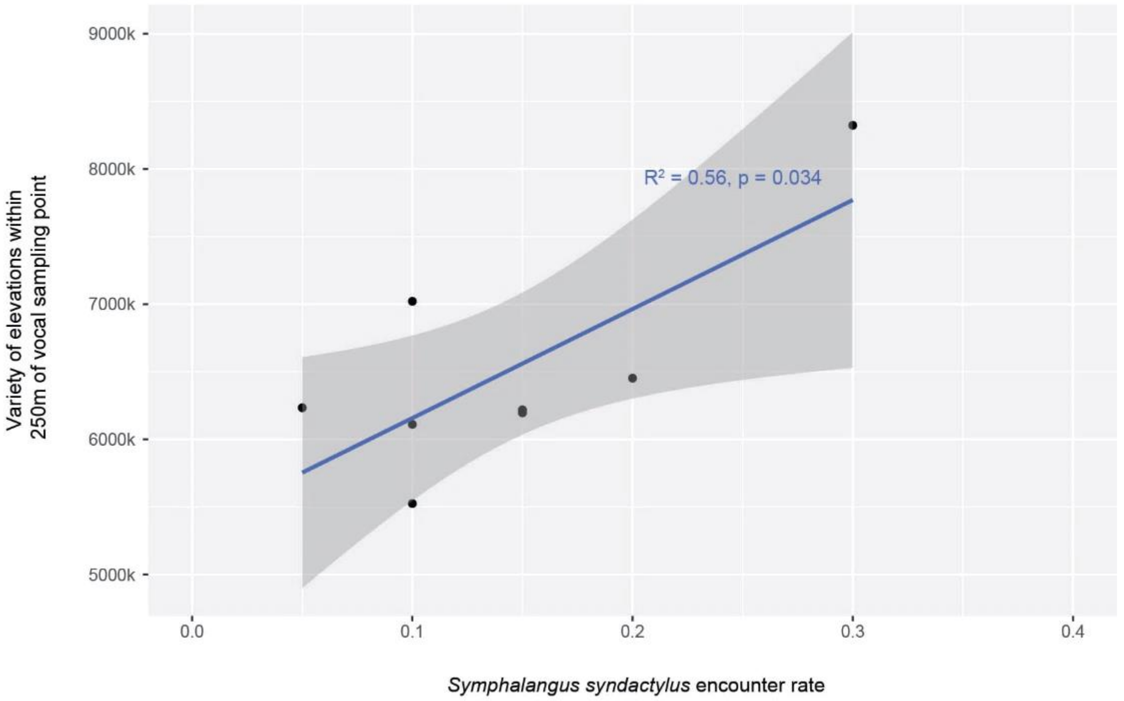


Figure 4.6 – Statistical relationships between ecological variables and *Hylobates lar* encounter rate

Figure 4.7 – Statistical relationships between ecological variables and *Symphalangus syndactylus* encounter rate

As shown previously, tree height and DBH are strongly linked (section 3.4.1). Therefore, ‘range of elevations’ as measured using a UAV extracted at a radius of 750 m and 1000 m is also related to mean DBH variables. However, whereas the relationship between tree height remains consistent with larger radius sample areas, the relationship between the range of elevations and mean DBH is weaker with increased radius sample areas (Range of elevations at 250m radius of vocal sampling post ~ Mean DBH, $\beta = 5.089$, $R^2 = 0.756$, $p = 0.005$, Range of elevations at 500m radius of vocal sampling post ~ Mean DBH, $\beta = 4.842$, $R^2 = 0.573$, $p = 0.029$), becoming non-significant beyond 500 m (Range of elevations at 750m radius of vocal sampling post ~ Mean DBH, $\beta = 3.8504$, $R^2 = 0.417$, $p = 0.08$). Additionally, minimum elevation at the 500m sample radius is correlated with plot-level range of tree heights within a given area (Minimum elevation at 500m radius of vocal sampling point ~ Tree height range, $\beta = 1.7258$, $R^2 = 0.751$, $p = 0.005$). No other UAV derived vegetation variables were related to plot level vegetation variables.

Counts of anthropogenic disturbance at differing radii from vocal sampling posts were negatively related to minimum elevations as measured by UAV surveys (Count of 25x25m cells containing anthropogenic disturbance at 500m radius of vocal sampling post ~ Minimum elevation at 500m radius of vocal sampling post, $\beta = -8.078$, $R^2 = 0.612$, $p = 0.022$. As also might be expected, increased anthropogenic disturbance had a positive relationship with the variety of elevations in an sampling area (Count of 25x25m cells containing anthropogenic disturbance at 500m radius of vocal sampling post ~ Variety of elevation at 500m radius of vocal sampling post, $\beta = 0.0001$, $R^2 = 0.808$, $p = 0.002$). No other UAV derived vegetation variables were related to counts of anthropogenic disturbance.

4.3.5 Primate encounter rates in relation to UAV vegetation structure

UAV surveys, measuring three-dimensional canopy structure, covered 8 of the 22 vocal sampling posts. In relation to the DSM elevation characteristics, *Presbytis thomasi* encounter rates were negatively related to the variety of elevations, a relationship which grew in strength with greater radius sample areas (Langur ER ~ variety of elevations within a 500m radius of vocal sampling post, $\beta = -0.0000002$, $R^2 = 0.403$, $p = 0.091$, Langur ER ~ variety of elevations within a 750m radius of vocal sampling post, $\beta = -0.0000001$, $R^2 = 0.611$, $p = 0.022$, Langur ER ~ variety of elevations within a 1000m radius of vocal sampling post, $\beta = -0.000000008$, $R^2 = 0.688$, $p = 0.011$). *Presbytis thomasi* encounter rates were also had positive relationship to the minimum elevation at a 500m radius of the vocal sampling post, though not significantly (Langur ER ~ 500 min elevation, $\beta = 0.019$, $R^2 = 0.481$, $p = 0.056$). *Hylobates lar* encounter rates were strongly related with the range of elevations at small radius sample areas (Gibbon ER ~ range of elevations within a 250m radius of vocal sampling post, $\beta = 0.014$, $R^2 = 0.856$, $p = <0.001$), a relationship that decreased in strength with larger radius sample areas (Gibbon ER ~ range of elevations within a 500m radius of vocal sampling post, $\beta = 0.012$, $R^2 = 0.661$, $p = 0.014$, Gibbon ER ~ range of elevations within a 750m radius of vocal sampling post, $\beta = 0.011$, $R^2 = 0.488$, $p = 0.054$). *Symphalangus syndactylus* encounter rates were related to the variety of elevations at 500 m radius sample areas (Siamang ER ~ variety of elevations within a 500m radius of vocal sampling post, $\beta = 0.00000006$, $R^2 = 0.556$, $p = 0.034$). No other UAV derived vegetation variables were significantly related to primate encounter rates, of any species.

4.3.6 Primate encounter rates in relation to sympatric species encounter rates

Comparing primate species encounter rates to one another, abundance of *Presbytis thomasi* were related to *Symphalangus syndactylus* (Langur ER ~ Siamang ER, $\beta = 0.136$, $R^2 = 0.17$, $p = 0.048$) but not *Hylobates lar. Symphalangus syndactylus* encounter rates were related to both *Presbytis thomasi,* and *Hylobates lar* (Siamang ER ~ Gibbon ER, $\beta = 0.262$, $R^2 = 0.30$, $p = 0.007$).

4.5 Discussion

Results from this study indicate that forms of forest degradation, be it recent land clearance or the effects of historical selective logging, impact habitat quality for primate species in different ways, depending on their habitat preferences. This study’s results support findings of previous research on the specific effects of anthropogenic disturbance on forest structure, namely that habitat degradation reduces tree height variation as large trees are removed (Felton et al., 2006; Franklin et al., 2002). This was supported by measurements of large trees, for example recorded as mean tree height in vegetation plots and elevation range using UAV surveys. These two measurements were strongly related ($R^2 = 0.97$), highlighting the potential for UAV data capture to rapidly assess habitat quality over large areas. Variation in tree height has previously been identified as an indication of old-growth forest (Franklin et al., 2002; Chen et al., 1992; Álvarez-Yépiz et al., 2008), and more uniform height a sign of forest regeneration (Harper et al., 2005; Greene et al., 1997) supporting these findings. Estimates of anthropogenic disturbance from supervised classification of satellite imagery were seemingly successful in identifying degraded areas, shown by a relationship between a reduction in tree height range as assessed in vegetation plots and by UAV surveys and counts of anthropogenic disturbance in the wider area (R^2 = 0.31 and R^2 = 0.81 respectively). This method of ground-truthing sites of discreet degradation may allow future studies to identify areas of forest degradation over large areas with minimal additional vegetation surveys and using widely (and freely) available satellite imagery. Additionally, that any relationship was shown between anthropogenic disturbance over a large area and mean values of vegetation plots suggests that even historic selective logging has an impact of vegetation quality for species inhabiting relatively small areas of forest, even 35 years after logging events (Knop et al., 2004). Whilst an effort was made to quantify the effects of historical degradation in this study, selective logging in tropical forests has been shown to target the largest trees, especially *ficus* spp. (Felton et al., 2006) which have previously been shown to be highly correlated to primate spesies' abundance, particularly Hylobates spp. (Mather, 1992, Barlett, 1999, Barlett 2007). In an area which is previously known to have been selectively logged, there is a high chance that large *ficus* trees have been damaged or removed. Identifying or quantifying the removal of important food trees and how this may impact primate species in the area still presents a challenge, even with the aid of UAV survey enabling the investigation of three-dimensional canopy topography.

Previous research has shown that changes in forest structure due to selective logging alter the behaviour and densities of primates (Marshall et al., 2009), and selective logging alters canopy structure (FAO, 1981, Jepson et al., 2001) and decreases potential habitat availability for arboreal primates (Johns, 1988). Vegetation structure has also been shown to be highly influential on the abundance of arboreal primate species (Matthiopoulos, 2003, Marsh et al., 2016), enabling travel (Emmons & Gentry, 1983), access to food resources (Felton et al., 2003), and resting and sleeping sites (Pruetz et al., 2008), although the location and availability of food resources has been shown to be the dominating factor in relation to habitat preference of frugivorous primate species (Garber, 1987; van Schaik et al., 1993). However, in environments in which preferred food resources are low, such as Sikundur (Wich et al., 2011), forest structure is increasingly important for arboreal primates. Tree connectivity is required to enable travel to dispersed food resources (Madden et al., 2010; Bernard et al., 2011; McLean et al., 2016), and when fruit is available, large fruiting trees produce more fruit than smaller trees (Chapman et al., 1992) and are often preferred sleeping sites for primate species (Merker et al., 2005; Cheyne et al., 2012; Feilen and Marshall., 2014). With degraded forests, areas in which large trees remain may become crucial for some primate species, especially frugivores (Marsh et al., 2016).

Tree height range in vegetation plots and range of elevations in sample areas of UAV survey data were both related with the abundance of *Presbytis thomasi* and *Symphalangus syndactylus,* both species with largely folivorous diets (Steenbeek and van Scaik, 2001;

Elder, 2009). Whilst both *P. thomasi* and *S. syndactylus* have been shown to have a large proportion of their diets consisting of fruit when it is in abundance (Gurmaya, 1986; Palombit, 1997), in Sikundur, in which fruit production is low (Figure 2.6) folivory is likely to make up a large part of their diet (Harrison and Marshall, 2011, Section 2.3, Figure 2.7). A larger range in the tree heights may therefore denote the presence of preferred food items (either dispersed fruit, or favoured young leaves) or potential sleeping sites. That these two species share some habitat preferences suggests some ecological overlap between them.

For the wide ranging, largely folivorus *Presbytis thomasi*, a high range of canopy heights, as measured on the plot level, within large areas of homogenous habitat structure appears to be favoured. A negative relationship between *P. thomasi* abundance and minimum elevation also suggests a preference for areas with large trees and high canopies. Where canopy homogeneity is compromised through anthropogenic disturbance, even at the largest sample area used in this study, *P. thomasi* appears to be less abundant. This assertion is reinforced by a negative relationship between *P. thomasi* abundance and the range of elevations ($R^2 = 0.69$). With the effect of canopy structure variety being stronger than anthropogenic disturbance (as measured by classification of satellite imagery), there is a suggestion that variety in forest canopy structure as opposed to anthropogenic effects, is an influence on *P.thomasi* abundance. This could suggest *P.thomasi* shows a preference for forest interiors, as opposed to forest edges, possibly in flat or alluvial land types. This suggests that for *P. thomasi,* in a continuous forest habitat with a high availability of low-quality food, there is a strong degree of habitat preference. Areas which are compromised by anthropogenic disturbance are avoided, as areas of undisturbed habitat of similar quality are readily available. Areas in which both *H. lar* and *S. syndactylus* are more abundant are not preferred by *P. thomasi*, instead they are most abundant where these two species are seemingly rare. Given that *P. thomasi* are generally characterised as folivores (Sterck, 1995), this may suggest a preference for areas with the least amount of interspecies competition with sympatric primate spp., although no clear statistical evidence for this is found in this study. A possible confounding factor to these findings relates to the method in which abundance was measured. Given that encounter rates were estimated from vocalisations made in the early morning, locations in which *P. thomasi* were encountered may not represent absolute habitat preference, but rather preferred areas for sleep sites, and other areas may be utilised later in the day. This could potentially dramatically alter this study's findings in relation to *P. thomasi*. However, *P. thomasi* has been shown to use relatively small home ranges (1.7ha – 15.7ha, Gurmaya, 1986) suggesting that early morning calls are to aid in territorial defence and abundance from early morning vocalisations may be a good indicator of preferred habitat.

Hylobates lar, is a highly arboreal frugivore, with fruit comprising ~60% of their annual diet (Bartlett, 2007), with figs (*ficus* spp.) making up a substantial portion of this (23% on average, Bartlett 1999, 2007). *H. lar* are socially monogamous and defend home ranges against neighbouring conspecifics (Bartlett, 2009). Their home ranges are extremely stable, not only year-round, but also year to year (Bricknell, 1999; Bartlett, 2009). They have been shown to favour areas in which large fruiting trees occur, and their territory size is limited by periods when resource abundance is low (Raemaekers, 1980). All these factors suggest that *H. lar,* in a degraded tropical forest with limited fruit availability, would defend small areas in which fruit availability was high and vegetation structure allowed access to food resources. In this study this was seemingly confirmed, with *H. lar* encounter rates were strongly related to the presence of large trees, as measured in areas with high mean tree diameter at breast height in vegetation plots ($R^2 = 0.36$) and by larger elevation ranges in UAV surveys ($R^2 = 0.86$), supporting findings in other studies (Brockleman and Ali., 1987; Nijman, 2001; Hamanrd et al., 2010). The strongest relationships between UAV variables and *H. lar* abundance occurred at the smallest spatial scales, suggesting that small home ranges in high quality habitat are preferred. Gibbon have been shown to be fairly adaptable to levels of anthropogenic disturbance, possibly due to their small home ranges and low group numbers (Johns., 1986; Nijman, 2001; Cheyne et al., 2016). Within Sikundur, historical anthropogenic disturbance such as logging roads may have seemingly little impact on the abundance of *H. lar*. However, such forms of disturbance may be discrete in their effects, and their impacts difficult to identify (Barlow et al., 2006; Chaves et al., 2012). Given the clear habitat preference of *H.lar,* if selective logging or encroachment into the Leuser Ecosystem were to continue (see Figure 1.4), a reduction of available habitat in the Sikundur would likely see a spike in *H. lar* population density, forcing some groups into areas of low-quality habitat, thereby impacting their health and potentially reproductive success. This has previously been shown in the variety of local gibbon densities between habitat types in the same landscape (O'Brien et al., 2004; Marshall, 2009; Yanuar, 2009). This very process is likely to have occurred in Sikundur previously during periods of selective logging (Abdulhadi et al.,1987). That historical logging roads occurred most in areas with large trees in this study may be potentially obscuring this relationship. Additionally, strong correlations between *H. lar* and variables produced using UAV surveys in this study enable the projection of habitat preference in areas covered by future UAV surveys, a method that could be used to highlight areas of conservation importance for this endangered ape species.

Symphalangus syndactylus is larger bodied than *H. lar* and differs in both diet and ranging from sympatric gibbon species (Chivers, 1972, MacKinnon, 1977). The siamang, tends to eat larger quantities of less calorific leaves compared to gibbon diets of fewer, more calorific fruits (Raemakers, 1979). Similar to *Pongo pygmaeus*, *S. syndactylus* appears to be an arboreal generalist, eating large quantities of leaves regularly, but utilising fruits when they are available (Wich et al., 2006; Lappan, 2009). As previously shown, *S. syndactylus* in

Sikundur may have larger home ranges than siamang in other areas (see Section 2.3.2 and 2.4), suggesting that this may be a response to anthropogenic disturbance or low fruit availability. Given the generalist nature of *S. syndactylus,* and the relatively unclear effect of anthropogenic disturbance on the quality of siamang habitat, it is unsurprising that few habitat variables were found to explain *Symphalangus syndactylus* encounter rates. Variety in canopy elevations, as measured using UAV surveys and standard deviation in vegetation plots, was shown to be correlated with *S. syndactylus* encounter rate. This suggests that siamang preference is for variety in their preferred habitat, with the potential to contain both large fruiting trees and regenerating forest to provide a source of young leaves, which make up the majority of their diet (see Section 2.3.1; O'Brien et al., 2003; Lappan, 2009). *S. syndactylus* abundance is correlated, albeit weakly, with both *P. thomasi* ($R^2 = 0.17$) and *H. lar* ($R^2 = 0.30$), which supports the idea that siamang share some ecological similarity to both these species, yet remains within its own ecological niche, that of a dietary and habitat generalist (Lappan, 2009). Siamang may be able to take advantage of habitats utilised by both sympatric primate species highlighted in this study, as well as other primate species in the area, *Pongo abelii*, *Macaca fascicularis* and *Macaca nemestrina.* Natural selection should favour behavioural flexibility in primates living in complex, unpredictable landscapes. Primate species with sufficient behavioural flexibility may even have altered diet and behavior between groups of the same species in the same area as shown by Chapman et al., (2002); for example, a group or red colobus shared a higher dietary overlap with a sympatric group of black-and-white colobus than another neighbouring group of red colobus. However, despite apparent habitat flexibility, siamang are large and exclusively arboreal and require the presence of vegetation with sufficient structural integration to locomote effectively (Fleagle, 1974, Fleagle, 1976). A possible confounding factor to these determinations is the uniformly low abundance of *S. syndactylus* throughout Sikundur. The population density of *S. syndactylus* is seemingly fairly low, with groups occupying large, low-quality home ranges (see Section 2.3.2). Given this, defense of these territories through calling may be infrequent, affecting *S. syndactylus* encounter rates. It has previously been proposed in *Hylobates spp*. that low density affects singing probability, as the 'contagious' nature of territorial calling results in there being infrequent stimuli to initiate calling bouts (Steenbeck et al., 1999; Brockelman & Srikosamatara, 1993; Geissmann & Nijman, 2006; Mitani, 1987; Nijman, 2004). This may be a confounding factor in the assessment of *S. syndactylus* abundance in areas of low forest quality.

4.6 Conclusions

This study highlights how ecological niche separation of sympatric primate species impacts their responses to anthropogenic disturbance. Seemingly *P.* thomasi, a group living folivore, was most affected by anthropogenic disturbance, despite its apparent abundance throughout the study area. *H. lar* abundance was strongly related with the presence of large trees, supporting previous findings, and highlighting the importance of old-growth forest in supporting a diversity of primate species. *S. syndactylus* were seemingly in relatively low abundance throughout the study site and show evidence of being habitat generalists. For the assessment of habitat quality for arboreal primate species, the use of UAV surveys may be of great benefit in future studies, enabling the identification of preferred habitat over large areas. Ecological niche separation of each species enables the use of differing variables produced by UAV surveys to be ascribed to separate species, allowing the clear identification of vegetation characteristics that may govern individual species' abundance. Furthermore, given the strong relationship between tree height measured in traditional vegetation plots and elevation range measured using UAV surveys, tree biomass and therefore carbon stock estimations may be possible with minimal further data collection and analysis.

Chapter 5. The simulated impacts of climate change on two sympatric arboreal ape species

5.1 Introduction

Land-use change and global warming are among the primary threats to biodiversity (Nowakowski et al., 2018). Land-surface temperatures in tropical rainforest regions have risen by approximately ~0.25°C per decade since the mid-1970s (Malhi and Wright, 2004) and are projected to rise by 3-8°C by 2100 (Malhi et al., 2009). Forest degradation, measured by reductions in canopy cover, has affected 185 million ha between 2000 and 2012, with the vast majority, over 155 million ha, occurring within tropical forests (van Lierop et al., 2015). Although tropical forest species are experiencing both, habitat modification and climate change, simultaneously, they are typically studied independently (Sirami et al., 2017, Oliver and Morecroft, 2014), despite habitat modification causing thermal landscape variation (Todd and Andrews, 2008; Arroyo-Rodrigues et al., 2016; Tuff et al., 2016).

Macro-scale climate patterns are known to influence the distribution and range of biota (Frey et al., 2016). However, at a smaller scale, microclimate may only be weakly correlated with macroclimate due to the influence of vegetation structure and microtopography (Graae et al., 2012; WallisDeVries et al., 2011; Potter and Hargrove., 2013). Forest systems have been shown to reduce heat exposure by more than 10°C (Scheffers et al., 2014a, Chapter 2), dramatically changing the microclimate that organisms experience, which is often more relevant to animal behaviour and demography than macroclimate (Potter et al., 2013; Chen et al., 1999). In a degraded forest the availability of microhabitats and the effectiveness of their thermal buffering are heavily influenced by varying levels of vegetation density (Pringle et al., 2003). The level of degradation, time since degradation and tree species establishment will affect forest structure and therefore microclimate (Pohlman et al., 2007; Norris et al., 2012; Harper et al., 2005; Brokaw, 1982; Mulkey and Pearcy, 1992; Laurance et al., 2006) The availability and distribution of thermal buffering microhabitats may lead to only a fraction of available habitat being frequently utilised by certain species, depending on their exposure and sensitivity to temperature variation (Williams et al., 2008). Organisms that have evolved inhabiting dense forests may already be reliant on the forest structure to buffer against solar radiation and be close to their thermal thresholds (Tewsbury et al., 2008; Thompson et al., 2016; Pörtner et al., 2006). For these species, only a moderate degree of warming caused either by a reduction in the thermal buffering effects of vegetation or by climate change, would lead to a marked decline in fitness (Deutsch et al., 2008). The two effects of forest degradation and climate change, impacting in synergy, could have profound effects on organisms which have evolved to survive in tropical rainforest environments (Ahumada et al., 2011, Corlett, 2011).

Under future predicted climate change, tropical regions which are largely landlocked will experience higher rates of warming than those with large areas bordering oceans, such as Sumatra (Graham et al., 2016). However, climate envelope models predict large declines of tropical biodiversity in a warming world, especially in the lowland tropics (Colwell et al., 2008). As a consequence of the stable climates that Southeast Asia experiences, both over seasonal and millennial timescales, many organisms that inhabit these areas have narrow thermal niches (Tewsbury et al., 2008). Species that have reduced access to microclimate refugia and reliance on the complex homogenous structure of tropical forests for locomotion, could be most adversely affected by selective logging and climate change (Brodie et al., 2012). One taxonomic group that falls under this classification is arboreal apes.

In Sumatra, tropical forests face a multitude of threats; including the spread of commercial agriculture, encroachment of a growing human population and selective logging, (Gaveau et al., 2011). A lack of law enforcement has led to widespread forest degradation and deforestation, with protected areas experiencing similar levels of deforestation to areas allocated for commercial logging (Gaveau et al., 2012). In Sikundur, a lowland dipterocarp forest in Northern Sumatra, selective logging took place from the late 1960s until 1982, during which an average of 11 large trees per hectare were felled (Knop et al., 2004; Cribb, 1988; Wind, 1996). Five years after the end of the logging operation, Abdulhadi et al. (1987) found that 54% of the remaining trees still showed some damage caused by the logging. However, there is still ongoing small-scale deforestation and degradation (Wich and Koh, 2018). There is a lack of robust scientific knowledge on how coupled effects of tropical forest degradation and climate change affects habitat suitability for keystone species (Chapin III et al., 2000; Walther et al., 2002). The direct effect of historical forest degradation may be marginal in terms of reduced habitat for arboreal ape species, but changes in forest structure due to selective logging alter their behaviour and densities by displacing resources and increasing the energetic costs of reaching them (Marshall et al., 2009; Chaves et al., 2012). Microclimate also drastically alters how and when primates use disturbed areas of forest (Takemoto, 2004; Suggitt et al., 2011), with some ape species coming to the ground to take advantage of the thermal buffering of vegetation (Takemoto, 2017). In a warming environment, the reduced effects of thermal buffering due to forest degradation may have a substantial impact on the habitat suitability of degraded forest areas for arboreal apes. Exclusive arboreality in apes is rare (Rodman, 1984), but the Asian apes are the most restricted to locomotion in the canopy (Thorpe and Crompton, 2006). Chimpanzees, bonobos, mountain and lowland gorillas spend a relatively large amount of time on the ground, as reflected in their morphological adaptations for quadrupedal knuckle-walking

(Hunt, 1991). Whilst arboreal living may confer some advantages in the location and extraction of preferred food items (Thorpe and Crompton, 2005), it limits the ability of arboreal apes to thermo-regulate behaviourally and potentially renders them more susceptible to habitat degradation.

This study aims to assess how two sympatric ape species, Sumatran orang-utan (*Pongo abelii*) and siamang (*Symphalangus syndactylus*), inhabiting the same degraded forest landscape will be affected by future predicted climate change. By recording each species' use of canopy structure, I develop a Habitat Suitability Index (HSI) based on each species' recorded habitat use. To adjust this Habitat Suitability Index to take into account future predicted climate change, a site-wide microclimate model was adjusted to reflect future predicted levels of warming, with areas reaching temperatures above the theorised thermo-neutral zone of each species reducing the Habitat Suitability of those areas. Areas which reach temperatures above the species' predicted thermoneutral zone for extended periods of time will have reduced habitat suitability, and modelling this will estimate the impacts of global warming on these two arboreal ape species. I change each species' HSI in relation to future predicted climate change scenarios in both the years 2050 and 2070 under four greenhouse gas concentration trajectories as adopted by the IPCC for its Fifth Assessment Report (AR5) in 2014 (Moss et al., 2008). Although within these time periods other organisms may be able to evolve or acclimate to new temperatures, the extremely slow life-history of primates (~20 years per generation, [Gienapp et al., 2008]) inhibits physiological adaption to new climates. The four Representative Concentration Pathways tested (RCPs; RCP 2.6, RCP 4.5, RCP 6 and RCP 8.5) are named after a possible range of radiative forcing values relative to pre-industrial values (+2.6, +4.5, +6.0 and +8.5 W/m^2, respectively). Furthermore, I estimate the experienced temperatures of each species in each climate change scenario if their ranging behaviours were to remain unchanged, to assess if differing levels of climate change would render their current ranges unsuitable.

5.2 Methods

5.2.1 Habitat Suitability Model

Habitat suitability models typically predict the spatial distribution of a species over large areas using presence-only or presence/absence data (Manly et al., 2002; Pearce and Boyce, 2006), producing spatial predictions indicating the suitability of locations for target species (Hirzel et al., 2006). Variables normally included in habitat suitability assessments for terrestrial species include topography, geology, climate, land cover and the presence of prey-species or predators (Kanagari et al., 2011). Parameter-specific suitability functions (PSSFs) assess the suitability of each variable to a known reference, such as previously studied abundances, growth, or yield rates (Vincenzi et al., 2007). In terms of a location's suitability, elevation, tree cover or other features can be identified using satellite data (but see Coop et al., 2016). Other species known ranges (be they food items, prey or predator species), are also typically used in the generation of suitability indices, with each species with an index for their own, representing their own relative abundance (Pereria et al., 1991; Dussault et al., 2006; Mezquida et al., 2010). For arboreal apes, and at small spatial scales, the use of these variables is not directly applicable. The presence of a primarily arboreal ape is dependent on tree cover. Given the broad range of diets of both orang-utan and siamang, which include leaves and bark (Palombit et al., 1997; Forss et al., 2019; Section 3.2.4) mapping potential food items presents a challenge. Assessment of habitat suitability for arboreal apes using traditional methods (e.g. vegetation plots or transects; Peres, 1997; Neilson et al., 2013; this study - Chapter 3), over large areas would be prohibitively expensive, and whilst high-quality satellite imagery has made the identification of potential primate habitat possible, it only provides an approximation of habitat suitability. More detailed vegetation data is required for accurate assessments of habitat suitability for arboreal apes, especially in areas where anthropogenic disturbance may alter habitat quality rapidly. Recent advances have made UAVs (Unmanned Aerial Vehicles or drones) an affordable and accessible technology, enabling users to monitor and map areas in unprecedented detail (Grenzdörffer et al., 2008). With the advent of Structure-from-Motion (SfM) software, UAVs can be used to create detailed 3D models of tropical forests (Turner et al., 2012, Fonstad et al., 2013), which can be used to assess habitat quality for arboreal primate species (Alexander et al., 2018) (For full details of UAV survey methods see Section 2.2.4). To overcome the potential pitfalls of using satellite imagery and the high cost of traditional vegetation plots for the creation of habitat suitability indices over wide areas, Unmanned Aerial Vehicles (UAVs) were used in this study to capture three-dimensional canopy topography data. This enabled the creation of habitat suitability indices, for both orang-utan and siamang. Canopy variables were derived from the canopy structures used at locations at which each species was recorded, with a lower threshold introduced to recognise that some canopy structures may not be favoured.

The locations of eight individual orang-utans were recorded as GPS points using a handheld Garmin GPS at 15-minute intervals each time the individual was followed for the day during behavioural follows from July to November of 2017 (n = 3687). For siamang, GPS points were taken at 10-minute intervals during behaviour follows of a single group of three siamang, during the same time period, July to November 2017 (n = 4363). Different data collection regimes were used as locations of multiple individuals in siamang groups required more frequent data collection to accurately record the group's centre. GPS points recorded during behavioural follows (Figure 4.1) were imported into GIS software (ArcMap, version 10.4). The aggregated Digital Surface Model (produced in section 2.2.4, 2.3.3, Figures 2.22 and 2.24) was then used to extract canopy topography variables from the GPS locations, producing multiple variables for each GPS location. Values of canopy topography variables were obtained using the "Extract values to points" function, at each GPS point of both ape species (Figure 3.7). These aggregated variables extracted from the Digital Surface Model were: 1) 'max minus mean' (mean elevation within the aggregated 25m spatial resolution subtracted from the maximum elevation within the aggregated 25m spatial resolution), 2) 'min' (minimum elevation within the aggregated 25m spatial resolution), 3) 'range' (range of elevations within the aggregated 25m spatial resolution), 4) 'mean 3 x 3' (mean elevation of cells within an aggregated 75m resolution), and 5) 'relative height' (mean elevation within an aggregated 75m spatial resolution minus the mean elevation within a 25m spatial resolution). Given that some canopy structure may be infrequently used and may not be suitable habitat for each species, a lower threshold for each variable was established, in lieu of a graded suitability index for each variable (as in Vincenzi et al., 2007). The frequency of use of each canopy topography variable was recorded for each species (Figure 5.2). The lower 10th percentile of each canopy topography variable was used as a threshold, with values above this considered suitable. Values below the lower threshold were considered unsuitable for each species. As canopy topography variables were used which were derived from elevation data, an upper 90th percentile threshold was not used as an additional upper threshold as this would have rendered areas at higher elevations (e.g. on hills) as unsuitable, which is not the case for either species (Reichard & Preuschoft, 2016; Wich et al., 2016), but would have rather been an artifice of where data collection took place. A binary classification was used for each variable above (1/yes) or below (0/no) the lower 10th percentile threshold to establish preferred canopy for each species over the entire study site. This was achieved using the 'raster calculator' function in ArcMap (version 10.4), using a binary selection for each variable (e.g. minimum elevation > 38.9m = binary zero/no, one/yes output). The resulting layers of each canopy structure variable were then added to each other to produce a habitat suitability index from zero to five with an index of zero describing areas in which no habitat structure variable met a species' canopy structure suitability and an index of five describing areas in which all habitat structure variable preferences were met.

5.2.2 Microclimate model

Within-canopy microclimate modelling was carried out for each hour between 7am and 4pm using equations produced from multiple linear regressions, in which the temperatures recorded by microclimate data loggers (n = 20) were predicted by vegetation and weather variables produced by UAV surveys and recordings at the Sikundur site. An alternative model was used to those in Section 2.3.4 (Table 2.3) as the use of the 'min' variable (minimum elevation within the aggregated DSM to a 25m spatial resolution) used over the entire site gave erroneous results in hilly areas, much like in habitat suitability modelling. For modelling purposes, only mean climatic recorded between the months of primate observation (July - November 2017) were used in this study. These models included variables measuring: height in canopy of primate, potential incoming solar radiation, cloud cover, (see section 2.2.3) minimum daily temperature (for hours 8 am – 1pm), maximum daily temperature (for hours 2pm – 4pm), and total daily precipitation (see Table 5.1). Each hourly microclimate model used structural vegetation variables taken from an aggregated Digital Surface Model of the site (see section 2.2.4). The model's incoming solar radiation was estimated across the forested study site using the Potential Incoming Solar Radiation tool in System for Automated Geoscientific Analyses (SAGA) software (version 2.3.2) using the Digital Surface Model (produced in Section 2.2.4) derived using a fixed-wing UAV. This allowed for the estimation of incoming solar radiation, measured in kWH/m^2, for each hour of the day. For the sake of simplicity, mean values across months were used in each hourly model (i.e. potential incoming solar radiation for 9am was the mean of potential incoming solar radiation between July to November at 9am). Similarly, microclimate models used mean values at each hour for cloud cover, averaged across the months of July to November. For microclimate projection, height of primate was set to 15m, the average height of both orang-utan and siamang during behavioural observations (See Section 2.3.4, Nowak, pers. comms.) Using these values, mean microclimate between the months of July and November were calculated for each hour from 7am – 4pm. Areas in which projected temperatures exceeded 32^{o}C (spatially identified with the 'Raster Calculator' argument 'Temp > 32^{o}C' = binary zero/no, one/yes on the output of the site-wide microclimate model) between 12pm-4pm were identified as unsuitable and subtracted from the habitat suitability index of both species. 32^{o}C was chosen as the temperature threshold as, even with the uncertainty in the microclimate model (mean residual standard error = 1.28 ^{o}C), this would be sure to be above the estimated 'Moderately Above Thermoneutral' threshold of Hill's (2005, 2006) thermal stress classification system for primate species.

To allow the effects of future predicted climate change on the site to be examined, Coupled Model Intercomparison Project Phase 5 (CMIP5) projections were accessed (using the 'raster' R package [Robert and van Etten, 2012] and the WorldClim dataset, [Hikmans et al., 2005]) across all four Representative Concentration Pathways (RCPs) predicting global climate in a number of emission scenarios (RCP 2.5, RCP 4.5, RCP 6.0, RCP 8.5, Moss et al., 2008). Only a single CMIP5 model was chosen for projections for the sake of simplicity

(Hadley Centre Global Environment Model version 2, HadGEM2-AO). Global climate scenarios were projected for 2050 and 2070, with variables for minimum and maximum average monthly temperature (°C) and average monthly precipitation (mm) extracted at the study site's location for the months of July to November and integrated into the microclimate model, detailed above, replacing the mean monthly 'minimum temperature', 'maximum temperature' and 'total precipitation' values. A total of eight possible future microclimate scenarios were modelled using these methods, at 2050 and 2070 across all four RCP scenarios.

To measure the changes in habitat suitability for each species in current and future scenarios, the 'zonal geometry as table' tool was used in ArcMap upon the resulting habitat suitability index for each species, in each scenario, to calculate the total area (in hectares) available within the study site under each value of the habitat suitability index and the changes between them.

To assess if differing levels of climate change would render the current ranges of orang-utan and siamang unsuitable, the same microclimate model detailed above was used, with 'minimum temperature', 'maximum temperature', 'daily rainfall', 'solar radiation' and 'cloud cover' variables replaced by recordings of those variables made during the time each primate location was recorded. Similarly, canopy structure variables used in the microclimate model for each hour were replaced by variables extracted from the primates' location at the time of recording using the ArcMap function 'multiple extract values from points'. As above, to predict the effects of possible future climate scenarios, 'minimum temperature', 'maximum temperature' and 'total precipitation' variables were replaced with values extracted from the various RCPs at both 2050 and 2070.

5.2.3 Statistical analyses

To compare canopy topography variables used by orang-utan and siamang, Mann-Whitney-Wilcoxon Tests for independent populations and F-tests of equality of variances were used. To compare changes in modelled temperatures experienced by both orang-utans and siamang in differing future climate change scenarios, pairwise comparisons using Wilcoxon rank sum test were used in relation to different climate scenarios. All statistical analyses were performed with R (version 3.4.1) using R studio (version 1.0.153), alpha was set to 0.05.

5.3 Results

5.3.1 Microclimate models

Multiple linear regressions were used to compare recorded temperatures with daily weather variables, potential incoming solar radiation and aggregated DSM canopy topography variables compared to recordings made between 7am – 4pm (n = 20,133). Best fitting models with the fewest possible variables were used to predict the temperatures across the whole site for each hour (Table 5.1, Figure 5.6). As previously found with the microclimate model in Section 2.3.4, the hourly ambient temperature and cloud cover had the biggest influence on temperature at any given location. For all but the warmest hours minimum ambient temperature was found to be the most influential on modelled microclimate, with maximum ambient temperature having a bigger impact from 2pm - 4pm. The height within the canopy and potential incoming solar radiation (measured as kWH/m^2), a measure of the geographical location of an area within the landscape in relation to sunlight, also had a significant impact on modelled microclimate. Canopy topography in the form of aggregated elevation values derived from the DSM influenced temperature across all times, with upper range (‘max – mean’ elevation) influencing temperature in the early morning (as the sun rises) and range and relative elevations having more influence on modelled temperature during the warmest parts of the day (10 - 2pm). Hourly microclimate models produced using mean environmental values for current (2017) temperatures had a mean residual standard error of 1.88^{o}C for the hours 8am - 4pm (Table 5.1, Figure 5.6). Hours beyond this were not modelled as minimum or maximum climate at the site (recorded using a weather station at base camp) were not significantly correlated in the microclimate model, meaning that adjustments for future predicted climate change models could not be applied to these hours. These microclimate models were adjusted to reflect potential changes by replacing current values of ‘local minimum temp’, ‘local maximum temp’ and ‘daily rainfall’ with projected values from differing climate scenarios (Figure 5.5).

Table 5.1 – Results of multiple linear regression microclimate models predicting microclimate based on (non-correlated) climatic and habitat variables across the Sikundur area

	7am		8am		9am		10am		11am	
Variable	β	p	β	p	β	p	β	p	β	p
Intercept	12.550	<0.001	15.692	<0.001	21.014	<0.001	24.153	<0.001	26.356	<0.001
Height above ground	-0.001	<0.001	0.033	<0.001	0.062	<0.001	0.095	<0.001	0.123	<0.001
Local Minimum Temp	0.392	<0.001	0.382	<0.001	0.335	<0.001	0.316	<0.001	0.299	<0.001
Local Maximum Temp										
Mean cloud cover at hour	1.493	<0.001	-1.177	<0.001	-3.380	<0.001	-6.410	<0.001	-9.630	<0.001
Daily rainfall	-0.004	<0.001	-0.004	<0.001	-0.005	0.002	-0.005	0.032	-0.010	<0.001
kWH/m2			0.002	<0.001	0.002	<0.001	0.001	0.033	0.001	<0.001
Max - mean elevation	0.015	0.002	0.129	<0.001	0.152	<0.001				
Range of elevations	-0.004	0.047	-0.072	<0.001	-0.123	<0.001	-0.051	<0.001	-0.126	0.487
Relative elevation							0.017	0.048	0.024	0.013
Adjusted R^2	0.344		0.245		0.323		0.435		0.494	
Res.stand.error	0.530		0.996		1.493		1.991		2.160	

	12am		13pm		14pm		15pm		16pm	
Variable	β	p	β	p	β	p	β	p	β	p
Intercept	27.178	<0.001	28.103	<0.001	27.370	<0.001	28.618	<0.001	31.378	<0.001
Height above ground	0.117	<0.001	0.103	<0.001	0.100	<0.001	0.092	<0.001	0.104	<0.001
Local Minimum Temp	0.182	<0.001	0.215	<0.001						
Local Maximum Temp					0.234	<0.001	0.185	<0.001	0.071	0.041
Mean cloud cover at hour	-8.469	<0.001	-8.840	<0.001	-7.801	<0.001			-10.326	<0.001
Daily rainfall	-0.012	<0.001	-0.011	<0.001	-0.011	<0.001	-0.010	<0.001	-0.016	<0.001
kWH/m2	0.002	<0.001	0.001	<0.001	0.001	<0.001	0.001	<0.001	0.002	<0.001
Max - mean elevation										
Range of elevations	0.026	0.047			-0.033	<0.001			0.019	<0.001
Relative elevation	0.058	<0.001	0.039	<0.001			0.025	0.002		
Adjusted R^2	0.512		0.513		0.526		0.475		0.459	
Res.stand.error	2.123		1.993		1.963		2.026		2.117	

5.3.2 Habitat Suitability

Habitat suitability significantly differed between siamang and orang-utan (Figure 5.2) with siamang using areas of forest which have higher minimum elevations and with significantly different degree of variance (Wilcoxon rank-sum test ; W = 6.30_6, p = <0.001, F test; F = 1.73, p = <0.001), lower range of elevations (W = 7.98_6, p = <0.001, F test F = 1.73, p = <0.001), lower ‘maximum minus mean’ elevation (W = 7.94_6, p = <0.001, F test; F = 1.55, p = <0.001), higher elevations at a coarser spatial scale (mean elevation of cells within a aggregated 75m resolution, W = 7.74_6, p = <0.001; F test; F = 3.636, p = <0.001) and using areas of forest with a higher elevation than those around it (relative height, W = 5.60_6, p = <0.001, F test; F = 1.094, p = 0.006) compared to areas used by orang-utans (Figure 5.2).

Orang-utan showed a broader range of habitat used in all measured variables with lower mean values and less defined peaks of frequency than those of siamang habitat use (Figure 5.2). Subsequently, in the total area sampled, siamang had less area that was classified in the upper two most suitable habitat categories than orang-utan (Table 5.2) (Figure 5.3).

5.3.3 RCPs

RCP results from the Hadley Centre Global Environment Model version 2 (HadGEM2-AO) for the Sikundur area produced four variations of predicted temperatures based on differing Representative Concentration Pathways, for the years 2050 and 2070. Each model produced three separate variables (minimum temperature, maximum temperature and monthly mean rainfall) which were subsequently used in microclimate modelling in eight different climate scenarios (Figure 5.4 and 5.5).

Table 5.2 – Total area within each Habitat Suitability Index for each species in 2017

Habitat Suitability Index	0	1	2	3	4	5	Total
area (ha) for orang-utan	0.1	37.9	52.1	117.6	422.8	1564.1	2194.6
area (ha) for siamang	0.1	77.9	99.4	301.4	379.4	1336.4	2194.6

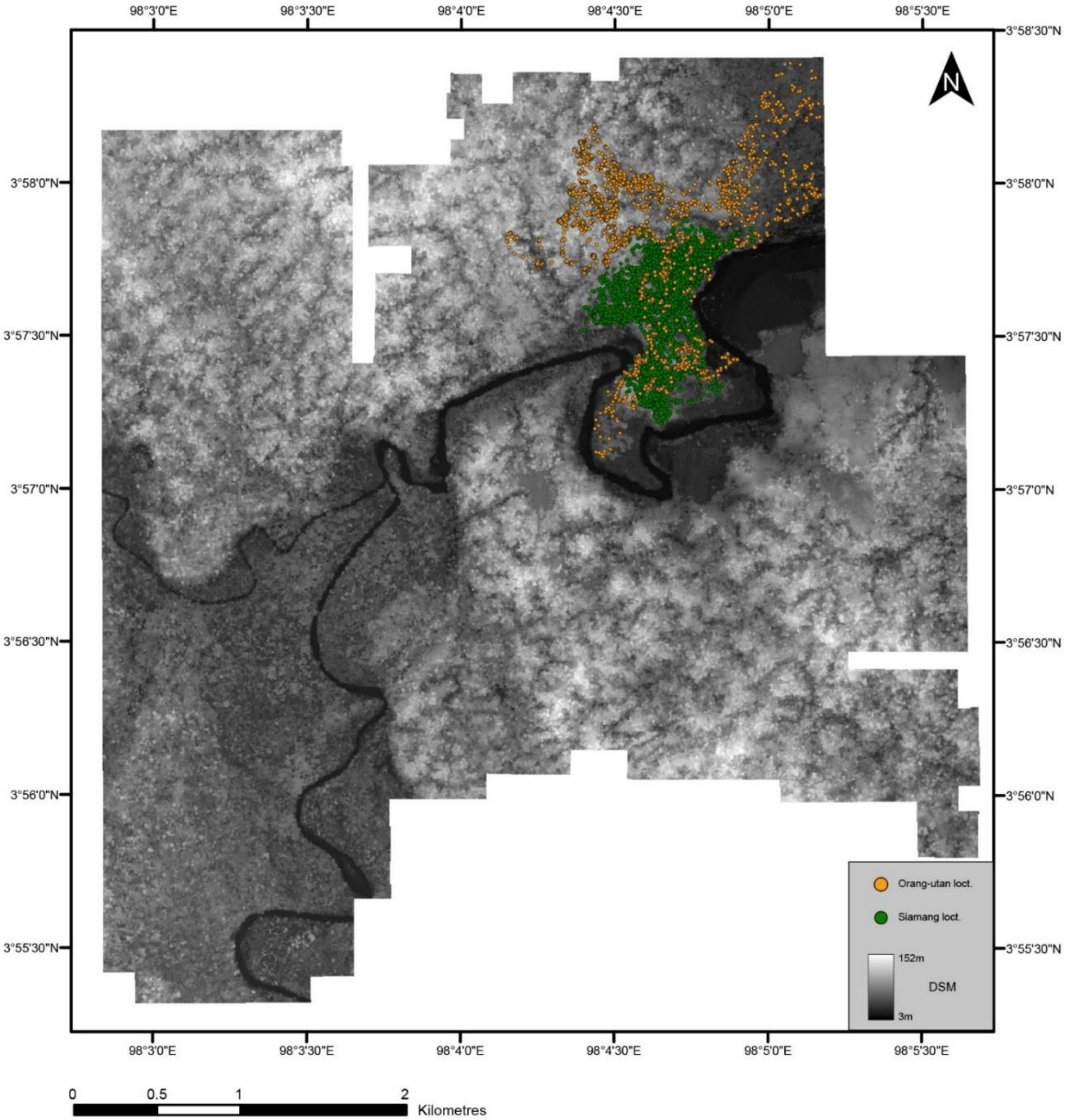
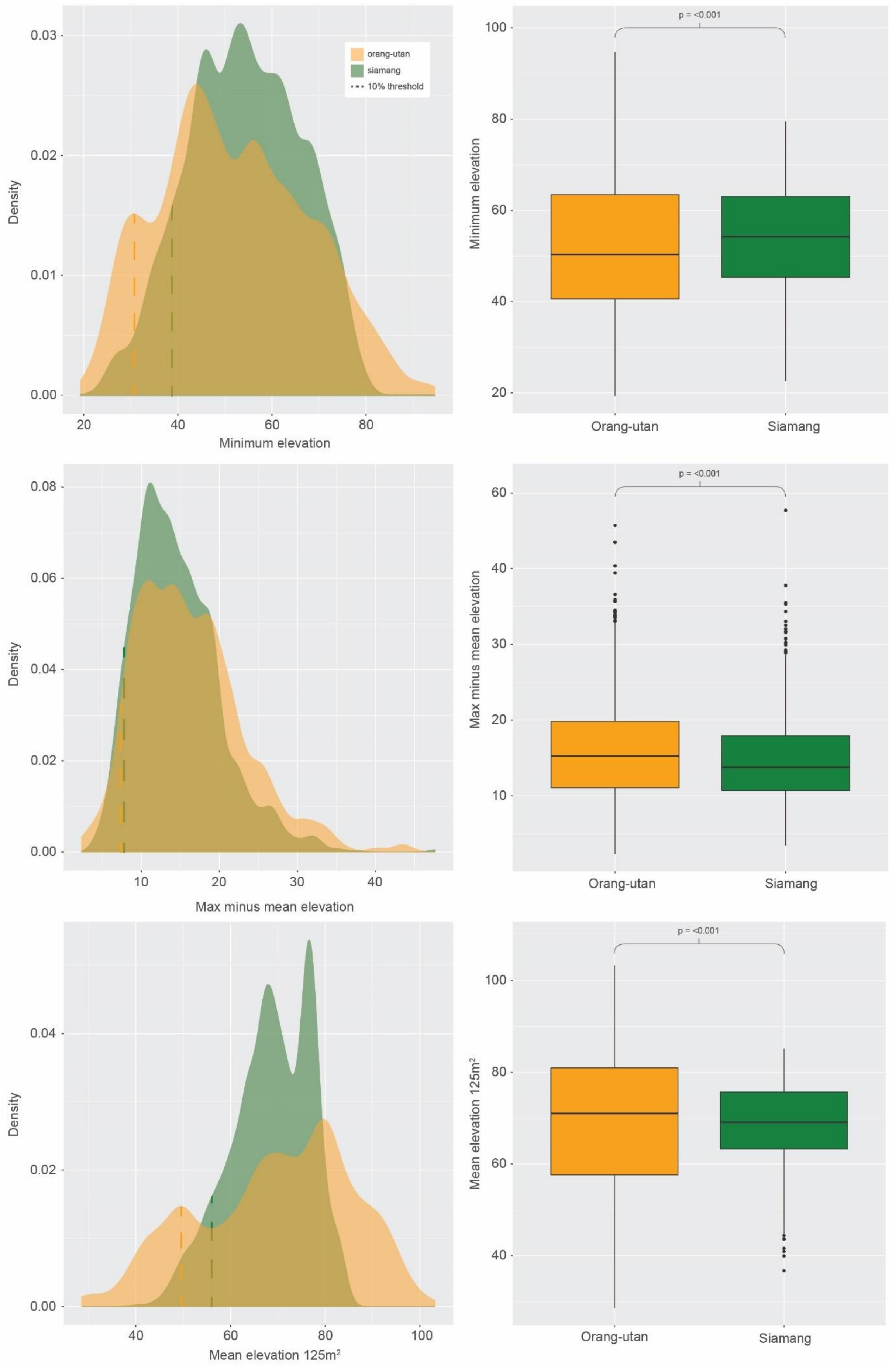


Figure 5.1 – Locations of orang-utan and siamang recorded between July and November 2017



0.03
0.02
0.01
0.00
Density
orang-utan
siamang
10% threshold
20
40
60
80
Minimum elevation
p = <0.001
100
80
60
40
20
Minimum elevation
Orang-utan
Siamang
0.08
0.06
0.04
0.02
0.00
Density
10
20
30
40
Max minus mean elevation
p = <0.001
60
40
30
20
10
Max minus mean elevation
Orang-utan
Siamang
0.04
0.02
0.00
Density
40
60
80
100
Mean elevation 125m²
p = <0.001
100
80
60
40
Mean elevation 125m²
Orang-utan
Siamang

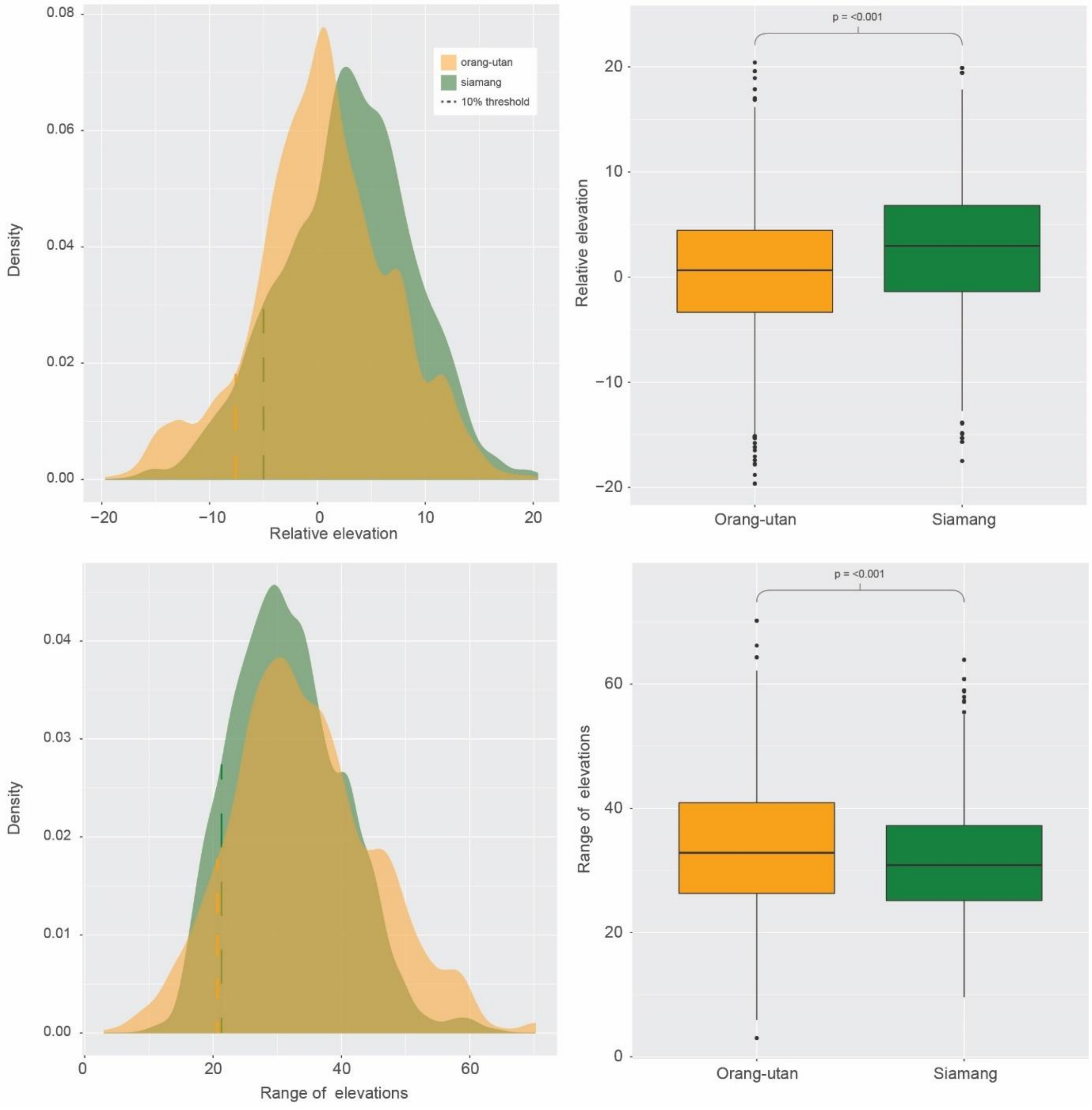


Figure 5.2 – Values extracted from canopy topography variables for siamang and orang-utan with statistical results of a Mann-Whitney-Wilcoxon test

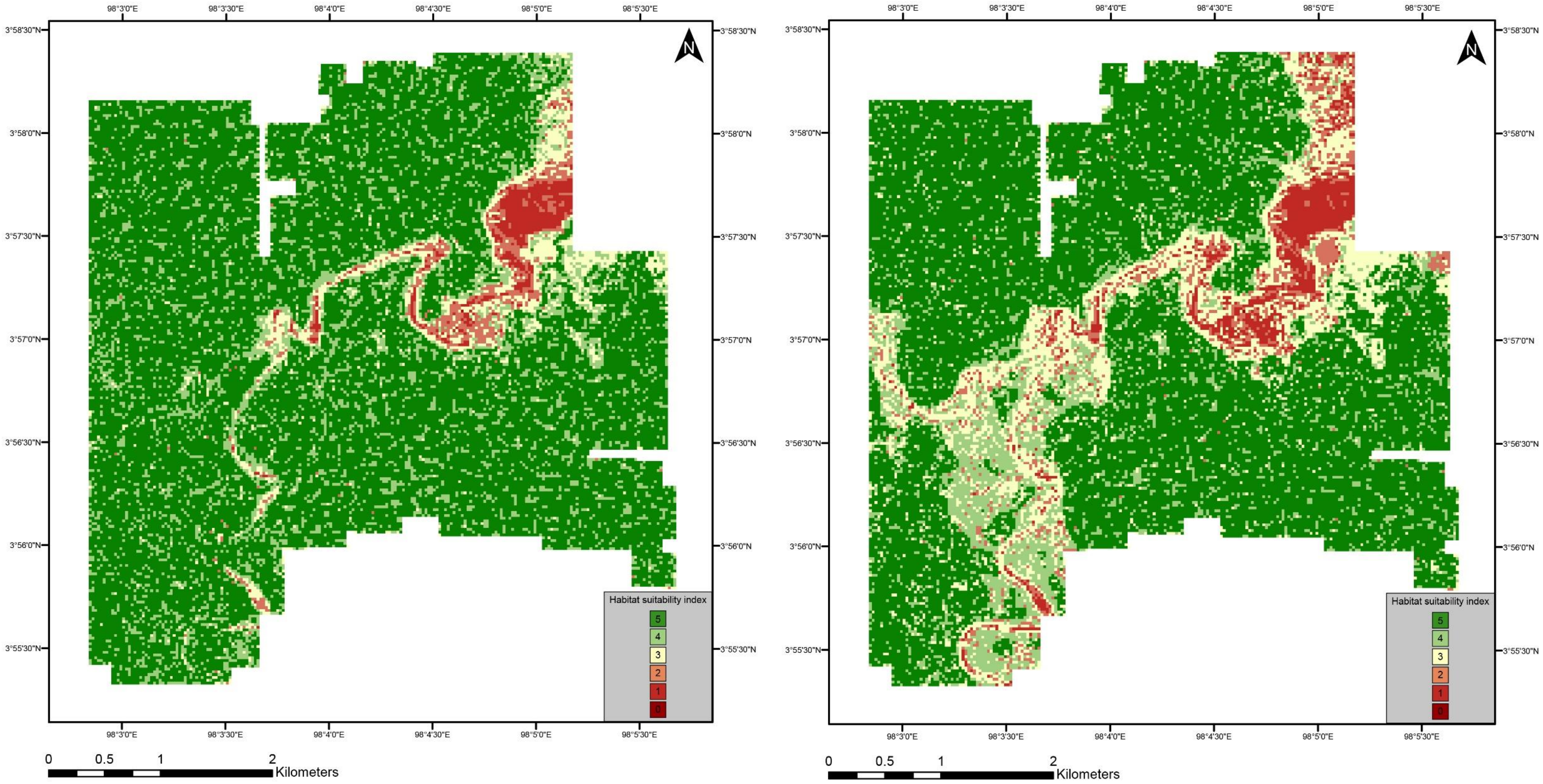


Figure 5.3 – Current habitat suitability index for orang-utan (left) and siamang (right)

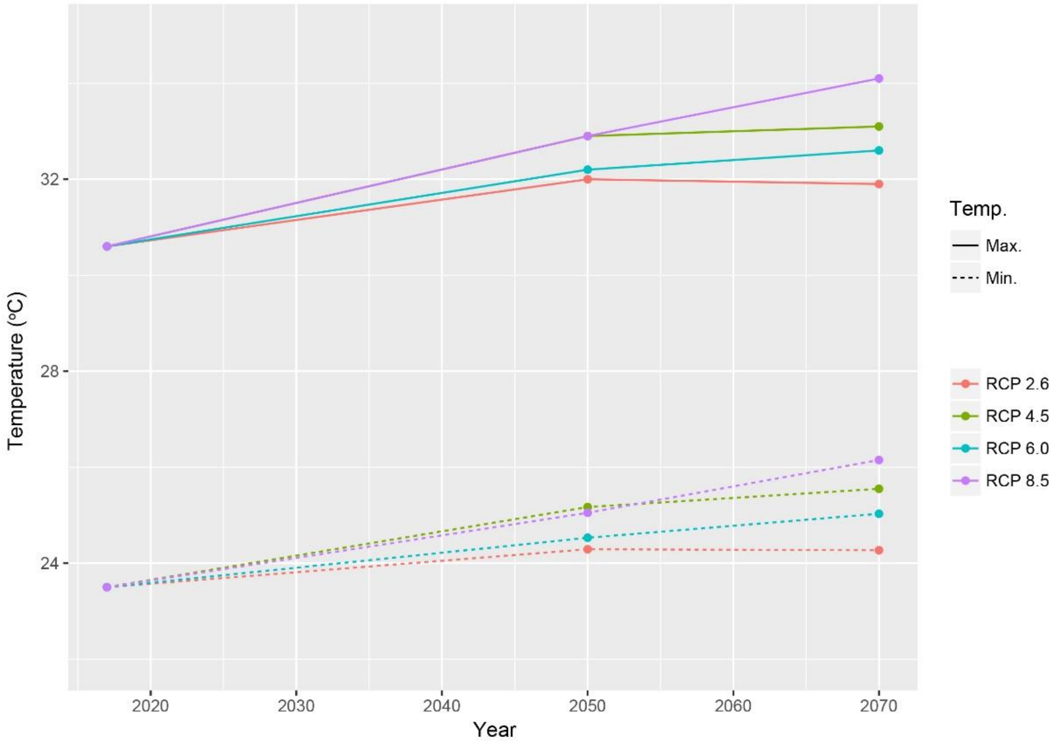


Figure 5.4 – current (measured) and projected (from HadGEM2-AO) minimum and maximum temperatures for the Sikundur area

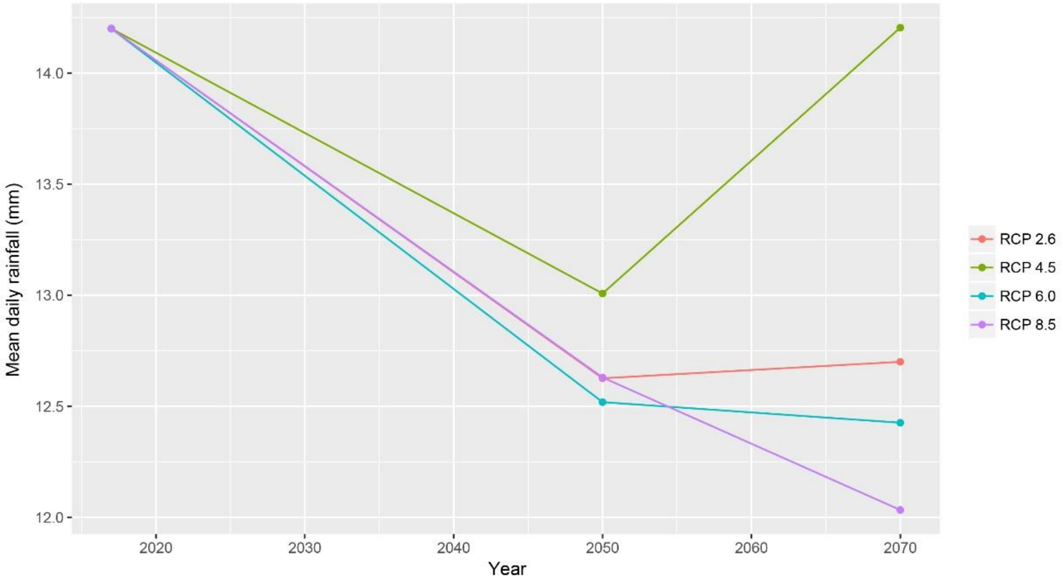


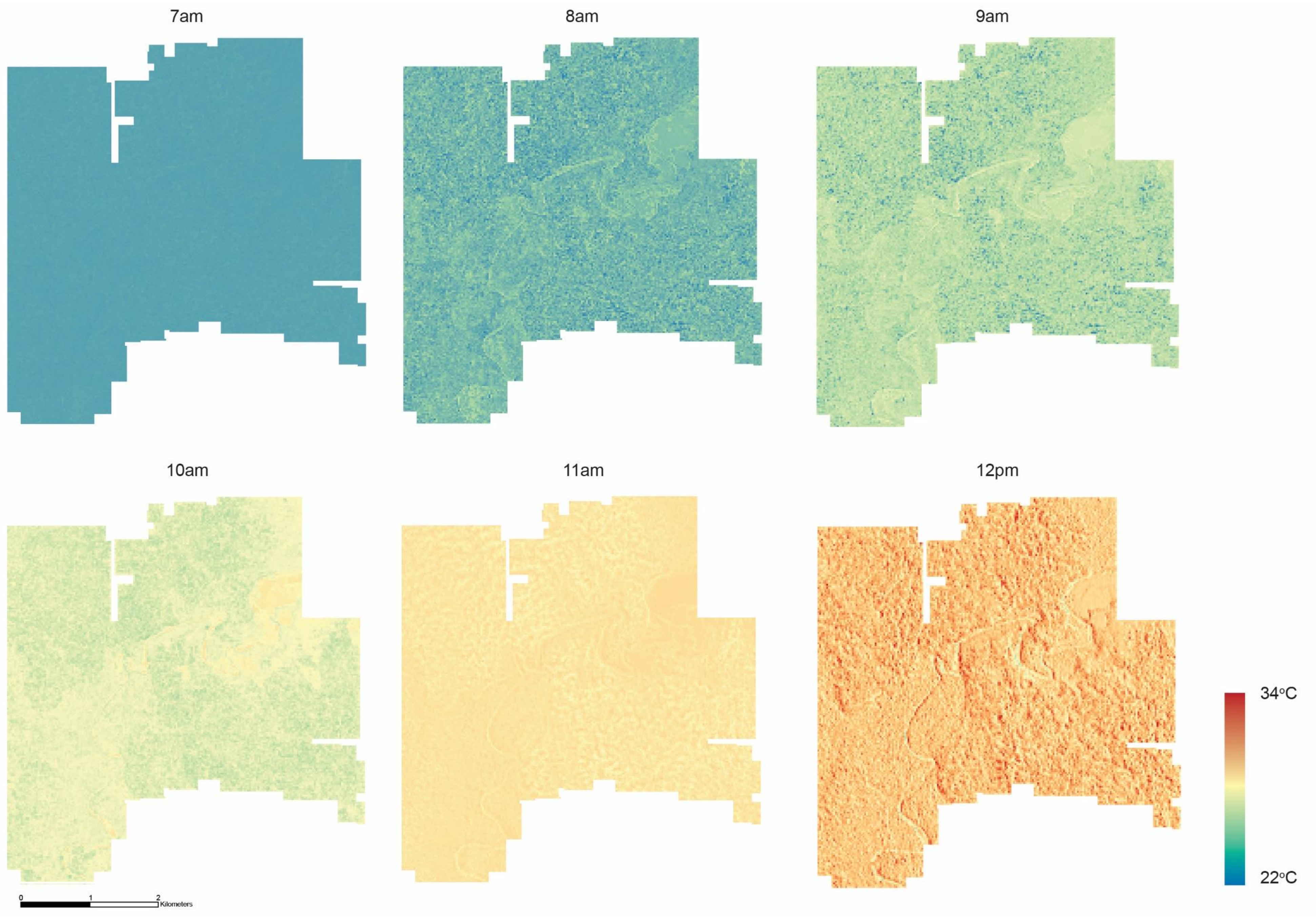
Figure 5.5 - current (measured) and projected (from HadGEM2-AO) mean daily rainfall for the Sikundur area

5.3.4 Projected Habitat Suitability Index for 2050 and 2070 using four RCPs

Using values from projected future climate change RCPs, microclimate measurements were modelled for each RCP in 2050 and 2070, with values equal to or exceeding 32°C reducing the Habitat Suitability Index of that area by one (Figure 5.7a-c). Percentage change from current (2017) habitat suitability in each predicted climate scenario is given in Table 5.3. Siamang lose proportionally more high-quality habitat than orang-utan in all climate change scenarios, as areas of the canopy which are exposed to more potential incoming solar radiation, which are seemingly favoured by siamang (Figure 5.3), reach above 32°C for large portions of the day, rendering them potentially unsuitable.

Table 5.3 – Habitat suitability index change under differing climate change scenarios

			Habitat Suitability Index change from 2017 levels (%)					
	RCP	year	0	1	2	3	4	5
orang-utan	2.6	2050	0.10%	0.50%	1.30%	5.80%	3.70%	-5.80%
	2.6	2070	0.10%	0.50%	1.30%	5.70%	3.20%	-5.60%
	4.5	2050	0.10%	0.70%	1.80%	7.50%	10.50%	-9.10%
	4.5	2070	0.20%	0.80%	1.90%	8.00%	12.80%	-10.10%
	6	2050	0.10%	0.60%	1.40%	6.20%	5.30%	-6.60%
	6	2070	0.10%	0.70%	1.60%	7.10%	9.20%	-8.40%
	8.5	2050	0.10%	0.70%	1.80%	7.40%	10.20%	-8.90%
	8.5	2070	0.30%	1.20%	2.70%	10.30%	24.30%	-15.20%
siamang	2.6	2050	1.00%	0.80%	3.20%	2.90%	11.80%	-7.30%
	2.6	2070	0.90%	0.80%	3.10%	2.80%	11.10%	-7.00%
	4.5	2050	1.20%	1.50%	4.40%	3.50%	20.40%	-11.00%
	4.5	2070	1.30%	1.80%	4.70%	3.70%	23.20%	-12.20%
	6.0	2050	1.20%	0.90%	3.40%	3.00%	13.80%	-8.20%
	6.0	2070	1.20%	1.30%	4.10%	3.30%	18.90%	-10.20%
	8.5	2050	1.20%	1.40%	4.30%	3.50%	20.20%	-10.90%
	8.5	2070	1.80%	2.90%	6.20%	4.80%	37.20%	-18.00%


7am
8am
9am
10am
11am
12pm
34°C
22°C
0
1
2
Kilometers

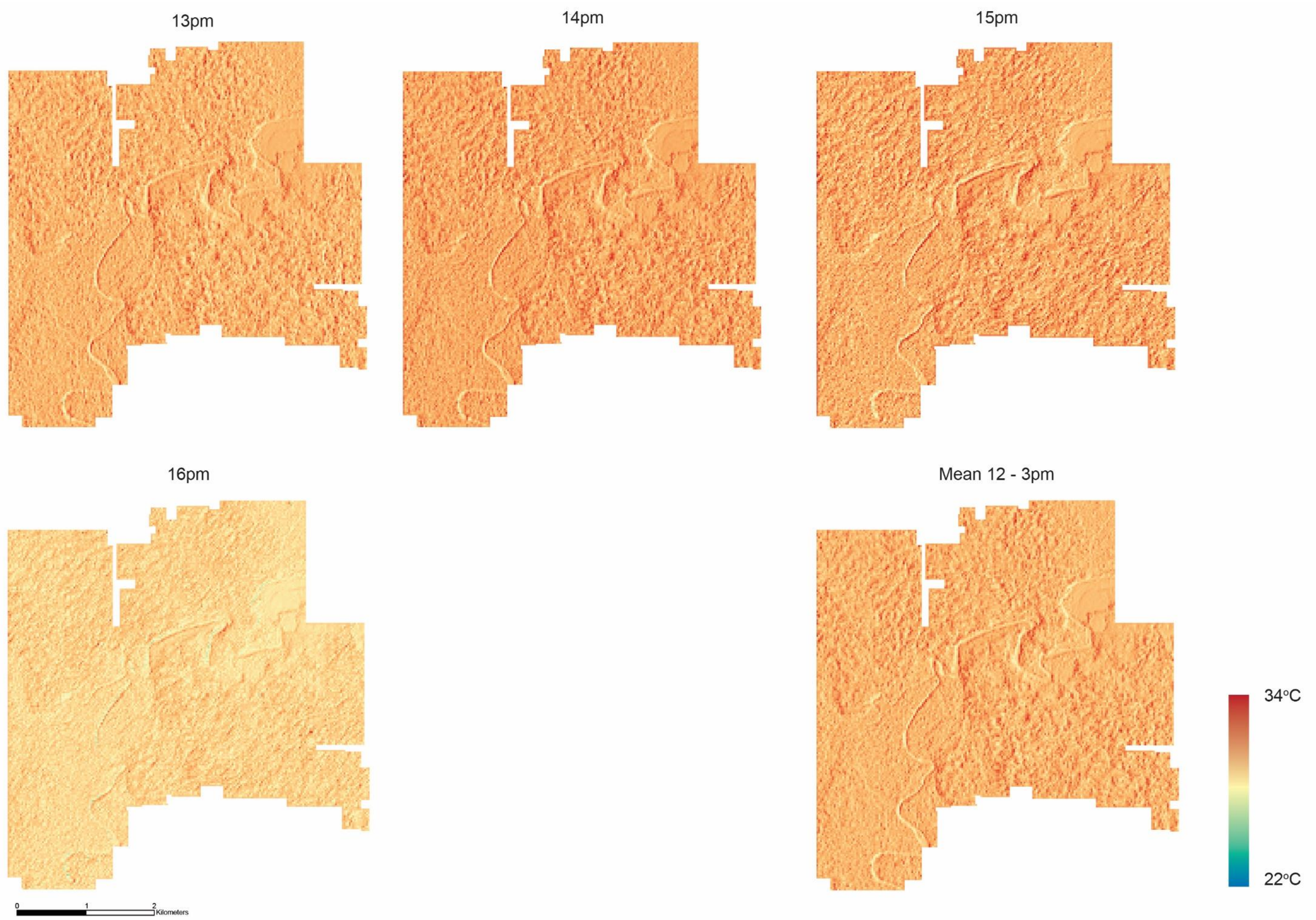


Figure 5.6 – Microclimate models from 7am – 4pm projected over the study site

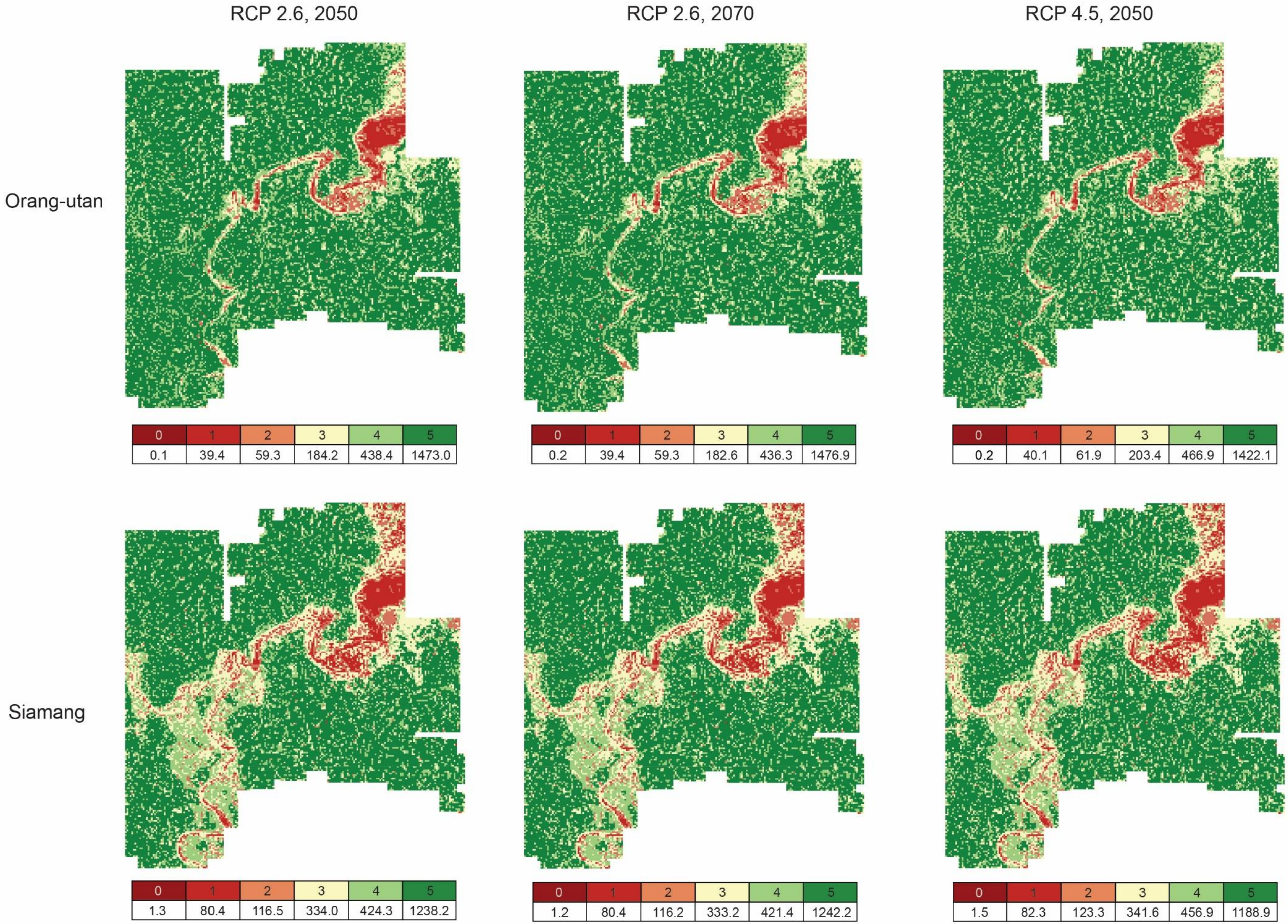


Figure 5.7a – Habitat suitability index of orang-utan and siamang under different RCPs in the years 2050 and 2070, areas in ha

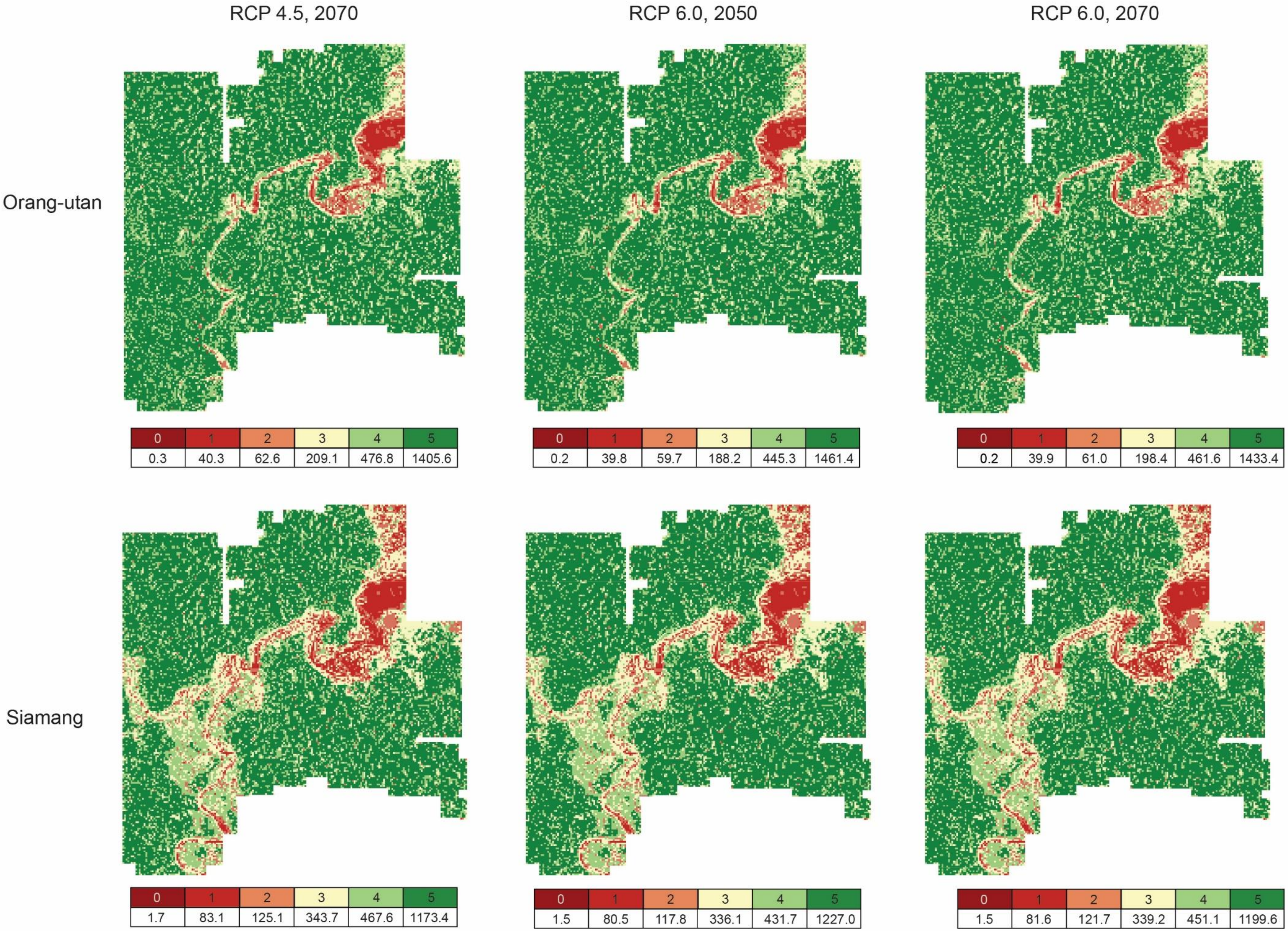


Figure 5.7b – Habitat suitability index of orang-utan and siamang under different RCPs in the years 2050 and 2070, areas in ha

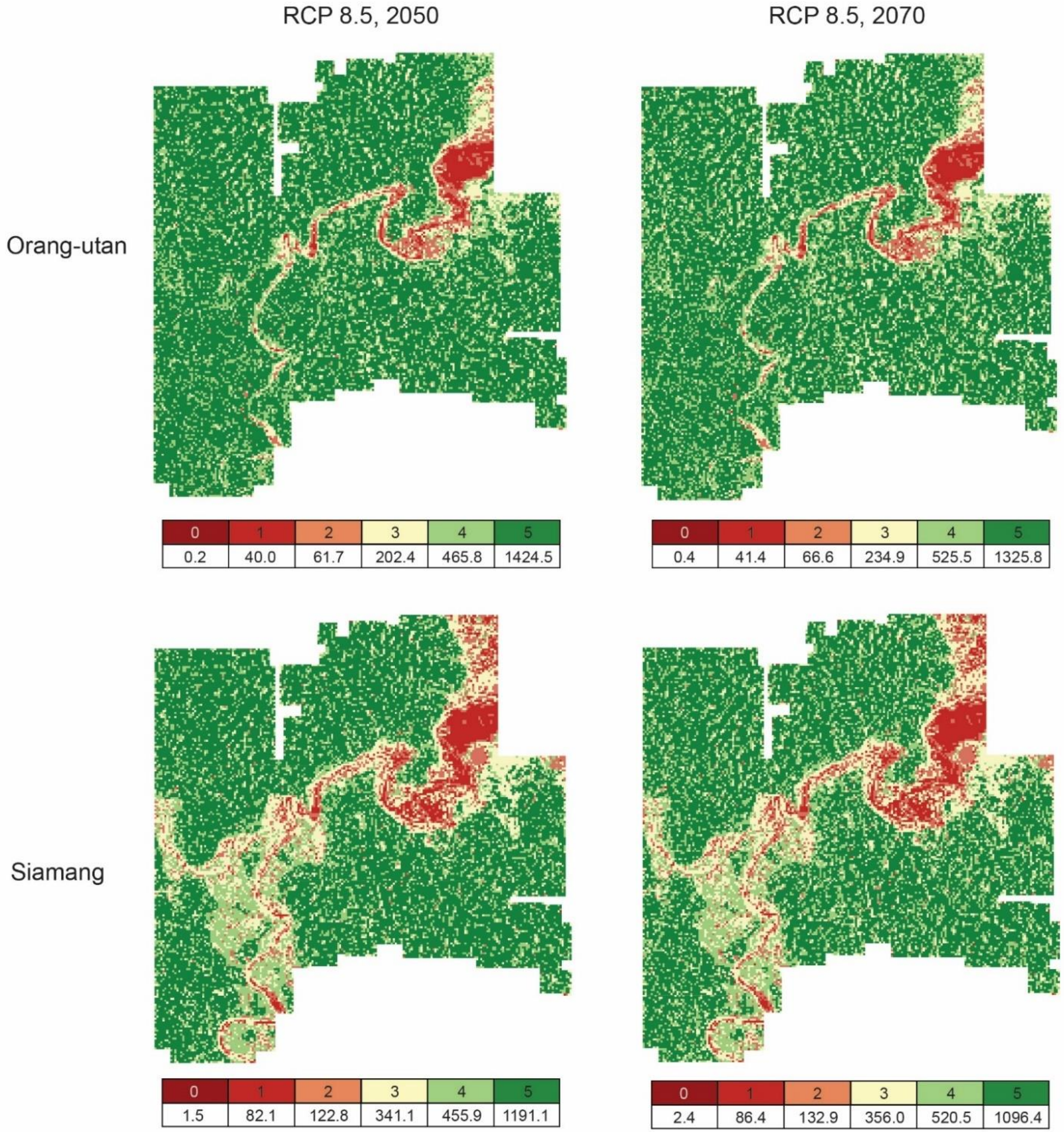


Figure 5.7c – Habitat suitability index of orang-utan and siamang under different RCPs in the years 2050 and 2070, areas in ha

5.3.5 Projected temperature of orang-utan and siamang for different years and RCPs

Using values from projected future climate change RCPs, microclimate measurements were modelled at the location of orang-utan and siamang in 2017, 2050 and 2070 (Figure 5.8a and 5.8b). The percentage of modelled temperatures equal to or exceeding 32ºC in each predicted climate scenario is given in Table 5.4, and a statistical comparison of modelled temperatures of both orang-utan and siamang in different climate change scenarios (using Wilcoxon rank sum test) is given in Table 5.5. Currently, both species are predicted to experience temperatures above 32ºC ~10% of the time, suggesting that both species are near the edge of their thermal threshold. In the 'worst case' scenario in 2070, the time spent above 32ºC is likely to double, suggesting that both species are likely to change their behaviour or ranging to reduce the amount of time spent at high temperatures. The modelled temperatures that both species experience in all climate scenarios are significantly different from current levels (Table 5.5). Most notable however, is the insignificant differences between RCP 4.5 in 2050 and other climate scenarios in respect to the difference in temperatures experienced by arboreal apes. This relative marginal degree of warming in the near future could have significant impacts on the well-being of arboreal apes inhabiting degraded tropical forest.

Table 5.4 - Percentage of modelled temperatures equal to or above 32ºC under differing climate change scenarios in 2017, 2050 and 2070

	RCP	year	% of recordings above 32ºC
orang-utan		2017	10.2%
	2.6	2050	13.1%
	2.6	2070	13.1%
	4.5	2050	15.9%
	4.5	2070	16.6%
	6.0	2050	14.1%
	6.0	2070	15.4%
	8.5	2050	15.6%
	8.5	2070	19.5%
siamang		2017	9.6%
	2.6	2050	13.0%
	2.6	2070	13.0%
	4.5	2050	16.2%
	4.5	2070	17.1%
	6.0	2050	14.4%
	6.0	2070	15.7%
	8.5	2050	16.0%
	8.5	2070	19.9%

Table 5.5 - Pairwise comparisons of modelled temperatures of both orang-utan and siamang in differing climate change scenarios, using Wilcoxon rank sum test, ‘ * ’ denotes a significant correlation (p=<0.05), ‘ ** ’ denotes a highly significant correlation (p=<0.01)

RCP			2.6	2.6	4.5	4.5	6.0	6.0	8.5
	year	2017	2050	2070	2050	2070	2050	2070	2050
2.6	2050	<0.001**	-	-	-	-	-	-	-
2.6	2070	<0.001**	1	-	-	-	-	-	-
4.5	2050	<0.001**	<0.001**	<0.001*	-	-	-	-	-
4.5	2070	<0.001**	<0.001**	<0.001*	0.18	-	-	-	-
6.0	2050	<0.001**	0.019*	0.019*	0.003*	<0.001**	-	-	-
6.0	2070	<0.001**	<0.001**	<0.001**	0.418	0.034*	0.028*	-	-
8.5	2050	<0.001**	<0.001**	<0.001**	0.656	0.077	0.012*	0.724	-
8.5	2070	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**

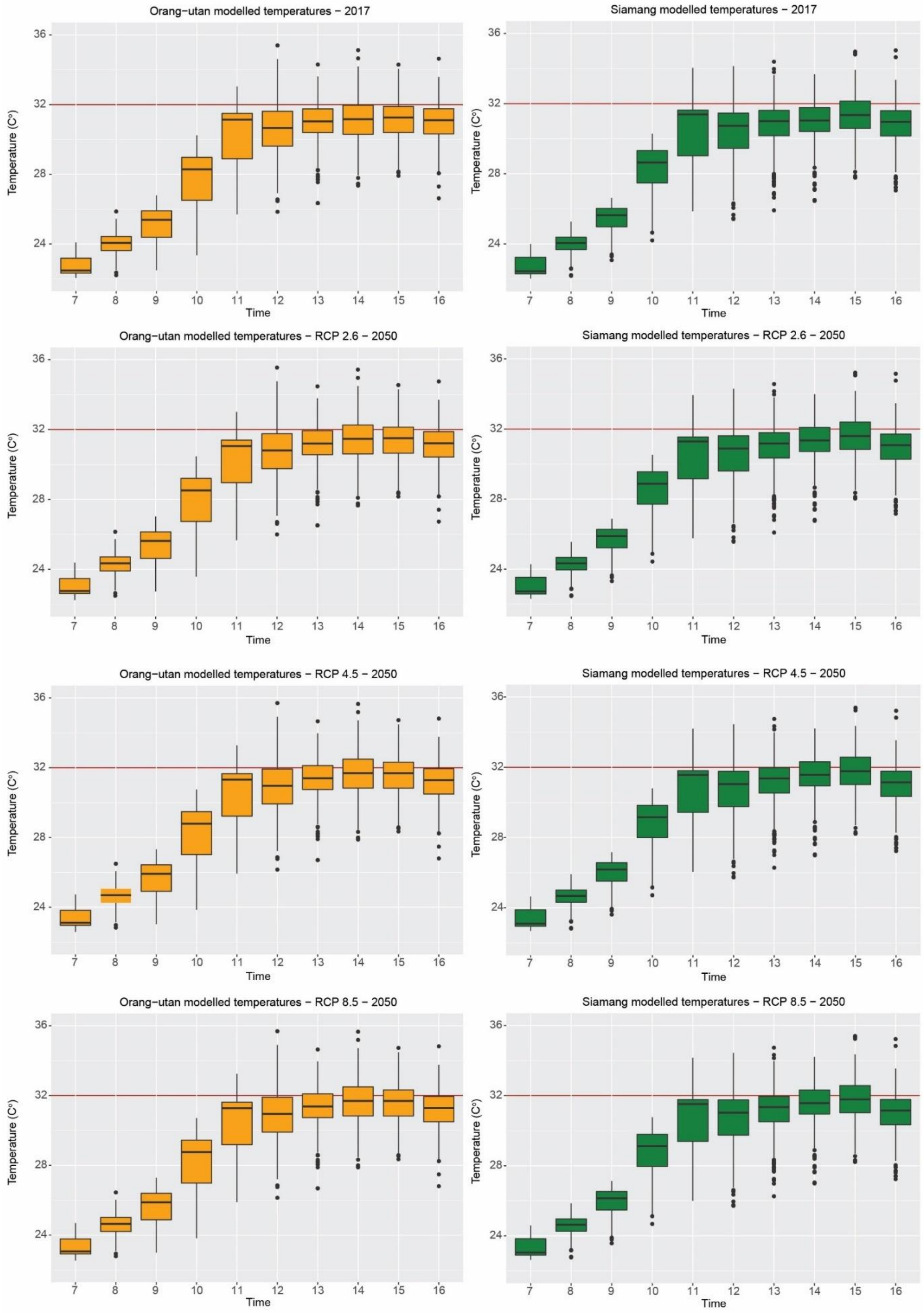


Figure 5.8a – Current and future predicted microclimate models for 2050 using different RCPs based on orang-utan and siamang recorded locations

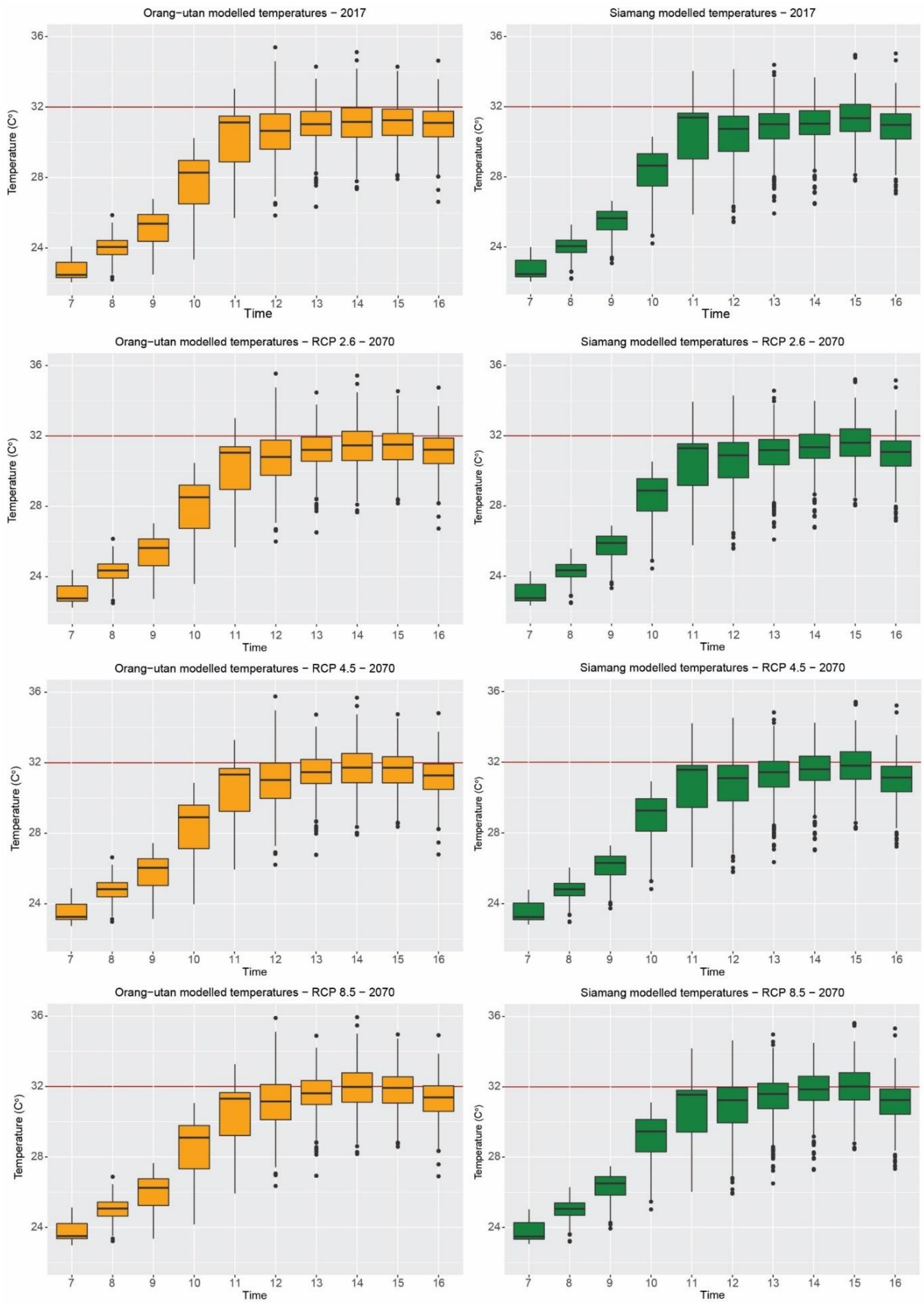


Figure 5.8b – Current and future predicted microclimate models for 2070 using different RCPs based on orang-utan and siamang recorded locations

5.4 Discussion

This study aimed to produce a habitat suitability index, uniquely based on microclimates, for two sympatric arboreal apes, the Critically Endangered Sumatran orang-utan and the Endangered siamang, and adjust this index to predict future conditions under different climate change scenarios. Orang-utan showed a broader range of habitat used than siamang, who more frequently used, what would be considered ‘higher quality’ habitat, with a prevalence of large, tall and therefore, old trees. Microclimate models suggests that areas that currently show signs of degradation (i.e. previously cleared land and historic logging roads for example), and areas of forest that are subject to higher degrees of solar radiation (through either microtopographic changes or their relative height to the surrounding canopy), will experience high temperatures for long periods, reducing these area’s suitability. Both species are impacted, though siamang, with their seemingly more defined habitat requirements will be more detrimentally affected.

Results from this study provide novel evidence that future climate change will have a significant impact on the habitat suitability for arboreal apes, impacting sympatric species unequally. This study’s findings that areas that were previously ‘prime’ habitat will be rendered less suitable by their exposure to solar radiation in an increasingly warming environment is potentially significant to the wellbeing of arboreal primates in relation to global warming. Whilst primates may still utilise these areas for resource extraction or for travel, the reduction in the availability of microclimate refugia due to increased temperatures may push large arboreal primates to the very edge of their thermal threshold, substantially reducing the overall availability of high-quality habitat in lowland areas.

Under all predicted future climate change scenarios, orang-utan and siamang are likely to see a significant change in their climatic environment (see Table 4.4). Even in the ‘best case’ scenario (RCP 2.6), both species are likely to see a substantial reduction in the availability of preferred habitat by the year 2050 (orang-utan: -5.8%; siamang: -7.3%), which almost doubles under the ‘worst case’ scenario (RCP 8.5, orang-utan: -8.9%: siamang: -10.9%). By 2014, some studies had already excluded model outputs using RCP 2.6 as unfeasible given global CO_2 output (Mora et al., 2013), suggesting that global warming from current levels is likely to be severe. Given that if both species were to stay within their current ranges they would experience considerable increases in temperatures above their potential thermoneutral zone (see Figure 4.3), with no immediately available substantially cooler environment available (with an increased elevation, for example) they will be faced with an immediate need to adapt their behaviour, as opposed to being given sufficient time for evolutionary change (Gienapp et al., 2008). Species response, and survival, in a warming environment will depend on their genetic diversity, the current availability of preferred habitats, the disruption of ecological interactions and their adaptive capacity (La Sorte et al., 2012; La Sorte et al., 2013). Under these foci, the future of each species may appear uncertain. The genetic diversity of each is hampered by dwindling numbers; the siamang is listed as Endangered and the Sumatran orang-utan as Critically Endangered by the IUCN (Nijman and Geissman, 2008; Singleton et al., 2017). In terms of preferred habitat, (though the siamang is further ranging) both species inhabit the Gunung Leuser Ecosystem which loses approximately 25,722 ha per year from human encroachment (from Hansen et al., 2013, see Figure 1.4). With the additional threat of global warming, their future is uncertain, though each species faces separate challenges based on their behavioural and morphological traits (Marsh et al., 2016).

The thermoneutral zone of the ambient temperature for primates usually has a range of less than 5°C, although the range differs depending on the species (Thompson et al., 1994; Muller et al., 1995; Aujard et al., 1998;). The upper critical temperatures for anthropoids range from 25°C (*Cercopithecus* mitis, Muller et al., 1983) to 34°C (*Cebulla pygmaea,* Genoud et al., 1997) and the lower critical temperatures range from 24°C to 28°C (Takemoto, 2004). The thermoneutral zone for naked humans is reported to be from 25–27°C to 28–31°C (Færevik, 2001). The behaviour and morphology of Asian apes suggest that they have evolved in a climatically and structurally stable environment (Hunt, 1991; Gebo, 1996). Given that simultaneous recordings of temperatures at Sikundur have differed by 15.2°C, and temperatures have exceeded 42°C (see Section 1.3.2), physiological adaptations for acclimatization will be exceeded, necessitating the utilisation of behavioural thermoregulation. Endotherms are likely to move to areas closer to their thermoneutral zones according to ambient temperature fluctuation (Takemoto, 2017). Arboreal primates are therefore likely already utilising areas of forest that provide the required buffering from solar radiation to remain within their thermoneutral zone (Figure 4.9). This and the needs of energy efficient locomotion, group cohesion requirements and potentially, territorial defence, likely governs the habitat suitability for each species (Figures 4.2 and 4.3).

Modern humans have been clearing forest in Sumatra for ~30 thousand years (Spehar et al., 2018). Whilst primate numbers have declined due to these anthropogenic disturbances as well as vegetative and climatic change since the Pleistocene (Jablonski et al., 2000), only now are these synergistic factors, vegetation structure and climate, being changed with such rapidity (Chatterjee, 2009). Currently, with climatic changes due to global warming, substantial areas within previously suitable habitat may be outside of the thermal limit of arboreal ape species, rendering significant areas of degraded lowland tropical forest unsuitable in the near future (Figure 5.7a - 5.7c).

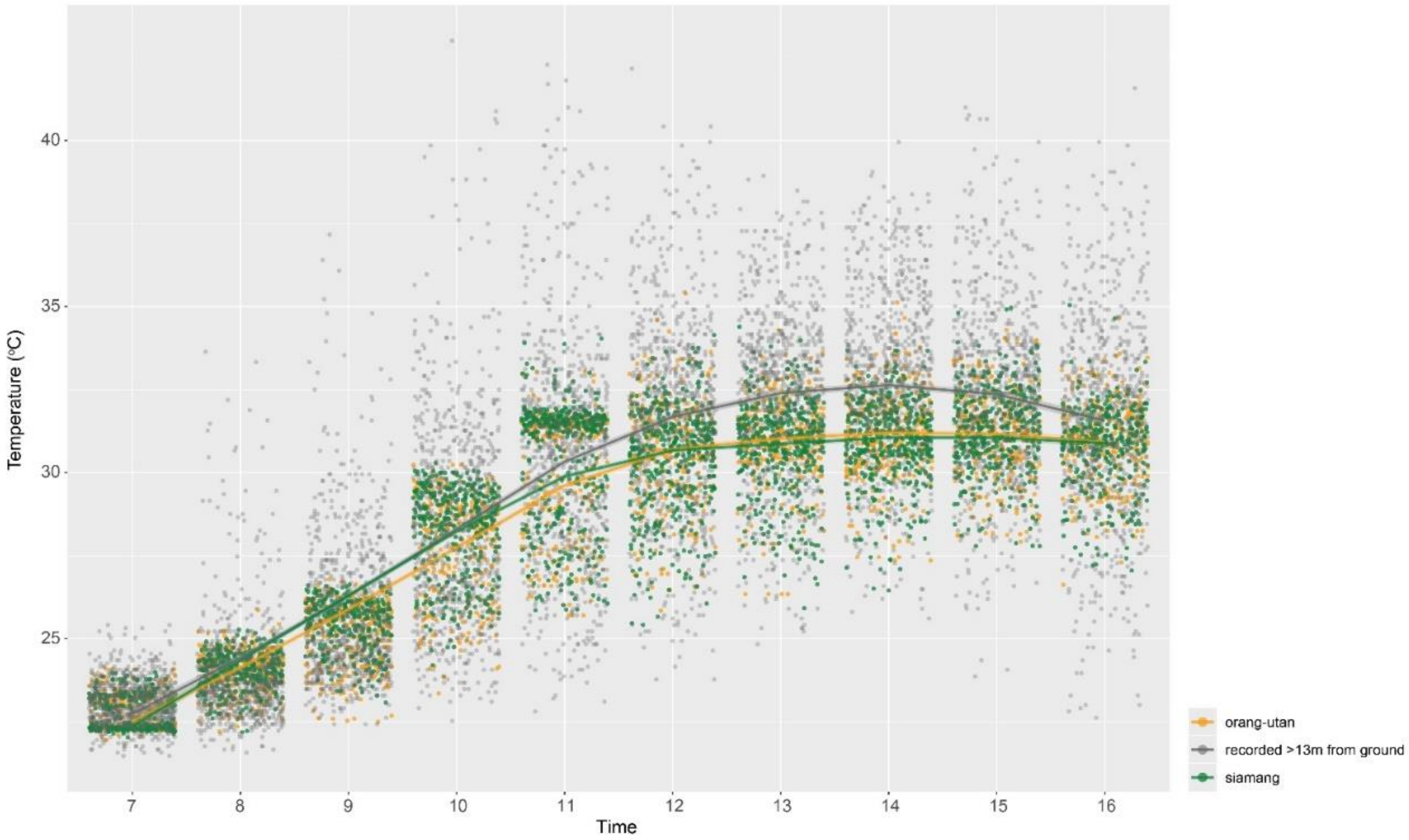


Figure 5.9 – Modelled temperatures from orang-utan and siamang locations compared to those recorded by microclimate data loggers recording more than 13m from the ground shown with loess lines

As a result, the habitat suitability of areas that have long been ‘prime’ habitat for arboreal ape species are now under threat, with land-use change slowly but surely reducing available habitat, and historical forest degradation and climate change reducing the quality of habitat which is remaining. However, primate species are highly adaptable, and researchers often record novel behaviours in response to environmental changes. (Hockings et al., 2015). In Bossou, chimpanzees exploit cassava stored underground by local human farmers, as well as transporting stone tools and crops bipedally (Hockings et al., 2010; Carvalho et al., 2012). In Kibale, chimpanzees engaged in nocturnal crop-raiding behaviour (Krief et al., 2014). It is likely therefore, that the arboreal apes of Asia will expand their behavioural repertoire in response to environmental challenges, likely in unexpected ways.

Both orang-utans and siamang can be considered relative generalists, with a broad range of diet and flexibility in social structures, compared to other primate species. Orang-utans, have a largely solitary fission-fusion social dynamic, possibly a diffuse gorilla-like harem social structure seemingly adapted to the low availability of favoured food items (Harrison and Chivers, 2006), but show markedly more social interactions in times of fruit abundance (Kanamori et al., 2017). Whilst relatively under-studied, siamang have a relatively fluid social system. Siamang have been observed as singular females, bonded pairs, up to six member groups with multiple males and females of reproductive age (Lappan, 2007), similar in many ways to elasticity of howler monkey social systems (Ostro et al., 2001; Treves., 2001). Siamang also have a broad diet, with less reliance on ripe fruit than other, smaller bodied gibbon species (Chivers et al., 1975). However, they show a narrower range of habitat requirements than the orang-utan, who are seen in the degraded peat swamps of Gunung Palung (Felton et al., 2003) and surviving in the highly degraded forests of Surya Hutani Jaya (Meijaard et al.,2010). Siamang are seemingly more adverse to habitat disturbance (O'Brien et al., 2002), and due to the demands of group living, territorial defence and black hair (Kosheleff and Anderson, 2009), are potentially more adversely affected by a warming climate in which less high-quality habitat is available and competition for territory may be increased. But given both species' apparent behavioural flexibility, as temperatures rise and high-quality habitat becomes less available, it is likely that these arboreal primates will adapt their behaviour to enable behavioural thermoregulation.

In other ape species, the adoption of more terrestrial behaviours has been associated with higher temperatures (Takemoto, 2004). This use of vertical microclimate gradients within forests may even have had an impact on the acquisition of terrestrial behaviour by human ancestors (Takemoto, 2017). Forest degradation has previously been linked to terrestrial activity in Bornean orang-utans, *Pongo pygmaeus* (Ancrenaz et al., 2014; Loken et al., 2015) and muriquis, *Brachyteles hypxanthus* (Mourthé et al., 2007; Tabacow et al., 2009), both previously thought to be exclusively arboreal species. However, in both these instances a potential terrestrial ecological niche could be exploited and risk from predation was low. In Sumatra, predation risks are somewhat higher, with tigers (*Panthera tigris sondaica)*, Sunda clouded leopards (*Neofelis diardi*), leopard cats (*Prionailurus bengalensis)* and humans (*Homo sapiens*) known to predate large arboreal apes (Rikksen, 1978; Morino, 2010; Meijaard et al., 2011; Cheyne et al., 2012; Fichtel, 2012; Davis et al., 2013). The terrestrial ecological niche is already exploited by southern pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*Macaca fascicularis*), frequently descending to the forest floor to take advantage of fallen fruit, as well as thomas langur (*Presbytis thomasi*) occasionally seen on the forest floor (personal observation, Steenbeck, 1996). Greater mouse-deer (*Tragulus napu*), serow (*Capricornis sumatransis*), red muntjac (*Muntiacus muntjak*), sambar deer (*Rusa unicolor*), wild boar (*Sus scorfa*) and sun bears (*Helarctos malayanus*) also forage on fallen fruit, meaning arboreal primates are unlikely to fulfil their dietary requirements terrestrially, though an increase in terrestrial behaviour could be advantageous to thermoregulation.

With the onset of a warming climate, arboreal primate species are more likely to have their time-budgets altered, as resting time during the hottest parts of the day becomes enforced (Dunbar et al., 2009; Korstjens et al., 2010). Time constraints can limit both a primate's ability to survive in a given habitat and the maximum group size (Korstjens et al., 2006; Korstjens and Dunbar, 2007; Pollard and Blumstein, 2008). Adopting fission-fusion social dynamics has been shown to reduce the cost of travel to dispersed food items in primate communities (Lehmann et al., 2007), and for siamang, foraging individually has potential benefits, allowing each individual or sub-group to quickly achieve their nutritional requirements. However, given the strict territoriality of siamang and their group territorial calls (O'Brien et al., 2003), the defence of favoured food sources, sexual partners and offspring may make this social dynamic risky. However, it should be noted that the siamang group observed in Sikundur used sleeping trees relatively early (mean time 4:56pm, see Section 3.3.3). This normally rendered them out of sight of researchers, but during this time they were seen to partake in resting and social behaviours (personal observation). There is therefore potential 'room' in their time-budget for resting during the hottest part of the day if evening resting/social behaviours were displaced temporally. With minimal time needed for social interaction, orang-utans have seemingly already stretched their time-budget allowance for maximum foraging and feeding time, especially in areas such as Sikundur with low fruit availability (Figure 1.6, SOCP, 2016). Enforced resting time during the hottest parts of the day may directly affect orang-utan overall health, as it could potentially limit their nutritional intake.

Other primate species have adopted more crepuscular behaviour in relation to environment pressures (Curtis and Rasmussen, 2006). *Lemur sp.* are theorised to have adopted cathemerality in a direct response to the threat of predation by fossa (*Cryptoprocta ferox)* (Hill, 2006). In the owl monkey (*Aotus sp.*), competition for resources with diurnal primate species may have favoured the development of nocturnality (Fernandez-Duque and Erkert, 2006), though increased predation risk is theorised to inhibit cathemerality in the majority of primate species (Hill, 2006). Large herbivores living in arid environments reduce heat stress by being more active at night and seeking shade during the day (Berger et al., 1999). In Brazil, the maned sloth, (*Bradypus torquatus*) are mainly nocturnal in warm Amazonian tropical forest, and diurnal in the cooler Atlantic montane tropical forest, highlighting the potential benefits of cathemerality for thermoregulation for arboreal mammals (Chiarello, 1998). Sloths, as well as other xenarthrans (armadillos and anteaters), likely evolved from subterranean forms, hence their rod monochromacy vision and their ability to locomote arboreally in low-light levels (Emerling and Springer, 2015). Some neotropical primate species also locomote arboreally in dim light, utilising their dichromatic vision to compete temporally for valued food resources (Snodderly et al., 2018). Due to their large body size and highly arboreal nature, arboreal locomotion before sunrise or after sunset for orang-utan and siamang presents a hazard of falling; both species are trichromats with three cone photopigments, without the potential advantages in dim light as possessed by dichromats or rod monochromatic xenarthrans (Emerling and Springer, 2015; Snodderly et al., 2018).

There are a number of disruptions and changes to ecological processes which may arise with climatic warming in tropical forest which the model used in this study did not take into consideration. For low fruiting areas such as Sikundur, masting events, in which many tree species fruit simultaneously, provide much needed abundance of favoured food items and are often synchronised with reproductive events. Whilst masting events occur in other areas, only in dipterocarp forest such as Sikundur does fruiting in mast years span so many tree species (Janzen, 1974). The theorised trigger for masting in dipterocarp forest is related to the El Ninõ Southern Oscillation. A 2-3^{o}C drop in night-time temperatures for a period of 4-8 days is thought to initiate masting (Appanah, 1993), with masting events normally correlated with El Ninõ years (Wright et al., 1999). With minimum temperatures rising in all potential RCP climate scenarios at Sikundur (see Figure 4.4), it is likely that masting events will be disrupted, which in turn could have impacts on the reproduction levels of vertebrates inhabiting these areas that have synchronised their reproduction to occur when food is abundant (Curran et al., 2000).

There are a number of opposing viewpoints on the potential health of tropical forest in a warming climate. Increases in CO_2 levels may lead to direct fertilisation of photosynthesis, reduced photorespiration and improved water-use efficiency at the leaf level, leading to biomass gains and increased maximum tree height at the stand level (Prentice et al., 2201; Malhi and Phillips, 2014). Conversely, plant growth may be limited by a lack of Nitrogen, Phosphorus, Potassium and Calcium, the increased dominance of large lianas, increased soil acidification, and climatic drying, leading to climate induced dieback and increased fire risks (Phillips et al., 2002). Habitat suitability for arboreal apes may dramatically increase or decrease depending on the outcomes of these theorised biomass increases or diebacks. Additionally, climate change has been predicted to increase the likelihood of extreme weather events, such as hurricanes, windstorms and landslides (Dale et al., 2001), but given the decrease in predicted rainfall for the Sikundur area (see Figure 4.5), drought is likely to have a larger impact on the well-being of orang-utan and siamang. Whilst some primate species have shown remarkable resilience to droughts, in Madagascar, infant mortality in *Lemur catta* reached 80% after a two-year drought, with 20% of all adult females also dying. However, four years after the drought the population had recovered to pre-drought numbers due to high birth rates, early sexual maturity and an increased range of food items (Gould et al., 1999). Given the relatively slow life-histories of orang-utan and siamang and their already broad diets, it is unlikely that these species would be able to adjust their fecundity in response to such detrimental effects on their population in a similar situation. Long term droughts are likely to be highly damaging to these sympatric populations, as these primates' access to water sources is almost entirely reliant on arboreal sources.

The environmental stress caused by climate change may exacerbate the dangers of disease to arboreal apes (Chapman et al., 2005). The interplay of host status, pathogen attributes and environment quality determines the effect of pathogen prevalence in primate populations. The presence of small organisms, such as mosquitoes or ticks, and the availability of high-quality food items can influence the likelihood of pathogen spread and the health of hosts (Wolfe et al., 1998). With a reduction in habitat quality for arboreal primates with climate change, pathogen prevalence is likely to increase. Human encroachment of tropical forest habitats is also likely to increase zoonotic infectious disease transfer to both both primate and human populations (Pedersen & Davie, 2010).

This study does not take into consideration microclimate measurements in open or transitional environments within the landscape, as microclimate data loggers were not placed in these areas. It is therefore likely that modelled microclimate changes for these areas are underestimated, and climatic edge effects will be a more dominant factor than is presented in this study. The microclimate model also does not take into account the nested nature of many microclimate processes (Adams et al., 2009; Hardwick et al., 2015). For instance, increased warming and reduced rainfall may reduce soil moisture, causing a feedback loop leading to reduced humidity and rising temperatures (Anderegg et al., 2013), a possible confounding factor for this, and many studies of this type, which attempt to model the possible effects of future climate change.

Many of the potential effects and responses of primate populations to climate change presented here are not included in the climate change model in this current study, but these potential additional effects of climate change should be taken into consideration when assessing the likely responses of species to climate change (Korstjens and Hillyer, 2016). Whilst the outlook for the two species of arboreal ape may appear threatened, many primate species have the behavioural flexibility to weather adverse environments and flourish, utilising previously cryptic resources (Pruetz, 2007; Pruetz and LaDuke, 2010; Gumert and Malaivijitnond, 2012; Hockings et al., 2015; Proffitt et al., 2016). It is perhaps relevant that similar environmental dynamics that may have led to adoption of terrestrial behaviour by human ancestors may be enacting on the arboreal apes of Sumatra (Takemoto, 2017), be it within generational, as opposed to millennial time periods. Given this, the long-term survival of both the Sumatran orang-utan and siamang may therefore be reliant on the speed at which they can adapt, as opposed to their capacity to do so, as the ability of primate species to adapt to environmental challenges should not be underestimated, given their cognitive and behavioural flexibility (Reader and Laland, 2001). Ultimately, the evolutionary pathway that each organism takes to its current state equips it with the means to weather future environmental change (Sih et al., 2011). This plasticity has often evolved in response to previous environmental disturbance (Crispo et al., 2010). Given that the arboreal apes of Sumatra are likely to have evolved in a relatively stable environment, both structurally and climatically (Gebo, 1996; Chaterdee, 2009), they may face novel challenges ahead.

5.5 Conclusion

Ecologists aiming to understand and predict the influence of climate change on species often use models based on macroclimatic variables, which are generally projected using records from standard meteorological stations (Moss et al., 2010). However, organisms experience climate at the microscale and temperature variation is highly scale-dependent (Chen et al., 1999). Due to the influence of vegetation structure and microtopography, microclimate may only be weakly correlated with macroclimate (WallisDeVries et al., 2011; Graae et al., 2012; Potter and Hargrove., 2013), as dense tree cover buffers against solar radiation (Section 2.17; Frey et al., 2016). In this study, using a microclimate model that incorporates vegetation structure has shown that the effects of climate change on arboreal primates may substantially reduce habitat suitability, though areas such as Sikundur will remain largely viable habitat even with ‘worst case’ climate scenarios (see Figure 5.7c). Highly adaptable ape species will likely adapt to these changes, though it places them under greater risk from other threats and those associated with a warmer climate. With the feedback loop of a warming climate, extreme weather events (Meehl et al., 2000) and drought are more likely (Allen et al., 2010; see Figure 5.5). In the low-fruiting forest of Sikundur, this may push the currently healthy population of arboreal primates closer to an energetic and climatic limit (Gould et al., 1999). Climate change alone may not cause the loss of these populations, but coupled with other anthropogenic disturbance, such as forest loss or hunting, apes with slow life-histories’ and low birth rates, may not be able to recover if multiple negative factors impact simultaneously (Cox, 1997). However, if large areas of forest are removed in Sikundur, as they have been in the past, the negative effects of climate change will be marginal in comparison to large-scale deforestation’s effects on primate species.

Chapter 6. Discussion

In this study I aimed to understand how arboreal primates might be affected by inhabiting a historically selectively logged forest. I aimed to quantify the structural and climatic variation in the canopy of a degraded forest and understand how this may impact on arboreal primates' current behaviour, ranging and abundance and also how future climate change may impact on the suitability of degraded forests.

6.1 Forest canopy microclimates

The climatic variability of tropical forest has previously been recorded (Chen, 1999; Dial et al., 2006), but the extreme variability of Sikundur, with simultaneous temperature recordings in different parts of the forest differing by as much as 14°C, shows that degraded forests are both structurally and climatically highly complex. Though vegetation structure dictates temperature only to a small degree in comparison to weather effects such as cloud cover and precipitation, structure can have a strong influence on the suitability of areas of forest for arboreal primates. Whilst other studies have concluded that forest canopy acts as a thermal buffer and may reduce the severity of potential future climate change (De Frenne et al., 2019), historical selective logging will likely reduce the effectiveness of this thermal buffering. Tropical forests have been shown to offset temperatures more than Boreal or Temperate forests, possibly due to their multi-layered canopy structure (Anhuf and Rollenbeck, 2001). In tropical forests, invasive plant species have been documented dominating degraded or deforested areas (Lynch et al., 2009), hampering forest regeneration after degradation or deforestation events. Whilst some areas of degraded forest clearly retain the ability to buffer against higher temperatures for invertebrates and small vertebrates (Senior et al., 2018), for larger mammals, particularly those that are arboreal, historically degraded forest may be climatically unsuitable at the hottest parts of the day.

The structure of anthropogenically disturbed forest may be changed in both expected ways (e.g. reducing mean tree height, Okuda et al., 2004) and unexpected ways (e.g. reducing potential overall tree height and biomass in the remaining trees, Rutisauser et al., 2016). For large, far-ranging mammals, particularly those that rely on canopy structure to locomote, historically degraded forest may be rendered unsuitable. As seen in this study, primate species that have a clear relationship with the presences of large trees (such as gibbon spp.) may see a direct reduction in suitable habitat with selective logging (Zhang et al., 2010). For other primate species with broader habitat requirements, degraded forest in a warming world may reduce its suitability, rendering large areas of forest unsuitable in the future, as shown in Chapter 5. However, there are a number of factors that were not taken into consideration in this study's investigation into the synergistic effects of vegetation structure and microclimate on the suitability of habitat for arboreal primate species. An oversight in this study was placing data loggers only within the forest itself, and not at forest edges, regenerating areas or within other cleared parts of the landscape. Whilst the initial focus of the study was documenting the microclimate experienced by arboreal primates, placing data loggers in a wider range of habitats would have enabled a more comprehensive view of the thermal landscape of the entire site (Zhu et al., 2007), and a more accurate landscape scale projection of the potential effects of climate change. It is notable that many tropical ecology studies, as repeated here, often collect data only within a forest system, and rarely collect data from forest edges or in neighbouring anthropogenically disturbed land unless this is a direct focus of the study (Arroyo-Rodriguez et al., 2013; Galán-Acedo et al., 2018; Galán-Acedo et al., 2019). Including data collection in a number of different landcover types across the matrix of a landscape could enhance the understanding of the effects of vegetation structure and microclimate across degrees of human disturbance and in multiple different habitat types, allowing more direct comparison between studies at different sites.

There are multiple recent studies which examine the effects of forest structure and geography on climate, both in the micro and macro scales (Scheffers et al., 2014; Mangnago et al., 2015; Frey et al., 2016). Vanwallegham and Meentemeyer's (2009) study of multiple forest patches concluded that differences in monthly mean temperature were primarily affected by elevation and coastal proximity, whereas daily or hourly mean temperature variation was primarily affected by forest structure. Most macroclimate models approach climate at a monthly or yearly scale, although animals' experience of temperature fluctuations is vastly different (Chen et al., 1999) as habitat structure and type is a major modifier of temperature extremes (Suggitt et al., 2011). It is therefore important to consider temperature fluctuations at a scale, both structurally and temporally, that is appropriate for the organism being studied. For long-lived endotherms, rapid anthropogenic disturbance may alter existing habitat faster than they can adapt their behaviour. Given the slow life-history of primates, many individuals that currently inhabit degraded forests were alive to experience those habitats when they were intact forests. Whilst it is likely that most primate species will possess the behavioural means to adapt to a changing climate in tropical forests (Chapman and Rothman, 2009), the survival of populations will largely be reliant on the behavioural plasticity of individuals. Socially flexible species such as orang-utans may possess the behavioural breadth to adapt to these conditions (van Schaik et al., 2009). Territorial species, such as gibbons or siamang, may have large areas of their territory rendered unsuitable by increased climatic warming within their lifetimes. Whilst primates will likely have the ability to utilise these areas for short periods or during cooler parts of the day, thereby avoiding the additional energetic costs associated with spending extended periods of time in high temperatures (Wheeler, 1991), large areas of forest which frequently reach high temperatures will have reduced overall habitat suitability, effectively reducing the quality of habitat and potentially placing additional energetic demands on territorial species (Pulliam and Danielson, 1991).

Given this greater understanding of within-canopy microclimates, this study's objective of assessing the impacts of forest structure on microclimate was largely achieved. The predictive model produced in this study, based on microclimate measurements, allows the estimation of the temperature at any given point within the canopy at Sikundur with a good degree of accuracy (mean residual standard error of 1.28^{o}C). In particular, the placement of microclimate data loggers vertically within the canopy highlighted variation (under different levels of cloud cover), which is directly driven by vegetation structure. However, a full understanding of the impacts of vegetation structure at the landscape scale was not achieved as the predictive model is only accurate with the forest canopy. Further study is required for the ability to produce an inclusive model which is of similar accuracy in various land-use types.

6.2 Siamang behavioural ecology

The habituation and behavioural follows of siamang marks, potentially, the first siamang group to be habituated in Northern Sumatra. They were found to be highly cohesive, rarely straying far from one another and maintaining markedly similar behavioural patterns throughout the study period within a well-defined home range. Within this relatively limited range, no strong or clear relationships were seen between activity budget changes in relation to temperature, or canopy structure (as measured using univariate statistics on a grid or cell system in this study). However, the group's position in relation to solar radiation during periods with low cloud cover showed a stark preference for shade during hot periods of the day. Despite this behavioural thermoregulation, modelled temperatures still suggested that siamang were likely experiencing significantly higher temperatures than in higher cloud cover, suggesting that they lack the capacity to behaviourly adjust their location to mitigate the effects of solar radiation and remain within their thermoneutral zone. Given the group's territorial extent, bordered by the Besitang river and historic logging roads on all sides, they may not have the capacity to utilise differing canopy structures as other groups may do. Similarly, the natural and anthropogenic barriers surrounding their territory may govern their diet, range use, and inter-group encounters. Initially the group's calling behaviour in reaction or response to the calls of neighbouring groups of siamang was set to be a focus of this study, but due to the extreme infrequency of their calls, statistical relationships could not be established. It may be that as opposed to the variables measured (i.e. distance to or frequency of neighbouring groups calling) governing their response to other siamang groups' vocalisations, the physical barriers to other siamang groups may mean the study group is able to avoid the additional energy expenditure of frequent vocalisations. This could possibly present evidence of their understanding of geographical barriers and use of sophisticated Euclidean mental maps of their surroundings (Normand and Boesch, 2009), unlike large arboreal monkeys (Di Fore and Suarez, 2007). The relative isolation of the study group no-doubt helped with the speed of their habituation, enabling the detailed study of their behaviour and ranging. However, it may render them a poor model for 'typical' siamang social and ranging behaviour. Although other recent studies of siamang have found remarkable flexibility in group dynamics and group size (Lappan, 2010), Lappan et al. (2007) found evidence of more frequent male than female dispersal in siamang, but it is notable that two single females, as well as four cohesive groups, were observed at Sikundur. Given their biparental care of young, variable group size and markedly different territorial calling rates between populations (this study, Lappan 2009; Lappan 2010; O'Brien et al., 2004; Chivers, 1976), siamang behaviour may vary considerably across their geographic range, between populations and potentially between groups depending on the ecology of each area (Chapman et al., 2002), perhaps signalling the ability of siamang as a species to adapt to ecological change.

There was clear evidence that the siamang at Sikundur used forest structure to shield themselves from thermal maxima (Figure 3.21), whilst forest structure itself had relatively little effect on their behaviour. This may be due to their structured home range use and relatively selective habitat requirements (Figure 5.4), effectively making variations to their use of habitat due to microclimate changes relatively subtle. This is however confounded by the findings in Chapter 4 of a lack of notably strong relationships between habitat structure variables and siamang abundance. This highlights the need for the study of multiple groups across a range of environments to adequately explore the ecological needs of the species. Whilst this study has gone some way to expand the understanding of the effects of forest structure and microclimate on siamang behaviour and ranging, as was an objective of the study, further studies of groups in differing environments would greatly aid in determining their ecological thresholds.

6.3 Abundance of primate species in relation to vegetation structure

The habitat requirements of three sympatric species, lar gibbons, Thomas langur and siamang were explored in Chapter 4, utilising UAVs and traditional vegetation surveys.

Surprisingly, UAV surveys were a substantially better predictor of the abundance of all three primate species than traditional vegetation surveys. This is possibly due to the more synchronous, wide-ranging data collection regimes of both vocal surveys and UAV vegetation surveys. Vegetation plots in continuous forests may not be capable of recording, either in sufficient detail or sufficient quantity, the habitat variables that dictate primate abundance within the typical constraints of time and cost for fieldwork (Hummel et al., 2011). Initially triangulation of primate vocalisations was attempted to enable the recording of primate population densities of each species at each site (Brockelman and Ali, 1987; Brockelman and Srikosamatara; 1993 Johnson et al., 2005 among others). However, possibly due to extensive microtopography, complex forest structure and human and equipment error, accurate triangulations of vocalisations were rare. Given the potential for compound errors in population density estimates based on Type I errors (Freckleton et al., 2006) due to un-triangulated detections of primates, encounter rate was chosen as a measure of primate abundance in each area. However, with the recent release of acoustic spatial capture-recapture (ascr) analysis application by the IUCN Primate Specialist Group Section on Small Apes (released in late April 2019), accurate interpretation of primate vocalisation data is now available, and may enable a more precise assessment of numbers of arboreal primates within the Sikundur area.

The pairing of these two methods, primate abundance surveys and UAV vegetation surveys, may prove to be a valuable methodological addition to the monitoring of primate populations. The abundance of primate species relative to vegetation structure variables obtained using UAVs presents an exciting prospect for the assessment of tropical forest habitat for arboreal primates. As both methods are relatively quick and cost-effective, large areas of forest could be surveyed for their relative suitability for various primate species and these assessments then checked with primate vocal surveys. In this study, clear relationships between differing species and vegetation structures were found, fulfilling the objective of the study. However, there are a number of confounding factors. Primates may not vocalise frequently in areas with low population densities and therefore areas of low-quality habitat (Steenbeck et al., 1999), effectively amplifying statistical relationships between ‘high quality’ vegetation structure and primate abundance. Conducting multiple surveys or using multiple methods for the assessment of primate abundance may rectify this potential problem.

6.4 Potential effects of climate changes on arboreal primates

Modelling the potential effects of future climate scenarios on arboreal primates, using microclimate models that include forest structure, revealed previously unexpected results. Whilst primate habitat has previously been theorised to be hardest hit by future predicted climate change (Graham et al., 2016), the buffering effects of forest cover may soften the effects of a warming climate. The study presented here shows that degraded areas and those exposed to high levels of solar radiation will potentially be most affected, reducing the suitability of these areas to primate species, but affecting sympatric species unequally. Whilst the microclimate model used highlights these previously unexplored areas, the analysis presented in this study does not take into account the feedback loop of reduced rainfall, or the predicted rise in extreme weather effects, which may have significant impact on the health of tropical forest ecosystems (Allen et al., 2010). Integrating vegetation health into future microclimate models may allow the prediction of these effects.

The thermoneutral zone as referred to throughout this study in relation to arboreal apes is hypothesised as opposed to measured. Whilst multiple studies have used the same classification of thermal niches for large-bodied primate species developed by Hill (Hill 2004; Hill, 2006; Barrett et al., 2004; Pruetz, 2007; Pruetz and Bertolani, 2009; Magill et al., 2013; Gesquiere et al., 2008), and some studies have measured the thermoneutral zone of different primate species (Aujard et al., 1998; Muller, 1995; Whittow et al., 1977; McNab and Wright, 1987; Genoud et al., 1997; Thompson et al., 1994), (to the author’s knowledge) none have examined the thermoneutral zone of primarily arboreal ape species. In contrast, the thermoneutral zone of hominins has been relatively well studied, particularly in relation to bipedalism and arboreality (Cross et al., 2008; Ruxton and Wilkinson 2011a; Wheeler, 1991; Takemoto 2017), loss of functional body hair (Ruxton and Wilkinson, 2011b; Wheeler, 1992a), body size (Wheeler, 1992b), physique (Tilkens et al., 2007; Wheeler, 1993), and shade-seeking behaviour (Wheeler, 1994). Given that behavioural thermoregulation of many primate species is well documented (for example; Japanese macaques *Macaca fuscata* bathing in hot springs to conserve heat [Zhang et al., 2007], Chacma baboons *Papio ursinus* reduce activity [Hill, 2006b], increase shade seeking [Hill, 2006a] and utilise cooler cave microclimates [Barrett et al., 2004]), this is somewhat surprising, particularly given the known effects of vertical temperature gradients in tropical forests (Freiberg, 1997; Kumagai et al., 2001; Pontes Riberiro and Bassest; 2007). The ‘catch-all’ figure of above 32°C has been used in this study to classify temperatures, above which thermal stress may be induced, but this figure may differ between species. Large bodied primates may be better suited to coping with intense solar radiation and heat stress (Wheeler, 1992a), particularly those with long limbs (Tilkens et al., 2007). Hair colour may also make a dramatic difference on the ability of some species to thermoregulate, as dark hair can heat to 56°C after five minutes in direct sunlight (Kosheleff and Anderson, 2009). Given this study’s findings, there may be evidence that suggests orang-utans, with large bodies and lighter pelage, are better suited to higher temperatures than the smaller, dark-haired siamang. This may well support the theory that the modern orang-utan may have evolved to inhabit relatively high temperature lowland tropical forests and siamang have adapted to cooler, higher elevations, despite their sympatricity (Smith and Pilbeam, 1980; Chaimanee et al., 2004; Yanuar, 2009).

Whilst the study presented here may not offer definitive answers to how climate change will affect arboreal primate populations, it does highlight a number of novel findings. Primarily, forest structure may play a vital role in the protection of arboreal primate species from climate change, with further forest degradation likely to substantially harm habitat suitability. Secondarily, sympatric primate species are likely to be affected by climate change unequally, due to differences in habitat requirements caused by ecological niche separation. Ultimately, species with narrower habitat requirements will likely be most adversely affected as the suitability of available habitats is reduced. Species which are able to use a wide range of habitats, that are not constrained by group-living or the defence of territory, will likely be able to use individual behavioural plasticity to adapt to new ecological challenges. However, it should be noted that efforts to predict primate species responses to novel problems, given their high degrees of behavioural innovation, are unlikely to be accurate. Given these new findings, the study objective of predicting species responses to future climate change has been largely successful, though new questions have been posed which further studies may answer regarding thermoregulatory thresholds of arboreal primate species and their behavioural plasticity.

6.4 UAVs in ecology

In this study I focused on forest structure and its ability to buffer against solar radiation, in relation to primate behaviour and abundance. This was achieved at a landscape scale using UAVs and structure-from-motion photogrammetry. Whilst this has proven to be an accurate, cost-effective method for the measurement and assessment of forest structure, it currently does not allow the identification of tree species without the use of hyperspectral imagery (Nevalainen et al., 2017, but see Lisein et al., 2015). Structure alone may not be the best indicator of forest health; the plant species which make up forests may have a dramatic impact of their ability to retain animal biodiversity (Kessler et al., 2011). Alpha-diversity (or dominant tree species) may largely govern a forest’s ability to survive the impacts of extreme weather events such as drought or fires (Goldammer and Serbert, 1990), with dipterocarp forest seemingly at particular risk (Tyree et al., 1998). However, in low-fruiting dipterocarp forests, primates are more likely to be dependent of tree beta-diversity, i.e. those trees which regularly bear fruit. It is currently unclear how beta-diversity will be affected in a warming world and is likely to be highly geographically dependent (Graham et al., 2016). Some tree species are highly dependent on obligate pollinators and climate change may alter these relationships (Koh et al., 2004; Gilmans et al., 2012). For example, *Ficus* spp., key food items for many primate species in Northern Sumatra (Ungar, 1995), may be particularly at risk, as the life span of fig wasps (*Agaonidae* spp.) may dramatically shorten in warming climates (Jevanandam et al., 2013). It is also possible that invasive species become useful food sources for primate species, as has been seen in other anthropogenically disturbed primate habitat (Voskamp et al., 2014) Understanding how tree species diversity may change could be of prime importance to understanding the potential impacts of climate change on tropical forests. In a warming climate, with a higher likelihood of extreme weather events and possible CO_2 fertilisation, tropical forest species diversity and health could be altered dramatically. The application of multi- or hyperspectral surveys of tropical forests could enable the monitoring of these potential changes (Féret and Asner, 2012). Given the relatively low-cost of using UAVs, they provide a faster, far-ranging and more accurate measure of vegetation structure than traditional vegetation surveys (Austin, 1991). However, the method used to classify vegetation here is univariate statistics of elevation data, and whilst seemingly appropriate does not fully capture vegetation structure per se, but rather an undefined mix of topographical and vegetation data, which is largely indistinguishable from one another. As tree species diversity, particularly beta-diversity, may be governed by slope aspect in tropical forests (Gallardo-Cruz et al., 2008), an understanding of microtopography may be essential to understanding the drivers of tropical forest productivity. Unlike LiDAR surveys, 'ground hits' are not as frequent using SfM photogrammetry (Wallace et al., 2016) and the elevation of the ground in relation to vegetation, therefore the measurement of vegetation height above ground, is not readily apparent. This differentiation may not be applicable to arboreal primate species using solely the upper canopy, nor for most ecological questions (Liu et al., 2017). However, new 'vegetation penetrating' LiDAR may allow direct measurements of tree height (The Optical Society, 2017). Till this new technology become readily available the use of paired oblique RBG cameras has potential to assist in generating point clouds with more vertical detail.

An additional possibility to indirectly measure tree size may be the implementation of algorithms to identify and measure individual tree crown size (Zarco-Tejada et al., 2014), which is correlated to both tree height and diameter at breast height (see Figure 2.14). Whilst implementing this over large scales may be computationally demanding, it could potentially enable the measurement of tree size, and therefore habitat quality for arboreal species (and biomass of forested areas) over large areas, with rapid and low-cost data collection (Panagiotidis et al., 2017).

The addition of multispectral data collection using UAVs could not only capture vegetation structure, but also vegetation health (Ismail et al., 2007). Whilst the use of RGB imagery may allow the potential identification of tree species or tree health within a single UAV flight, changing cloud cover, light and weather conditions render direct colour comparisons between flights problematic, even if they are completed within hours of each other (see Appendix I). Multispectral data collection would permit the comparison of vegetation quality over extended time periods, allowing the effects of rainfall, drought, seasonality and a warming climate on vegetation quality to be studied (Barna et al., 2017; Minařík et al., 2016; Milton et al., 2007). Vegetation quality could be studied in even further detail by utilising hyperspectral and LiDAR sensors (Näsi et al., 2015). Currently the availability of affordable, lightweight sensors is prohibitive for many users, but with ever decreasing costs and sizes of advanced sensors, UAVs using hyperspectral and LiDAR may be common place within only a few years, allowing the identification of individual tree species from their field reflectance signatures and direct measurements of their dimensions (Nevalainene et al., 2017; Adam et al., 2009; Rosso et al., 2005).

The pairing of UAVs and thermal infrared cameras, enabling the identification of arboreal mammals, has recently seen great success, (Kays et al., 2019). Spaan et al. (2019) recently used UAVs fitted with infrared cameras to identify the numbers of *Ateles geoffroyi* within groups at sleeping trees, enabling accurate surveys of population density, as well as examination of sleeping sites and sleeping behaviour. Combining these imaging sensors could lead to a great leap forward in the accuracy of both forest structure surveys and arboreal vertebrate behavioural ecology. By mapping large areas of forest using SfM photogrammetry to enable the classification of forest structure, analysing the health of the vegetation using multispectral sensors, and sampling the abundance of arboreal vertebrates using UAV-mounted thermal infrared cameras, correlations between the three survey techniques could allow the detailed identification of what constitutes preferred habitat for arboreal species, and could also assist in estimating their population density. Additionally, the use of UAV-mounted thermal infrared cameras could be used to detect microclimate variation in forest canopies, remotely assessing climatic changes, canopy gaps and signs of disease (Smigaj et al., 2015). The application of these technologies could potentially revolutionise the study of forests canopy and the animals that reside within them. However, the full use of UAV technologies which are currently available has not yet been fully realised.

Applying existing UAV technology in repeatable, predictable ways holds great promise for conservation biology. Repeated surveys of the same area to document land-use and forest structure change could be one of the most useful applications of UAV technology, enabling the near real-time study of land-use change, documentation of anthropogenic disturbance as well as vegetation growth and die-back. Yet given that most of its current users are western researchers, these applications are not yet viable in a Southeast Asia context. UAV technology has seemingly yet to reach the “plateau of productivity” that many new technologies face (Van Lente et al., 2013), and with each new facet of UAV technology, be it a new sensor or application for UAVs, a technological rush is triggered with research documenting its possible use in a number of contexts (Goerzen et al., 2010; Roberge et al., 2012; Nex and Remondino, 2014). Yet the routine use of these technologies by the organisations that could put them to the best use (e.g. ‘in-country’ conservation NGOs or national park officers/rangers in a conservation biology context, for example) has yet to be established. Given this, it is essential that conservation minded researchers focus on both the potential applications of emergent technologies as well as capacity building in their areas of study to ensure that these technologies are put to best use, data acquisition is maximised and a ‘technology gap’ does not separate conservation biology researchers and practitioners.

The implementation of UAV surveys for the assessment of vegetation quality does not negate the need for on-the-ground surveys. Whilst UAVs may be able to conduct vegetation structure and phenology surveys (Berra et al., 2016; Klosterman et al., 2018; this study) they will not be able to identify the onset of disease, increased insect activity or other factors that may influence vegetation health. Similarly, without local knowledge and experienced botanists assisting with the identification of tree species, detailed inventories of forest would not be possible, even with the assistance of multi- or hyperspectral imagery. The advent of technologies such as UAVs should not preclude the use of more traditional, and potentially detailed, methods. As well as producing valuable botanical data that are not directly available to non-native researchers (Sujarwo et al., 2016; Brush, 1993), collaborations with local researchers, botanists and field assistants can foster revenue streams, healthcare and educational opportunities and protect local traditional knowledge (Gadgil et al., 1993; Twarog and Kapoor; 2004; Chapman et al., 2015; Hance, 2015). Emergent technologies such as UAVs will show their true strengths as data collection aids when used alongside existing methods, not as a means to replace them.

There are still further considerations for the use of UAV technology. In this project, UAV flights were halted by local authorities before the planned area could be mapped in full. A lack of clear regulations on the correct permits needed or which government agency would grant such permits led to an administrative impasse that caused all data collection using UAVs to be stopped. Paradoxically, it is vital that all users of UAV technology adhere to the guidelines of their host country and hold the appropriate permits and licences, as infractions of the law, the constraints of permits or licences can deter the granting of future permits for UAV use by local authorities, increase the scrutiny of UAV use and hamper future research. As mentioned by Vincent et al. (2015), the approval process for UAVs can render them a time-consuming and potentially expensive method for data collection. As the use of UAVs has recently become more wide-spread, clearer guidelines and legal requirements have been defined by many authorities in a number of countries (Gillespie and West, 2010). The adherence to all relevant guidelines as well as the sharing of results with local authorities may pave the way for more cohesive workflows and fewer issues with UAVs in future research.

6.5 Future recommendations

Whilst UAVs and other emergent technology may aid in the understanding of canopy processes and surveys of biodiversity, in terms of the effective conservation of habitats, the rapid identification of further anthropogenic disturbance and land-use change is the field where they may have the largest impact. Whilst the synergistic impacts of climate change and degradation may have an impact on arboreal primate species, and warming temperature may reduce overall habitat availability, further deforestation will have the largest immediate impact on the arboreal primate population in Sikundur. With encroachment into the Sikundur area periodically removing large sections of forest (personal observation; Szantoi et al., 2017; see Hansen et al., 2013), the impacts of forest degradation may be eclipsed by deforestation. Between 1985 and 2007, 43.3% of forest within the North Sumatra province has been lost (Riswan et al., 2011). This has likely led to increased human-wildlife conflict, with orang-utans that stray into plantations being killed with relative frequency (Nantha and Tisdell, 2009), highlighting the compound effects of anthropogenic disturbance on forest habitat (Buma, 2015; Gillespie et al., 2015).

Pervasive small-scale encroachment into the larger Sikundur area (see Figure 2.4) could have substantial effects on the primate populations. Those areas remaining which are adjacent to anthropogenic disturbance are most suitable to a higher number of species (Chapter 4), as opposed to alluvial areas which make up large tracts of the larger Sikundur area. Given large areas of high-quality habitat will likely be less suitable for primate species with the effects of climate change, minimising further encroachment into lowland forest areas is key to safeguarding the biodiversity of these areas. Here there is great promise in the full utilisation of emergent technologies. The deployment of UAVs working in synergy with local law enforcement could rapidly identify areas of deforestation or degradation (Messinger et al., 2016). UAVs coupled with soil surveys and locally scaled climate modelling could mitigate the effect of future climate change and human-wildlife conflict by increasing yields of locally grown crops or alternative crops with higher worth (Sweain et al., 2010; Hunt et al., 2010; Geipel et al., 2014). Both UAVs fitted with thermal infrared cameras and passive acoustic monitoring systems (PAMs) offers the potential for tracking potentially destructive animals and alerting those that live at the human-wildlife interface of their locations, removing the need for long hours spent protecting crops (Gonzales et al., 2016; Vermeulen et al., 2013; Hill, 2000). Together with local education project and healthcare initiatives, effective conservation of protected areas can add revenue streams for the local population and markedly improve quality of life (Chapman et al., 2015; Kugonza et al., 2009).

However, in Indonesia, corruption has been a powerful and pervasive force that has been hugely detrimental to the protection of forest (Dauvergne, 1994). Recently, large tracts of tropical forest have been removed for large scale agriculture, with the majority of profits from this agricultural and industrial growth not remaining within the nation (Pichler, 2015; McCarthy, 2010). Corruption has directly contributed to forest loss. President Suharto (1967 - 1998) was renowned for his distribution of logging licenses to key military officials to secure their support for his long, dictatorial rule (Poffenberger, 1997). In recent years an increase in palm oil production, largely funded by foreign investors as well as the Indonesian government, has led to environmental degradation (Davis et al., 2015; Wicke et al., 2011), ‘land-grabbing’ (Casson, 1999; Colchester, 2011) and extensive forest fires (Van Nieuwstadt and Sheil, 2005) which has had a global impact (Harrison et al., 2009). The global awareness of these issues has led to western consumer markets boycotting products that contain palm oil (Cova and D’Antone et al., 2016), a trend that could lead to the destabilisation of an industry that, in Indonesia, contributes $4.1 billion to the gross national income (TWB, 2006). Given these rapid developments, and the legally grey area in which land acquisition can take place in Indonesia (Carlson et al., 2012), there are few factors deterring small-scale encroachment of protected areas in Sumatra (Gaveau et al., 2007; Lee et al., 2014). But stemming the small-scale deforestation and degradation events in protected areas may be key to the long-term survival of biodiversity in areas such as Sikundur. With a multitude of threats from climate change, extreme weather events, droughts and the plethora of ecological responses to these, the addition of further anthropogenic disturbance may seal the fate of the highly biodiverse lowland forests of Sumatra. However, there is hope. Wright and Muller-Landau (2006) predict that a slowing of human population growth and rapid urbanisation will lead to a decrease in deforestation rates, and natural forest regeneration through secondary succession to increase. This may potentially avoid a predicted mass extinction event (Aide and Grau, 2004), and present those species with sufficient behavioural adaptability to flourish in regenerating forest areas.

6.5 Conclusion

Habitat and climate change are reshaping thermal landscapes and will likely create novel environments for many species, changing community assemblies, population dynamics and habitat suitability (Nowakowski et al., 2018). The degree of change the tropical forests will undergo from current levels will be governed by both future and historic levels of anthropogenic disturbance and the trajectory of future climate change (Dale et al., 2005; Laurance, 2004; Wright 2005). The ability for each species to adapt to these new environments will likely be governed by their adaptability, behavioural plasticity and ultimately, their evolutionary history (Moritz and Agudo, 2013; Pacifici et al., 2015). The arboreal apes of Sumatra have evolved to inhabit structurally complex, climatically stable environments, each specialising within their own ecological niche to minimise interspecies competition and when appropriate, exhibiting territorial behaviour to minimise intraspecies competition. Each species' survival in the Anthropocene will be governed by the breadth of their ecological niche and its resilience in the face of anthropogenic disruption.

In terms of their abundance, Thomas langurs (*Presbytis thomasi*) were the most frequently recorded in Sikundur, across all areas surveyed. Their primarily folivorous diet (Ungar, 1995), fluid social dynamics, relatively fast life-history (Wich et al., 2007), large population and apparently adaptability to multiple environment types (see Table 4.1 and Figure 4.4a-d), suggest that, though they may not show a high degree of behavioural adaptability, their ecological niche is broad enough to weather all but the most severe future environmental changes.

Lar gibbons (*Hylobates lar*) were the next most abundant species, with strong correlations found between their abundance of large trees, with sites of anthropogenic disturbance having little to no negative impact. As a highly arboreal, territorial and frugivorious species with low group numbers, gibbons in Sikundur are seemingly in high numbers in favoured habitats, and low densities in less suitable areas. Whilst this is expected given previous studies' findings (O'Brien et al., 2004, Marshall., 2010), lar gibbons' dependence on habitats which have previously been targeted by selective logging suggests that many of the areas in which they are most abundant will likely be threatened in the future. Although it was not explicitly studied in this project, the lar gibbons tendency to favour resting and locomotion in large trees high in the canopy potentially mean that this species will be the first within the sympatric primate species of Sikundur to experience the detrimental effects of future climate change. Whilst gibbons may have the behavioural capacity to adjust their behaviour to counter these effects by descending further into the canopy, potentially altering their time-budget and adopting a more folivorous diet, this will likely put them in direct competition with other sympatric primate species occupying other ecological niches.

Orang-utan within Sikundur, whilst seemingly the least abundant (Knop et al., 2004), show perhaps the broadest range of habitat types used. Together with their highly dispersed social structure (Harrison and Chivers., 2007), extremely broad diet (Vogel et al., 2015), and use of tools (Fox et al., 2004), orang-utan are the most adaptable of primate species within Sikundur. However, their low population numbers, slow life-history and high inter-birth interval (Galdikas and Wood, 1990; Knott, 2001; Wich et al., 2004) make them extremely vulnerable to direct anthropogenic threats such as hunting or human conflict. With the seemingly steady removal of forest in the larger Sikundur area (Figure 2.4), these threats will only increase in the future. Small decreases in orang-utan numbers could dramatically reduce orang-utan population viability in areas such as Sikundur (Leighton et al., 1995). However, if these pressures were not present, orang-utan in Sikundur are likely able to adapt to a dramatically different environment, the species having been likely to have lived at much higher population densities in the recent past (Meijaard et al., 2010) and be relatively abundant in swamp land, peat swamp, and highly degraded areas when hunting is not present (Marshall et al., 2006).

Siamang within Sikundur present a more complex picture than the other species studied in this project. Seemingly, they are relatively adaptable, with a largely folivorious diet, adaptable group structure and a wider range of habitat use than the smaller lar gibbon species. Whilst at seemingly low densities throughout the region, they were present in all but the lowest habitat quality areas. In these terms siamang seemingly inhabit an ecological niche half-way between the more specialised, frugiovorus lar gibbon and the adaptable, generalist, orang-utan. Siamang are likely susceptible to both habitat removal, degradation and sharp population declines, but likely to a lesser degree than lar gibbons or orang-utan. However, due to their seemingly low population numbers and limited ability to behavioural adaptability, they may be more susceptible to the less obvious pressures of the synergistic effects of forest degradation and climate change. The siamang group that was the focus of this study showed a clear preference for relatively high-quality habitat, avoiding areas of anthropogenic disturbance (see Figure 5.3). Similarly, the group showed a markedly different ranging in times of low, moderate and high cloud cover (Figure 3.21), further reducing the amount of potential habitat used at times when temperatures were high, which is likely to exacerbate with future predicted climate change. These cryptic effects may have relatively small negative effects over short time periods, but may form the basis of extinction debt, slowly reducing infant survival, increasing energetic demands and increasing inter- and intra-species competition for less lower quality food items. The severity of these effects will be determined by the resilience of tropical forests to future degradation, removal and climate change.

In this regard, tropical forest environments still present an enigma, with multiple studies predicting their downfall (Brook et al., 2008; Mueller-Dombois and Goldammer, 1990; Harrison, 2000; Malhi et al., 2009) or durability (Huntingford et al., 2003; Thompson et al., 2009; Hirota et al., 2011) in the face of climate change. The results of this study generally suggest the latter, though some sections of forest, through degradation or their position in relation to the rest of the canopy, will likely be more affected by climate change than others. This is due to the breakdown of canopy integrity, lessening the capacity of tropical forests to buffer against solar radiation, as shown in chapter 2. In the short term this is likely to lead to reduction in the availability of preferred habitat for arboreal primates, as shown in chapter five. However, it is unclear whether this will lead to the breakdown of tropical forest ecosystems in the long-term as suggested by Brook et al. (2008). Canopy gaps, degradation and invasive plant species currently alter the climatically stable environment beneath the canopy (Fetcher et al., 1985; Brown, 1993; Blonder et al., 2018), but climate change potentially introduces a pervasive increase in temperature, subjecting plant species, invertebrates and vertebrates to a novel thermal environment. Arboreal primates, without the availability of terrestrial microclimate refugia, are likely to experience these changes earlier under global warming than terrestrial species. As shown in chapter 3, arboreal primates alter their position within the canopy to regulate their temperature but are only partially successful in doing so in low cloud cover. This may render significant portions of their habitat, especially degraded forests, unsuitable in the future. As shown in chapter 4, canopy structure governs the abundance of different primate species, with habitat suitability of different areas altering depending on the behavioural and ranging requirements of each species. The disruption of habitat suitability by future predicted climate change may significantly alter the interactions between sympatric primate species, and the behaviour of individuals, likely in unexpected ways. However, arboreal primates are likely to reduce their use of degraded forest areas in a warming climate, seeking the climatic stability of old-growth forest (Blonder et al., 2018). Intact forest canopy is key to their continued survival in a changing climate. Protecting areas such as Sikundur from land-use change and degradation will be essential for the survival of the arboreal primate populations that have been the focus of this study.

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