

Spatial Distribution and Density of the Lar gibbon
Hylobates lar and Siamang *Symphalangus*
syndactylus in relation to canopy structure and
disturbance in a lowland dipterocarp forest,
Sumatra.

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This thesis is submitted in partial fulfilment of the requirements of the
degree Masters by Research (MRes).

January 2016

Bournemouth University

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Abstract

Forest structure is an important factor in the persistence of arboreal primates, and understanding the relationship between primate populations and habitat characteristics is essential for their conservation. Indonesia is experiencing one of the highest rates of deforestation globally, and with such a large amount of historical logging having taken place, only ~3.8% of the remaining forest is classified as primary. Sumatran lowland forests are one of the most threatened habitat types, though few studies have been conducted on primate populations within this habitat. The aim of the study was to ascertain forest vegetation structure between four different land units (*hills, plains, alluvial* and *hill-swamp*), and identify which structural variables are important indicators of habitat suitability for the two sympatric gibbon species, the lar gibbon *Hylobates lar*, and the siamang *Symphalangus syndactylus*. The field study was conducted from 1st March to 1st August 2016 within the Sikundur region of the Gunung Leuser National Park, North Sumatra, where both large and small-scale logging practices have been undertaken. At ten forest survey locations, auditory sampling methods using fixed points counts were used to produce hylobatid density estimations, and 4-6 vegetation plots per site were undertaken to identify differences in forest structure. Lar gibbon densities ranged from 1.19 – 3.56 groups/km² and were found to be correlated with median tree height and crown area ($F_{(9)} = 5.604$, $p = 0.031$, $R^2 = 0.459$), and negatively correlated with frequency of trees <20m ($F_{(9)} = 6.775$, $p = 0.035$, $R^2 = 0.616$), and with canopy connectivity <15% ($F_{(9)} = 22.45$, $p = 0.001$, $R^2 = 0.737$). Siamang densities ranged from 0.40 – 2.11 groups/km², and were correlated with frequency of trees between 10-20m in height ($F_{(9)} = 5.576$, $p = 0.046$, $R^2 = 0.411$), and with canopy connectivity between 50% -75% ($F_{(9)} = 5.930$, $p = 0.041$, $R^2 = 0.426$). These results indicate these hylobatid species exhibit a degree of tolerance and behavioural flexibility to habitat disturbance, though the preservation of tall trees and the provision of a significant amount of canopy connectivity is required for their continued presence in lowland forests. It is hoped that the results of this study will contribute to the preservation of Sumatran's lowland forest, and the gibbon species that inhabit them.

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Acknowledgements

First of all, I would like to thank my supervisors Amanda Korstjens and Ross Hill, without whom this would not have been possible. I am so grateful for their continued patience and support, both whilst undertaking the fieldwork in Indonesia and additionally in producing this thesis. I appreciate all the support and encouragement you have provided. I could not have asked for better supervisors.

I would like to extend a special thank you to Matthew Nowak and the staff from the Sumatran Orangutan Conservation Programme (SOCP) for their help not only through the visa process, but the continued support they provided whilst I was in Indonesia. This study would not have been possible without their help. I would like to say a huge 'terima kasih banyak' to all the Sikundur field staff who provided help with both the language and logistics of undertaking this fieldwork, which would not have been possible without them. These include; Suprarudi Rimba, Supri, Ben, Logga, Rikki, Mister Ukok and Yangsa. Additionally, I would like to thank my co-worker Christopher Marsh, not only for help with collection of fieldwork but friendship and laughter whilst in Indonesia. An extra thank you goes to John Abernathy and James Askew who provided well needed laughter and support both at Sikundur and in Medan.

I would also like to give a special thanks to my mom and Paul, who have always supported me in achieving my dreams. Their immense help this year both financially and emotionally has allowed me to undertake this study and get back on my desired career path. I could not have done this without you and appreciate this more than you will ever know.

Last, but not least, I would like to thank my best friend Ellesse Janda; she never fails to make me smile every day and has been a huge support whilst writing this study. I couldn't have done it without her.

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1. Introduction

South-east Asian rainforests are home to a significant proportion of the world's biodiversity and demonstrate high species richness and endemism (Wilcove et al. 2013). Many of these areas have become the last strongholds for numerous unique, endangered species and encompass approximately 25% of the world's flora and fauna (Woodruff 2010). However, these forests are in rapid decline, and are experiencing one of the highest rates of forest loss across the globe (Sodhi et al. 2010). In Indonesia alone, Margono et al (2014) recorded a loss of 0.84MHa of primary forest in 2012, with 51% of this occurring in lowland forests. If the current rate of habitat loss is maintained, the region could lose 75% of its forests and 42% of its biodiversity by 2100 (Sodhi et al. 2010). With habitat loss being a significant threat, many forest species are critically endangered and are at a high risk of extinction. Anthropogenic activities are the primary causes of this loss including complete clearance of forest areas for large scale plantations and intensive logging practices. These logging practises (both intensive and selective) alter the structure of the remaining forest by removing only the large target tree species (Hall et al. 2003). This in turn alters species composition and micro-climate, increases 'edge effects', creates canopy gaps and modifies understorey vegetation. In Indonesia, such a large amount of historical logging has taken place that only approximately 3.8% of remaining forest has been classified as primary (Cheyne et al. 2013). It is therefore important to increase our understanding of how this ecosystem will respond and/or adapt to these structural changes, and how this will affect endemic forest dwelling species; especially arboreal species, such as the gibbons, that depend on the vertical structure of the forest in order to maintain sustainable populations.

1.1: Relationship between primates and forest habitats

Primates are a highly-threatened taxon with a large number of species being dependent upon tropical forest ecosystems. Almost 90% of all primate species are found within this biome, and worryingly, more than half of the extant species are threatened by extinction (Chapman and Peres, 2001). Primates inhabit a variety of forest types including lowland and montane rainforests, savannah, woodland and swamp forest, each

with their own distinct structural characteristics (Mittermeier et al. 2013). The evolution of both forest habitats and primates are closely linked; with each habitat's distinct characteristics leading to specific morphological and behavioural developments, allowing for the adaption of an arboreal lifestyle (Gouveia et al. 2014). Currently, some of the most threatened primate species survive only in fragmented forest habitats, therefore understanding the ecological flexibility within and across species and adaptation limits in terms of survival are extremely important (Anderson et al. 2007) and necessitate further investigation. South-east Asia has more critically endangered primate species than any other tropical region (IUCN 2015) and as unhabituated arboreal primates are difficult to census and study (Brockelman and Srikosamatara 1993), data on population sizes are lacking in many areas (O'Brien et al. 2003). Even though forest loss and degradation is known to negatively impact most forest dwelling primates (Phoonjampa et al. 2011) it is difficult to quantify the effects of forest degradation due to the lack of any long-term data. Some primate species exhibit morphological adaptations and behavioural plasticity to allow them to subsist in these structurally modified habitats, although others appear to be more vulnerable due to greater specialisation both morphologically and behaviourally (Marsh et al. 2016).

The main factors influencing population size and abundance of primate species in forest habitats are food availability, predation and disease, though population densities are also highly correlated with forest structure (Hamard et al. 2010; Phoonjampa et al. 2011). Arboreal species that rely on the forest canopy for food, travel and sleeping sites are more affected by habitat disturbance than other terrestrial forest dwelling species. This is especially true for the hylobatidae family (gibbons and siamangs) which spend the majority of their life high in the canopy, rarely descending to the ground (Bartlett 2007). These apes are obligate canopy dwellers, and require intact canopy structure for all aspects of their behavioural ecology (Cheyne 2010; Hamard et al. 2010; Marshall 2010).

The survival of all extant gibbon species are threatened by habitat loss from anthropogenic factors and although several species are the focus of behavioural and ecological studies (Brockelman and Srikosamatara 1993; Chivers 1984; Mitani 1990; Bartlett 2007; Cheyne 2007a), there is still little understanding of their resilience to forest disturbance (Lee et al. 2014). The majority of gibbon species are allopatric except for the sympatric lar gibbon *Hylobates lar*, and siamang *Symphalangus syndactylus*, which live in Sumatra and peninsular Malaysia (Cheyne 2010). Although the lar gibbon is most

widespread in its Sumatran range, it is listed as Endangered by the IUCN (IUCN 2015) almost certainly due to this island having the highest deforestation rates in South-east Asia (Miettinen et al. 2011). Although imperative to gibbon conservation initiatives, there are still relatively few population estimates for the species in Sumatra, especially within the lowland forests (Lee et al. 2014; O'Brien et al. 2004).

1.2: Focus of Study

Relationships between vegetation structure and population densities have been found for several primate species (Phoonjampa et al. 2011) and recent studies have suggested such relationships between forest structure and gibbon populations exist as well (Hamard et al. 2010; Lee et al. 2014). Furthermore, gibbons are highly territorial, suggesting groups may remain within their former ranges even following intensive forest disturbance such as the removal of a high proportion of trees (Cheyne et al. 2013) as documented in orangutans (SOCP 2014). For this reason, alongside their ecological characteristics (long maturation and inter-birth intervals, highly frugivorous feeding behaviour and large territory size) their recovery ability from large population crashes is reduced (Phoonjampa et al. 2011; O'Brien and Kinnaird 2011). Therefore, it is imperative that research into this area is undertaken urgently to preserve these endangered apes. Investigation into the spatial distribution of the species in relation to canopy and vegetation structure will provide information and improve our understanding on habitat preferences and levels of adaptability, as well as providing a baseline population estimate for Sumatran lowland forests.

This study was undertaken in a Sumatran lowland dipterocarp rainforest located in the Gunung Leuser National Park (GLNP), Sumatra. The GLNP is 7927km² and is located between the boundaries of Northern Sumatra and Aceh provinces. Several arboreal primate species reside here including; the lar gibbon, siamang, thomas leaf monkey *Presbytis thomasi*, two macaque species *Macaca spp*, and the critically endangered Sumatran orangutan *Pongo abelii*.

1.3: Research aims, objectives and hypotheses

The aim of this study was to ascertain forest structure and group density of the lar gibbon and siamang within a block of lowland forest in the Sikundur region of North Sumatra, Indonesia. It is anticipated that this study will provide an understanding of how

forest structural characteristics influence habitat choice of primates. Understanding the relationship primates have with their environment will provide a valuable insight into the level of habitat disturbance these species can tolerate, and the effect this will have on their survival ability. This information can assist in the planning and implementation of future conservation strategies that will benefit both arboreal primates and Sumatra's highly threatened lowland tropical forests. This will be achieved through the following objectives:

1. Identify differences in rainforest structure between four different forest types located within the Sikundur lowland forest of the GLNP. These are hill forest, plains forest, alluvial forest and hill-swamp forest. This will be established through measurements of various vegetation structural features.
2. Estimate group densities of two sympatric hylobatid species in each survey area and forest type, and identify any relationships between species densities in association with each other.
3. Compare results of two different gibbon density estimation methods; triangulation and Spatially Explicit Capture-mark Recapture (SECR).
4. Identify relationships between forest structural characteristics and hylobatid density to ascertain ecological requirements and habitat preferences to allow species' survival.

Consequently, this study's hypotheses are:

1. Forest types will show structural differences through various vegetation characteristics including; tree height, stem diameter, connectivity, crown area and tree density. Additionally, forest disturbance through historical logging is expected to have had an effect on forest vegetation, resulting in fewer taller trees and a less connected canopy in these areas.

2. There are several different methods for estimating density in wild primate populations based on fixed point measurements, though the accuracy of these methods is difficult to assess. It is expected that densities calculated from these two estimation methods will not show significant differences in densities to each other.
3. Primate densities will differ within and between habitat types. It is expected that areas with the most stratified, structurally complex and uninterrupted canopies will have the highest primate densities, whilst low forest with large canopy gaps will hold the lowest primate densities. As these species' live sympatrically it is expected that less disturbed, highly stratified structurally complex, uninterrupted canopies with necessary ecological requirements will allow the species to co-exist in closer proximity when compared to more disturbed, less structurally complex habitat.

2: Background

2.1: Introduction

Deforestation and habitat fragmentation have been identified as one of the biggest drivers of global biodiversity loss (Norscia and Palagi 2010). Forest loss and modification has placed significant pressure on the remaining rainforest ecosystems. This is especially prevalent in south-east Asia, where ~15% of the world's tropical forests are located (FAO, 1995). South-east Asia's tropical forests make up the one of the last strongholds for many important populations of endemic and specialist species (Lee 2009), and how these animals are responding to habitat changes alongside their adaption abilities is of crucial importance if we are to prevent future mass extinctions. These habitats are essential in aiding 'species restocking' of restored forest and human dominated landscapes, and this can only be achieved if large, healthy populations are surviving in these increasingly remnant environments. Further research within this area of study can provide information on adaptation levels of species, as well as identifying the necessary requirements needed within a habitat to ensure species' survival. Research into the distribution and abundance of south-east Asian biodiversity in relation to anthropogenic impacts will highlight how well native species might survive in human dominated landscapes in the future, providing information and management strategies to enable conservation initiatives to be implemented to achieve this.

2.2: Tropical forest loss: causes, threats and implications

Tropical rainforests are one of the most threatened habitat types, with between 8-12 million square kilometres (35%-50%) of original closed canopy tropical forest already lost (Wright and Muller-Landau 2006). Forests are recognised for their high biological diversity, their role in maintaining global climate cycles, regional and local weather patterns and precipitation levels, as well as providing some of the most important ecosystem services to the planet. The main drivers of tropical forest loss are anthropogenic activities; clearing vast expanses of land for the growing global demand for food, biofuel and other commodities (Sodhi et al. 2010), which in turn leads to massive biodiversity declines and endemic species extinctions. Conversion causes notable changes in forest structure and ecosystem processes; i.e land-atmosphere

interactions, global carbon budget, hydrological cycles and soil properties have all been shown to be significantly impacted by land use changes in forests (Reiners et al. 2015). Additionally, tropical forests contain over 30% of global carbon stocks (Dura et al. 2013), consequently significant modifications and destruction of these hugely important ecosystems will have a major impact on the global carbon cycle and climate change worldwide.

2.3: South-east Asia deforestation

Although a worldwide phenomenon, South-east Asia has one of the highest rates of deforestation (Gaveau et al. 2009a) due to the continued escalations and expansions in agriculture, logging, fragmentation and urbanisation. Between 1990 and 2010, Stibig et al (2014) documented a loss of 6.5% of the region's land area, equivalent to forest loss of ~320,000km². Anthropogenic threats to these forests are increasing in severity, putting enormous pressure on the remaining intact forests and their biodiversity, with a plethora of species declines and extinctions predicted in this region if the present rate of deforestation continues (Sodhi et al. 2010; Sodhi and Brook, 2006b). The major drivers of deforestation within South-east Asia include the rapid expansion of oil palm plantations and paper and pulp industries at the expense of lowland dipterocarp forests. Clearing of these lowland forests, as well as increased droughts and forest fires has become a major source of global carbon emissions. These changes bring with them a number of issues exacerbating the problem, including the construction of infrastructure and roads, with increasing disturbance levels within forests from human traffic. The construction of roads due to logging and connection of human habitation significantly fragments forest complexes and consequently disrupts habitat use and behavioural patterns of many species, especially mammals (Austin et al. 2007; Laurance et al. 2009). Animals are killed through vehicle collisions, their hunting and foraging patterns disturbed and the creation of canopy gaps restrict the movement of particular primates, as well as providing greater accessibility to hunters and poachers targeting threatened animals (Pattanavibool and Dearden 2002; Wich et al. 2008). Many mammals learn to avoid roads as a survival technique, and studies show occurrences of species negatively correlate with distance to roads (Linkie et al. 2008). This reduces 'useable' habitat even more, and potentially causes both intra- and inter-specific competition in species, as individuals are forced to share territories and compete over reduced availability of food resources and favoured sleeping sites.

Another major factor in reducing abundance of species comes from the establishment of human settlements around the edges of forest reserves. These settlements scare away and disturb species, consequently contracting species' home range. A study by Ngoprasert et al (2007) showed habitat use by leopards in a Thai National Park increased with distance from human settlements. Therefore, the conservation of Asian tropical lowland forests is a matter of urgency, both to mitigate against climatic change and carbon emissions and to conserve biodiversity (Wich et al. 2008).

In order to curb losses in forest cover, governments and conservation organisations have established networks of protected areas, restricting human access and activities through law enforcement (Gavaeu et al. 2009b). However, these areas cover less than 17% of the total land cover of South-east Asia, and the laws are not always enforced, with many illegal activities continuing inside the boundaries of these reserves (Nowak 2015). Not only is South-east Asia's annual deforestation rate the highest in the tropics, but it has increased between the periods 1990–2000 and 2000–2005, and is still increasing at present. This could result in projected losses of 13–85% of biodiversity in the region by 2100 (Sodhi et al. 2010).

The highest forest losses recorded in south-east Asia occur within Indonesia. A study undertaken by Miettinen et al. (2011) identified areas with extreme levels of deforestation include the peat swamps of Borneo and the eastern lowland forests of Sumatra, which additionally have one of the highest biodiversity values of any terrestrial ecosystem (deWilde and Duyfjes, 1996). High levels of disturbance within these Sumatran lowland forests are attributed to their relatively easy accessibility in contrast to other areas and even though they are under threat, remain largely understudied in comparison. Less than a quarter of Sumatra's landmass remains forested (Miettinen et al. 2011) and over the past decade alone, 6.2 million hectares of Sumatra's forests have been assigned to oil plantations (YOSL-OIC 2009).

2.4: Anthropogenic effects on forest structure

As well as the complete clearance of forests, the structure of forests is changing through human activities, in particular selective logging (Hall et al. 2003). Selective logging homogenises forests, creating a simplified vertical structure and lower species richness (Norris et al. 2010). This practice is the greatest anthropogenic threat to remaining forested areas, and the impacts on vegetation structure varies depending on

the method used, spatial scale, size and amount of timber harvested (Sodhi et al. 2010). Plants inevitably are the first organisms to be impacted upon, and the ones that are the most important for the overall ecosystem stability, structure and function, playing an important role in nutrient cycling, maintaining soil structure and flood regulation (Cardinale et al. 2012). Although logging does not result in a dramatic loss of vegetation cover in comparison to complete land clearance, logging activity can cause a marked disruption and small-scale fragmentation of the forest under-storey (Pereira et al. 2002) due to the production of large clearances. This decreases canopy continuity and tree density by removal of the large emergent trees (Kakati et al. 2009). Logged forests have a lower canopy height, which indirectly alters micro-climate, humidity, increases 'edge effects' and increases the recruitment of under-storey vegetation. Clearances provide the perfect conditions for shade intolerant species to grow as they fair better from the change in climatic conditions and become dominant. Invasive species from farm and crop land also colonise such areas.

Plant species configuration changes as well with clearances, leading to compositional changes in the number of specialised and endemic species that survive. The once dominant native tree saplings are outcompeted by the invasives, preventing future re-colonisation and decreasing plant species diversity. Edge effects (the product of forest fragmentation) cause many abiotic (microclimate and light availability) and biotic effects (leaf turn over, nutrient cycling and dispersal) to both the flora and fauna of a habitat (Kunert et al. 2015). Creating edges exposes the forest to other potential threats, both natural and anthropogenic, including higher susceptibility to natural disasters, decreased food resources and an increase in hunting through enhanced visibility. The structure of upper storey vegetation has also been shown to influence recovery abilities from past disturbance, dependent upon the duration and extent of the logging undertaken (Barbeito et al. 2009). The detrimental impacts of selective logging can extend for many years, especially when considering that forest structural properties and deep canopies associated with wildlife habitats are not likely to be regained for 30–50 years post logging (Broadbent et al. 2008). Impacts of selective logging vary between countries; some showing little effect and others displaying large negative effects on vegetational structure and composition (Sodhi et al. 2010; Hall et al. 2003). Usually selective logging targets specific large tree species, causing local extinctions due to poorly planned, exhaustive timber extraction and loss of essential seed banks required for regeneration. Hall et al. (2003) found after 18 years' post-harvest in a Cameroon

forest, areas had significantly lower densities of African mahogany (target species for logging), with a very low number of seedlings. Other effects include trees not recovering to their original height from micro climate changes, decreases in soil nutrient levels, and remaining trees becoming the 'living dead'; they exist but cannot reproduce due to lack of pollination and dispersal from declines in faunal seed dispersers. However, Berry et al. (2008) found tree diversity in a Bornean forest was not significantly affected 20 years after logging. Nevertheless, high tree diversity does not necessarily equate to high conservation value. Old growth forests have less floristic diversity but contain higher abundances of range-restricted species (Slik et al. 2004), and these can be hugely important for specialised forest fauna.

2.5: Species responses to structural changes

Species vary in their response to forest degradation depending on a variety of factors, features and functional processes which the animal needs to survive (Fischer and Lindenmayer 2007). These include but are not limited to; shelter, protection, predation pressure, food resource availability, locomotor abilities, species' dispersal and reproduction abilities. Several studies on these variables have shown the effect they have on the animal's use of space (Saracco et al. 2004), with marked differences between species as they experience their habitat at different spatial and temporal scales. Previous studies (Posa and Sodhi 2006; Scales and Marsden 2008) have shown that forest endemic species are the most extinction prone in these modified tropical landscapes. Studies on the effects of clearing old growth, primary forest have identified a set of specialist forest species highly vulnerable to land-use change include plants, insects, amphibians, reptiles, birds, bats and primates (Barlow et al. 2007; Faria et al. 2007; Basset et al. 2008).

Discovering which endemic forest species can maintain viable populations in these human modified landscapes continues to pose a challenge to conservationists (Chazdon et al. 2009). Obligate forest species that are only found in large remnants of native forests (including several arboreal primate species) are intrinsically more vulnerable to extinction from forest loss than species only partly dependent on forest habitat, and their functional roles such as seed dispersal are not easily replaced (Gardner et al. 2009). Studies on an animal's use of space in regards to food resources and shelter are numerous, although research into the effect of canopy and vegetation structure on animal movement, independent of these variables has received relatively little attention.

The general consensus is that the structural complexity of the forest vegetation plays a significant role in species occurrence and movement (Arroyo-Rodríguez and Fahrig 2014), and can provide a crude proxy of biodiversity value across land use intensification gradients (Gardner et al. 2009). Usually, forest biodiversity declines along a gradient of old growth primary, secondary, plantations, arable crops and pasture (Philpott et al. 2008), reflecting the decline in floristic and structural diversity. However, the structural recovery of a forest following human modification (i.e. logging) can occur at a much faster rate than biotic recovery, therefore structural diversity does not always reflect species and functional group composition, which can take many years to increase to its original level (Liebsch et al. 2008). Knowledge of historical logging practices within an area can be of great importance when considering effects on biodiversity and evaluating forest structure, and is crucial when considering forest dependent species (Peres 1993). Forest structure has been shown to be related to changes in the composition of bird assemblages (Barlow & Peres, 2004a) and important in driving bird species distributions (Griesser & Lagerberg, 2012) and functional diversity (Hidasi-Neto et al. 2012). Vegetation structure is also an important component of habitat quality for terrestrial birds (Hinsley et al. 2008) influencing both nesting and foraging activities, as well as affecting the ease of movement for these birds both physically and behaviourally (Desrochers and Hannon, 1997).

2.6: Primate relationships, adaptations and vulnerabilities to habitat structural change

Primates have a complex relationship with their habitats, and understanding this relationship is essential for effective conservation planning (Hamard et al. 2010). The majority of tropical primate species are arboreal, and as they lack the ability to move large distances between forest patches, changes in forest structure may have a more adverse impact on their survival. Recently, forest structure has been highlighted as an important factor in driving primate species abundance. Gouveia et al. (2014) showed that vertical forest structure is a strong predictor of primate species richness due to the increasing availability of arboreal microclimates in taller, more stratified tropical forests. Palminteri et al. (2012) showed the importance of forest structural diversity in the bald faced saki *Pithecia irrorata*, which are more frequently present in uniform forest with a taller inter-connected canopy and absent from low, highly fragmented patches. Engstrom (2000) showed that Bornean orangutan *Pongo pygmaeus* densities were reduced in disturbed forests with high gap frequencies, which may be a result of an

increase in energy demands experienced in order to reach more dispersed food resources. Thus, a reduction in forest cover can potentially reduce the range and distribution of forest dwelling primates. The arboreal nature of neotropical primates decreases their ability to cross non-forest areas (Chiarello and de Melo 2001), though anecdotal evidence exists that some arboreal primates will disperse across plantations (Umapathy and Kumar 2000). These behaviours are still fairly uncommon reflecting the higher energy expenditure involved and the increased exposure to predation this form of travel conveys. Anderson et al. (2007) documented colobus monkeys *Colobus angolensis palliatus*, traveling through a diverse range of modified habitats, though height and coverage of vegetation (>6m tall and coverage of 50-79%) predicted relative use with a preference for taller, more connected areas. Variance in density of the Tana river red colobus *Piliocolobus rufofasciatus*, was explained by high basal area of food trees, density of food trees and basal area per tree for all trees (Mbora and Meikle 2004), so factors influencing the occurrence and abundance of certain tree species is also an important consideration in species presence.

Two main predictors of primate species vulnerability to habitat encroachment and destruction have been highlighted: 1. proportion of fruit in the species' diet, and 2. home range size. Primates with large home ranges who are primarily fruit eaters are thought to be the most vulnerable to the negative effects of forest degradation and fragmentation. These include; bearded saki monkeys *Chiropotes satanas chiropotes*, and southern gentle lemurs *Hapalemur meridionalis* (Boyle and Smith 2010; Schwitzer et al. 2011; Eppley et al. 2011). Factors that enable species to persist in fragmented or disturbed habitats include a small home range, a broad ranged diet and small group size (Purvis et al. 2000). Species include; howler monkeys *Alouatta spp*, mantled howler monkeys *Alouatta palliata* and white-faced capuchins *Cebus capucinus* (Bicca-Marques 2003; Estrada 1999; Panger et al. 2002). Spider monkeys *Ateles spp* with a highly frugivorous diet and large home range size are not commonly found in forest fragments (Boyle et al. 2010), whereas the increased ability of howler monkeys to live in such fragments has been attributed to flexibility and adaptability in their feeding strategies (Bicca-Marques 2003). Yet, this species was still found to be negatively affected by forest fragmentation (Arroyo-Rodríguez and Dias 2009). Brown capuchin monkeys *Cebus paella* and titi monkeys *Callicebus moloch* are capable of living in extensive areas of disturbed primary and secondary growth forest owing to having a wide dietary breadth, adapting highly conservative energy budgets and increasing the amount of foliage in their diet

relative to fruit pulp (Michalski & Peres 2005b). Although, caution should be applied when assessing species' presence in forest fragments, as this may not indicate lower sensitivity to fragmentation. Bearded sakis *Chiropotes Satanu* in Brazil showed flexibility in their behaviour in secondary forest; but lack of infants and juveniles suggested these animals did not have adequate resources to successfully breed (Boyle and Smith 2010), thus affecting long term species stability. The 'quality' of the forest area; size, shape, amount of disturbance, canopy height and food availability are also important factors to consider. These factors can impact on the sustainability of larger populations and multiple species of primates (Mbora and Meikle 2004).

2.7: Hylobatids

Asia has more critically endangered primate species than any other region (O'Brien et al. 2003) constituting ~7-20% of the total primate density and ~10-25% of primate biomass within these communities. The majority of Asian primate communities are distributed across the east and west of the region, though species are found across Japan, China and the Philippines (Reed and Bidner 2004). Asia harbours relatively few large bodied primates, and the majority fall into the 5-10kg range (Reed and Bidner 2004) and most are frugivores. Frugivorous, larger primate species need a larger home range to satisfy their ecological requirements, and reviews by Johns and Skorupa (1987) found that these species are the most sensitive to forest disturbance and show a lower survival ability in light of disturbance and forest loss. Primate species within this category include the Hylobatidae: gibbons and siamangs. These are small arboreal apes inhabiting rainforests of south-east Asia, north-west India and Bangladesh (Chivers 1984). Within Asian rainforests, there are only one or two gibbon species co-existing with other primates including similar sized leaf monkeys, macaques and on Sumatra and Borneo, the much larger orangutan (O'Brien et al. 2003).

Within the family hylobatidae, there are four genera of gibbons: *Bunopithecus* (hoolock gibbon), *Hylobates*, *Nomascus* (crested gibbons) and *Symphalangus* (siamangs), containing 16 species in total. Gibbons live in small family groups and are mostly socially monogamous, with males and females forming stable, long-term pairs (Mitani, 1990). Gibbons are highly territorial and pairs use a 'duet' which consists of a sequence of calls (Cheyne et al. 2007) usually performed in the morning. These calls not only defend their territory but also strengthen their pair bond. These 'duets' are useful as they can be used for population estimates through auditory sampling (Brockelman and Ali 1987).

The majority of gibbons are allopatric, apart from the sympatric lar gibbon and siamang in Sumatra (Cheyne 2010). To allow co-existence within this arboreal environment, each species distributes their daily activities (feeding and travelling) between different canopy layers within different time periods. Where these two species co-exist in a certain area, their highly territorial morning callings are also undertaken at different times, preventing overlap of calling activity. These differences in resource and substrate use, time allocation of ecological behaviours and modes of locomotion reduce resource competition and promote niche separation between them (Raemaekers et al. 1980; Cannon and Leighton 1994; Reed and Bidner 2004). Hylobatids are generally found at low population densities, have long generation times, a delayed onset to sexual maturity and long inter-birth intervals (Yanuar 2009). This suggests reduced abilities to respond demographically to habitat disturbances (O'Brien and Kinnaird 2011; Lee et al. 2014) and longer recovery rates following escalated habitat losses and degradation. In areas showing severe habitat disturbance and forest loss, hylobatids will be faced with locomotor challenges caused by large canopy gaps and reduced size of branch supports. This may result in increased energy expenditure from travelling longer distances and on different pathways from their preferred routes, and changes in their travel mechanisms as they are physiologically limited to the distances they can cross through brachiation (Cheyne 2011; Cheyne et al. 2013). A gibbon's range of locomotory behaviours include climbing, leaping, brachiation and bipedal walking (Cant 1992). Leaping and brachiation are the most commonly used, preferred modes of transport through the canopy (Cheyne et al. 2012). Leaping is defined as discontinuous progression where the hind limbs provide all the propulsion, and brachiation (arm swinging), defined as discontinuous progression in which the forearms are used in a suspended posture (Cant 1992). These two forms of locomotion require a more uniform canopy, and an uneven canopy or one with large canopy gaps poses a crucial problem for these primates. Gibbons select established travel routes known as arboreal highways (Chivers 1974) which minimise their chance of encountering gaps. Gibbons may have the ability to tolerate some forest disturbance from selective logging by adapting locomotor behaviour, however, there may be a limit as to how much they can adapt to. Cheyne et al (2012) found gibbons reduce brachiation and increase other modes of travel in areas of selective logging, though no gap crossing over areas >12m was observed, potentially being a constraint on the gibbon's physical abilities. In addition, Nijman (2001) found that gibbons in disturbed habitats shifted activities from the upper to the middle canopy and increased time spent

resting. This negatively impacted on other vital behaviours, with individuals showing decreased time spent singing, feeding and travelling. Cheyne et al (2012) also found an increased time spent in 'broken canopy', therefore suggesting disturbance has a significant effect on behaviour. Furthermore, Nijman (2001) recorded a lower fecundity and higher mortality of individuals in disturbed forest. Likewise, O'Brien et al. (2003) found that siamangs in recently burned habitats had reduced reproductive success compared to individuals in non-degraded habitats.

2.7.1: Hylobatids and sleeping trees

As primates spend a significant proportion of their lives in sleeping trees, selection of a suitable tree for this purpose is crucial for survival and individual fitness (Cheyne et al. 2012). Features such as height, diameter (reflecting stability) and safety influence tree choice (Lutermann et al., 2010; Phoonjampa et al., 2010). Cheyne et al (2012) found gibbons most frequently slept in Dipterocarpaceae trees, which were taller than the average tree height in the area. Tall, emergent trees are additionally used for singing at dawn (Anderson et al. 2007). Therefore, presence of a sufficient number of tall trees may be required for gibbons to thrive in an area. Furthermore, Phoonjampa et al (2010) found predator avoidance, proximity of feeding trees and neighbouring groups played a major role in the choice of sleeping sites by pileated gibbons *Hylobatides pileatus*.

2.7.2: Hylobatids and feeding

Evidently, availability of vital food resources is an important consideration within a primate's habitat, and a limiting variable of occupation (Marshall and Leighton 2006; Marshall et al. 2009). However, a study by Paciulli (2010) showed that Kloss gibbon, *Hylobates klossii*, densities did not change according to the availability of favoured food resources such as figs, suggesting absence of favoured food items does not always limit densities. This species demonstrates the ability to switch diets to less desirable, less nutritious food items during periods of food scarcity (Paciulli 2010); natural occurrences within rainforest habitats. Sumatran forests display pronounced seasonal variations of rainfall and mast fruiting events, causing temporal variation in food availability which may be dramatic and unpredictable (Kinnaird and O'Brien 2005). Therefore, it is thought natural selection should favour behavioural plasticity in primates living in these unpredictable, complex landscapes, and gibbons are known to show this level of

flexibility in their diets (Bartlett 2007). For example, lar gibbons and siamangs may switch to a more folivorous diet when fruit resources are less abundant (O'Brien et al. 2003), however, they may not be able to endure this for very long due to physiological adaptations not allowing effective digestion of tanins found in leaves, limiting their ecological plasticity.

2.7.3: *Hylobatids and vegetation structure*

Recent studies (Muzaffar et al. 2007; Cheyne 2010; Hamard et al. 2010; Paciulli 2010; Phoonjampa et al. 2011; Akers et al. 2013) have begun to examine relationships between hylobatid density and forest vegetation characteristics. As of yet, these studies have provided little insight into the exact important structural variables and habitat characteristics needed to support hylobatid populations. Gibbons prefer higher canopies (Whitten 1982) and Hamard et al. (2010) found gibbon density in Kalimantan was highly correlated to canopy cover and tree height, alongside density of large trees and the availability of food trees within an area. Pileated gibbons in Thailand depend on undisturbed forests but can persist in degraded areas (Phoonjampa et al. 2011), and the density of Bornean white-bearded gibbon *Hylobatides albibarbis* in Kalimantan is positively associated with vegetation parameters indicative of tall, relatively undisturbed forest with good canopy cover (Hamard et al. 2010). Furthermore, yellow cheeked crested gibbons *Nomascus gabriellae* in Cambodia also appear to be associated with undisturbed forest with a high canopy (Traeholt et al. 2006), but could persist in selectively logged forests. Reproduction and survivorship in siamangs is linked to the availability of strangler figs which can be used as a proxy for habitat quality (O'Brien et al., 2003). Lee et al (2014) found gibbon density and group size in Sumatra increased with forest quality, though gibbons were still present within degraded areas of forest.

2.8: *Conclusion*

Today, few truly undisturbed tropical forests exist, whereas degraded, logged, secondary and plantation forests are rapidly expanding (Gibson et al. 2011). Species that are found within primary forests are highly specialised taxa that have evolved a broad continuum of habitat requirements and life history strategies over millennia (Chazdon et al. 2009). To identify the ability of species to survive in modified, disturbed, fragmented and secondary growth habitats it is important to accurately assess the abundance and distribution of these highly specialised forest taxa in undisturbed, old growth forests,

alongside a detailed understanding of their individual habitat requirements and dispersal limitations. The survival of these primate species is dependent on the protection of these habitats (Chapman et al. 2006), and understanding the links between primate abundance and specific habitat attributes (such as vegetation structure), that are key in determining population distribution and abundance, will greatly aid in the effective conservation of resident populations (Hamard et al. 2010). This knowledge can be used to assess the necessary requirements that species need to successfully survive, and to focus harvest strategies to avoid removing certain tree species most important to primate species. Species with large home range sizes and with a high degree of frugivory, such as hylobatids, are the ideal model for investigating the impact of these vegetation changes. The following chapters discuss a field study into how forest structure differences, such as those created by disturbance, affect hylobatid densities in a lowland forest in Indonesia.

Chapter 3: Methods

3.1: Study Species

Gibbons are small-bodied apes, classified under the superfamily Homonoidea and part of the Hylobatidae family (Bartlett 2007), all which are found in Asia. There are four recognised genera of gibbons, and 16 recognised species (Bartlett 2007; Cheyne 2010). All species of gibbons are considered threatened with extinction, with four critically endangered, 11 endangered and one listed as vulnerable. This is largely due to habitat loss and habitat degradation (Geissmann 2014). Hylobatids are therefore the ideal model for understanding how primates react to different levels of habitat degradation and recovery (Phoonjampa et al. 2011). Although the majority of gibbon species are allopatric, the lar gibbon *Hylobates lar* exists sympatrically with the siamang *Symphalangus syndactylus* in a few parts of its range, one of these being the lowland forests of North Sumatra.

Lar gibbons are the most widespread of the gibbon species, with the broadest north to south distribution (Bartlett, 2007). Lar gibbons are small lesser apes, with adults weighing between 5-6kg and varying in colour from black to blonde. Their main defining characteristic is the white colouration on their hands and feet, giving them their other recognised name of the white handed gibbon (Geissmann 2014).

Siamangs, in contrast, have only two recognised sub species (*Symphalangus syndactylus* and *Symphalangus continentis*) and are less widely distributed, being restricted to Sumatra, Malay Peninsula and Thailand (Gron 2008). Siamangs are the largest living extant hylobatid species, with adults weighing between 10-12kg. Both sexes are black in colouration and have large air sacs on their throat which inflate when singing and act as sound resonators (Gittins and Raemaekers 1980).

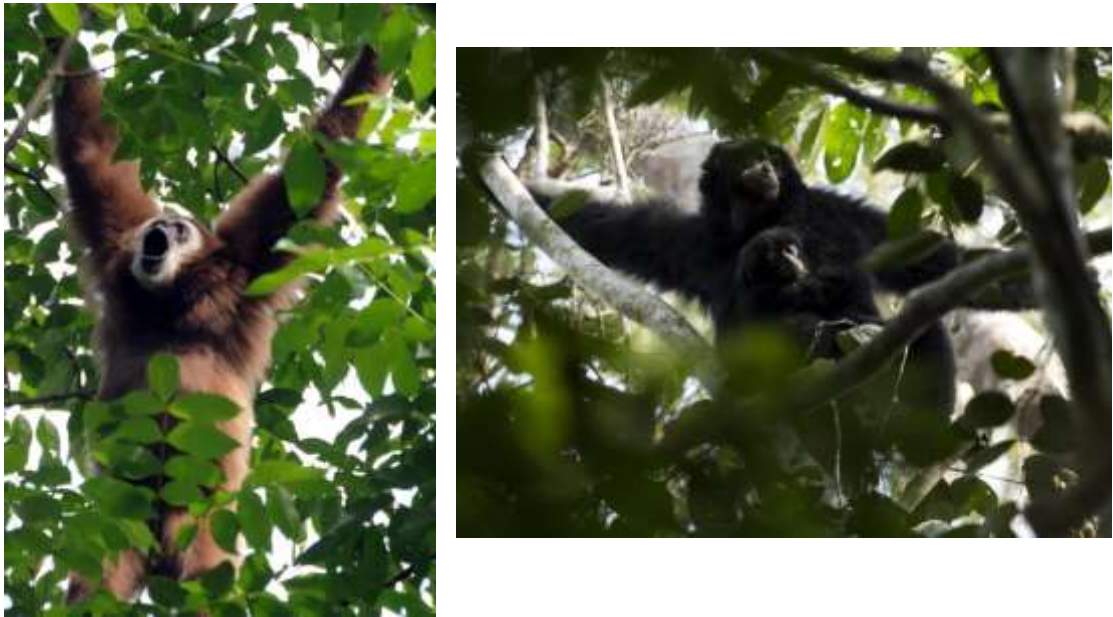


Figure 3.1. Left: Lar gibbon *Hylobates lar* vocalising, and on the right a Siamang *Symphalangus syndactylus* with an infant in Sikundur. Photo credit by A.H Korstjens and E.L. Hankinson

3.1.1: Ecology

Both the siamang and lar gibbon live sympatrically in Sumatran lowland dipterocarp forests, but are also known to inhabit hill and peat-swamp forests (Gron 2010). Lar gibbons prefer these lowland forest habitats and do not typically venture above 1200m elevation, whereas the siamang in has been known to inhabit higher elevations. Both species exploit similar feeding niches and use similar locomotive strategies; both sing and sleep in the highest emergent trees whilst using the middle and lower upper canopies to feed and travel (Gittins and Raemaekers 1980). Home range sizes vary between the species (Table 3.1), undoubtedly due to differences in diets. Siamangs are more folivorous whilst the lar gibbon utilises more widely dispersed food resources and are more frugivorous (Bartlett 2007). Due to these dietary differences, the lar gibbon travels more each day; ~1.4km with siamangs travelling <1km daily (Gittins and Raemaekers 1980; Table 3.1). Consequently, travel makes up a higher proportion of the lar gibbon's daily activity budget, whereas siamangs spend relatively more time feeding (MacKinnon and MacKinnon 1980). Within the species' home range, these gibbons fiercely defend a territory from neighbouring groups. Territory size between the

species relates to home range size, with the siamang defending a smaller territory, as shown in Table 3.1.

Table 3.1. Home range sizes, territory sizes and travel distance of the lar gibbon and siamang (Gittins and Raemaekers 1980)

Species	Daily travel (km)	Home Range Size (Ha)	Territory Size (Ha)
<i>Hylobates lar</i>	1.4	40	29
<i>Symphalangus syndactylus</i>	0.8	26	18

3.1.2: Diet

Fruit constitutes the majority of food items for both species of hylobatidae, though siamangs are more folivorous than lar gibbons and eat less fruit; 61% and 71% respectively (Bartlett 2007). Gron (2010) showed figs featured largely in the diets of both species, whilst Geissmann (2014) observed that figs made up ~50% of food for both the lar gibbon and siamang in Ketambe. While fruit is clearly a significantly important food for both species, they complement their diet with other items such as insects, flowers and young leaves (Bartlett 2007; Cheyne 2010). Fruit species from the families *Annonaceae* and *Moraceae* are also recorded as important food sources for lar gibbons (Cheyne 2010), which may also be the case for siamangs.

3.1.3: Locomotion

Lesser apes exhibit a unique set of morphological adaptations which is associated with their form of locomotion. Four different forms of locomotion have been recorded for the species; climbing, leaping, bipedal walking and brachiation. Cheyne (2013) found that brachiation was the most common form of locomotion (66%) followed by leaping (34%). Leaping seems to be used for travelling shorter distances and used to cross small canopy gaps, whilst brachiation is employed on longer travel routes. Morphological adaptations for this form of locomotion include elongated forelimbs, ridged ribcages, highly mobile wrist, shoulder and elbow joints, and an inflexible lower spine (Cheyne 2011). Hylobatid hands and feet are slender with their four fingers used as hooks to grasp tree branches, and thumbs folded down to ensure successful movement (Cheyne 2011). Brachiation (Figure 3.2) is thought to be the preferred choice of locomotion as it is energy efficient, reduces travel time, predation risk (by remaining in the canopy) and allows rapid travel across continuous canopies (Cheyne, 2011). Additionally, this specialised locomotive repertoire allows these lesser apes to access fruit and leaves on the thin

outer branches of trees, unavailable for most competitors (Greissmann 2014) creating an exclusive ecological niche for this family of primates.



Figure 3.2. Lar gibbon (*Hylobates lar*) (after a photo series in Eimerl & DeVore, 614 1969, pp. 72-73). (Geissmann 2014)

3.1.4: Vocalisations

One of the most recognisable and important behaviours of hylobatids is the production of their highly-specialised vocalisations or ‘duets’. These are produced by each monogamous pair (a single male and female) and are typically given in the mornings. Single males or females are also known to sing. Call times can differ between habitat, species and presence of others. Geissman (2014) found in Malaysia, where siamangs and lar gibbons occurred sympatrically, the siamang duets were heard ~2 hours after that of the lar gibbon groups. This possibly occurs to prevent inter-specific competition. The purpose of these morning duets serves as a dual function; territory defence and strengthening pair bonds (Bartlett 2007). The songs are loud, can last for half an hour or more and can be heard as far as 1km away (Cheyne 2010), providing an extremely useful tool for auditory sampling of the visually cryptic hylobatid family.

3.2: Study Site

3.2.1: Location, temperature, rainfall and phenology

Gunung Leuser National Park (Figure 3.3) forms part of the Tropical Rainforest Heritage of Sumatra UNESCO World Heritage Site (YOSL-OIC 2009) and is approximately 1,094,692ha in size. The park is encompassed by the larger Leuser Ecosystem and measuring 2.6MHa, is one of the largest expanses of tropical rainforest remaining in south-east Asia. Containing a range of unique habitats and a huge diversity of flora and fauna it is not surprising this area is of enormous importance for the world’s climate, and one of the last strongholds for many endemic, critically endangered species including the Sumatran tiger *Panthera tigris sumatrae*, the Sumatran rhinoceros *Dicerorhinus*

sumatrensis, and the Sumatran elephant *Elephas maximus sumatranus*. Nonetheless, despite being protected by law from any form of destructive encroachment, illegal logging and clearing is still occurring, with primary forest disappearing at a rate of 21,000 hectares per year (Laurance et al. 2012).

The study site is situated on the eastern edge of the park, located in the Langkat district of North Sumatra (04°58' - 04°59' N and 98°04' - 98°05' E). This area was first established as the Sikundur Reserve in 1938, prior to the formation of the government body 'Taman Nasional Gunung Leuser' (TNGL) in 1980 when it received full national park protection (Nowak, 2015). The 'Sikundur area' (Figure 3.3) now encompasses a monitoring post established and maintained by the Sumatran Orangutan Conservation Programme (SOCP) due to the importance of this rare habitat and the high suitability of the forest for many Asian primates, specifically the critically endangered Sumatran orangutan *Pongo abelii*. SOCP are collaborators of this project, and have been the leading source of information on behavioural, ecological and distribution data on Sumatran orangutans in the area since 2012, and full-time staff are present at the post all year round.



Figure 3.3. Gunung Leuser National Park, the larger Leuser Ecosystem and the location of the Sikundur monitoring post (Nowak 2015).

Sikundur is located approximately 30-500m above sea level, and has been described as '*a mixture of lowland dipterocarp forest with rich alluvial forests along rivers*' (Knop et al. 2004). The climate is superhumid, receiving 2000-3000mm/yr of rainfall (Laumonier, 1997). Sikundur's annual rainfall during 2014 was recorded at 3,042.8mm (Nowak 2015). The average monthly rainfall is recorded as 256.4mm (measured between August 2013-February 2015) with a range of 12.4 – 535.4mm (Figure 3.4). Highest levels of rainfall generally occur between April-May, September-October, and December (Nowak 2015). Low levels of rain are observed during the months January-

March, June-July and November. Average monthly temperatures recorded were 27.3°C, ranging from 26.1-29.2°C, with the highest recorded between February-July, and lowest between October-January (Figure 3.4).

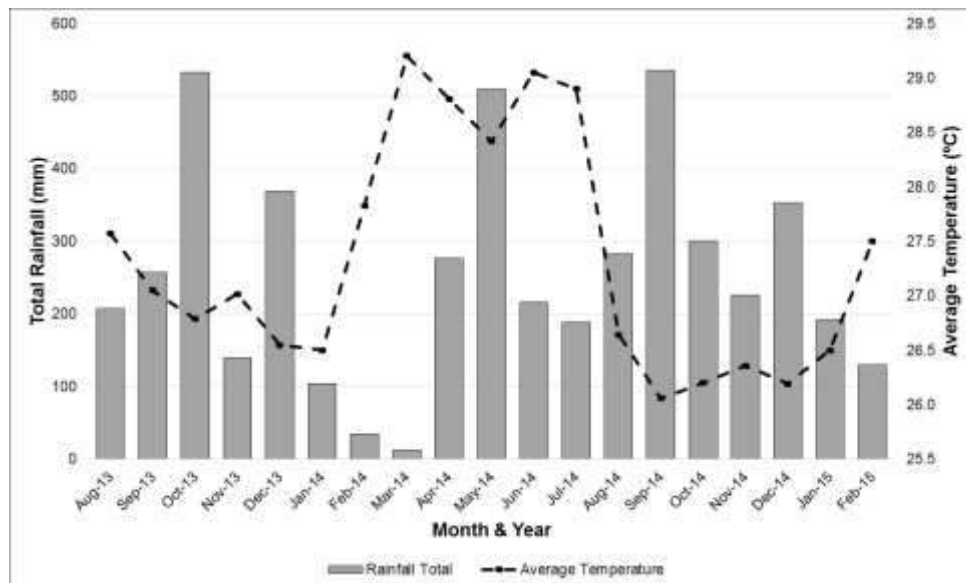


Figure 3.4. The average rainfall and temperature for the Sikundur Monitoring Post from August 2013 – February 2015 (SOCP 2014).

Phenology and fruiting within the Sikundur area shows the average percentage of trees and lianas bearing fruit between June 2013-February 2015 being 3.6% (Nowak 2015). High fruiting months were recorded during May and July-September, whereas low fruiting between December and April (Figure 3.5). The average fruiting score of 3.6% is of interest as this is similar to scores recorded for Bornean field sites (3.0-6.8%) rather than Sumatran areas (6.9%-30.57%) including Ketambe and Suaq Balimbing (Wich et al. 2011). This suggests that this is a low productivity area of Sumatra, and that Sumatra is far less homogeneous than previously thought.

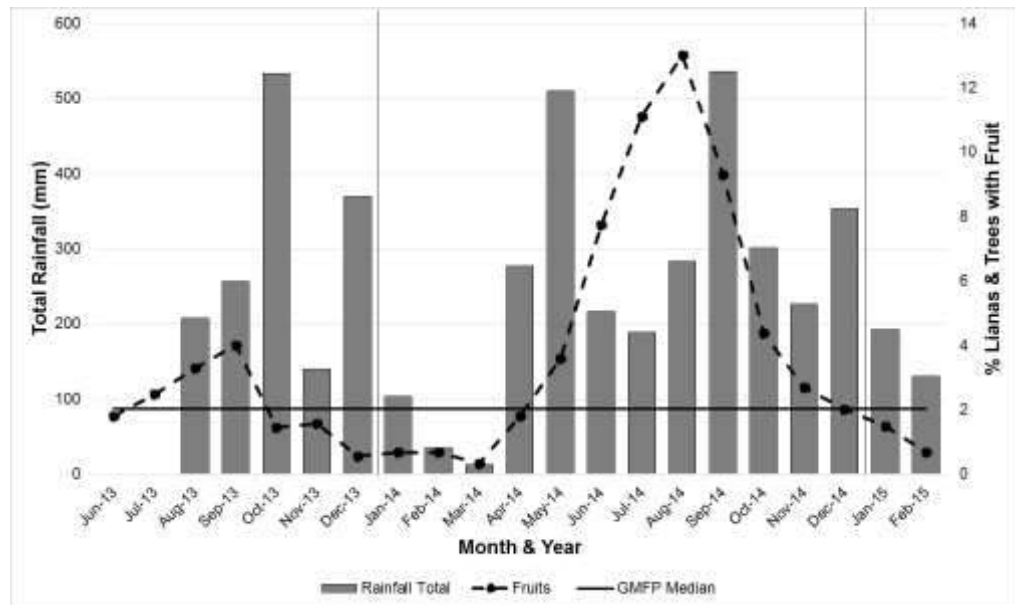


Figure 3.5. The average rainfall and percent fruit productivity for the Sikundur Monitoring Post from June 2013 – February 2015 (SOCP 2014).

3.2.2: History of Disturbance

Sikundur was subjected to both large-scale and small-scale logging commencing in the late 1960s, peaking in intensity between 1976-1988, and again intermittently in the 1990s (Nowak 2015). Currently, even with full protection, illegal logging within the area as well as complete land clearing is still occurring, in addition to other illegal activities such as resin extraction, bird trapping and fishing (SOCP 2014).

Due to these illegal activities, SOCP undertook an analysis of forest disturbance/loss throughout the Langkat district between 2013-2014 using monthly FORMA forest loss data downloaded from the Global Forest Watch website (www.globalforestwatch.org; Hammer et al. 2013; Hansen et al. 2013). Results of the analysis showed 409 forest disturbance hotspots; with 94 of these within 10km of the Sikundur monitoring post (SOCP 2014) shown below in figure 3.6.

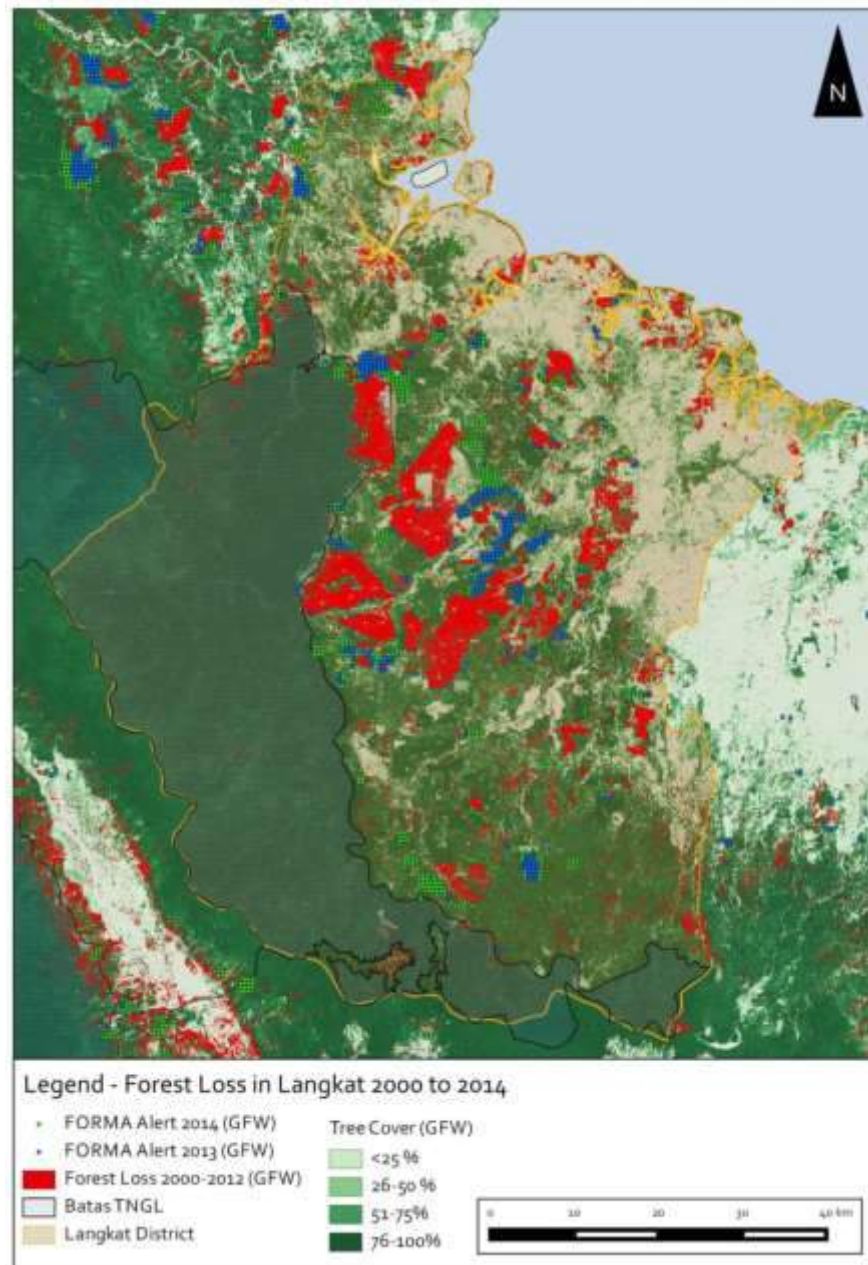


Figure 3.6. Forest loss in the Langkat District. The spatial data was collected from the Global Forest Watch website (www.globalforestwatch.org; Hammer et al. 2013; Hansen et al. 2013). The black circle shows the Sikundur monitoring post location and the study area.

This study area was chosen for several reasons: 1. Sikundur is one of the few remaining places that the lar gibbon and siamang live sympatrically; 2. Density and abundance of the species within this location are unknown; 3. Vegetation composition and structure varies hugely across the area due to differences in habitat type and disturbance levels (historical logging together with current anthropogenic activities) providing a structural gradient to evaluate these effects on hylobatid abundance; 4.

Future proposed studies across the area using unmanned aerial vehicles (UAV's) will require ground truthing of forest areas which this study will provide, supplying an invaluable data set aiding future habitat assessments, primate research and disturbance levels.

3.2.3: *Habitat characteristics*

Sumatran rainforest habitats vary dramatically, and a recent study by Laumonier et al. (2010) has demonstrated the ability of the forest's floral diversity to differ significantly in locations only a few kilometres apart. Furthermore, the plant communities and species compositions in North Sumatra differ distinctly from the rest of the island (deWilde and Duyfjes 1996). The heterogeneity found within this region can be illustrated when compared to the Ketambe area. Ketambe's tall lowland forest varies in both structure and composition from the dry lowland forests of Sikundur. Therefore, providing initial population densities for this structurally different habitat within the same national park will provide insights into Sumatran hylobatid adaptations to this dry lowland forest habitat.

The study area was divided into ten forest areas located to the south and south-west of the Sikundur research station (Figure 3.3). The forest is predominantly lowland dipterocarp, with elevations ranging from the flat alluvial plains adjacent to rivers, to the hill areas extending to an altitude of ~500m (Laumonier 1997). As well as natural structural and compositional differences between locations, levels of anthropogenic disturbance varied between locations, with almost no area surveyed being completely undisturbed. The study area consisted of four topographical forest types:

1. Alluvial forest contains flat, non-inundated areas with tree heights ranging from 20-25m and emergent trees reaching 50m. Dipterocarps are the dominant tree species, but others include *Anacardiaceae*, *Moraceae*, *Euphorbiaceae* and palms. Alluvial forest is located in close proximity to rivers, extending 2-5km inland from the river and flooding periodically. This habitat is within ~2km of the Besitang River.

2. Plains forest occurs on flat elevated area away from rivers, and is not subjected to flooding. It is characterised by 2-8% slopes ranging 5-30m in length. Large trees are present, ranging from 35-40m in height, with dense undergrowth, although herbaceous vegetation is sparse.

3. Hill forest shows steep inclinations and summits of 450-500m, with slopes ranging from 8-30%. These areas consist of a high tree species diversity and a dense, well connected canopy. Tree heights are between 35-40m, with emergent trees averaging 50m in height.

4. 'Hill-swamp' forest is hill forest habitat within high areas, showing the same characteristics as described above (summits of 450-500m). However, these hill areas are intersected with various areas and valleys consisting of 'swamp habitat': wet areas comprising of a high density of small diameter trees with extensive root systems, and a dense undergrowth of rattans and climbers.

Disturbance within these habitats varies historically. Alluvial habitat has been frequently disturbed by humans due to its close location to the rivers corresponding to the ease of transporting forest goods out. The plains have been logged extensively due to ease of access (flat ground, easy to enter forest) from an abundance of road networks, and many of these areas have been converted to palm oil and rubber plantations. The hills areas were relatively spared from logging until the 1980s due to difficult terrain (Laumonier 1997) however, some low hill areas are now completely destroyed and occupied by local villages, and therefore have become highly influenced by human activities. Despite this, the Siknudur region has become one of the few remaining areas of lowland forest that still maintains suitable forest habitat for several species of arboreal primates. In addition to the residing gibbon populations, five other primate species inhabit the region: long tailed macaque *Macaca fascicularis*, pig tailed macaque *Macaca nemestrina*, thomas leaf monkey *Presbytis thomasi*, slow loris *Nycticebus coucang* and the Sumatran orangutan *Pongo abelii*.

3.3: Data collection

Fieldwork was undertaken from 1st March 2016 to 1st August 2016. Vegetation data and hylobatid density surveys were undertaken in ten sample locations (Figure 3.7) during the five-month study. The location of the sample areas were chosen to cover the largest possible area consisting of a range of forest types and disturbance levels.

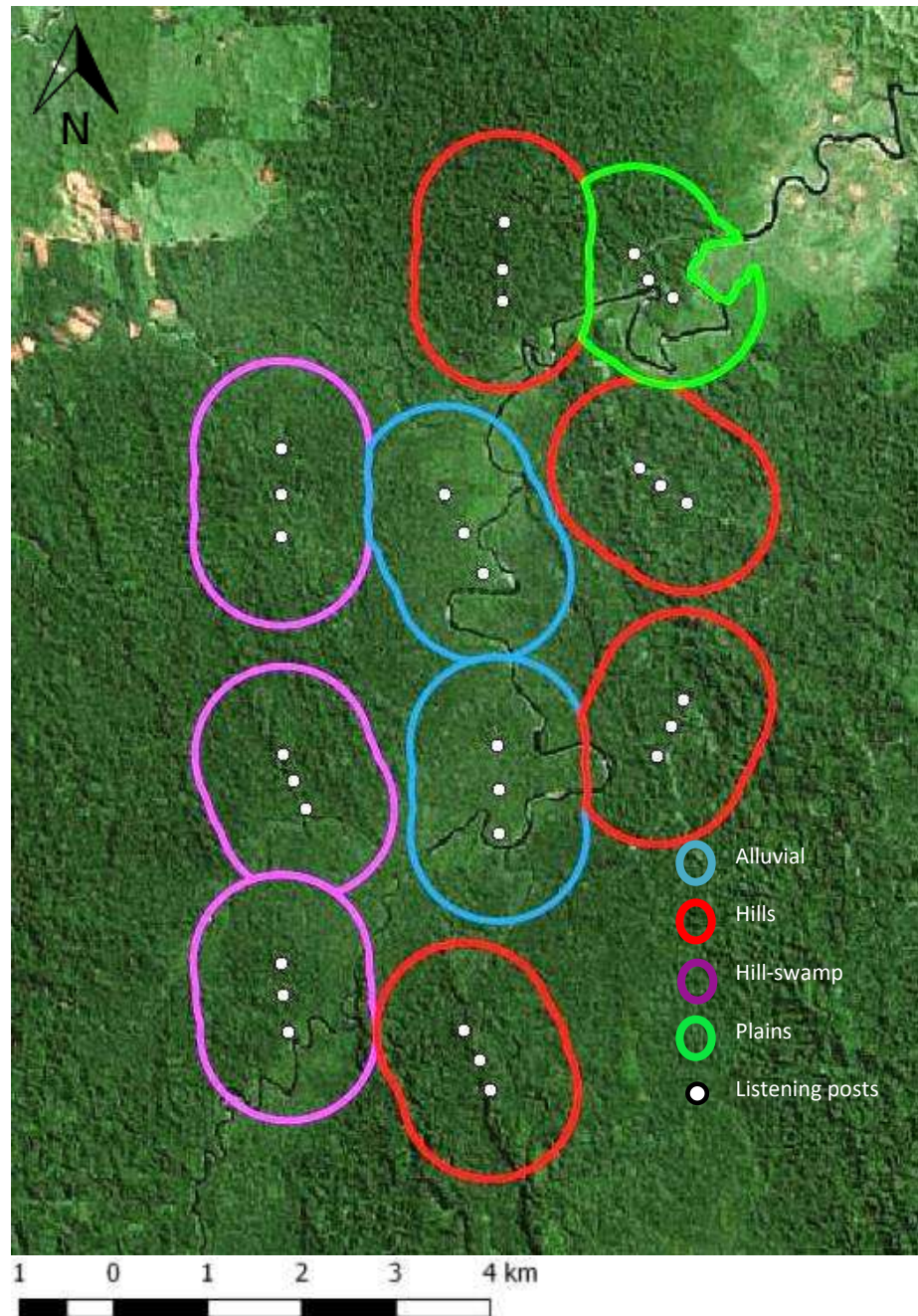


Figure 3.7. Study area. Coloured circles show habitat types and sample area locations. Bersitang village is located north-east of plains forest, and the Bersitang River runs north to south through the study area.

3.3.1 Forest structural analysis

To ascertain vertical and structural complexity, randomly placed 25x25m plots (minimum of 4 and maximum of 10) were sampled within each forest location around the listening posts and conducted within the same time frame as the primate auditory sampling, representing a sample of the habitat (Table 4.1). Ten plots were undertaken in the plains habitat due to extra surveys being conducted within this habitat not relating to this study. However, data from all ten plots was used within this study as it provided a more sufficient representation of the forest habitat. Within each plot the following measurements were recorded for any tree with a diameter at breast height (DBH) $\geq 10\text{cm}$ (Table 3.2).

Table 3.2. Vegetation variables measured within each other the vegetation plots undertaken

Variable	Units	Methodology
Diameter at Breast Height	m	Diameter of trunk at approximately 1.3m
Basal Area	cm^2	$BA = \pi \left(\frac{DBH}{2} \right)^2$
Tree height	m	Distance from base of trunk to top of crown.
Bole height	m	Distance from base of trunk to first major bough.
Height-DBH ratio	-	Tree height divided by DBH indicating tree age and growth patterns.
Crown area	m^2	$A = \pi \left(\frac{N - S \text{ width}}{2} \right) \times \left(\frac{E - W \text{ width}}{2} \right)$
Crown connectivity	%	Visual estimate of connectivity of crown in relation to neighbouring crowns by the same observer throughout the surveys.
Number of branches	-	Number estimated in five categories; 0-2cm, 2-4cm, 4-10cm, 10-20cm >20cm. Conducted by the same observer throughout the surveys.
Total number of trees per plot	-	Number of trees with DBH $\geq 10\text{cm}$ occupying plot
Tree Density	Per hectare	Total number x 16

3.3.2: Group density estimates of hylobatids

The most common survey methods used to assess distribution and abundance of primate species are strip census and line transects (Buckland et al. 2010; Nijman and Menken 2005). These methods rely on observer ability to visually detect groups of primates both sides of the survey transect. Although highly efficient for density estimates on a range of primate species, these methods have been shown to be unreliable for unhabituated hylobatid species. Hylobatid preference for high canopy and inconspicuous

behaviour decreases visible detection, in addition to their unpredictable behaviour on detecting humans: fleeing, mob calling and hiding (Brockelman and Srikosamatara 1993 and Dacier et al. 2011). These factors can lead to an under-estimation of density, and line transect surveys conducted in the Sikundur trail system between February and July 2015 yielded almost no primate sightings (Consiglio 2015). Fixed point count surveys 'map' gibbon species using long calls and are considered preferable and more efficient (Lee et al. 2014). Their loud audible morning vocalisations provide efficient mapping of triangulated points (Cheyne et al. 2016). Additionally, fixed point counts allow for quick, time-efficient surveys and more reliable results, already proving efficient in numerous primate studies (Cheyne et al. 2008; Hamard et al. 2010). Consequently, it has become common practice amongst hylobatid researchers to use auditory sampling methods to estimate gibbon densities which additionally provides comparative hylobatid density data across a range of different sites. Preliminary surveys conducted using this method yielded more accurate data than line transects at the study site in 2015 (Consiglio 2015).

3.3.2.1: Auditory sampling

A total of ten sample locations were surveyed over the 5-month period. To achieve the most reliable density estimations, a preliminary survey was undertaken to train surveyors in recording techniques. The same surveyors were used in all sample areas to increase consistency in bearing and distance estimation and to limit bias between sample areas. Each sampling area consisted of a 3 by 1 linear array of listening posts spaced ~500m apart (Figure 3.7). A linear array design was chosen over the traditional equilateral triangle used by most studies as recent studies by Kidney (2013; 2016) showed linear arrays yielded a lower variance and reduced bias than non-linear arrays of the same size. In the present study, listening post positions were adjusted up to 100m between forest locations to avoid difficult terrain, impassable vegetation and deep valleys, where vocalisations could be missed or direction misinterpreted due to summits. It has been argued that this is more important than ensuring the distance between each listening post is uniform (Phoonjampa et al. 2011). Furthermore, all array locations were situated at the highest point possible to maximise hearing distance and avoid 'missing' any singing groups. This resulted in some variation in the sampling area (range: 3.5km² – 5.12km²). Observers were placed at each post between the hours of 4:30h and 10:00h; the optimum time of day for singing. On each survey occasion,

observers recorded start and end time of song, compass bearing and estimated distance to each hylobatid group heard duetting.

A gibbon duet is comprised of the female's great call and the male's answering call (Cheyne et al. 2007). All lone male calls were omitted as these did not represent a mated pair or family group inhabiting an exclusive home range (Cheyne 2008). Gibbons do not call every day, despite favourable weather conditions, and calling frequencies are density dependent; groups call less at lower densities (Cheyne et al. 2007). Each sampling area was surveyed for four consecutive days as prior studies found calling stabilised after four days (O'Brien et al. 2004; Lee et al. 2014). Rainy mornings were excluded as rain has been found to negatively influence singing behaviour (Brockelman & Srikosamatara 1993; Cheyne 2008; Lee et al. 2014; Cheyne et al. 2016). Nine of the ten sites were surveyed for four days, and only one site surveyed for three days due to weather conditions.

3.3.2.2: Group mapping

To ascertain the location of primate groups through triangulation, groups were identified at the intersection of compass bearings, which originated from different listening posts and had a matching time stamp (Phoonjampa et al. 2011). Following each survey day, a map was created based on all groups heard from each listening post (Figure 3.8). However, estimating distance is difficult in rainforest habitats and even a small bearing error can prevent the intersection of lines from two points recording the same group. Therefore, groups were distinguished not only through bearing and distance, but time and length of each singing bout. This allowed correct identification of groups heard over the four-day period and ensures any groups singing twice in one day were not recorded as a separate group. Previous research has suggested 500m is the approximate width of any given gibbon territory (O'Brien et al. 2004; Buckley et al. 2006; Phoonjampa et al. 2011; Cheyne et al. 2014). Consequently, any groups calling more than 500m away were considered to be separate groups. Any groups heard $\geq 500\text{m}$ away was considered to represent separate groups if heard simultaneously. Additionally, any groups heard from only one listening point but which were located $>500\text{m}$ from any other identified group on the same day were included in the analysis (Rawson 2010).

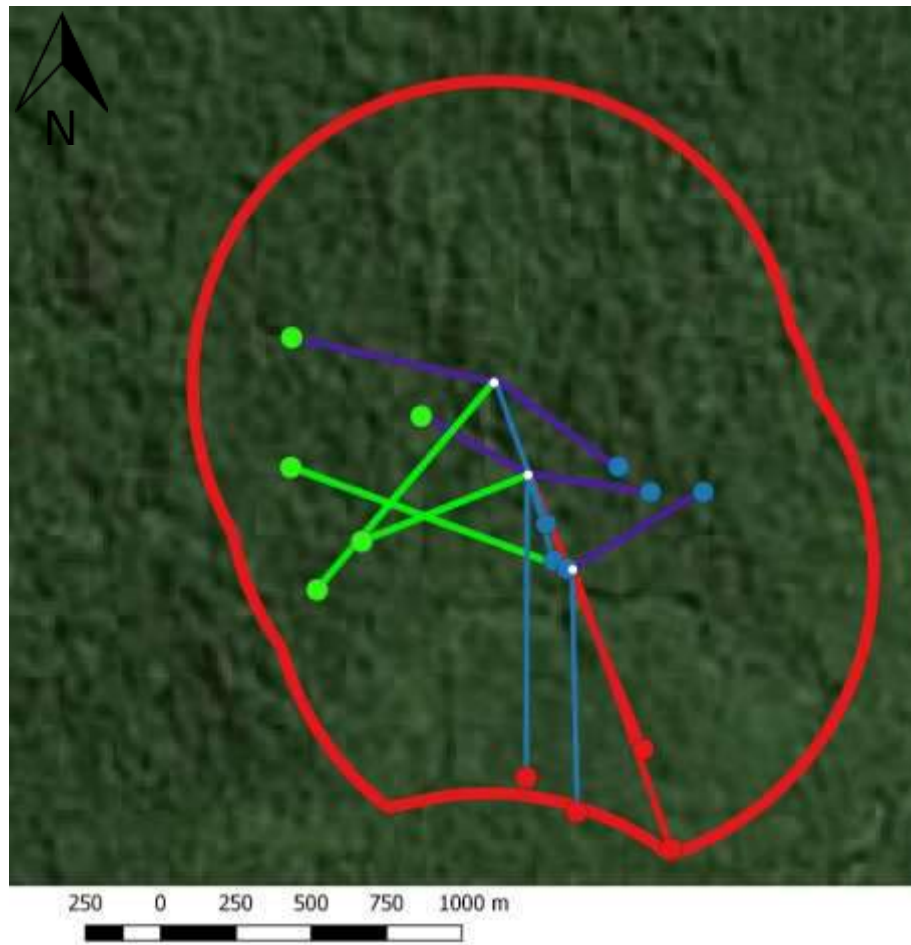


Figure 3.8. Example of array mapping in QGIS. Different coloured dots signify separate gibbon groups and different coloured lines signify separate survey days.

3.3.2.3: *Effective listening area (E)*

The effective listening area (E) is the maximum area that gibbon vocalisations can be heard from a listening post. As a general rule of thumb, gibbon calls can usually be heard at a maximum distance of 1.5km (Rawson 2011), though this can vary greatly due to habitat terrain. Specific maximum hearing distance for each individual location can be estimated using field data from each survey undertaken. However, this was not possible due to time limitations. Hence a fixed radius of 1km was defined around each listening post, omitting overlapping areas to avoid incorrect estimation of the sampling area (Figure 3.8). This 1km 'effective listening area' is used by established gibbon researchers (Cheyne et al. 2016; Hamard et al. 2010) therefore is assumed to be reliable. Areas without forest cover (i.e farmland) were removed from the effective listening area. All listening areas were calculated using the program QGIS (v.2.16.3).

3.4: Data Analysis

Two density estimation methods were used to assess hylobatid density. 1. Triangulation; a standard method known throughout the research community and used in a large range of countries developed by Brockelman and Ali (1987), and 2. gibbonSECR, a Spatial Explicit Capture mark-Recapture method in R Studio, developed by Kidney et al. (2013). The total survey area was 46.65km² across four different forest types over a total of 39 days.

3.4.1: Standard Triangulation

Density estimates were obtained using the following formula developed by Brockelman and Ali (1987):

$$D = n/[p(m) \times E] \quad (1)$$

where n = number of groups heard in an area determined from mapping, $p(m)$ = estimated proportion of groups expected to sing during a sample period of m days, and E = effective listening area.

The correction factor $p(m)$ was determined at each survey area using the following formula;

$$P(m) = 1-[1-p(1)]^m \quad (2)$$

Where $P(1)$ = singing probability for any given day and m = number of survey days. This was calculated in Excel (Microsoft office professional 2013), using the package for calculating gibbon population density from auditory surveys developed by Rawson (2011).

3.4.2: SECR

The second method used to estimate gibbon density was calculated using Spatially Explicit Capture mark-Recapture models (SECR) using the software package 'gibbonsSECR' with the programme R studio (version 3.1.1) and developed by Kidney et al. (2013). Prior to analysis, calling probabilities were calculated for each survey area using the formula above in triangulation. Once number of groups had been determined through mapping, each separate group was assigned an occasion number and input into the model. The buffer radius (m) was selected based on the Akaike Information Criterion (AIC). A half normal detection function was applied to the analysis as this assumes the

probability of detection has a half normal distribution (commencing at 1, and exponentially decreasing as distance from the listening post increases).

3.5: Statistical Analysis

3.5.1: Forest structural analysis

All continuous vegetation variables were tested for normality through both Shapiro-Wilkinson and Kolmogorov-Smirnov tests. As all variables were non-normally distributed a log10 transformation was performed in an attempt to achieve normality. Following transformation, vegetation variables were still non-normal and therefore to compare structural differences between the four land units, nonparametric Kruskal-Wallis tests were performed, followed by pairwise Mann-Whitney *U* post-hoc tests (Fowler et al. 1998). Critical values for post hoc tests were obtained through sequential Bonferroni correction. Following the above tests, non-parametric Spearman's rho correlations were performed on all vegetation variables to identify any collinearity between the variables.

3.5.2: Hylobatid Density Analysis

Parametric tests were used to compare hylobatid density estimates between all ten survey locations, to test for differences in densities between species and to test for differences between densities for both density estimation methods using independent sample T-tests. A Spearman's rho correlation and a least squares linear regression was performed to evaluate any relationships between the densities of the two species.

3.5.3: Relationships between hylobatid densities and forest structure

Pearson's rho correlations were undertaken on all structural variables. To ascertain the strength of the relationship, *r* values were categorised into; moderate relationship ($r = 0 - 3$), strong relationship ($r = 4 - 6$) highly strong relationship ($r = \geq 7$).

Following Pearson's rho correlations, a multiple regression analysis was undertaken to identify relationships between hylobatid density and forest structure. Any variables which were significantly correlated with other vegetation variables were omitted from the regression as this can cause the model to over-parameterize. These included: DBH, basal area, height-DBH ratio, and total number of trees per plot. Additionally, branch counts were not included in the analysis, as many categories were

highly correlated to DBH or with other variables (i.e tree number and tree density) ultimately producing the same relationships twice. Furthermore, branch counts were not regarded to be highly influential variables relating to hylobatid densities. Tree height and canopy connectivity are important forest structural variables previously correlated to gibbon density (Hamard et al, 2010; Lee et al. 2014). Therefore, to establish if there are stronger relationships between hylobatid densities and if a tolerance level of tree height and canopy connectivity can be identified for both species, these variables were further categorised into the following: Tree heights less than 20m (<20m), tree heights between 20-30m (<20m >30m and tree heights above 30m (>30m). Connectivity was classified into the following categories: Connectivity less than 15% (<15%), connectivity less than 25% (<25%), connectivity between 25-50% (>25% <50%), connectivity between 50-75% (>50% <75%) and connectivity over 75% (>75%). All tests were carried out using SPSS v.23, and a significance level of $P < 0.05$ was applied. Following categorisation, backwards stepwise multiple regression analysis was undertaken on the height categories and connectivity categories, to ascertain which influenced gibbon density most strongly.

Chapter 4: Results

4.1: Forest structural analysis

Ten forest areas were surveyed for both hylobatid density and forest structure giving a total survey area of 46.25km² over a sampling period of 39 days. Four distinct habitat types were recognised, 49 vegetation plots sampled and a total of 1418 individual trees measured. A minimum of four vegetation plots were undertaken in each area with a maximum of ten in array 1 (Table 4.1).

Table 4.1. Summary showing number of vegetation plots, vocal arrays and individual trees measured during the study.

<i>Array Number</i>	<i>Number of days per array</i>	<i>Habitat Type</i>	<i>Number of vegetation plots</i>	<i>Number of trees measured per array</i>
1	4	Plains	10	234
2	4	Hills	6	168
3	4	Hills	4	104
4	4	Hills	4	183
5	3	Alluvial	4	131
6	4	Alluvial	4	118
7	4	Hill-swamp	5	149
8	4	Hills	4	132
9	4	Hill-swamp	4	106
10	4	Hill-swamp	4	93
Total	39	4	49	1418

4.1.1: Normality tests

None of the continuous vegetation variables showed a normal distribution (even after a log₁₀ transformation) based on Shapiro-Wilkinson and Kolmogorov-Smirnov normality tests. Therefore, non-parametric tests were used to explore differences in forest structural variables between the four identified land units across the ten surveyed forest areas.

4.1.2: Structural Differences Between land units

Kruskal-wallis non-parametric tests showed the land units differed significantly from each-other for all continuous vegetation variables (Table 4.2). Therefore, further pairwise Mann-Whitney *U* post hoc tests were performed to compare land unit types (using a sequential Bonferroni correction for multiple tests, α' is set to 0.0083; Table 4.2). Tree heights differ significantly between all land units apart from plains and hill-swamp (Figure 4.2). The hills habitat contained the tallest trees (median = 18.0m) whilst alluvial

forest possessed the shortest trees on average (median = 13.0m). Height to first major bole shows a similar pattern as the top height of trees with the hill forest containing the greatest bole height (median = 12.0m), alluvial the smallest (median = 8.0m), and plains and hill-swamp forest with heights in between these extremes (median=9.9m and 10.0m respectively; Table 4.1, Figure 4.2). There is a significant difference in stem diameter (DBH) of trees between all land units except within the plains and hills forest (Table 4.2; Figure 4.3). Crown areas (m^2) of individual trees are comparable between the plains and hill-swamp forest, and were significantly larger in the hill forest (median = $84.4m^2$). The smallest crown areas were located in the hill-swamp forest (median = $58.9m^2$; Figure 4.4). Tree connectivity significantly differed between all habitat types except plains and alluvial forests and hills and hill-swamp forest (Figure 4.5; Table 4.2). The highest percentage of canopy connectivity between individual trees was seen in the hill-swamp forest (median=30%, Table 4.1), whilst the lowest connectivity was recorded in the alluvial habitat type (median = 20%, Figure 4.5).

Table 4.2. Kruskal-Wallis non-parametric tests conducted on all continuous vegetation variables. Significant P-values are highlighted in bold.

	<i>Plains Forest</i>			<i>Alluvial Forest</i>			<i>Hills Forest</i>			<i>Hill-swamp Forest</i>			<i>Kruskal- Wallis</i>	
	<i>N</i>	<i>Median</i>	<i>Mean</i>	<i>N</i>	<i>Median</i>	<i>Mean</i>	<i>N</i>	<i>Median</i>	<i>Mean</i>	<i>N</i>	<i>Median</i>	<i>Mean</i>	<i>χ²</i>	<i>P</i>
<i>Top Height (m)</i>	234	16.8	18.04	249	13	14.88	455	18	20.07	480	16	17.66	95.59	<0.001
<i>Height to first bole (m)</i>	234	9.95	11.25	249	8	8.95	455	12	13.67	480	10	11.07	108.43	<0.001
<i>DBH (cm)</i>	234	21	52.92	249	17.80	22.89	455	21	27.40	480	18.2	23.76	25.63	<0.001
<i>Crown Area (m²)</i>	234	63.95	84.84	249	62.80	95.10	455	84.40	170.51	480	58.90	82.40	30.83	<0.001
<i>Connectivity</i>	234	20	25.15	249	20	21.55	455	25	32.84	480	30	31.01	53.74	<0.001
<i>Branches over 20cm</i>	234	0	0.16	249	0	0.42	455	0	0.26	480	0	0.08	30.16	<0.001
<i>Branches 10-20cm</i>	234	0	0.76	249	0	1.45	455	0	0.85	480	0	0.36	34.01	<0.001
<i>Branches 4-10cm</i>	234	3.00	6.52	249	14.00	21.03	455	2.00	5.72	480	1.00	4.89	153.55	<0.001
<i>Branches 2-4cm</i>	234	27	44.82	249	65.00	97.03	455	20.00	32.39	480	20.00	34.52	194.63	<0.001
<i>Branches 0-2cm</i>	234	200.00	271.18	249	300.00	455.24	455	100.00	182.71	480	200.00	289.38	155.44	<0.001

Table 4.3. Pair-wise comparison of the land units for all continuous vegetation variables. Significant P-values following sequential Bonferroni correction are highlighted in bold.

	<i>Plains vs Hills</i>		<i>Plains vs Alluvial</i>		<i>Plains vs Hill-Swamp</i>		<i>Hills vs Alluvial</i>		<i>Hills vs Hill-Swamp</i>		<i>Alluvial vs Hill-Swamp</i>	
	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>
<i>Top Height (m)</i>	45853.5	0.003	19489.5	< 0.001	51546	0.074	32656.5	< 0.001	87156.5	< 0.001	45445.5	< 0.001
<i>Height to first bole (m)</i>	41591	<0.001	21455	<0.0001	54898.5	0.626	30924	< 0.001	83379	< 0.001	45820.5	< 0.001
<i>DBH (cm)</i>	51747.5	0.548	23570	< 0.001	46256.5	< 0.001	48028	< 0.001	94906.5	< 0.001	58363.5	0.604
<i>Crown Area (m²)</i>	44439.5	<0.001	28987	0.924	53981	0.400	47134.5	< 0.001	88053.5	< 0.001	57838	0.476
<i>Connectivity</i>	41970	< 0.001	26888.5	0.138	48095.5	0.002	39399.5	< 0.001	10232.5	0.093	46184	< 0.001
<i>Branches over 20cm</i>	53235	1.000	29016	0.332	56160	1.000	56420	0.176	10920	1.000	59056	0.172
<i>Branches 10-20cm</i>	52994.5	0.509	28672	0.117	55932	0.542	56006	0.201	10915	0.939	59056	0.172
<i>Branches 4-10cm</i>	52873.5	0.829	18377	< 0.001	54747.5	0.407	35485	< 0.001	10721	0.464	36401	< 0.001
<i>Branches 2-4cm</i>	42862.5	< 0.001	18284	< 0.001	47160.5	< 0.001	26428.5	< 0.001	10657	0.482	30519	< 0.001
<i>Branches 0-2cm</i>	33153	< 0.001	25032.5	0.002	50343.5	0.015	29819.5	< 0.001	80433	< 0.001	46343	< 0.001

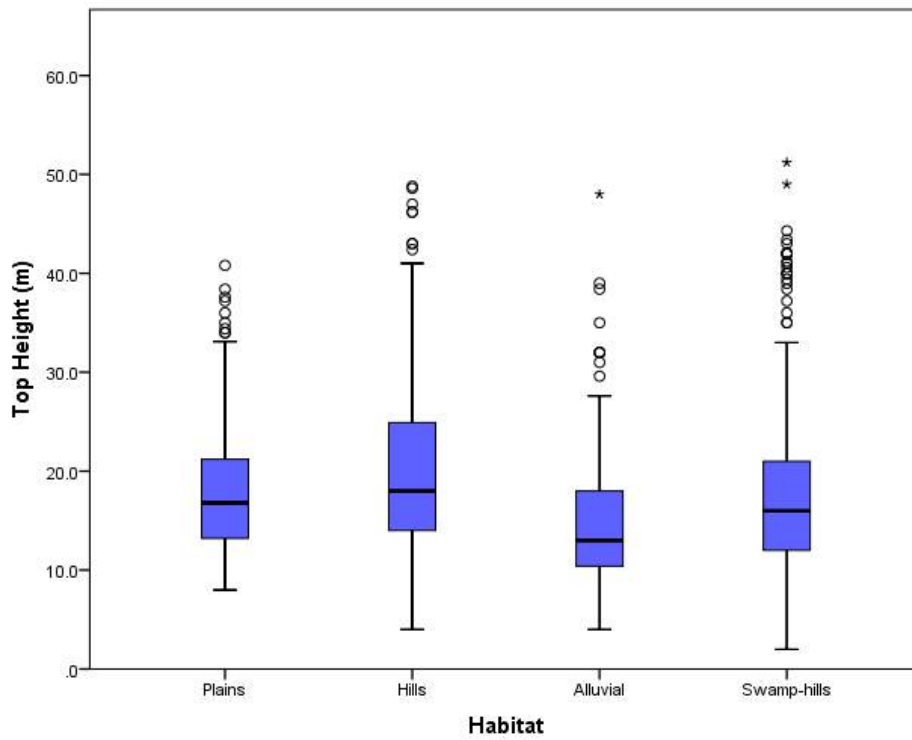


Figure 4.1. Top Height of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

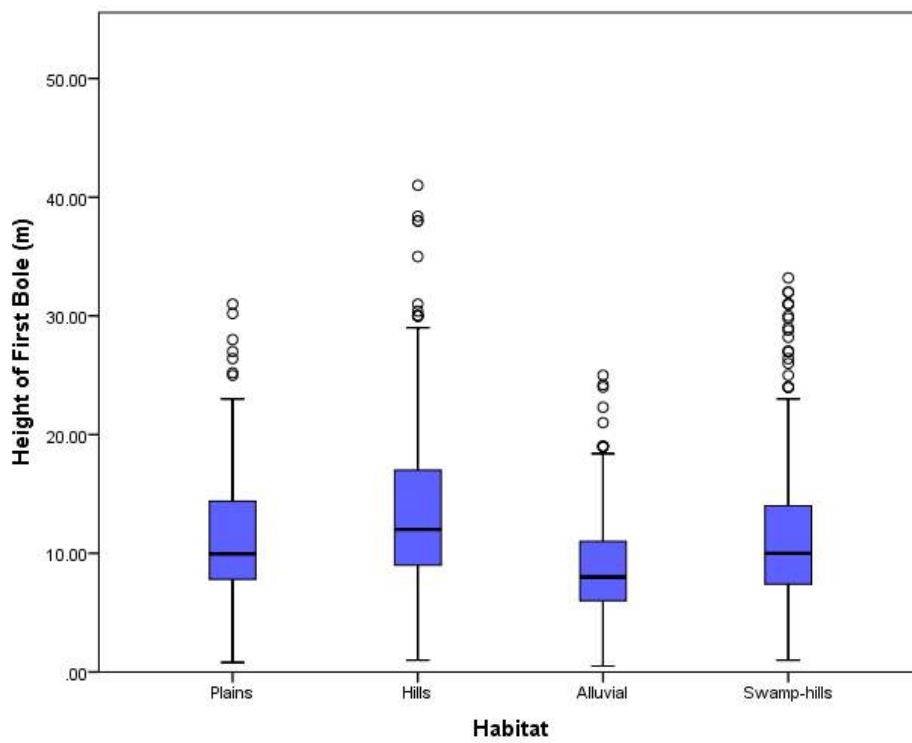


Figure 4.2. Height of first bole of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

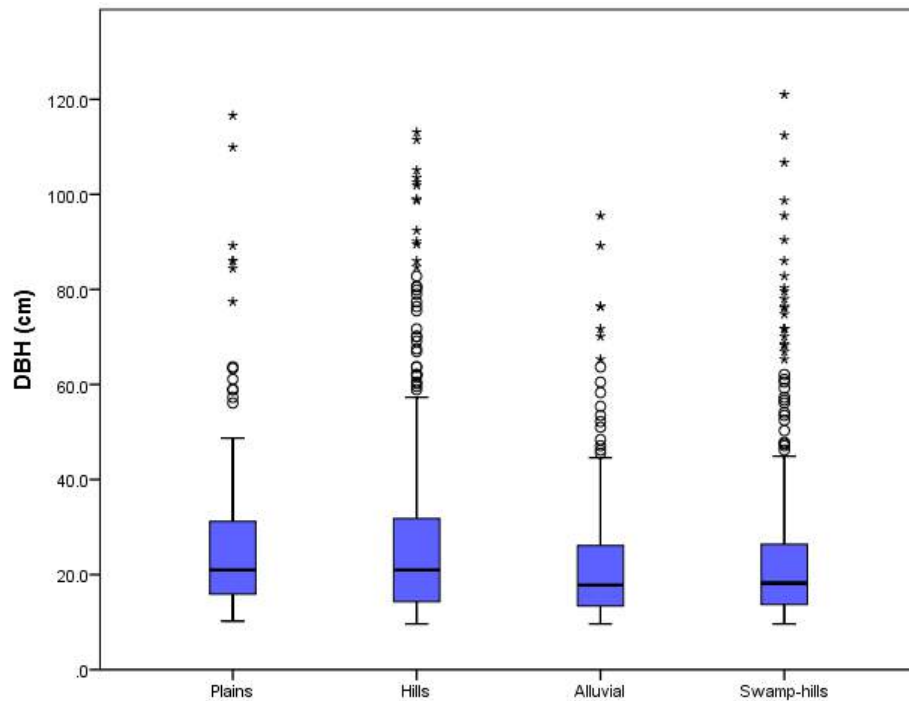


Figure 4.3. DBH of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

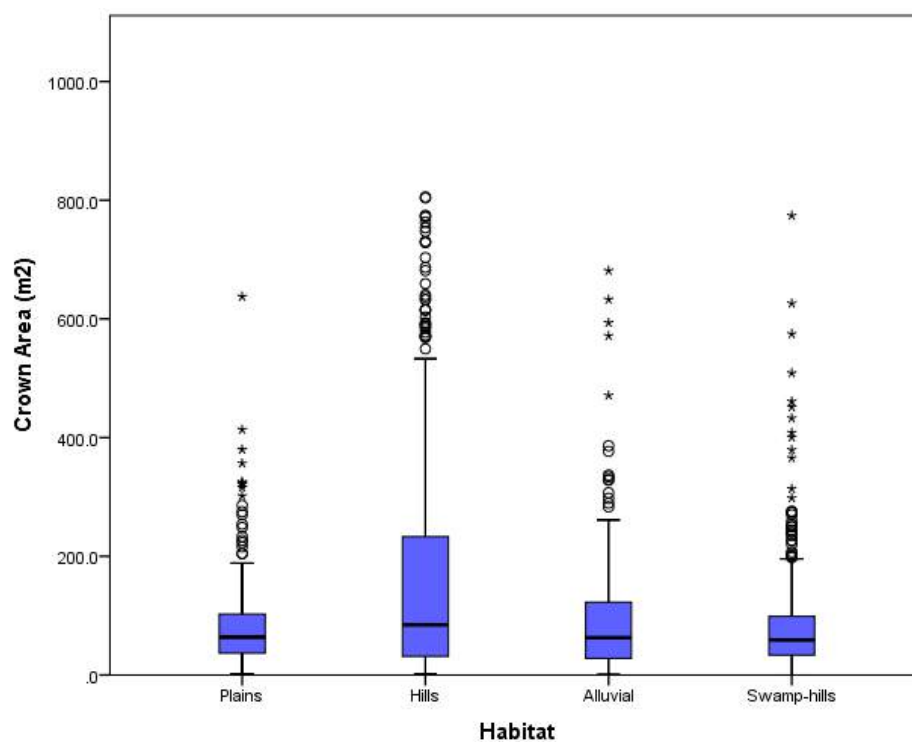


Figure 4.4. Crown Area of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

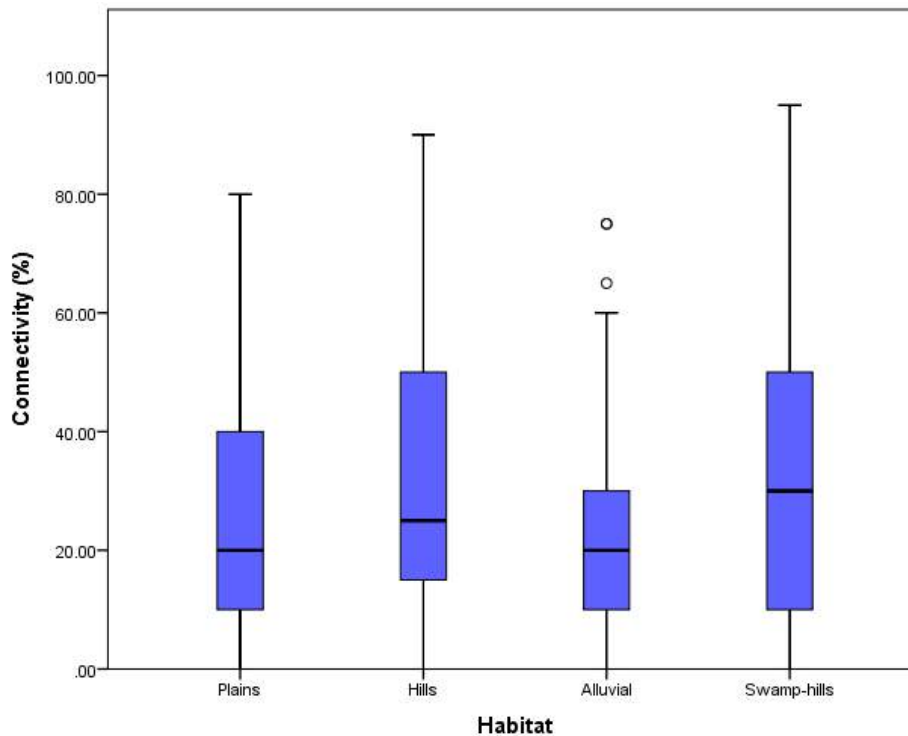


Figure 4.5. Connectivity of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

The number of larger branches over 20cm and between 10-20cm in diameter were not significantly different between habitat types. The number of smaller branches (0-2cm diameter and 2-4cm) showed more variation between land units (Table 4.2).

There was a significant difference in the density of trees >10cm DBH (ha) between the land units (Kruskal Wallis test: $X^2_{(4)} = 10.491$, $p = 0.015$) due to a significant difference between the plains and alluvial forest (Table 4.3). The smallest density of trees was found in the plains forest (median=360trees/hectare), whilst the hill and alluvial forest contained the highest density of trees DBH (median=496, 496trees/hectare, respectively).

Table 4.4. Summary of pairwise Mann-Whitney U post hoc tests on tree density between the different land units. Significant P-values following sequential Bonferroni correction are highlighted in bold and underlined.

	<i>Plains vs Hills</i> <i>N = 28</i>	<i>Plains vs Alluvial</i> <i>N = 18</i>	<i>vs Hills vs Alluvial</i> <i>N = 23</i>	<i>Hills vs Swamp</i> <i>N = 26</i>	<i>vs Hills vs Hill-Swamp</i> <i>N = 31</i>	<i>Alluvial vs Swamp</i> <i>N = 21</i>
<i>Tree Density (ha)</i>	U = 36.5 P = 0.01	<u>U = 10.5</u> <u>P = 0.006</u>	U = 42.0 P = 0.152	U = 67.5 P = 0.802	U = 84.0 P = 0.185	U = 22.0 P = 0.02

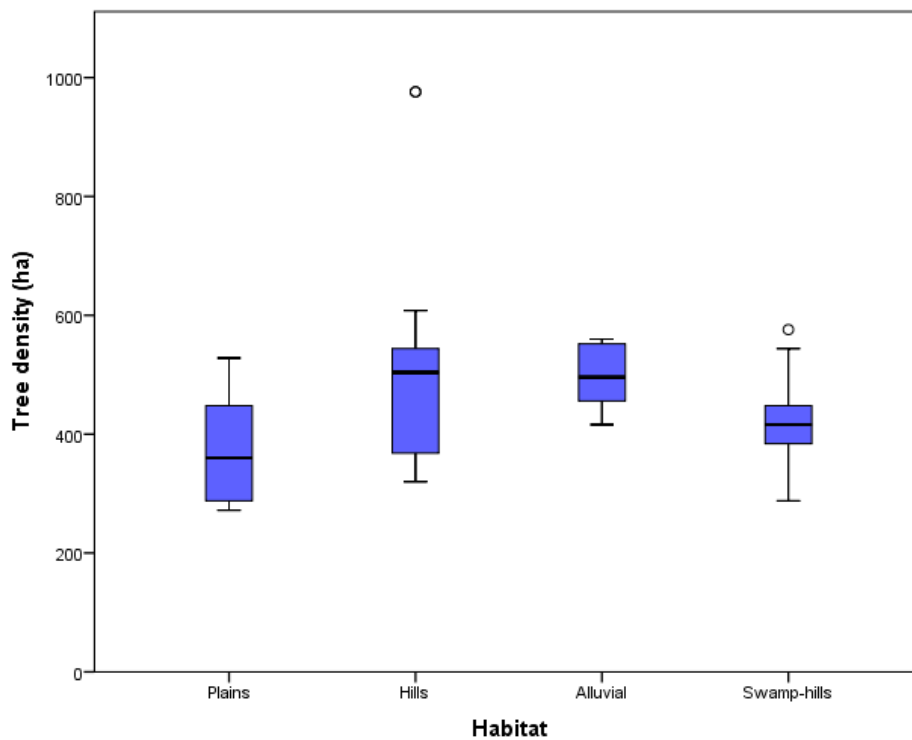


Figure 4.6. Density of trees (>10cm DBH) in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

4.1.3: Correlations between vegetation variables

All vegetation variables correlated significantly with each other within the entire dataset, however many relationships represented weak correlations (Spearman's Rho correlations; Table 4.4). Correlations were ranked on the strength of the relationship, as all variables showed significance. Moderate correlations if $r = 0 - 3$, strong correlations if $r = 4-6$, and very strong correlations if $r = \geq 7$. The strongest positive correlation was found between tree height and height to first bole ($r = 0.790$, $p < 0.001$; Table 4.4; Figure 4.7). Tree diameter was strongly positively correlated with numerous variables (Table

4.4); including height ($r = 0.757$, $p < 0.001$; Figure 4.8), height to first major bole ($r = 0.591$, $p < 0.001$; Figure 4.9), and crown area ($r = 0.606$, $p < 0.001$; Figure 4.10). Crown area was strongly positively correlated to both top height and height to first bole, as well as tree diameter (Table 4.4).

Canopy connectivity of individual trees showed no strong correlations to any of the other tree variables (Table 4.4). Number of branches of all size categories were strongly positively correlated to each other (table 4.4) and to tree diameter. Additionally, the two largest branch sizes were strongly correlated to crown area.

Table 4.5. Summary of Spearman's Rho Correlations on all continuous vegetation variables showing significance in all variables between the different land units. Correlations between variables showing, bold highlighted signify moderate correlations, * signifies strong correlations and **signifies very strong correlations.

	<i>DBH (cm)</i> <i>N = 1418</i>	<i>Top Height (m)</i> <i>N = 1418</i>	<i>Height first bole (m)</i> <i>N = 1418</i>	<i>first Crown Area (m²)</i> <i>N = 1418</i>	<i>Connectivity (%)</i> <i>N = 1418</i>	<i>Branch >20cm</i> <i>N = 1418</i>	<i>Branch 10-20cm</i> <i>N = 1418</i>	<i>Branch 4-10cm</i> <i>N = 1418</i>	<i>Branch 2-4cm</i> <i>N = 1418</i>	<i>Branch 0-2cm</i> <i>N = 1418</i>
DBH (cm) N = 1418	–									
Top Height (m) N = 1418	r=0.757** P<0.001	–								
Height first bole (m) N = 1418	r=0.591* P<0.001	r=0.790** P<0.001	–							
Crown Area (m²) N = 1418	r=0.606* P<0.001	r=0.583* P<0.001	r=0.440* P<0.001	–						
Connectivity (%) N = 1418	r=-0.100 P<0.001	r=-0.079 P=0.003	r=-0.089 P=0.001	r=-0.073 P<0.001	–					
Branch >20cm N = 1418	r=0.462* P<0.001	r=-0.326 P<0.001	r=-0.201 P<0.001	r=0.427* P<0.001	r=-0.053 P=0.044	–				
Branch 10-20cm N = 1418	r=0.542* P<0.001	r=0.421* P<0.001	r=-0.289 P<0.001	r=0.400* P<0.001	r=-0.070 P=0.008	r=0.644* P<0.001	–			
Branch 4-10cm N = 1418	r=0.433* P<0.001	r=-0.304 P<0.001	r=-0.146 P<0.001	r=-0.334 P<0.001	r=-0.061 P=0.02	r=0.512* P<0.001	r=0.593* P<0.001	–		
Branch 2-4cm N = 1418	r=0.411* P<0.001	r=-0.284 P<0.001	r=-0.159 P<0.001	r=-0.272 P<0.001	r=-0.080 P=0.003	r=0.412* P<0.001	r=0.466* P<0.001	r=0.733** P<0.001	–	
Branch 0-2cm) N = 1418	r=0.431* P<0.001	r=-0.333 P<0.001	r=-0.192 P<0.001	r=-0.286 P<0.001	r=-0.067 P=0.012	r=0.446* P=0.001	r=0.494* P<0.001	r=0.570* P<0.001	r=0.750** P<0.001	–

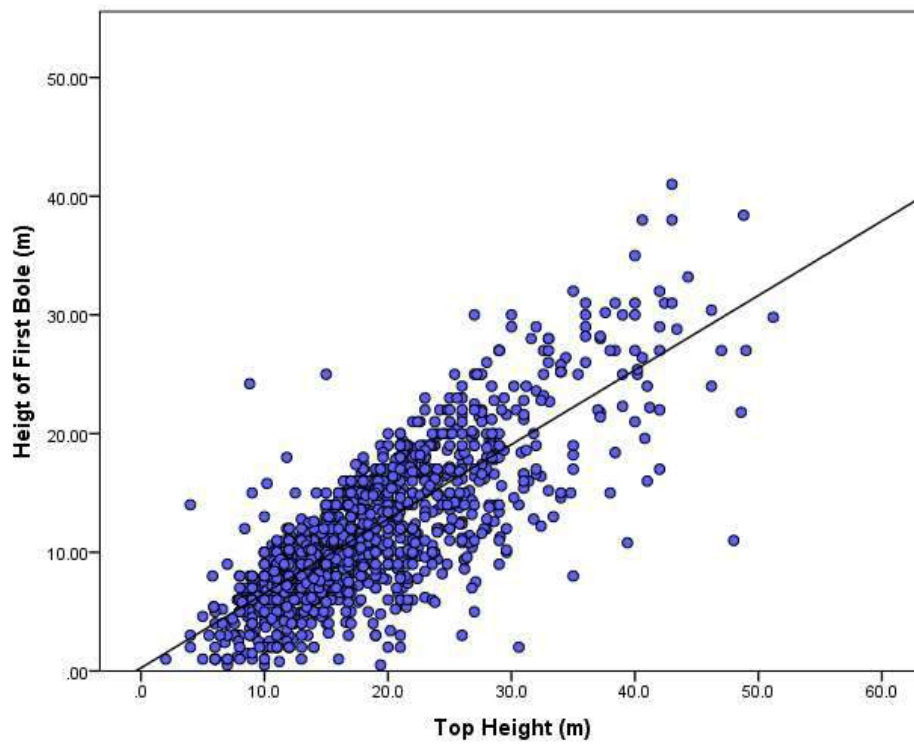


Figure 4.7. Relationship between tree height (m) and height to first bole (m) for all trees ($r = 0.790$, $n = 1418$, $p < 0.001$).

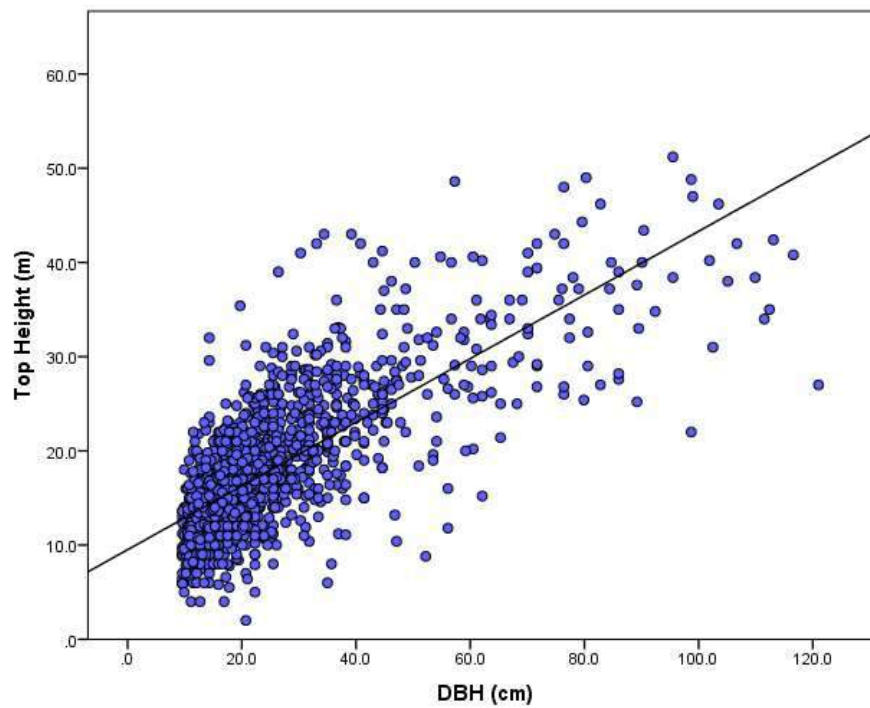


Figure 4.8. Relationship between DBH and tree height (m) for all trees ($r = 0.751$, $n = 1418$, $p < 0.001$).

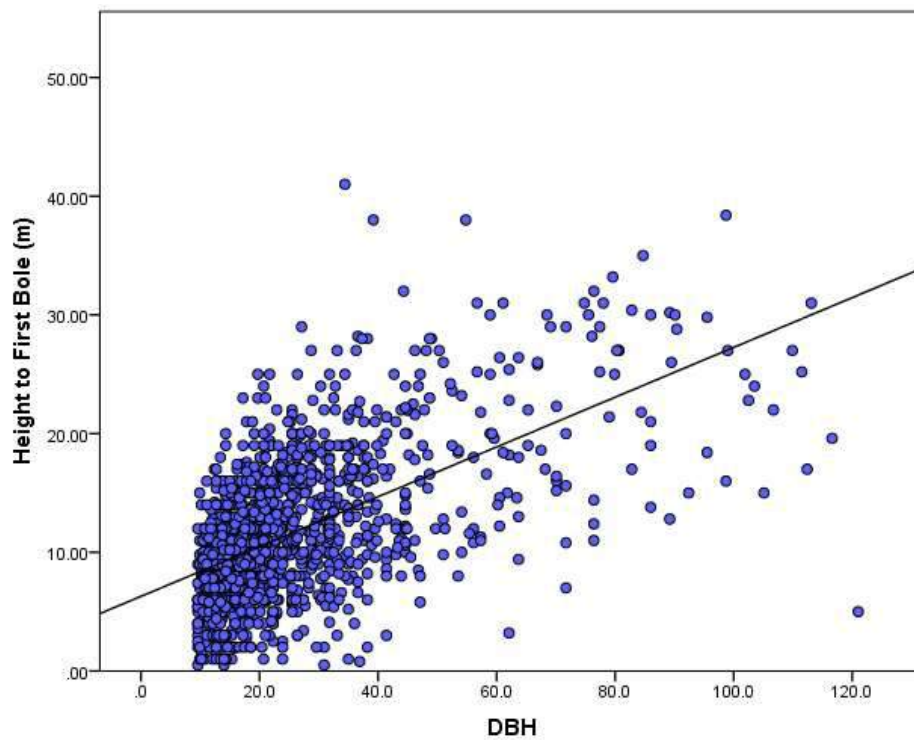


Figure 4.9. Relationship between DBH and height to first bole (m) for all trees ($r = 0.591$, $n = 1418$, $p < 0.001$).

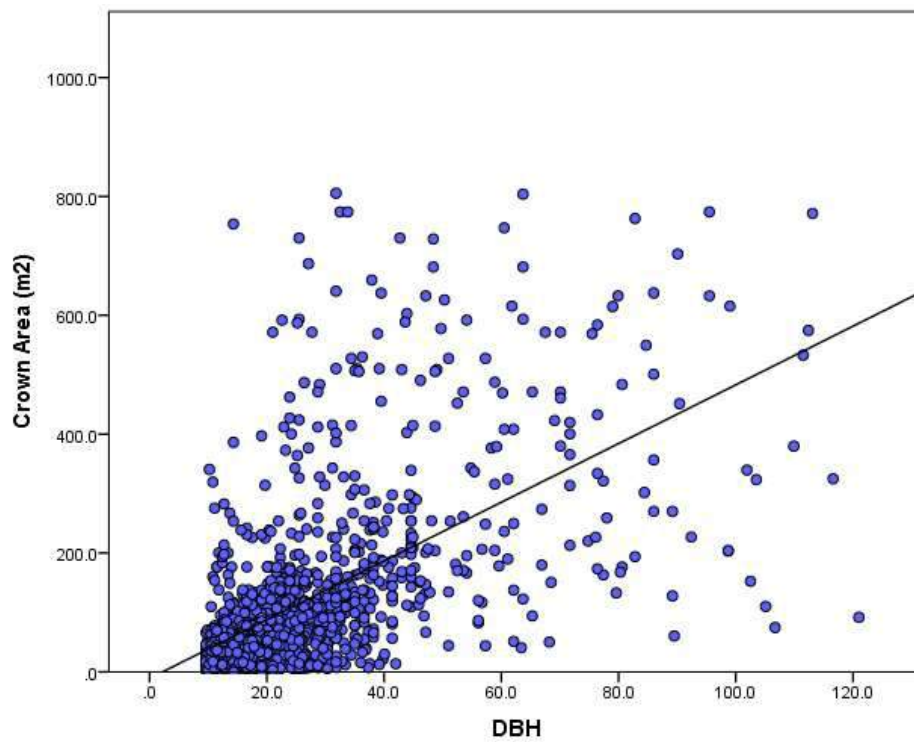


Figure 4.10. Relationship between DBH and crown area (m²) for all trees ($r = 0.606$, $n = 1418$, $p < 0.001$).

Density of trees above $\geq 10\text{cm}$ DBH (ha) did not correlate with any other vegetation variable (table 4.6).

Table 4.6. Summary of Spearmans Rho Correlations on tree density and all continuous vegetation variables.

	<i>DBH (cm)</i> <i>N = 10</i>	<i>Height (m)</i> <i>N = 10</i>	<i>Height to first bole (m)</i> <i>N = 10</i>	<i>Crown Area (m²)</i> <i>N = 10</i>	<i>Connectivity (%)</i> <i>N=10</i>
Tree Density (ha) N = 10	$r=0.004$ $p=0.990$	$r=0.100$ $p=0.783$	$r=0.115$ $p=0.753$	$r=-0.043$ $p=0.906$	$r=-0.125$ $p=0.730$

4.1.4: Variation in tree heights and tree connectivity

Because hylobatids prefer tall trees with a well-connected canopy for travel, tree heights and connectivity were placed into categories to assess preferred height by the species'. Number of tall trees $>30\text{m}$ differed significantly across the land units (Kruskal-Wallis test: $X^2_{(3)}=14.12$, $p = 0.003$). Hill forest contained a significantly higher percentage of tall trees (10.57%) than all the other land units. Conversely, alluvial forest habitats contained the lowest number of tall trees ($>30\text{m} = 3.3\%$, Figures 4.12 and 4.13).

Alluvial forest had the highest percentage of trees with a low canopy connectivity (73.5%; post hoc tests with subsequent Bonferroni correction - $\alpha'=0.0083$, Table 4.7; Figure 4.14), whilst only approximately half (48.9-56.8%) of trees in the other three habitat types possesses trees with low canopy connectivity.

Significant differences in high tree connectivity were found between alluvial and hill forest habitats, and alluvial and hill-swamp forest (Table 4.7, Figures 4.16 and 4.17). Hill forest had the highest percentage of trees with $>75\%$ connectivity (10.1%) whilst alluvial contained no trees within this category. Plains habitat contains only a minimal number of high connectivity trees ($>75\% = 0.4\%$, $50-75\% = 3.3\%$, Figure 4.17).

Table 4.7. Summary of pairwise Mann-Whitney U post hoc tests on all tree height and connectivity categories between the different land units. Significant P-values following sequential Bonferroni correction are highlighted in bold and underlined

	<i>Plains vs Hills</i> <i>N = 28</i>		<i>Plains vs Alluvial</i> <i>N = 18</i>		<i>Plains vs Hill-Swamp</i> <i>N = 23</i>		<i>Hills vs Alluvial</i> <i>N = 26</i>		<i>Hills vs Hill-Swamp</i> <i>N = 18</i>		<i>Alluvial vs Hill-Swamp</i> <i>N = 21</i>	
	U	P	U	P	U	P	U	P	U	P	U	P
<i>Tree Height <20m</i>	72.00	0.384	12.50	0.014	46.50	0.803	22.00	0.005	90.00	0.277	17.50	0.012
<i>Tree Height >20m <30m</i>	34.50	0.008	35.00	0.653	59.50	0.729	21.00	0.005	36.5	0.001	50.5	0.912
<i>Tree Height >30m</i>	34.00	0.006	34.00	0.574	59.00	0.702	20.00	0.003	52.50	0.009	37.00	0.257
<i>Connectivity <15%</i>	83.00	0.735	10.50	0.008	60.50	0.779	23.00	0.006	111.00	0.809	9.50	0.002
<i>Connectivity <25%</i>	53.00	0.735	8.00	0.003	61.00	0.803	25.00	0.009	65.00	0.038	3.00	<0.001
<i>Connectivity 25 - 50%</i>	63.00	0.193	36.00	0.721	54.00	0.492	33.00	0.032	99.00	0.468	35.00	0.213
<i>Connectivity 50 - 75%</i>	60.00	0.144	28.00	0.254	38.00	0.089	24.00	0.006	112.00	0.840	12.00	0.003
<i>Connectivity >75%</i>	68.00	0.164	36.00	0.371	45.50	0.116	48.00	0.007	112.00	0.814	32.00	0.052

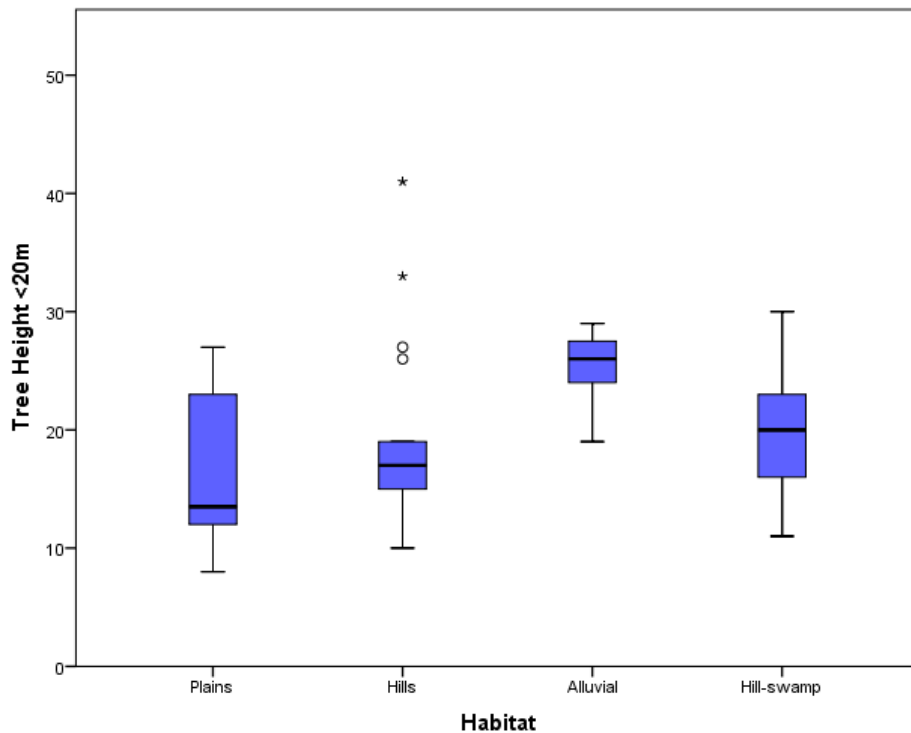


Figure 4.11. Tree height <20m (>10cm DBH) in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

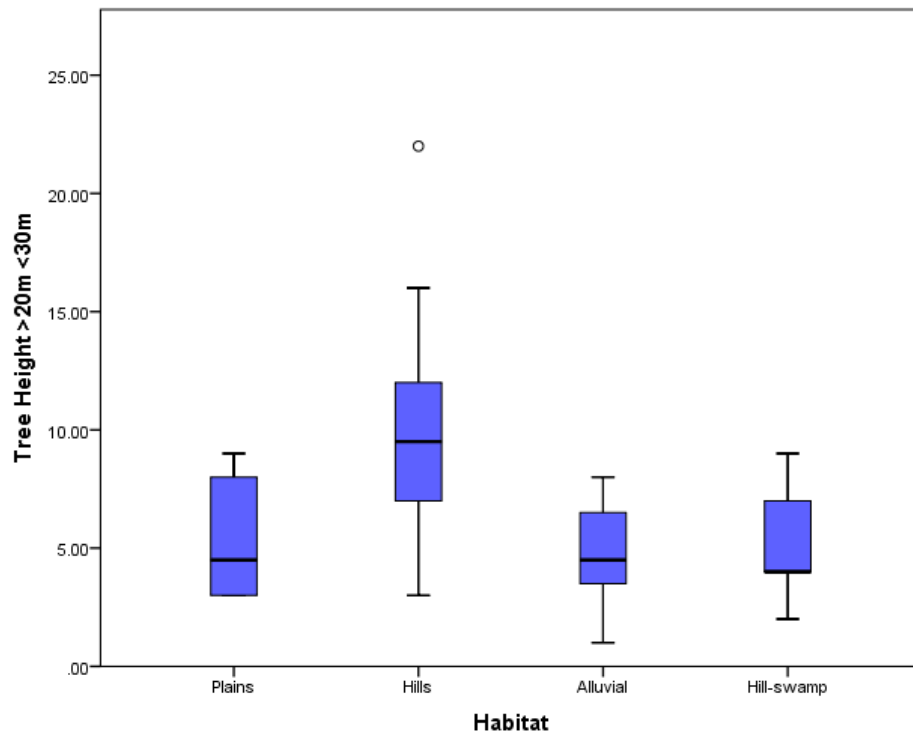


Figure 4.12. Tree height >20m <30m (>10cm DBH) in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

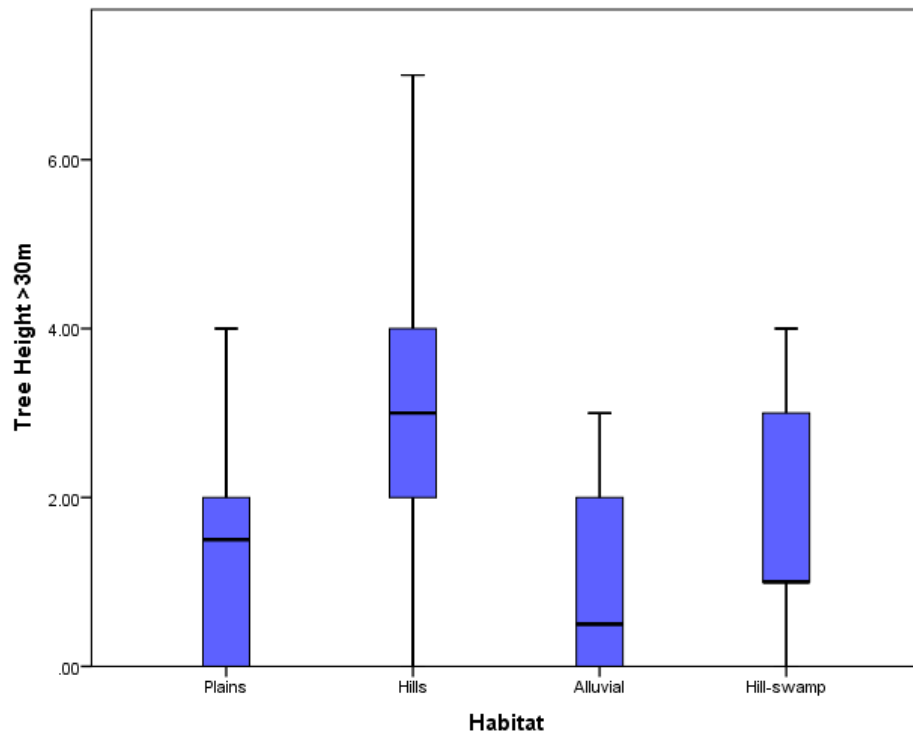


Figure 4.13. Tree height >30m (>10cm DBH) in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

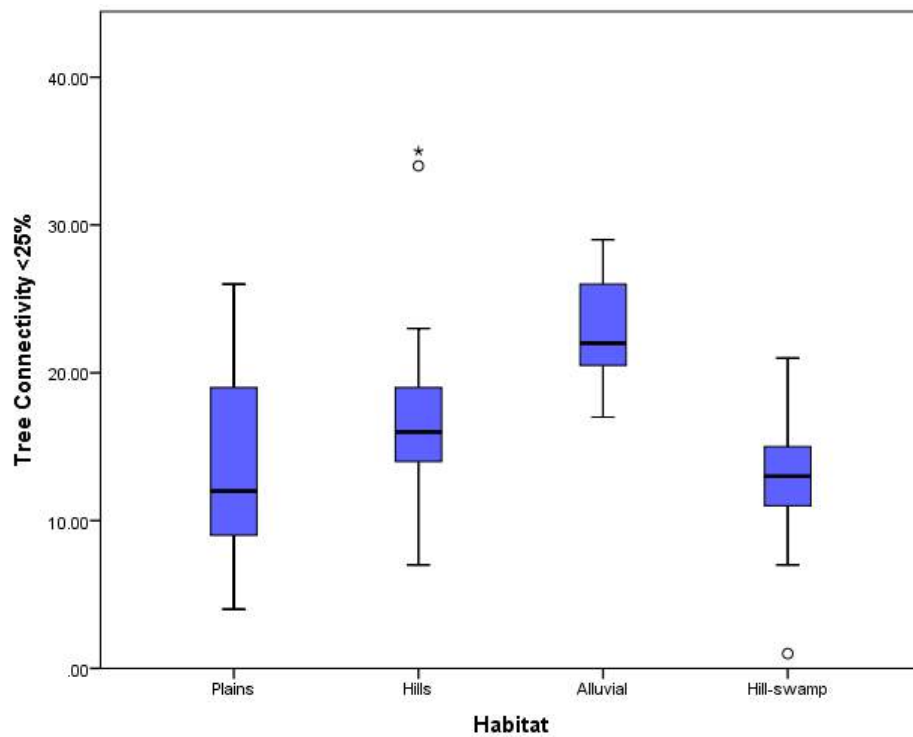


Figure 4.14. Tree Connectivity <25% in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

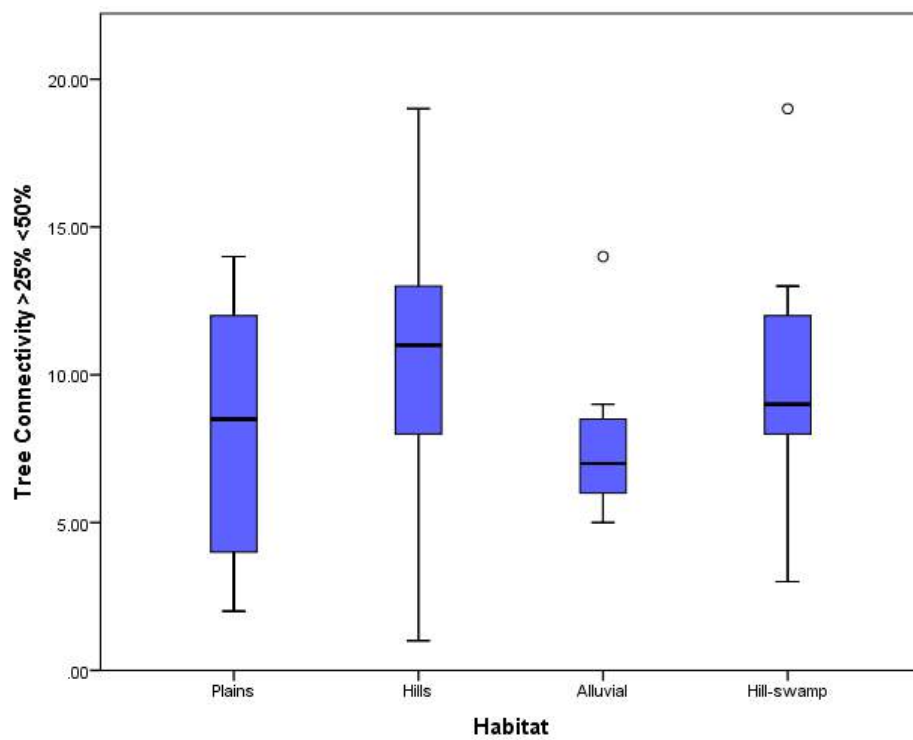


Figure 4.15. Tree Connectivity >25% <50% in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

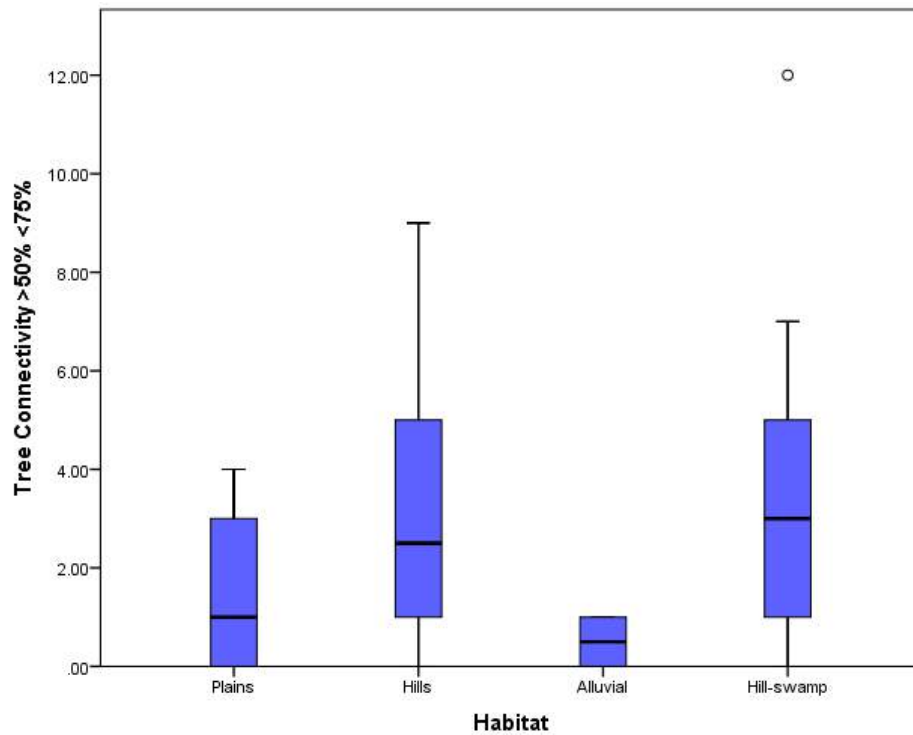


Figure 4.16. Tree Connectivity >50% <75% in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

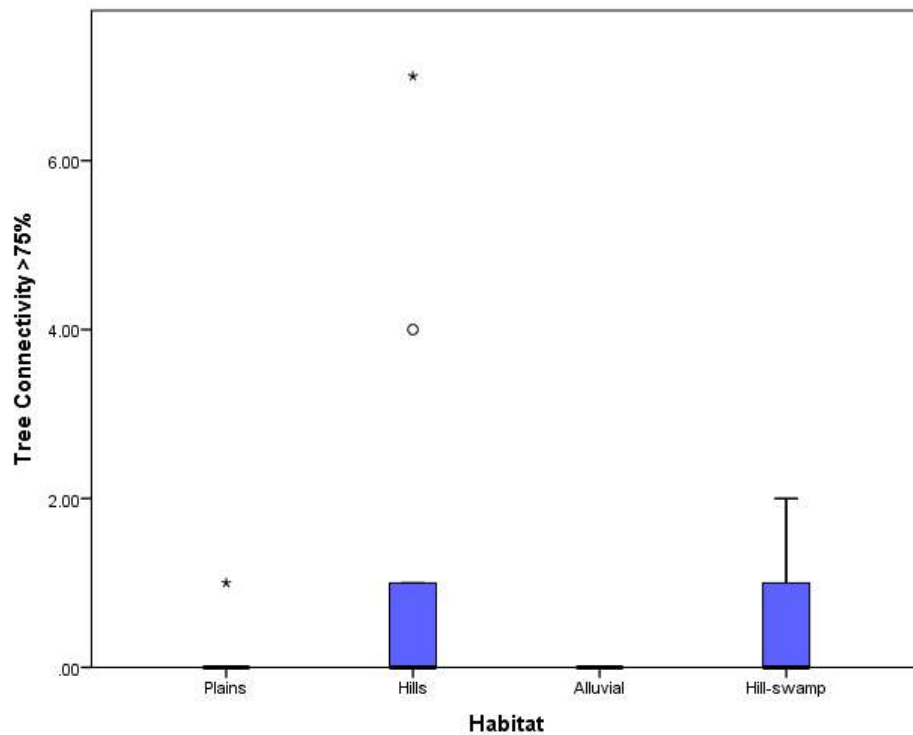


Figure 4.17. Tree Connectivity >75% in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values and * and ° represent the extremes and outliers, respectively.

In summary, hill forest habitats contain the largest trees (DBH), the tallest trees with the largest crown areas, the highest canopy connectivity and the largest density of trees compared to the other habitat types. Hill-swamp forest contains some tall trees but also contains a significant number of shorter trees <20m. However, trees showed high connectivity with neighbouring trees within this habitat. Plains forest on average has a low tree density with a low number of tall trees and low connectivity between trees. The alluvial forest habitats have a high tree density; however, these trees had a lower DBH, are less connected and are shorter than trees found within any of the other forest types.

4.2: Hylobatid densities

Seventy gibbon and siamang groups were identified during the study period, consisting of 213 recorded gibbon vocalisations and 108 siamang vocalisations. After mapping, this resulted in a total of 45 groups of lar gibbon (Figure 4.18), and 25 siamang groups identified (Figure 4.19). Sampled survey areas were calculated using QGIS (v.2.16.3) and all effective listening distances were based on a radius of 1km around each listening post. A section of plains habitat (array 1, green in figure 4.18) was removed due to consisting of farmland and therefore completely unsuitable for any hylobatid groups. Effective sampling areas differ, due to differences in distances between listening posts and difficult terrain and to allow all posts to be positioned at the highest point maximising chances of hearing all groups calling within an area (table 4.8).

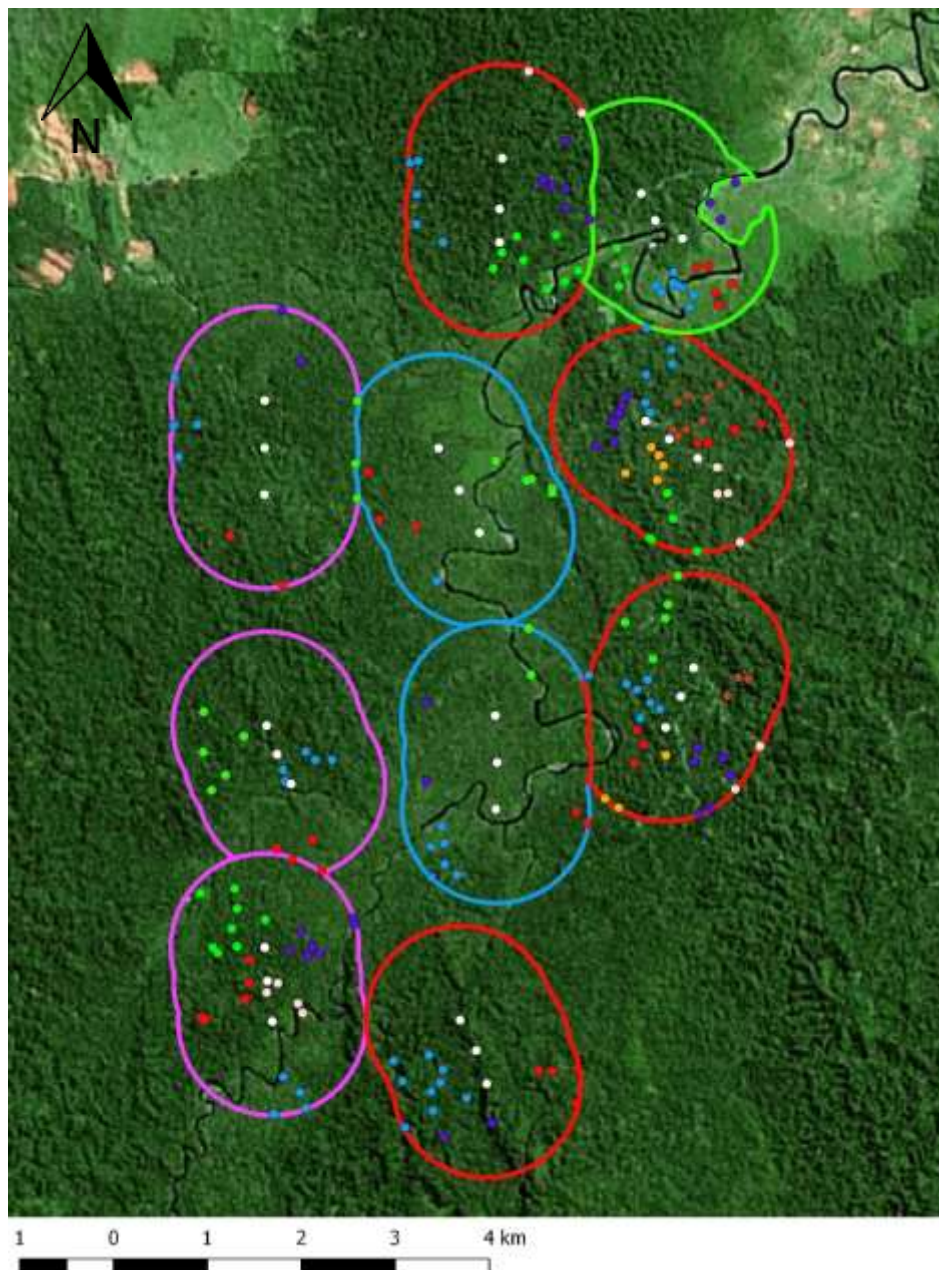


Figure 4.18. Approximate location of each gibbon vocalisations. Each coloured circle represents a separate identified group. Different coloured arrays represent habitat types; green = plains, red = hills, blue = alluvial, purple = hill-swamp.

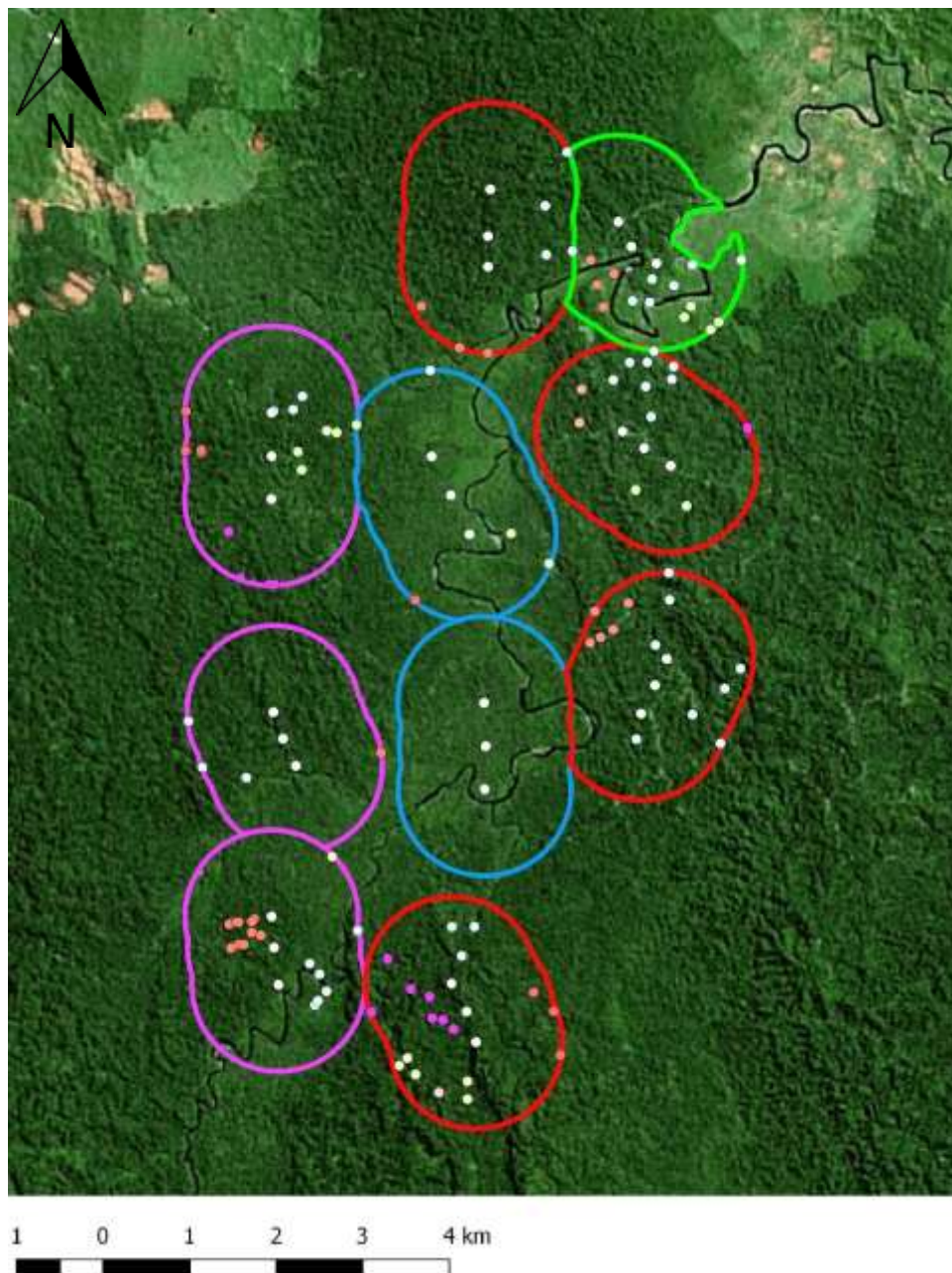


Figure 4.19. Approximate location of each siamang vocalisations. Each coloured circle represents a separate identified group. Different coloured arrays represent habitat types; green = plains, red = hills, blue = alluvial, purple = hill-swamp.

4.2.1 Density estimation through standard triangulation method

Table 4.8 and 4.9 shows results of gibbon and siamang population information as calculated through triangulation and described by Rawson (2011).

Table 4.8. Results of triangulation method for calculating lar gibbon density within the survey area.

Array Number	Habitat Type	Sample Area (km²)	Raw Group Number	Calling Probability p(call)	Estimated Group density (group/km²)	Upper 95% confidence interval	Upper 95% confidence interval
1	Plains	3.54	4	1	2.82	3.15	2.51
2	Hills	4.91	4	0.736	2.26	2.92	1.60
3	Hills	4.5	7	0.904	3.56	4.22	2.90
4	Hills	4.39	7	0.694	3.45	4.26	2.63
5	Alluvial	5.12	4	0.634	1.44	1.98	0.89
6	Alluvial	5.01	3	0.634	1.19	1.46	0.93
7	Hill-swamp	5.12	4	0.475	2.11	3.10	1.13
8	Hills	4.61	4	0.736	1.74	2.13	1.36
9	Hill-swamp	4.72	5	0.933	2.75	3.19	2.32
10	Hill-swamp	4.33	3	0.475	1.99	2.80	1.02

Lar gibbons were found in all sample locations, with the highest densities recorded within the hills habitat (3.56 groups/km², Table 4.8). The lowest density of lar gibbons was recorded within the alluvial forest (1.44 and 1.99 groups/km²). Plains habitat showed the second highest density of lar gibbons (2.82 groups/km²), followed by hill-swamp areas. There was a significant difference in lar gibbon densities between all forest locations $t_{(9)} = 9.22$, $p < 0.001$.

Table 4.9. Results of triangulation method for calculating siamang density within the survey area.

Array Number	Habitat Type	Sample Area (km²)	Raw Group Number	Calling Probability p(call)	Estimated Group density (group/km²)	Upper 95% confidence interval	Upper 95% confidence interval
1	Plains	3.54	2	0.50	2.11	2.83	1.39
2	Hills	4.91	2	1.00	0.82	1.05	0.58
3	Hills	4.5	4	0.52	1.64	2.24	1.05
4	Hills	4.39	3	0.63	1.62	2.04	1.20
5	Alluvial	5.12	-	-	-	-	-
6	Alluvial	5.01	2	0.67	0.40	0.74	0.40
7	Hill-swamp	5.12	4	0.63	1.99	2.78	1.20
8	Hills	4.61	4	0.52	2.52	3.39	1.66
9	Hill-swamp	4.72	2	0.63	1.33	1.58	1.08
10	Hill-swamp	4.33	2	1.00	0.92	1.19	0.66

Siamang groups were found in all sample locations with the exception of one alluvial forest type (table 4.9). This species followed a similar pattern to the lar gibbon; with the highest population density recorded within hill forest habitat (2.52 groups/km²) and the lowest within alluvial habitat (0.44 groups/km²). However, higher densities were also found in the plains habitat (2.11 groups/km²). There was a significant difference in siamang densities between all forest areas $t_{(9)} = 5.31$, $p < 0.001$.

Overall, hylobatid densities were highest in hill forest areas, whereas the lowest densities were recorded in alluvial forest types. There was no significant difference between lar gibbon and siamang densities overall $t_{(18)} = 2.79$, $p = 0.968$. Nevertheless, lar gibbon population densities were consistently higher than siamang densities in all forest locations with the exception of one hill forest location (mean difference 1.75 SE=0.30). Although lar gibbon densities were consistently higher than siamang densities, there was no significant relationship between the densities of these species in relation to each other ($r = 0.442$, $p = 0.200$ (Figure 4.19).

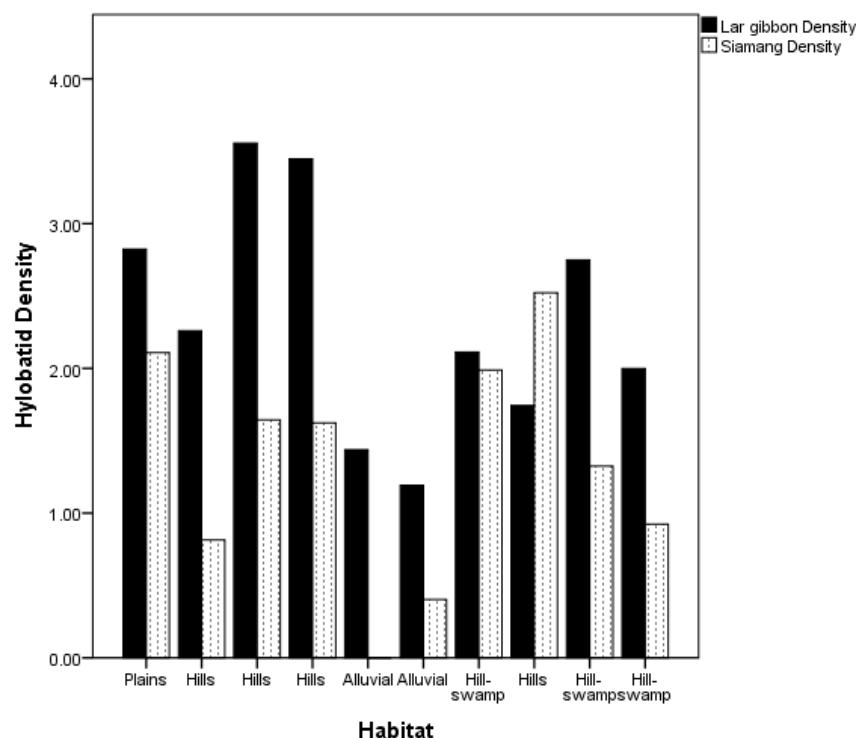


Figure 4.20. Lar gibbon and siamang densities in all survey locations.

4.2.2: Density estimates using gibbonSECR method

Density estimates were additionally calculated using the program gibbonSECR in Rstudio for the two species. For both species and across all sample locations the density estimates followed the same pattern as triangulation, with the highest recorded

densities of lar gibbon and siamang within hill habitats (1.46 groups/km², 0.96 groups/km² respectively), and the lowest within alluvial forest (0.30 groups/km² and 0.16 groups/km² respectively Tables 4.10 and 4.11). However, the calculated density estimates in all cases are lower than those calculated by the standard triangulation methods, with an order of magnitude difference of between 2.11- 4.86. There was a significant difference in the densities calculated from the two different methods for both lar gibbons ($t_{(18)} = 6.05$, $p=0.023$) and siamangs ($t_{(18)} = 3.06$, $p=0.014$).

Table 4.10. Density estimates of Lar gibbon calculated from both triangulation and SECR and showing the order of magnitude difference.

<i>Array Number</i>	<i>Raw Number</i>	<i>Group</i>	<i>Triangulation Density Groups/km²</i>	<i>SECR Density Groups/km²</i>	<i>Order of magnitude difference</i>
1		5	2.82	0.58	4.86
2		4	2.26	0.52	4.35
3		8	3.56	1.46	2.44
4		7	3.45	0.92	3.75
5		4	1.44	0.37	3.89
6		3	1.19	0.30	3.97
7		4	2.11	0.59	3.58
8		5	1.74	0.36	4.83
9		5	2.75	0.98	2.81
10		3	1.99	0.42	4.74

Table 4.11. Density estimates of Siamang calculated from both triangulation and SECR and showing the order of magnitude difference.

<i>Array Number</i>	<i>Raw Number</i>	<i>Group</i>	<i>Triangulation Density Groups/km²</i>	<i>SECR Density Groups/km²</i>	<i>Order of magnitude difference</i>
1		2	2.11	0.47	4.49
2		2	0.82	0.29	2.81
3		4	1.64	0.78	2.11
4		3	1.62	0.73	2.22
5		0	0.00	0	
6		2	0.40	0.16	2.53
7		4	1.99	0.79	2.52
8		4	2.52	0.96	2.63
9		3	1.33	0.57	2.32
10		2	0.92	0.34	2.72

As the standard triangulation method is well known and widely used by many gibbon researchers, these density estimates were used to ascertain any relationships between hylobatid densities and vegetation variables.

4.2.3: *Hylobatid densities in relation to vegetation variables*

Lar gibbon density across the 10 sites was significantly positively correlated with tree diameter ($r = 0.701$, $p = 0.024$), tree height ($r = 0.666$, $p = 0.035$) and crown area ($r = 0.722$, $p = 0.018$; Table 4.12). Additionally, lar gibbon density was significantly negatively correlated with frequency of trees with low connectivity <15% ($r = -0.859$, $p = 0.035$) and a high frequency of small trees <20m ($r = 0.667$, $p = 0.031$). Tree density, frequency of tall trees (all categories >20m) and high percentage of tree connectivity were not significantly correlated with gibbon density (Table 4.13).

Siamang density per site correlated significantly positively with frequency of trees with high tree connectivity ($r = 0.652$, $p = 0.041$) and with tree height of between 20m to 30m ($r = 0.641$, $p = 0.046$). Furthermore, siamang density was significantly negatively correlated with frequency of trees with intermediate connectivity >50% <75% ($r = -0.745$, $p = 0.013$). Tree height was weakly positively correlated with siamang number, however no correlation was found in relation to tree diameter, crown area, tree density, low connectivity classes and low tree height classes (Table 4.12).

Table 4.12. Pearson's correlations between predictor variables (forest characteristics) and gibbon and siamang densities. * signify strong correlations, ** signify Very strong correlations.

<i>Predictor Variables</i>	<i>Gibbon Density</i>	<i>Siamang Density</i>
DBH (cm)	$r = 0.701^{**}$ $p = 0.024$	$r = 0.421$ $p = 0.226$

<i>Height (m)</i>	r = 0.666* p = 0.035	r = 0.584 p = 0.076
<i>Crown Area (m²)</i>	r = 0.722** p = 0.018	r = 0.376 p = 0.284
<i>Tree Density</i>	r = 0.088 p = 0.809	r = -0.020 p = 0.957
<i>Tree Connectivity <15%</i>	r = -0.859** p = 0.001	r = -0.554 p = 0.097
<i>Tree Connectivity <25%</i>	r = -0.516 p = 0.127	r = -0.745** p = 0.013
<i>Tree Connectivity >25% <50%</i>	r = 0.502 p = 0.139	r = 0.620 p = 0.056
<i>Tree Connectivity >50% <75%</i>	r = 0.573 p = 0.084	r = 0.652* p = 0.041
<i>Tree Connectivity >75%</i>	r = -0.247 p = 0.491	r = 0.447 p = 0.195
<i>Tree Height >30m</i>	r = 0.049 p = 0.892	r = 0.387 p = 0.269
<i>Tree Height >20m <30m</i>	r = 0.465 p = 0.176	r = 0.641* p = 0.046
<i>Tree Height <20m</i>	r = -0.677* p = 0.031	r = -0.505 p = 0.137

4.2.4: Multiple regression analysis

Prior to undertaking a multiple regression, any variables that were highly correlated to other vegetation variables were omitted as this may cause the model to over-parameterize. Therefore, tree diameter was omitted as this variable was highly correlated with most other vegetation variables (Table 4.5). This left tree density, crown area, height and connectivity. A backwards stepwise regression was performed, which removes variables which are most statistically insignificant to the model. Tree crown area was the most influential in determining gibbon density (model 4: $F_{(9)} = 8.7$, $p = 0.018$, $R^2 = 0.521$, Figure 4.21), but the best model also included tree height (model 3; Table 4.13). There were no significant relationships between any variable and siamang density, although height somewhat influenced siamang density (Table 4.14).

As connectivity and height showed the strongest influence on hylobatid densities, two further backwards stepwise regression analysis were performed using the height and connectivity classes. This was undertaken to ascertain specific constraints by the species regarding these variables (Table 4.15 – 4.17).

Table 4.13. Stepwise Regression results of habitat variables on gibbon density. P-values highlighted in bold show significant relationship between density and vegetation variable.

<i>Model</i>	<i>R</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
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<u>Model 1</u>				
Tree Density				
Crown Area	0.802	0.643	2.255	0.198
Height				
Connectivity				
<u>Model 2</u>				
Crown Area	0.797	0.636	3.491	0.090
Height				
Connectivity				
<u>Model 3</u>				
Crown Area	0.785	0.616	5.604	0.035
Height				
<u>Model 4</u>				
Crown Area	0.722	0.521	8.700	0.018

Table 4.14. Stepwise Regression results of habitat variables on siamang density. P-values highlighted in bold show significant relationship between density and vegetation variables.

<i>Model</i>	<i>R</i>	<i>R</i>²	<i>F</i>	<i>P</i>
<u>Model 1</u>				
Height				
Crown Area	0.737	0.543	1.487	0.332
Connectivity				
Tree Density				
<u>Model 2</u>				
Height	0.736	0.542	2.370	0.170
Crown Area				
Connectivity				
<u>Model 3</u>				
Height	0.687	0.472	3.126	0.107
Connectivity				
<u>Model 4</u>				
Height	0.584	0.341	4.138	0.076

The regression analyses for lar gibbon density for trees within height classes (Table 4.16) and connectivity classes (Table 4.18) as the independent variables showed that the frequency of tree <20m in height and tree connectivity <15% were the most influential in determining gibbon density ($F_{(9)} = 6.755$, $p = 0.031$, $R^2 = 0.459$, Figure 4.22, 4.23). In regards to siamangs, frequency of trees of between 20m and 30m in height (Figure 4.24, Table 4.17) and tree connectivity >50% <75% were the most influential in determining siamang density (Table 4.19, Figure 4.25).

Table 4.15. Stepwise Regression results of Tree Height variables on lar gibbon density. P-values highlighted in bold show significant relationship between density and vegetation variables.

<i>Model</i>	<i>R</i>	<i>R</i>²	<i>F</i>	<i>P</i>
<u>Model 1</u>				
Height <20m	0.701	0.492	1.936	0.225

Height >20m <30m				
Height >30m				
Model 2				
Height <20m	0.700	0.490	3.359	0.095
Height >20m <30m				
Model 3				
Height <20m	0.677	0.459	6.775	0.031

Table 4.16. Stepwise Regression results of Tree Height variables on siamang density. P-values highlighted in bold show significant relationship between density and vegetation variables.

<i>Model</i>	<i>R</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
Model 1				
Height <20m				
Height>20m <30m	0.779	0.606	3.081	0.112
Height >30m				
Model 2				
Height>20m <30m	0.738	0.544	4.177	0.064
Height >30m				
Model 3				
Height >20m <30m	0.641	0.411	5.576	0.046

Table 4.17. Stepwise Regression results of Tree Connectivity variables on gibbon density. P-values highlighted in bold show significant relationship between density and vegetation variables.

<i>Model</i>	<i>R</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
Model 1				
Connectivity <15%				
Connectivity>25% <50%	0.880	0.774	4.293	0.071
Connectivity>50% <75%				
Connectivity >75%				
Model 2				
Connectivity <15%	0.880	0.774	6.868	0.023
Connectivity >25% <50%				
Connectivity >75%				
Model 3				
Connectivity <15%	0.878	0.772	11.826	0.006
Connectivity >75%				
Model 4				
Connectivity <15%	0.859	0.737	22.450	0.001

Table 4.18. Stepwise Regression results of Tree Connectivity variables on Siamang density. P-values highlighted in bold show significant relationship between density and vegetation variables.

<i>Model</i>	<i>R</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
Model 1				
Connectivity <15%				
Connectivity <25% >50%	0.794	0.630	2.127	0.215
Connectivity >50% <75%				

Connectivity >75%				
<i>Model 2</i>				
Connectivity <15%	0.787	0.619	3.252	0.102
Connectivity >50 <75%				
Connectivity >75%				
<i>Model 3</i>				
Connectivity <50% >75%	0.753	0.568	4.593	0.053
Connectivity >75%				
<i>Model 4</i>				
Connectivity >50% <75%	0.652	0.426	5.930	0.041

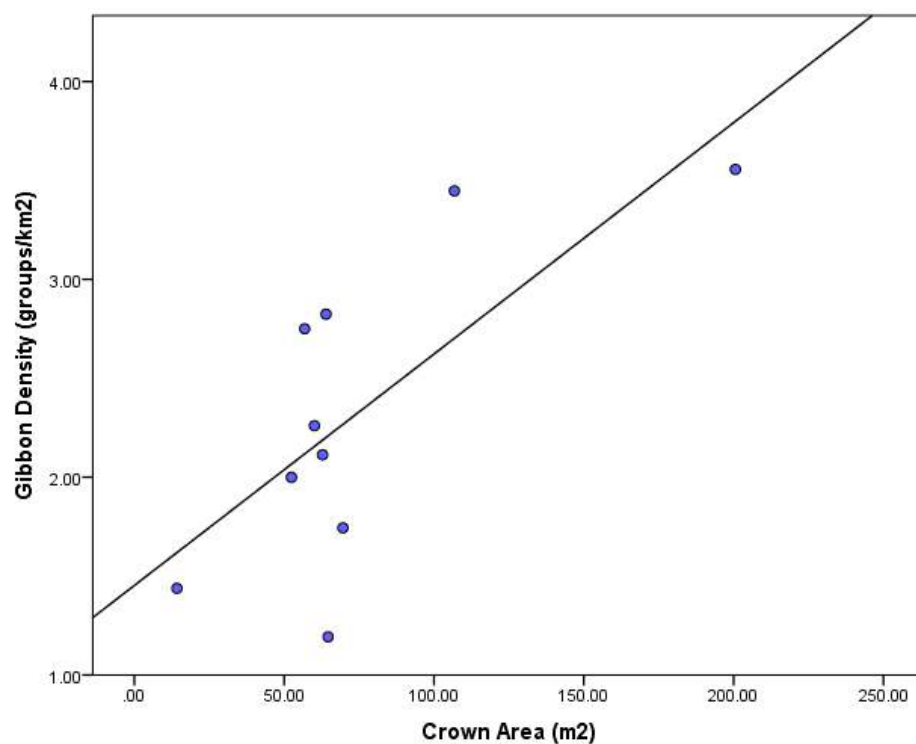


Figure 4.21. Significant linear relationship between lar gibbon density and tree crown area (m²).

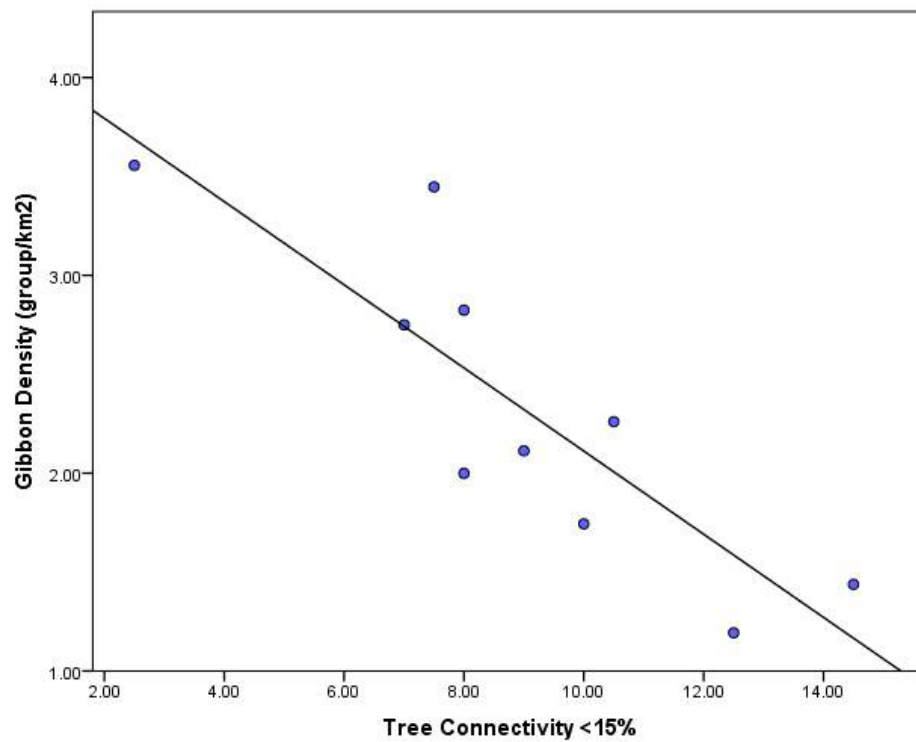


Figure 4.22. Significant negative linear relationship between lar gibbon density and tree connectivity <15%.

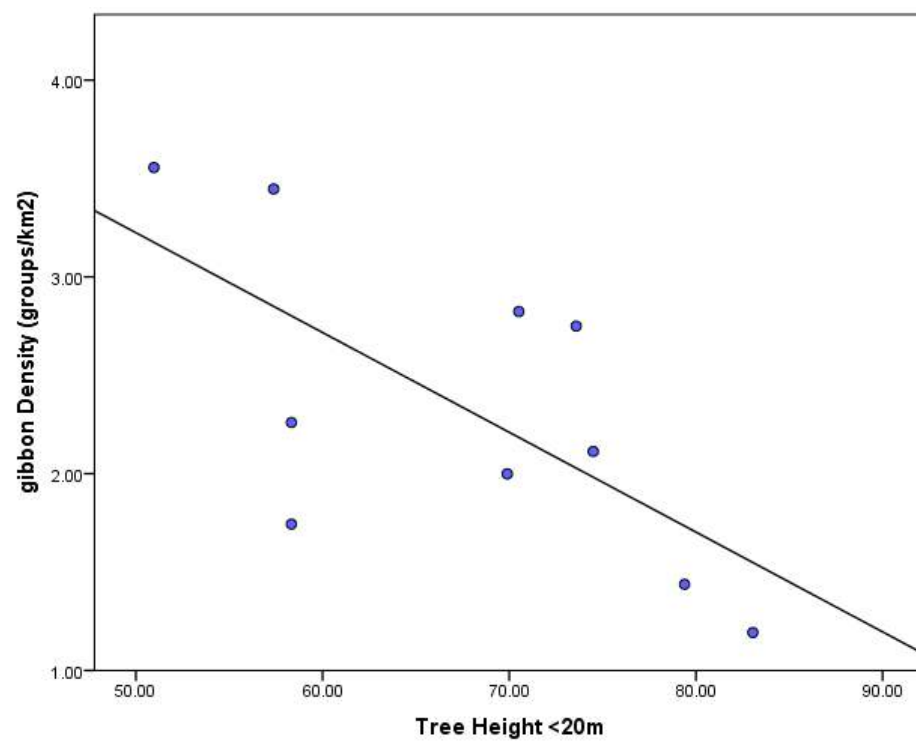


Figure 4.23. Significant negative linear relationship between gibbon density and tree height <20m.

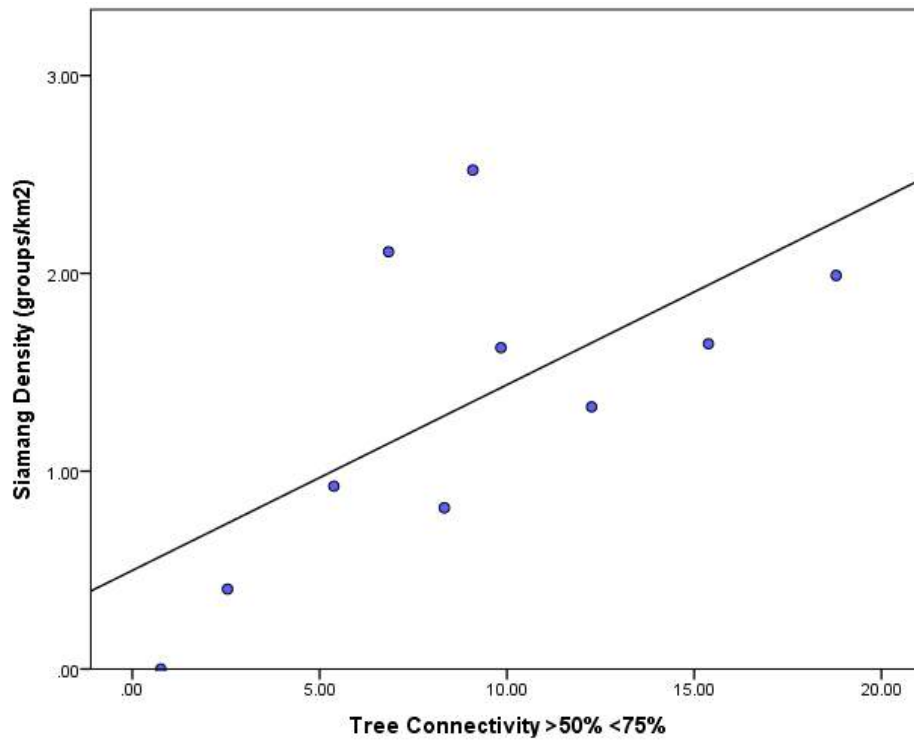


Figure 4.24. Significant negative linear relationship between siamang density and tree connectivity between 50-75%.

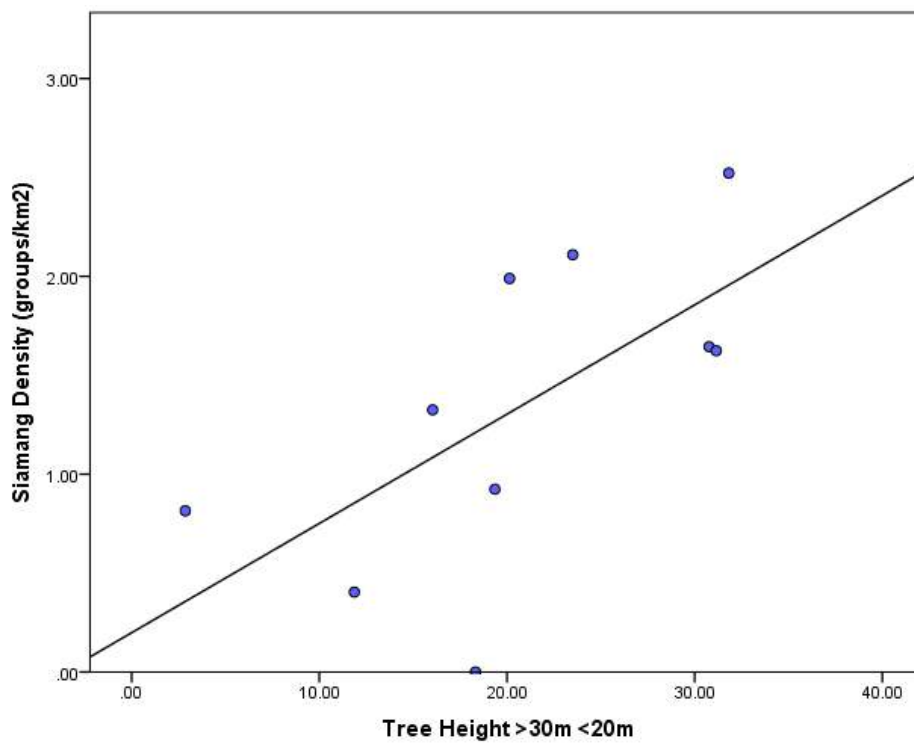


Figure 4.25. Significant negative linear relationship between siamang density and tree height between 20-30m.

4.2.5: Relative density of hylobatids

The relative density of siamangs was calculated (siamang density/lar gibbon density) to ascertain if the number of lar gibbon groups within an area had any effect on the number of siamang groups present within a survey area. There was a significant difference in the relative density of siamangs between survey areas ($t_{(9)} = 4.570$, $p = 0.001$) and a linear regression revealed that relative siamang density was strongly influenced by lar gibbon density ($F = (1,8) = 27.641$, $p = 0.001$, $R^2 = 0.776$). Figure 4.26 shows that the relative density of siamangs is highest in the hill habitat, where gibbon density is highest, and lowest within alluvial forest, where gibbon density is also lowest.

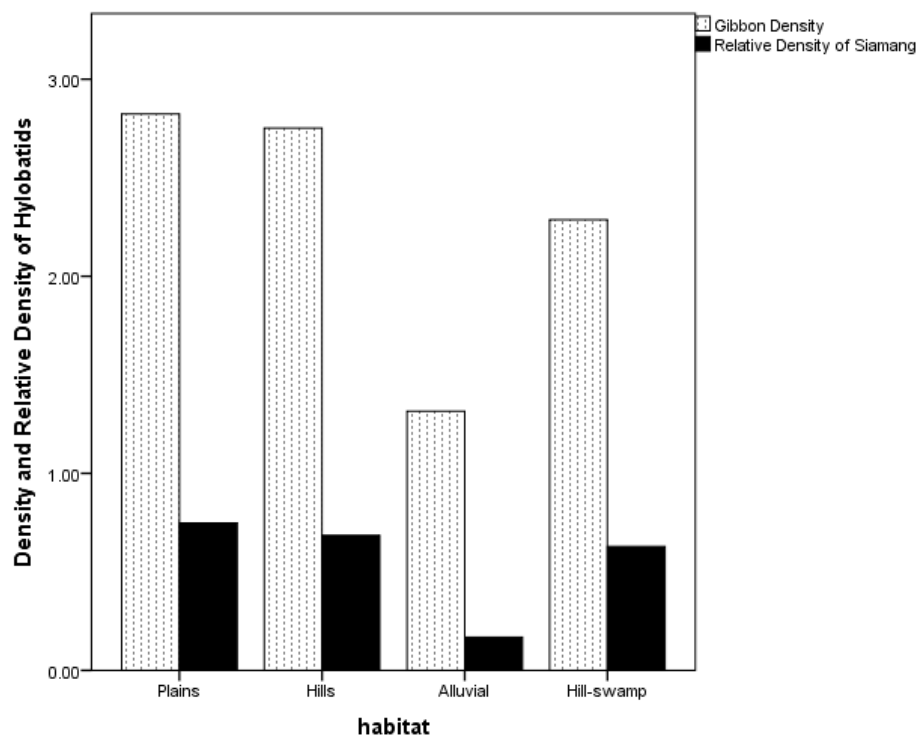


Figure 4.26. Relative Density of Siamang in relation to gibbon density between the four land units.

4.2.6: Calling probabilities

Calling probabilities can have an effect on density estimations, and low calling probabilities can result in under-represented density estimates. Therefore, correlations between calling probabilities and gibbon densities were undertaken for all survey areas to assess the likelihood that calling probability may affect the density estimates. There were no significant correlations between densities and calling probabilities for either the

lar gibbon ($r = -0.340$, $p = 0.337$) or the siamang ($r = -0.587$, $p = 0.074$). Hence, the density estimations for lar gibbon and siamang can be presumed reliable.

Chapter 5: Discussion

This study investigated forest characteristics and hylobatid densities across varying types of forest; in terms of habitat and structure. All four identified land types showed differences in vegetation structure, especially in regards to stem diameter, tree height, height to first bole, crown area and connectivity. Forest classified as hill forest contained trees with the largest average diameter (21.0cm), highest average height (18m), highest frequency of tall trees >20m (41.2%), trees with the largest crown area (84.4m²) and the highest percentage of canopy connectivity >25% (86.6%). Alluvial forest types contained trees with the smallest average diameter (17.8cm), lowest average height (13m), highest frequency of short trees (81.2%) lowest frequency of tall trees >20m (18.4%), smaller crown areas (62.8m²) and least frequency of tree canopy connectivity >25% (21.0%). Plains habitat contained trees with large diameters compared to hill forest (21cm), but contained significantly less tall trees >20m (29.5%), small crown areas comparable to alluvial (63.9m²) and with an average tree height of 16.8m. Hill-swamp habitat contained trees with large diameters (18.2cm), overall tree height comparable to plains habitat (16m), the smallest crown areas (58.9m²) and a large canopy connectivity >25% (74.6%). Frequency of tall trees were similar to that of plains habitat (24.7%). Differences due to these structural aspects between forest types influenced hylobatid densities, with highest densities found in the hill forest and lowest densities within the alluvial habitat for both species. This suggests that it is possible to extrapolate from current wide-scale land unit descriptions to predict gibbon densities in structurally similar habitats.

5.1 Differences in forest structure between habitat types

All four identified land units showed significant differences between tree variables and vegetation structure, with the largest differences seen in stem diameter, tree height, height to first major bole, crown area and canopy connectivity. There is a significant difference in the diameter of trees between habitat types, with both hill and plains forest showing a larger average diameter than both alluvial and hill-swamp forest, but equal to plains habitat. However, trees across all areas showed small stem diameters

in comparison to expected stem diameter size of primary undisturbed lowland forest, originally identified through vegetation studies by Laumonier (1997). This study identifies average tree height in hills and plains habitats between 25-30m, with emergent trees reaching 50m in height. Large diameters generally denote tree age, irrespective of species. Small tree saplings must first grow vertically, reaching the canopy and gaining access to light to photosynthesise, prior to using resources for trunk and branch growth, thus older trees tend to have a larger diameter. It is apparent from the study that many trees located within the study area are relatively young and in general small, with few trees with diameters >60cm existing within the area. A study in Sikundur assessing vegetation structure 22 years' post logging (Priatna et al. 2004) showed 67.6% of trees had diameters of 10-20cm and only 17% with diameters 21-30cm within a 2ha plot.

Hill forests show the largest percentage of trees with a diameter >60cm (7.33%), though this is still relatively low indicating more secondary, regenerative forest is still present, and that although many areas are showing signs of regeneration, the process is very much still ongoing. Alluvial forest was found to possess the lowest average tree diameter (17.8cm) with only 3.61% of trees within this land unit having a tree diameter >60cm. Nevertheless, all habitat types possessed a few trees with large diameters; the largest found in hill-swamp (121cm), followed by plains (116.6cm), hills (113cm) and alluvial (95.5cm). This provides evidence of remnant primary forest existing within the area. Unfortunately, the rare presence of such trees reflects the amount of disturbance this forest has undergone, and the considerable timescale needed in order to regain comparable measurements to undisturbed primary rainforest.

Frequency of tall trees between land units differed significantly, with the hill forest containing the largest percentage of large trees (41.45% >20m) whilst alluvial contained the lowest percentage of trees >20m (18.4%) and the highest percentage of trees <20m (81.22%). Tree height is a significant factor in forest structure in regards to supporting highly arboreal primates such as gibbons and siamangs (Hamard et al. 2010). Cheyne et al (2013) have shown gibbons prefer to travel in high canopies and will avoid low canopies if possible. As such, hill forest containing the largest density of gibbon groups, had significantly greater frequencies of trees between 20-30m (30.58%) and >30m (10.57%), with plains and hill-swamp forest containing the lowest densities of gibbon groups, possessing a significant proportion of trees 20-30m in height (23.5%, 18.5% respectively). Thus, hill forest habitats provided a more layered heterogeneous canopy structure, preferred by gibbon and siamang species. Tree heights overall were low, with

the majority of trees in all land units not exceeding 30m in height. From 1418 trees sampled across the four forest habitat types, only eight trees reached a height above 45m; seven found within hill forest and one in the plains habitat. This shows a stark difference in comparison to Laumonier's study (1997), where Sumatran lowland forest contained a mean canopy height of 25-30m, with emergent trees between 45-55m. Only a single tree was recorded >50m (51.2m) which was located within the hill-swamp forest. These reduced tree heights and low numbers of tall emergents, appear to reflect Sikundur's logging history and disturbance levels. The once tall emergent trees have been harvested, and secondary regrowth has not yet had a significant amount of time to reach former primary forest heights. Even so, the presence of these reduced height emergent trees represents regeneration within these areas, and if anthropogenic pressures remain absent, demonstrates the potential for the forest to regain its original height.

The connectivity of individual trees is an important component of habitat preference for the persistence of gibbon and siamangs in forest habitats. Brachiation, the most frequently used form of locomotion by these species requires a connective canopy which allows travel to essential food resources and avoids using other less energy inefficient modes of travel and ground dwelling predators (Anderson et al. 2007). A sufficient amount of tree connectivity allows the formation of arboreal pathways, and recent studies have shown that canopy cover significantly influenced the density of gibbons within forest habitats (Hamard et al. 2010; Phoonjampa et al. 2011). Hill and hill-swamp habitat have significantly higher tree connectivity than other habitat types; higher frequency of trees within the hill forest showed connectivity between 50-75% (42.64%). Tree crown area within the hills habitat was also significantly larger than other land units. It would be expected that larger, older, taller trees would have a more established crown area and therefore a higher level of connectivity, whereas younger trees will be expected to possess a smaller crown area. Indeed, hill forest contains the largest and tallest trees. The alluvial and plains forest contains shorter trees which have smaller crown areas and a less well connected canopy, relating to the smallest gibbon densities recorded there. Priatna et al (2004) showed logging caused severe damage to Sikundur's forest canopy, with a recorded canopy gap size of 6200m² within a 2ha plot four years after logging. After 18 years, canopy recovery had reduced gaps within the area to 4920m², a rate of 1.14% in-filling per year. It is suggested that at this rate of recovery, the canopy at Sikundur would reach a canopy cover similar to primary forest

in 35 years. In comparison, canopy gaps in undisturbed lowland primary forest in Malaysia make up only 10-17% of the entire forest canopy (Whitmore 1984).

Density of trees showed little variation across habitat types, with only a significant difference found between plains (360trees/ha) and alluvial (496trees/ha). This suggests that although the forest had a relatively low tree height for a Sumatran lowland forest, tree regeneration seems to be successful, with many trees having already reached substantial heights and stem diameters >10cm. Twenty-two years after logging, Priatna et al (2004) found that within the 2ha plot, tree number had reached 1145 trees in comparison to 837 trees found only four years post logging. Overall tree density does not necessarily signify more suitable forest for arboreal primates, as lower tree height classes are unsuitable as they are too small and weak to sustain the weight needed for locomotion. However, a higher percentage of tall trees (>20m) was identified in hill (41.15%), plain (29.48%) and hill-swamp forests (24.73%) which are required by gibbon species for travel, feeding and providing safe sleeping sites.

This study has shown that areas of primary forest still exist within Sikundur, albeit in low densities. Nonetheless, the effect of historical logging has had a large impact on the structure of the vegetation. Structure measurements within the area in 2000 (22 years post logging) has shown recovery is ongoing, with increases in tree species and tree density. Priatna et al (2004) estimated that the forest will require at least 56 years post logging to show features which will resemble an undisturbed primary forest.

5.2 Hylobatid density surveys

The results indicate that healthy populations of both lar gibbon and siamang populations persist within the Sikundur region; as all density estimates found during the study are within the mid-range of published density estimates for the species, in comparison to field sites with similar forest (Table 5.1). Moreover, it shows that the auditory sampling method is replicable. Lar gibbons are found within all habitat types surveyed and always at higher densities than siamangs, although lar gibbon groups do not negatively affect siamangs and densities were not correlated. Both gibbon and siamang densities were greatest within the hill forest, which possesses the most stratified, structurally complex uninterrupted canopies that have been found to be preferred by gibbon species in other areas. Alluvial forest, possessing lower, more disturbed and less structurally complex forest with a high frequency of canopy gaps, holds the lowest gibbon densities. Results show that the carrying capacity of this

historically disturbed, rejuvenating forest is greater for lar gibbons than that for siamangs. Lar gibbons seem to fair better. This may be due to their reduced body size enabling them to cross weaker, less well connected canopies, and thus are able to access food sources, sleeping trees and travel routes potentially inaccessible to siamangs. The larger bodied siamang requires larger, more structurally robust canopies to allow travel, and is therefore more limited within the area. However, the highest density of lar gibbons found in an area are comparable to the highest density of siamangs, showing the sympatric nature of these species and their ability to co-exist.

The ratio of species densities are comparable to range-wide densities; gibbons tend to increase from southern to northern latitudes on Sumatra, Borneo and Peninsular Malaysia, and contrarily, siamang tend to decline south to north (O'Brien et al. 2003). Sikundur is located at the northern extreme of their range, where gibbons are at their highest and siamang lowest densities, and results from this study concur.

Table 5.1. Group Density Estimates of lar gibbons and siamangs showing comparisons from this study and past studies

<i>Species</i>	<i>Group Density (groups/km²)</i>	<i>Habitat Type</i>	<i>Site</i>	<i>Reference</i>
Lar Gibbon <i>Hylobates lar</i>	1.32	Lowland (alluvial)	Sikundur, Sumatra	This study
Lar Gibbon <i>Hylobates lar</i>	2.82	Lowland (plains)	Sikundur, Sumatra	This study
Lar Gibbon <i>Hylobates lar</i>	2.75	Lowland (hills)	Sikundur, Sumatra	This study
Lar Gibbon <i>Hylobates lar</i>	2.28	Lowland (hill-swamp)	Sikundur, Sumatra	This study
Lar Gibbon <i>Hylobates lar</i>	2.85	Lowland (alluvial)	Sikundur, Sumatra	Consiglio (2015)
Lar Gibbon <i>Hylobates lar</i>	0.44	Lowland (plains)	Sikundur, Sumatra	Consiglio (2015)
Lar Gibbon <i>Hylobates lar</i>	0.86	Lowland (hills)	Sikundur, Sumatra	Consiglio (2015)
<i>Lar Gibbon Hylobates lar</i>	2.6		Phu Khieo Wildlife Sanctuary, Thailand	
Agile Gibbon <i>Hylobates agilis</i>	1.7		Sabangau catchment, Kalimantan	Hamard et al. (2010)
Agile Gibbon <i>Hylobates agilis</i>	2.0	Lowland forest	Kerinci-seblat National Park, Sumatra	Yanuar (2009)
Agile Gibbon <i>Hylobates agilis</i>	3.8	Hill dipterocarp	Kerinci-seblat National Park, Sumatra	Yanuar (2009)
<i>Bornean Agile gibbon Hylobates agilis albibarbis</i>	2.16		Sabangau catchment, Kalimantan	Buckley et al. (2006)
Agile gibbon <i>Hylobates agilis</i>	1.4	Lowland forest	BBSNP	O'Brien (2003)
Agile gibbon <i>Hylobates agilis</i>	2.8	Hill forest	BBSNP	O'Brien (2003)
Agile gibbon <i>Hylobates agilis</i>	1.9	lowland	Way kambas, sumatra	Yanuar and Sugardjito (1993)
Siamang <i>Symphalangus syndactylus</i>	0.40	Lowland (alluvial)	Sikundur, Sumatra	This study
Siamang <i>Symphalangus syndactylus</i>	2.11	Lowland (plains)	Sikundur, Sumatra	This study
Siamang <i>Symphalangus syndactylus</i>	1.65	Lowland (hills)	Sikundur, Sumatra	This study
Siamang <i>Symphalangus syndactylus</i>	1.41	Lowland (hill-swamp)	Sikundur, Sumatra	This study
Siamang <i>Symphalangus syndactylus</i>	1.52	Lowland (alluvial)	Sikundur, Sumatra	Consiglio (2015)
Siamang <i>Symphalangus syndactylus</i>	0.45	Lowland (plains)	Sikundur, Sumatra	Consiglio (2015)
Siamang <i>Symphalangus syndactylus</i>	0.67	Lowland (hills)	Sikundur, Sumatra	Consiglio (2015)
Siamang <i>Symphalangus syndactylus</i>	2.1	Hill dipterocarp	Kerinci-seblat National Park, Sumatra	Yanuar (2009)
Siamang <i>Symphalangus syndactylus</i>	5	Lowland forest	Kerinci-seblat National Park, Sumatra	Yanuar (2009)
Siamang <i>Symphalangus syndactylus</i>	10.3	Lowland forest	BBSNP	O'Brien (2003)
Siamang <i>Symphalangus syndactylus</i>	4.2	Hill forest	BBSNP	O'Brien (2003)
Siamang <i>Symphalangus syndactylus</i>	2.8	lowland	Way kambas, sumatra	Yanuar and Sugardjito (1993)
Siamang <i>Symphalangus syndactylus</i>	7	lowland	ketambe	Mackinnon & Mackinnon (1980)

5.3 *Hylobatid* Densities estimations through triangulation method

Auditory sampling is a technique widely used, especially in cases of unhabituated primates where line transects are not possible due to limited visual detections. Fixed point counts using auditory sampling do however, have a number of biases associated with this method (Hamard et al. 2010; Rawson et al. 2010). Firstly, the method excludes lone animals from the estimate as only duets are taken into account in the analysis. A study of Bornean agile gibbons *Hylobates albibarbis* in West Kalimantan by Cowlishaw (1992) estimated lone animals make up approximately 5.5% of the total population. As this only affects individual density estimates, and not density of groups/km² this remains unchanged in this study. Second, auditory sampling is thought to be dependent on weather conditions, and factors such as rain are known to influence singing frequency and start times of singing bouts (Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993, O'Brien et al. 2004, Cheyne et al. 2013, Hamard et al. 2010). To prevent bias of data, surveys were avoided on rainy mornings and any mornings following a night of heavy rain. Rain only affected one of the study areas (in alluvial forest) reducing the survey to three days in this location. Furthermore, Brockelman and Srikosamatara (1993) found wind affected singing in siamangs (but not gibbons). Wind conditions were calm on every survey morning, and therefore this factor was not likely to have an effect on singing frequency. Although detailed weather conditions were not collected, no other extreme weather conditions affected data collection or survey effort. Duration of time spent at each vocal array extended for at least half an hour past the last vocalisation heard to avoid missing any groups delaying singing due to any adverse weather conditions. Several studies (Brockelman and Srikosamatara 1993; Geissmann and Nijman 2006) have suggested that low densities of gibbons within an area (<2 groups/km²) may affect singing, as singing can be stimulated by duets from neighbouring groups. No correlation was found between calling probability $p(1)$ and density of either gibbon or siamang in this study and calling probabilities over the four-day period were relatively high (siamang= 0.52-1, gibbon 0.48-1). It has been suggested that for reliable density estimates, calling probability should be ≥ 0.5 (Brockelman and Ali 1987). Four days were conducted at each array (except one) and calling probability was only recorded lower than 0.5 on two occasions; both for lar gibbon with a value of 0.48 on both occasions. This value was close enough to 0.5 to warrant effective density estimates have been obtained through the study. Another bias associated with gibbon surveys is a non-random survey design. This is usually due to topography; situating listening posts on high

elevation maximises the distance to which gibbons can be heard and prevents groups being missed. This approach violates assumptions of random sampling designs and therefore cannot be extrapolated to the population as a whole (Rawson et al.2010). However, the most problematic issue in conducting auditory surveys for gibbons is calculating the area surveyed from a listening post; i.e the effective listening area. Brockelman and Ali (1987) avoided this issue by setting a predetermined radius around each listening post. Only vocalisations heard within the predetermined survey listening radius are counted, vocalisations heard from more than one post and triangulate are counted, and all vocalisations occurring outside of this listening radius are discarded. This raises many issues including: omitted vocalisations recorded from single posts may affect density estimates, additional survey effort relative to survey coverage is required, and bearing error is not taken into account. This study used a fixed radius of 1km and several measures were undertaken to limit the above bias; 1. Vocalisations heard from a single post were included within the analysis if located more than 500m away from any other identified group on the same day following guidelines used by Rawson (2010); 2. Survey areas were set in a grid formation adjacent to one another to maximise coverage; if groups were heard from two different arrays within the same approximate location, one of these groups was eliminated to avoid double counting, 3. The same observers were used throughout the whole study to limit bearing error, with two people located at each listening post.

5.4: Hylobatid Densities estimations through SECR

GibbonSECR designed by Kidney (2013) has provided an alternative for analysing visually cryptic species through auditory sampling in attempting to address some of the issues in the above estimation methods. For example, this model accounts for the imperfect detection of groups through the use of a detection function, providing a more reliable estimate of the effective sampling area, and allows for bearing error through the inclusion of a bearing error model (Kidney 2013). Additionally, it produces reliable model-based estimates of uncertainty for all parameters such as the Akaike Information Criterion (AIC) to be used for the model selection. However, use of the gibbonSECR model in this study produced considerably lower density estimates than calculated from standard triangulation, with values averaging 3.35 (SE 0.22) lower on all occasions. This has been observed in other studies (Cheyne, pers coms, 21st August, 2016). Reasoning for the lowered density estimate is unknown, though may be due to the fact that the

program is unable to account for multiple sampling occasions and data are entered as one single sample period, creating a potential source of error. However, gibbonSECR is a promising tool which has the potential to improve the accuracy and reliability of primate density data. Manipulating the model in a more robust way may lead to more efficient data analysis and a preferred density estimation method for future density estimations. Studies comparing various techniques have concluded that using the manual triangulation method to estimate density remains an important tool for hylobatid surveys at present through its efficiency in locating gibbon groups using acoustic detection.

5.5: Relationships between forest structure and gibbon density

Hylobatids depend on the forest canopy for survival, in terms of food shelter and movement due to their almost total arboreality (Bartlett 2007). Hence, structural characteristics of the forest in terms of tree height, tree density, canopy cover and percentage of tall trees (as well as feeding trees) are important factors linking to population densities. The use of vegetation plots for forest structural analysis has proved efficient in identifying structural differences in forest characteristics. This is a time efficient method that can easily be associated with auditory sampling as a small number of plots can be undertaken each day after the vocal arrays in each survey area. Within the Sikundur survey area, gibbon groups ranged from 1 to almost 4 groups/km², whilst siamangs between 0 to almost 3 groups/km². This suggests that hylobatid density is tightly correlated with local habitat quality or carrying capacity of the habitat to support a given population density (Marshall 2010; Phoonjampa et al, 2011), and that lar gibbons and siamangs can be highly adaptable and flexible to environmental changes.

Lar gibbon density was observed to be highly correlated to several vegetation parameters, especially tree height, crown area and canopy connectivity. This result is not surprising as gibbons are known to prefer to use high forest canopy layers for all activities (Brockelman and Ali, 1987, O'Brien et al. 2004, Hamard et al. 2010). The presence of tall trees within a habitat has similarly been linked to presence and densities of other species: Di Bitetti et al (2000) found that tufted capuchin monkeys *Cebus apella nigrilus* spent the night in mature forest that contained taller trees and Phoonjampa et al (2010) found pileated gibbons prefer to use tall emergent trees as sleeping sites.

Hylobatids are relatively adaptable, and have been shown to use a lower forest canopy following disturbance (such as logging) to their habitat (Nijman, 2001). Gibbons are

known to use large emergent trees to conduct morning vocalisations and for sleeping trees. However, the frequency of very tall trees (>30m) and trees 20-30m in height and high frequency of tree connectivity did not relate to gibbon density in this study. The most significant finding is the negative correlation and relationship found between lar gibbons and tree heights of <20m, and connectivity of <15%. This suggests that lar gibbons can tolerate low frequencies of high trees and low connectivity of trees as long as this remains above a certain threshold. Overall tree canopy connectivity and tree height seem to be the most influential variables in relation to gibbon density, which is found to be an important factor in other study sites (Hamard et al. 2010; Phoonjampa et al, 2011).

Siamang density was more influenced by trees in the height range of 20-30m and tree connectivity between 50-75%. Siamangs are found to live at lower canopy levels than lar gibbons. The majority of tree heights within Sikundur's forest fall within this category. Siamangs seem to have a lower level of tolerance to low tree connectivity, as their densities were negatively correlated with connectivity of <25% compared to the lar gibbon's seemingly 'cut-off point' of <15%. Siamangs are considerably larger than lar gibbons (Chivers 1974) which could account for the larger canopy needed to hold their body weight when travelling. Siamangs are also more folivorous (O'Brien et al. 2003), meaning they need to travel less to food resources, as edible leaves are more uniformly distributed than fruits. This means they can remain in lower canopy levels to reach food and populations can be sustained in relatively smaller forest patches. However, the presence of a high frequency of trees <20m in an area would prevent exploitation of the forest as trees would not be sufficiently strong and canopy connectivity not sufficiently well developed to support their larger body weight limiting arboreal travel routes. Whereas the smaller body size of lar gibbons means they can survive more disturbance as they can reach food sources located in more disturbed areas, as these smaller trees and less well developed canopies can hold their weight and allow arboreal movement. The highest densities of nearly 4 groups/km² of lar gibbons were found within the hill forest areas. These areas, although showing signs of historical logging, such as large logging roads and a lower than average tree height, have the largest frequency of emergent trees, highest canopy connectivity and larger crown areas in comparison to all other habitats. Hill-swamp areas also have good quality habitat characteristics similar to hill forest, however the presence of swamp areas containing relatively small trees decreases available habitat for the species which is reflected in the lower densities

recorded there. Alluvial forest has much less suitable habitat for both gibbons and siamangs, offering very little canopy connectivity for brachiation, and small trees unsuitable for sleeping and territorial vocalisations. Even without historical logging these areas have been a less suitable habitat choice for hylobatids.

Although density gradients of these species are related to forest structure and composition, they are influenced by preferred food items (Marshall & Leighton, 2006; Marshall, 2009; Hamard et al. 2010). Siamangs are found to be more frugivorous on Sumatra in comparison to Malaysia (Palombit 1997), increasing competition with the lar gibbon and explaining why siamang numbers are less when living sympatrically with the lar gibbon. Palombit (1997) suggests that the increased frugivory in GLNP is due to increased feeding on strangler figs, rather than increased feeding on other fruits. These grow in mid-range canopy levels also explaining why siamangs are influenced by this tree height class. This higher availability of figs and fruiting trees in Sumatra may increase dietary overlap between gibbons and siamangs, and as siamangs have a larger body size and longer feeding bouts, this may give them a competitive advantage. However, Sikundur's fruiting score is low and strangler figs are much rarer in comparison to other Sumatran sites in the GLNP (A. H. Korstjens pers. comm. 20th July, 2016), being more similar to Bornean field sites than Sumatran areas (SOCP, 2014), potentially explaining the lower densities of siamangs in relation to gibbons. Therefore, these hylobatids may be more folivorous within this forest.

The findings of this study are comparable to other studies conducted on hylobatid relationships with vegetation structure, supporting the observation that hylobatids rely on tree height and a high level of connectivity to sustain healthy population numbers. Although Sikundur has been subjected to a large degree of selective logging, hylobatid densities within these areas have been well sustained, with densities comparable to other forests in Sumatra, Borneo and Malaysia (Table 5.1). A reason for this may be that the site is well connected to less disturbed areas of the National Park. Research has shown an increased ability for a habitat and associated species to recuperate if there is a primary, undisturbed habitat and a healthy species population within an adjacent habitat. As no density estimates have been undertaken within the area prior to this study, it is difficult to speculate the effects that logging has had on the population and the carrying capacity of the forest prior to the onset of logging.

5.6: Implications for forest conservation

Deforestation is still the largest threat to biodiversity and forest loss in Indonesia (Brun et al. 2015) and despite the protection of national park status, many lowland forests within Sumatra are still subjected to much illegal logging, land clearance and species removal (Jepson and Mulyani 2013). Due to these anthropogenic factors, few undisturbed primary forests exist, whereas secondary, degraded and fragmented habitats are continually increasing (Gibson et al. 2011). Studies assessing differences in population densities of species in primary and secondary forests have indicated a level of tolerance exhibited, with many disturbed habitats still maintaining viable levels of biodiversity (Berry et al. 2010). Although selective logging can generally be viewed slightly better than complete land clearance, damage to the forest exceeds just the felled tree. Johns (1988) found a tree removal rate of 3.3%, resulted in 50% of surrounding trees additionally destroyed from the extraction. This study has revealed that these two sympatric hylobatid species can not only tolerate specific levels of disturbance, but have the ability to recover from past large-scale logging of their habitat. Nevertheless, this is the first study conducted on these hylobatid populations 30 years post logging. Recovery of these species is impeded by the slow regeneration of tropical forests (Priatna et al. 2004; Brockelman et al 2009) and compounded by gibbon's slow reproductive rates and late age of maturity (Bartlett 2007). To ensure the long-term persistence of these species Indonesian government organisations will need to gain control over illegal logging and anthropogenic disturbances that are on-going within the national parks boundaries. Although this study has provided relatively stable population estimates of hylobatids within the lowland forest of Sikundur, the future of these primates is still relatively uncertain, and will depend heavily on improved conservation efforts and protection of these rare and decreasing forest habitats.

5.7: Recommendations for future research

Though many studies on the density and abundance of hylobatid species have been undertaken, relatively few of these are in Sumatra, especially within the lowland forests, which are quickly becoming one of the rarest habitats due to continued destruction. This study provided the first density estimate of the two sympatric hylobatid species residing within these lowland forests; the lar gibbon and the siamang. However, with slow reproducing primate species such as hylobatids, population trends require long

monitoring periods, and repeated surveys within the area will provide detailed information on population trends in Sikundur. A repeated survey would not only monitor population trends, but will highlight differences in seasonal variation, and health of populations in the long term.

In order to better understand habit preferences of hylobatids, additional data would be beneficial in understanding species preference to habitat selection. A larger amount of vegetation plots within each survey area may provide a better idea of habitat preferences. Due to a random sampling design, vegetation plots may have been placed in areas unrepresentative of the habitat as a whole, or areas used by hylobatids that contained more structurally suitable trees may have been missed. A large vegetation coverage by additional 25 x 25m vegetation plots may reveal insights this study may have missed.

Additionally, it would be a huge advantage in habituating a group of both lar gibbon and siamang in the area. Preference of sleeping trees and limitations to choice of sleeping site would provide an insight into restrictions within their range. Additionally, habituation would allow a further study on feeding behaviours. Due to the low productivity of this site in terms of fruit, it would be of great interest to examine the flexibility these species have in relation to diet, and how this relates to densities, abundance and group size.

Historical and current disturbances within the area are known, however, these disturbances have not been quantified in any useful way to be able to analyse them. A study design incorporating measurements of disturbance levels within the forest would be of interest in relation to not only hylobatids, but other species that inhabit the area, and to overall effects these disturbances have on biodiversity.

Chapter 6: Conclusion

A forest's suitability in supporting primate populations may be partially dependent upon the structural characteristics of its vegetation. This study provides an initial assessment of two species of gibbon; lar gibbon and siamang within the Sikundur forest, and how density of these species is affected by habitat quality and post logging recovery. As this study is the first large scale assessment of these species within the area, it is impossible to assess recovery abilities prior to heavy logging. The highest density of

lar gibbon was 3.56 groups/km², which is lower than a population recorded in a pristine mountainous forest at the Khao Soi Dao Wildlife Sanctuary, where populations reached 5 groups/km² (Brockelman and Srikosamatara, 1993) but comparable to many other Indonesian study sites. Hylobatid populations within the study area are largely influenced by tree height, tree crown area and a low canopy connectivity, with highest densities located within areas containing the tallest trees, largest crown areas and highest canopy connectivity. However, Sikundur's forest is still in a post logging recovery stage, with a lower than average canopy height and emergent trees, predicted to reach a recovery level similar to primary forest within a further 35 years (Priatna et al. 2004). Nonetheless, it is encouraging to find that these species have survived 30 years in historically logged, recovering forest. With further repeated population studies within this area, population trends and recovery rates can be ascertained, which will provide essential information in aiding the conservation of these important primate species.

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