Forest structure and group density of Thomas' langur monkey, *Presbytis thomasi*

Helen Slater

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Abstract

Tropical forests contain a substantial portion of global biodiversity, and provide a wide range of ecosystem services. Anthropogenic activities such as logging and agriculture alter the physical structure of forests and thus impact arboreal primates through altered availability of food and suitable sleeping sites and reduced ability to move through the forest canopy. There are many studies detailing the negative impacts of anthropogenic disturbance on primate populations in tropical forests, however few of these adequately explain the mechanisms behind these impacts. This study investigated the structure of disturbed forest at Sikundur, North Sumatra, Indonesia and the group density of an arboreal primate, *Presbytis thomasi*, in order to identify links between forest structure and primate density. Quantitative data was collected on forest structure from line transects and plots and compared between three land units: alluvial, hills and plains. Group densities of *Presbytis thomasi* were estimated using line transects and vocal arrays. Prior to this study, vocal arrays had not been applied to *P. thomasi*, however this method is more effective, especially in disturbed forest where visibility is poor, and primates are unhabituated.

Top height and the proportion of large, emergent trees was consistently low throughout the study site due to selective logging in the 1970s and 80s. However, alluvial forest has a significantly higher diameter at breast height, and lower height-DBH ratio than hills and plains, indicating that these trees are more mature. Illegal logging remains a regular occurrence in this area, but appears to be less in alluvial forest, which is less accessible than plains and hills. Plains forest was observed to be the most frequently exploited by local villagers. Group density of *P. thomasi* was highest in hills forest, which has a significantly higher bole height. Habitat preferences of *P. thomasi* may be linked to density of suitable sleeping trees and levels of human traffic within the forest.

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Chapter 1 : Introduction

Anthropogenic activities are having an increasing impact on tropical forests, which will have implications for species which dwell within these ecosystems. The total loss of tropical forests between 1996 and 2010 was estimated at approximately 100 million hectares (Food and Agriculture Organization, 2012). Habitat degradation has been identified as one of the main drivers of global biodiversity loss (Mantyka-pringle et al. 2012). Activities such as logging and agriculture will impact on forest-dwelling species by altering the composition and vegetative structure of ecosystems. These changes have been shown to have negative impacts on some wildlife populations (Sussman and Phillips-Conroy 1995, Pinto et al. 2014), while others appear to have been able to adapt to this disturbance (Schwitzer et al. 2011). A better understanding of the varying responses of animals to habitat alteration will enable improved conservation planning to protect forest ecosystems from further degradation. Therefore, this project looks at disturbed forests in Indonesian lowland forest and how forest characteristics affect primate densities.

1.1: Anthropogenic effects on forests

At present, the total globally remaining forest cover is estimated at 50% of its original extent, with only 40% of this being unaltered by human activities (Bryant et al. 1997). A reduction in forest cover will, in many cases, directly lead to declines in wildlife populations due to resource shortages (Schwitzer et al. 2011). Other human impacts are often exacerbated by deforestation; for example, hunting and human-wildlife conflict often increase as logged forests become more accessible (Dickman 2012). Remaining forests are being degraded through selective logging, agriculture and fragmentation. Fragmentation has been shown to negatively impact populations by isolating them and reducing gene flow, although there has been variation observed on this effect (Mantyka-Pringle et al. 2012). Agriculture can also degrade forest ecosystems by removing native species, and reducing habitat heterogeneity, leading to increased competition for limited resources (Estrada et al. 2012). All of these changes will fundamentally alter the structure and composition of forests, and this can have unknown impacts on the animal populations that use them.

Vegetation structure is likely an important factor influencing forest dwelling populations of primates, although there is little data available to quantify this relationship. While there has been a great deal of work on primate populations, much of this has focussed solely on describing their distribution and/or population trends, and has not satisfactorily explained the factors which drive them (Kamilar and Beaudrot 2013). There is indirect evidence to suggest that forest structure influences distribution. Several studies have noted that certain species seem to prefer particular types of forest (Peres and Janson 1999, Warner 2002, Lwanga 2006, De A. Moura 2007, Ortiz-Martínez et al. 2008, Boyle and Smith 2010, Valsecchi et al. 2010). There have been very few studies which have looked directly at the effect of forest structure on primate species (Manduell et al. 2012, Palminteri et al. 2012, Gouveia et al. 2014). The main reason for this lack of data is that collecting detailed data of forest structure is time-consuming and often impractical, however the developments of new methods are making these data easier to collect, for example Manduell et al. (2012) adapted the point centre quarter method to efficiently map vegetation and forest structure along transects. Employing these new methods to correlate forest structure with primate distribution will likely prove useful for predicting the potential impact of continued alterations to forests through human activities.

Human disturbance will cause significant changes to the composition and structure of vegetation in forests (Priatna et al. 2000, Sodhi et al. 2010, Reiners et al. 2015). Conversion to agricultural land, for example, will often homogenise an ecosystem and make it unsuitable for many species which previously occupied it, although this is not always the case (Estrada et al. 2012). Selective logging, which is often hailed as a sustainable logging practice, also results in notable changes to forests (Pinto et al. 2014). Often, during selective logging, the tallest trees are targeted, resulting in major differences in vertical canopy structure, as well as reduced canopy connectivity and an increase in gaps, which will further alter the forest structure through edge effects (Schwitzer et al. 2011). Human activities will change the composition of tree species within an ecosystem, and this will have implications for the rest of the forest community; either directly, by altering the availability and distribution of food resources, or indirectly, by increased exposure to predators and competition (Isabirye-

Basuta 2004, Schwitzer et al. 2011). Understanding the ways in which human activities change forest structure is an important step in conserving forest ecosystems.

1.2: Responses of species to changes in habitat structure

The effects of habitat loss and fragmentation on animal populations have been well documented, however, there is relatively little data available on the ways in which forest structure shapes communities, although it is likely to play an important role (Palminteri et al. 2012). A study by Emmons (1984) found that habitat heterogeneity was a more important determinant of density and diversity of mammal species than rainfall and seasonality; while several studies of primate distributions have linked densities of some species to forest type, implicating structure as a determinant of species distributions (Sussman and Phillips-Conroy 1995, Karere et al. 2004, Lwanga 2006, De A. Moura 2007, Valsecchi et al. 2010). As mentioned above, selective logging often removes the tallest trees and creates gaps in canopy cover, which can lead to an increase in predation; arboreal species may have to use the lower levels of the canopy, exposing them to ground predators, while reduced canopy cover improves visibility for aerial predators (Schwitzer et al. 2011). Selectively removing trees will also reduce overall canopy cover and create gaps, which will result in changes in forest microclimate, which will have a knock-on effect for the rest of the ecosystem (Ries et al. 2004). Canopy connectivity is also reduced, which will have implications for arboreal species and their ability to move through the forest (Manduell et al. 2012). Despite this evidence, there have been, to date, few attempts to directly correlate forest structure variables with species distributions for arboreal primates.

1.3: Primates as ecosystem indicators

Primate species are an ideal model for studying patterns in species distribution and modelling the potential impacts of disturbance on populations. Primates resonate well with both scientists and the public alike, making them a popular focus of research, leading to a substantial body of work on their ecology and distribution. Compared with other, more cryptic species, measuring the densities and distributions of primates is relatively easy. This means that population parameters for predictive models, which are usually lacking in endangered species research, are available for many primate species. They are widely used as indicators of ecosystem health, and it has been shown that primate distribution patterns are often closely correlated with those of other mammal species, suggesting that habitat alterations will impact them in a similar way (Emmons 1999). As such, conserving primates will benefit a range of other species within an ecosystem. This also means that data collected on primate species can be used to predict how less well-studied species with similar characteristics may respond to environmental changes, such as those resulting from logging. It is for the above reasons that primates have been chosen as a focus for this study.

1.4: Focus of study

This study focuses on the arboreal Thomas' langur monkey, *Presbytis thomasi*; endemic to Sumatra, Indonesia. *P. thomasi* is found predominantly in primary forest and shows a strong preference for lowland alluvial forest. They have a lower tolerance for disturbance than two other *Presbytis* species, *P. cristata* and *P. melalophos*, found within similar habitats in Sumatra. Lower densities of *P. thomasi* have been found in secondary forest compared with primary forest, with reported group densities of 2.7 groups/km^2 in secondary and plantation forest compared with 3.7 groups/km^2 in primary forest (Gurmaya 1986, Sterck 1996). *P. thomasi* is listed as vulnerable on the IUCN red list, as a result of population declines of more than 30% over the past 40 years, mostly due to forest degradation and loss (Supriatna and Mittermeier 2008). This species is also listed on appendix II of CITES (CITES 2014). The behaviour and ecology of *P. thomasi* has been well studied at two sites, Ketambe and Bohorok, within the Gunung Leuser National Park of Northern Sumatra. However, there has been little data gathered on the population within the Sikundur region and there is currently no available data to explain why *P. thomasi* is less able to cope with disturbance than other *Presbytis* species in the area. *P. thomasi* usually prefers tall trees, although Gurmaya (1986) observed that they will use lower canopy in areas where the proportion of tall trees is less. Their diet is predominantly made up of leaves, although they have demonstrated dietary flexibility, feeding on fruits, flowers, fungi and gastropods (Supriatna and Mittermeier 2008). There is also a marked difference in the dietary composition of the Ketambe and Bohorok study populations (Wich and Sterck

2010). Understanding the extent of their behavioural flexibility will be immensely helpful towards conservation efforts for the species.

This study was conducted within the Sikundur region of the Gunung Leuser National Park in North Sumatra, Indonesia. The chosen study area comprises of three distinct land units, identified by Laumonier (1997). These are classified as follows; alluvial, characterized by low-lying land located next to rivers, with fine-textured poorly-drained soils; plains, typically consisting of flat to undulating land at low elevation, with porous, acidic soils; and hills, found at higher elevations (100-500m), and comprised of fine-medium textured, leached soils with low organic content. More information on these land units is given in chapter 3 of this thesis. Since the chosen study area contains parts of all three land units, this enables comparison of forest structure between them, and can provide insight into the habitat preferences exhibited by *P. thomasi*.

1.5: Study aims and objectives

The aim of this study is to survey the forest structure and group density of *P. thomasi*, within a block of lowland forest in the Sikundur region of Northern Sumatra, Indonesia, with a view to gaining an insight into the ways in which forest structure influences the distribution of primates. Better understanding of this relationship will enable more powerful predictions of the potential impact of anthropogenic changes on forest dwelling species, which will be vital to planning and implementing effective conservation strategies. This will be achieved by completing the following objectives:

1. Establish any differences in structural characteristics across three different land units (shown in figure 3.2), which have previously been identified in the region by Laumonier (1997). The structure is expected to be reflective of the disturbance history and relative accessibility of each land unit. Areas which are more accessible are predicted to be more disturbed, and therefore have lower top and bole height; lower diameter at breast height; smaller crown

area; and reduced support availability and canopy connectivity for *P. thomasi*.

2. Estimate the group density of *P. thomasi* at Sikundur. This is predicted to be lower than densities reported from previous studies in primary forest at Ketambe by Assink & Van Dijk (1990). The group density is expected to be higher in the land unit which demonstrates the lowest level of anthropogenic disturbance.
3. Compare the traditional line transect method to a method employing vocal arrays for surveying populations of *P. thomasi*. Due to their arboreal nature, visual census data is challenging to collect, especially in areas where the animals are not habituated to humans. Therefore a method utilising morning vocalisations as a proxy for group density could prove to be more effective for this species.
4. Identify possible links between structural characteristics and group density which can be explored further to provide information on habitat preferences and ecological requirements for *P. thomasi*. It is expected that langurs will prefer forests with taller canopies and better connectivity, as well as a higher availability of supports, all of which facilitate safe sleeping site selection, predator avoidance and locomotion.

Chapter 2 : Forest structure and primate populations

2.1: Introduction

Forest ecosystems represent an important resource for human populations. Sequestering carbon helps to mitigate the effects of anthropogenic climate change, while forest vegetation plays an important role in nutrient cycling, maintaining soil structure and flood regulation (Cardinale et al. 2012). Forests support a substantial portion of the world's biodiversity, which provides a number of valuable resources, such as timber, food and medicines (Myers et al. 2000). Chemicals found in tropical forests are used in medicines and pharmaceutical products, and their estimated economic value is around $147 billion (Gavin 2009). Eco-tourism is another important economic benefit of forests. This is of particular importance to developing countries, where eco-tourism projects are often paired with sustainable development of local communities (Naidoo and Adamowicz 2005). Forests provide a substantial number of economic and social benefits to people, and protecting their biodiversity should be a priority in order to promote sustainable development.

Human activities have altered forest habitats in a number of ways. Clear felling will reduce available habitat and resources for populations. This deforestation has resulted in many forests becoming fragmented, with fragments subjected to various other structural changes as a result of edge effects. Edge effects involve abiotic changes, such as changes in microclimate and light availability, which in turn influence the biotic components of an ecosystem, affecting factors such as leaf turnover, nutrient cycling, dispersal and invasive species (Ries et al. 2004). According to the World Resources Institute only 10% of tropical forests remain relatively undisturbed (Bryant et al. 1997). Selective logging is a major contributor to this degradation, as it alters the composition and vertical structure of vegetation. Often the tallest trees are targeted, which will reduce the number of emergent trees and create canopy gaps. If a particular species is being harvested preferentially, this will also alter the species composition within the forest community. Both clear felling and selective logging have wide-ranging impacts on the physical characteristics of forest habitats, and so understanding the relationship between forest structure and primates will be key to predicting how disturbance will impact them.

Primates are an ideal model for measuring species responses to environmental change. They resonate well with the public and are therefore valuable, both as flagship species for forest conservation and for eco-tourism. Of the 426 primate species listed on the IUCN red list, 257 are classified as either vulnerable, endangered or critically endangered (IUCN 2014). Logging activities are a major contributor to the threatened status of many of these species, as they dwell primarily within forest ecosystems. For many species, their ecology, life history and distribution have been well documented, and there is data available on their past distribution trends (Schwitzer et al. 2011, Lynch Alfaro et al. 2014). Distributions of primate species have also been shown to correlate well with other mammal species (Emmons 1999). This can be of use in modelling future changes of species which are more difficult to study. Conservation of primate populations will benefit forest ecosystems as a whole, while understanding their distribution patterns can shed light on other, less well known animal species.

2.2: Disturbance impacts on forest structure

One of the major ways in which humans alter forest ecosystems is through conversion to agricultural land. Agroecosystems make up an estimated 25% of the world's total land area and the demand for agricultural land is considered to be one of the main drivers of deforestation (Estrada et al. 2012). Indonesia currently has the highest conversion rate of forest to agricultural land, and recent studies in the area have demonstrated the destructive impact this conversion has on wildlife populations (Sodhi et al. 2010). Conversion causes notable changes in forest structure and ecosystem processes, for example 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). Increasing conversion to agriculture also opens up forests to further human disturbance, such as hunting, poaching and logging, further compounding the effects of habitat loss on wildlife populations. Agroecosystems will generally support lower numbers of species compared with primary forest (Norris et al. 2010). Loss of habitat through conversion to plantations is considered to be one of the major drivers of declines in orang-utan populations (Knop 2004, Wich et al. 2008), and have also led to declines in populations of new world monkeys (Ortiz-Martínez et al. 2008). However, some species have been able to adapt to and exploit agroecosystems, for example, capuchins in Central America have been observed making frequent use of coconut and oil palm plantations, and raided crops make up more than 50% of their diet (Estrada et al. 2012). As a result of this, conversion to agriculture will result in changes to interspecific interactions and composition of primate communities. Conversion of primary forest into agricultural land fundamentally alters the structure and functioning of forest ecosystems, and has wide-ranging impacts on forest-dwelling species.

In addition to clearance for agriculture, humans also extensively alter forest environments through logging practices. Selective logging generally homogenises forests, leaving them with a simplified vertical structure and lower tree species richness (Norris et al. 2010). Generally, there will be decreased canopy continuity, tree density and a lower proportion of large or emergent trees in forests which are undergoing systematic or prolonged logging (Kakati et al. 2009). As well as a simplified canopy structure, logged forests will also have lower canopy cover, which alters the abiotic environment within the understorey layer (Scott et al. 2005). Gaps will change the amount of solar radiation penetrating the forest canopy, thereby altering forest microclimate and changing recruitment of understorey vegetation. This leads to an altered species composition within the forest understorey, and an increase in invasive and pioneer plant species (Clinton 2003, Frelich et al. 2003). The structure of upper storey vegetation has also been shown to influence the ability to recover from past disturbance in pine forests, demonstrating that forest regeneration is dependent upon the duration and extent of the logging carried out (Barbeito et al. 2009). Logging practices drastically alter both the biotic and abiotic characteristics of forest communities.

Clearance of forests has profound impacts on populations living within them. Srivistava et al. (2001), for example, reported dramatic population declines in all large-bodied primate species following forest clearance in the Borajan Reserve, India, with some species being at imminent threat of extinction; while Dunham et al. (2007) predicted an extinction risk of 35.6% for Milne-Edwards’ sifakas, *Propithecus edwardsi*, based on estimates of the current deforestation rates in Madagascar. Deforestation and habitat fragmentation have been identified as one of the biggest drivers of global biodiversity loss (Norscia and Palagi 2010). Despite this, there have been surprisingly few studies documenting the mechanisms by which fragmentation drives declines in mammal populations (Sodhi et al. 2010). It has been suggested that there is a general linear relationship between habitat area and species richness. Fragmented forests with larger patches and connectivity have been shown to have higher mammal species richness (Pattanavibool and Dearden 2002). A species' ability to persist in fragmented landscapes has been correlated with patch size and connectivity (Schwitzer et al. 2011). Habitat fragmentation is usually accompanied by an increase in other human activities, which further compound the effects of habitat loss, such as timber extraction, road construction, hunting and agriculture. Many species are unable to cross human-modified matrices, and become trapped in isolated fragments, and this has implications for the fitness of these populations (Michalski and Peres 2005). Populations within isolated fragments can have reduced fecundity and juvenile survival (Kakati et al. 2009), and lower genetic diversity, e.g. sportive lemurs, *Lepilemur* species in Madagascar (Craul et al. 2009). This makes them more vulnerable to environmental changes, such as El Niño events, drought or food shortages. Isolation can also result in higher densities or larger group sizes, which leads to increased competition for limited resources (Lee et al. 2014). Populations living in degraded or fragmented forests are likely suffering from the long term effects of stress as a result of increasing levels of human interference, therefore it is important to monitor such species and understand their capacity to adapt, as these effects may manifest themselves as increased mortality and population declines in the future.

2.3: Effects of forest structure on primate populations

Structure determines the distribution and abundance of resources, such as food and sleeping trees, which will in turn impact primate abundance, distribution and behaviour. Species diversity has been shown to correlate with habitat heterogeneity and food availability, both of which are normally reduced following periods of logging (Lehman 2004). In a recent review Gouveia et al. (2014) found that, generally, forest canopy height is positively correlated with primate species richness, providing further supporting evidence to the influence of canopy structure on primate communities. The structure of a habitat will exert significant influence over the ways in which primates utilise their available space. Usually, primates will demonstrate a preference for better quality habitats with a higher abundance of resources, and a more layered, structurally complex canopy (Warner 2002, Barelli et al. 2015). Arboreal primates, in particular, will spend more time in areas with taller canopies and better connectivity; bald-faced saki monkeys, *Pithecia irrorata*, spend a large proportion of their time in areas of their home range with these characteristics, and tend to avoid areas with lower tree heights and poor connectivity (Palminteri 2010). Since selective logging results in significant changes to the physical structure of forest habitats, it can be inferred that it will also alter primate ecology and behaviour.

Habitat quality can be linked to forest structure. In general the more heterogenous the forest canopy, the more species can persist in that environment. The availability of food resources has been shown to be a significant influence on the distribution of many primate species. Boyle & Smith (2010) found that the proportion of fruit trees was the strongest predictor of primate species presence/absence within forest fragments within the Brazilian Amazon, while Wich et al. (2004) reported a positive correlation between orang-utan, *Pongo abelii*, density and the density of strangling figs within the Leuser ecosystem in Sumatra. Where logging removes food trees for a particular species, it is likely that the species in question will decline or even go extinct within the affected area. Although food resources are an important determinant of distributions, primates will also tend to remain in areas with a higher habitat heterogeneity. A preference for taller, more structurally diverse canopies has been noted in many primate species, including: mottled faced tamarins, *Sanguinus inustus;* black and gold howler monkeys, *Aloutta caraya*; common marmosets, *Callithrix jacchus*; bearded capuchins, *Cebus apella libidinosus*; Tana river red colobus monkeys, *Procolobus rufomitratus*; and saki monkeys, *Pithecia* species (Karere et al. 2004, Boyle and Smith 2010, Palminteri 2010, Valsecchi et al. 2010). In saki monkeys a multi-layered, well connected canopy is essential for their mode of locomotion, and improves their access to food and escape routes from potential predators (Palminteri 2010). Canopy connectivity and height has also been found to exert a significant influence on the distribution of gibbons, most likely since these characteristics allow them to brachiate efficiently and with ease. Canopy structure affects the ability of a species to survive in forest habitats, and will therefore influence their distribution, however this effect is not universal across species.

The differing ecological requirements of primate species means that some species will cope better in particular types of forest than others, therefore forest structure will also influence primate community composition. Mammalian species richness in forests has been positively correlated with undergrowth density, and it has been theorised that this relationship is due to higher habitat heterogeneity and availability of niches (Emmons 1984). The differing ecological requirements of individual species results in different levels of sensitivity to disturbance. For example, the local extinction rates in Singapore are far higher in specialist species at 33 %, compared with generalist species at 7% (Tuomainen and Candolin 2011). Typically, specialist species will suffer and generalist species will be less affected, or may even benefit, from human changes to forest structure. Generally, larger bodied species have various traits making them more vulnerable to disturbance, such as long interbirth intervals and gestation periods, while smaller bodied species tend to be more resilient to change. This effect can be seen in the Tapiche River catchment in Peru, where all species of larger-bodied primate have either become locally extinct or have drastically declined, while smaller-bodied species have remained unchanged over the past thirty years (Bennett et al. 2001). It has also been observed in Guyana, where Sussman & Phillips-Conroy (1995) reported higher rates of decline in larger-bodied primates than smaller-bodied species. Disturbance can be beneficial to those species which are able to adapt and exploit novel resources within anthropogenically altered environments. It will also cause changes to interspecific interactions, by forcing overlap between species which would not normally come into contact with one another. For example, nilgiri langurs, *Trachypithecus johnii*, and hanuman langurs, *Semnopithecus entellus*, are rarely found living sympatrically, most likely an adaptive mechanism to prevent competition and interbreeding, but habitat degradation has caused their ranges to overlap in some parts of India (Kumara and Singh 2004). This will result in increased competition and could also result in hybridisation of the two species. Anthropogenic disturbance has variable impacts depending upon a species' ecological traits and requirements, causing notable changes to the structure and composition of primate communities.

Forest structure can indirectly affect primate species survival by impacting on their ability to disperse. Limitation of dispersal has been identified as a major factor shaping primate communities, more so than any other ecological factor (Beaudrot and Marshall 2011). A lack of dispersal opportunity in isolated forest fragments can result in larger group sizes, which will in turn increase intraspecifc competition for limited resources, and can result in higher levels of intergroup aggression (Lee et al. 2014). For some species, dispersing from the natal group has a high cost. When individuals move to an unfamiliar area, they can have a poorer diet, higher vulnerability to predation and be at risk of running into conflict with unfamiliar conspecifics (Isbell and Van Vuren 1995). In some cases, disturbance will increase the likelihood of individuals facing the risks associated with dispersing from their natal home range. Habitat disturbance can limit a species' ability to disperse, which impacts their fecundity and population dynamics, or it can force them to disperse due to poor resource availability, which will potentially increase mortality from starvation, aggression or predation.

Vulnerability to predation can be linked to forest structure in some primate species. Habitat structure plays an important role in predator avoidance, particularly for arboreal species, by providing escape routes and safe hiding spots. Small-bodied primates are more vulnerable to predation in lower, more open canopies, and as such will preferentially use parts of their home range with higher canopies and higher understorey visibility. This has been observed in bald-faced sakis and samango monkeys, *Cercopithecus albogularis* (Palminteri 2010, Coleman and Hill 2014). An increase in human activity can also increase perceived predation risk, which can result in maladaptive vigilance behaviours; for example ververt monkeys, *Chlorocebus pygerythrus*, have been shown to alter their ranging behaviour according to perceived predation risk (Willems and Hill 2009). An increase in human traffic can therefore result in an increase in vigilance behaviours at the expense of foraging and reproductive success. Habitat disturbance is also often associated with the introduction of new species, some of which can be novel predators for native primates. An example of this was recorded by Mckinney (2009), who observed an attempted predation of juvenile mantled howlers, *Aloutta palliate*, by a crested caracara, *Caracara cheriway*, a raptor typically introduced by human activities. Novel predators pose a significant risk to primates, as they may not possess the necessary adaptations to avoid these new species. Habitat disturbance can impact on primates by altering either actual predation risk, or perceived predation risk, both of which can influence their survival.

Anthropogenic disturbance can also make primates more vulnerable to disease and parasitic infection. There is, for example, some evidence to suggest transmission of pathogens from human populations to primates. Red colobus, *Procolobus,* species living close to the edge of forest fragments in the Kibale national park, Uganda, have a higher occurrence of concurrent infections than those in interior forest. Some of the pathogens found in these individuals were those which were typically associated with humans (Chapman et al. 2006). Two parasite species, *Ascaris* and *Giardia*, were identified in populations of red colobus monkeys in disturbed forest, but not in primary forest; these species are also highly prevalent in humans (Gillespie et al. 2005). It is important to note that, although these studies suggest sharing of pathogens between humans and primates, there is not yet any evidence confirming that this is the case. Since disturbance can increase the density of primates in some areas, it can also increase the likelihood of transmission, thereby increasing disease prevalence. *Piliocolobus* and *Cercocebus* species have higher parasite prevalence in fragmented forests, and prevalence seems to correlate with host density, although this relationship has not yet been tested properly (Gillespie and Chapman 2008, Mbora and Mcpeek 2009). Primates in disturbed forests may have supressed immune function, as a result of increased stress and poor diet, making them more susceptible to infection. Red-tail guenons, *Cercopithecus ascanius*, in Kibale National Park, Uganda, have a higher prevalence of gastrointestinal parasites in logged versus unlogged forest, and this is likely to be a result of suppressed immune function due to poor diet (Gillespie et al. 2005). Some populations living in disturbed habitats could be experiencing considerable stress, which has not yet manifested as population declines. Identifying these populations is an important step in conservation, and will enable protective measures to be put in place, before these populations begin to decline dramatically. Measures of parasitic infection and population stress should be used in conjunction with population trends to identify those populations which are most in need of protection.

2.4: Behavioural responses of primates to habitat disturbance

Habitat disturbance causes new challenges for primates by altering the distribution and availability of resources, forcing them to change their behaviour to balance opposing needs, such as avoiding predators and foraging for food. The ability to alter behaviour and adapt to a changing environment varies across species, and even populations. Where high quality food is less abundant, primate species will often alter their diet to include a higher proportion of lower quality foods. Gibbons have been shown to shift from eating fruit to leaves in times of low fruit availability (Kakati et al. 2009); red colobus monkeys feed less selectively in degraded areas, enabling them to maintain the same density as in primary forest (Milich et al. 2014); and Sumatran orang-utans spend a higher percentage of time bark feeding in degraded forest compared with primary forest (Campbell-Smith et al. 2011). For some species, prolonged periods eating lower quality foods can be detrimental, particularly in frugivorous species. Gibbons are unable to feed on leaf material for long periods, since their digestive system is unable to tolerate secondary compounds and toxins in leaves, and reductions in fruit abundance are often associated with declines in gibbon populations (Kakati et al. 2009). Where primates are eating a less nutritious diet, they will have more enforced resting time (the amount of time required to digest their food and conserve energy), which can limit their survival ability (Korstjens et al. 2010). Some primates in degraded areas compensate for this by altering their activity budgets. Sumatran orang-utans, *Callicebus* species and *Papio* species all spend less time resting and engage in less social activity in degraded versus primary forest (Michalski and Peres 2005, Wich et al. 2008, Bettridge et al. 2010). Lemurs, howler monkeys and bearded sakis also show reduced sociality, and have larger home ranges and bigger group sizes (Irwin et al. 2010, Schwitzer et al. 2011). By changing the availability of resources, habitat disturbance creates new ecological constraints for primate species and alters their behavioural ecology.

Disturbance will alter the distribution of resources within forests, which will in turn cause changes in how primates move throughout their environment. Lion-tailed macaques, *Macaca Silenus*, and lemurs show more concentrated ranging behaviour in degraded forests, with a preference for areas with the highest abundance of resources (Riley 2008, Kelley 2013). A sparse distribution of resources will also force primates to travel more. Some species have larger home ranges to compensate for fewer resources; this has been documented in lemurs (Ganzhorn 2002, Kelley 2013), bald-faced sakis (Palminteri 2010) and lion-tailed macaques (Riley 2008). Where deforestation has reduced the area of available forest, this will limit the number of groups which can be supported, and will therefore result in population declines in disturbed forests. This will be particularly true for territorial species, who will likely have an increase in aggression due to more intense competition for limited resources and territories.

For arboreal species, the structure of the forest also plays an important role in facilitating locomotion. Hamard et al. (2010) suggested a correlation between canopy connectivity, tree height, the number of available supports and gibbon density, and theorised that this is since taller, better connected and layered canopies are better at facilitating brachiating through the trees. Bald-faced sakis prefer to use larger diameter branches in order to minimise propulsion loss of energy during leaping, and logging may reduce the availability of these (Palminteri 2010). Geoffroy's tamarin, *Sanguinus geoffroyi*, also show a preference for specific types of vegetation, which enables them to maximise foraging efficiency and minimise predation risk simultaneously (Madden et al. 2010). Mantled howlers use specific learned arboreal pathways throughout their home range, and plan their routes to maximise foraging success (Hopkins 2010); regular removal of trees will interfere with this mental map and limit their ability to navigate through their home range. Generally, logging will simplify canopy structure and reduce overall canopy cover and connectivity, which will make it harder for arboreal primates to move throughout their habitats, and may force them to take more dangerous routes. For example, *Macacus* species in disturbed areas spend more time foraging on the ground (Riley 2008), while brown capuchins and colobus monkeys have been known to cross matrices between forest fragments, thus making them more vulnerable to predation or persecution by humans (Michalski and Peres 2005, Anderson et al. 2007, Riley 2008). Primates living in anthropogenically disturbed forests will have to learn to use their space and available resources differently. It is important to understand to what extent a species is able to do this in order to predict how current and future levels of disturbance will affect them, and identify those species which are most in need of protection.

2.5: Conclusions and future directions of research

Habitat alteration will have profound and far-reaching implications for primate communities in forests. It will alter species richness, community composition and cause changes in the distribution, abundance, ecology and behaviour of individual species. With current knowledge, however, it is not yet possible to identify universal trends in the relationship between environmental change and primates; nor is it possible to make predictions about how any given population will respond to disturbance. Most primate studies are either species or site-specific, and many only focus on one particular aspect, e.g. food availability or fragment area (Kamilar and Beaudrot 2013). It is necessary to undertake long-term studies which look at all aspects of primate ecology and the landscapes in which they live, in order to identify trends and improve the power of predictive models of primate responses to disturbance. In particular, landscape scale studies identifying the relationship between landscape features, forest structure and primates will be immensely useful in predicting how forest clearance and timber extraction will impact on primate populations.

Most studies related to habitat structure and landscape ecology only suggest correlations between species distributions or presence/absence (e.g. Hamard et al. 2010; Gouveia et al. 2014) and do not adequately explain the mechanisms which drive this relationship. Landscape studies require large amounts of ground data which is costly and time-consuming to collect, especially in remote areas with poor accessibility (i.e. tropical forests). More detailed research linking the landscape and habitat structure to primate ecology and behaviour will shed light on these mechanisms. Understanding this will then, in turn, help to explain species' ecological requirements and habitat preferences and identify those species or ecosystems which are most vulnerable to disturbance and highlight priority areas for conservation (Palminteri et al. 2012).

A better understanding of species' habitat preferences will aid in predicting the effects of future changes and planning conservation action accordingly. Conserving primate species will not be as simple as protecting the remaining primary forest. It is also necessary to focus on conserving and regenerating secondary forests, many of which have been found to hold large numbers of species (Lwanga 2006, Sodhi et al. 2010). Species richness is often used as an indicator for areas of conservation importance, however, it should not be used exclusively to highlight these areas. Peat swamps, as an example, have received little to no attention, but they have now been recognised as being hugely important habitats to endangered populations of orang-utans and gibbons (Hamard et al. 2010). Utilising improved methods for ground surveys will provide a deeper understanding of how environmental change and anthropogenic activities will impact on primate communities. It will also highlight areas of focus for conservation action and help to inform policies, such as protected areas or species trade restrictions, which are designed to protect forest biodiversity.

Chapter 3 : Methods

3.1: Study site

This study takes place in the Sikundur region of the Gunung Leuser National Park (GLNP) in Northern Sumatra, Indonesia, $3^{o}30'$ N, $97^{o}30'$ E (see figure 3.1). The GLNP covers C. 1,094,692 ha and forms part of the Tropical Rainforest Heritage of Sumatra UNESCO World Heritage (YOSL-OIC 2009). This area has been highlighted as being of particular conservation importance due to the high levels of biodiversity, including rare and endemic species, found throughout the region. Sumatra comprises part of the biogeographic area of Sundaland, identified by Myers et al. (2000) as being among one of the top 5 global hotspots of biodiversity, and has been highlighted as a priority area for conservation. The GLNP represents important habitat for a number of critically endangered species, including the Sumatran orang-utan (*Pongo abelli*), Sumatran tiger (*Panthera tigris sumatrae*), Sumatran elephant (*Elephas maximus sumatranus*) and Sumatran rhinoceros (*Dicerorhinus sumatrensis sumatrensis*). Despite its national park status, illegal logging and hunting continues to be a problem in this area. The annual rate of forest loss in the Leuser ecosystem, which includes the GLNP, has been estimated at 21,000 $\text{ha}^{-\text{year}}$. Conversion to plantations is also a major problem, with around 15% of Sumatra's total land area being converted to palm oil plantation since the 1980s. However, there are still large areas of primary forest in the region, along with previously logged secondary forest which has been left undisturbed long enough to allow the forest to recover somewhat (Priatna et al. 2000). This provides a useful opportunity to investigate the relationship between disturbances, forest structure and group density of *P. thomasi*.

This study was based at the Sikundur research station belonging to the Sumatran Orang-utan Conservation Project, SOCP. The chosen study area comprises of 3 distinct land units, identified by Laumonier (1997) and described in table 3.1. These are hitherto referred to as alluvial, hills and plains (see figure 3.2). The land units have been defined according to tree species composition, topography and climate; however there is little data available on how forest structure differs across these units. The location of this study allows comparison between these land units, and will give an indication of *P. thomasi* habitat preferences.

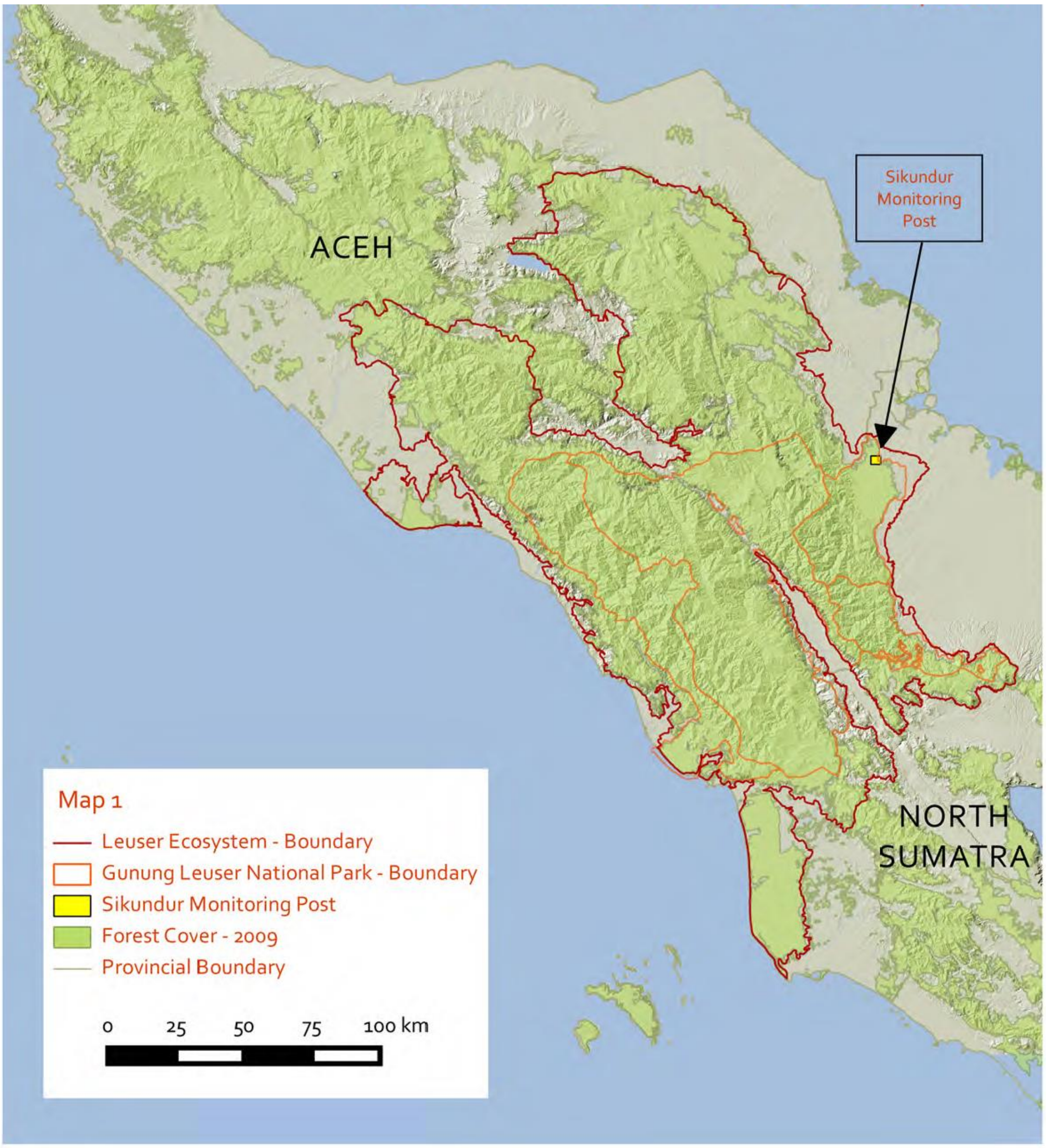

Figure 3.1: Boundaries of the Leuser ecosystem and Gunung Leuser National Park, and the location of the Sikundur research station in North Sumatra, adapted from PanEco (2013).

Table 3.1: The three land units found within the Sikundur region, as described in Laumonier (1997).

Land unit	***Topography***	***Climate***	***Soil***	***Composition and structure***	***Exploitation***
Alluvial	Located next ro rivers, and flooded periodically. Typically flat land at low elevations.	Superhumid: rainfall ~2,500 - 3,000 mm/year.	Fine-textured with high organic content, and some peat accumulation.	Diversity varies depending on frequency and duration of localised flooding. Typically dominated by dipterocarp and palm species. Canopy height usually 30-40m, with emergents reaching up to 50m.	Historically used extensively due to proximity to waterways. Most often converted to paddi fields or palm plantations.
Hills	Found at altitudes of 100-500m. Slopes ranging from 8-30% incline, and 50-300m in length.	Superhumid (rainfall ~2,500 - 3,000 mm/year) to hyperhumid (rainfall ~3,000-3,500 mm/year)	Fine-medium textured leached soils made up of a variety of rocks, pH between 5-6.5 and low organic content (3-15%).	Diverse plant species, dominated by dipterocarps. Dense, closely interwoven canopy, usually 35-45m in height, with emergents between 45-55m.	Minimal logging, but small scale exploitation by local populations for resources such as timber, rubber and sap.
Plains	Flat, undulating land at altitudes of 50-100m. Slopes ranging from 2-8% incline, and 5-30m in length.	Superhumid: rainfall ~2,500 - 3,000 mm/year	Porous, acidic soils with small amount of leaf litter.	Diverse plant species, dominated by dipterocarps and other woody plants. Large lianas, bryophytes and epiphytes also common.Canopy usually 30-40m tall, with emergents from 45-55m. Gaps are fairly common.	Has been degraded extensitvely, most often being cleared for agriculture and plantation land. This zone is now dominated by young secondary forest.

3.2: Study species

This study focuses on the Thomas' langur monkey, *Presbytis thomasi.* The reproductive success of males depends upon them becoming resident in a mixed-sex group, and as such competition between males can be intense, and, in some cases, even lethal. Groups usually consist of 8-10 individuals; one male, a harem of several females, and their offspring (Sterck 1996). Males will normally spend a portion of their lives in an all-male band, or as a solitary bachelor. This is either a result of them being ousted from their natal group upon maturity, or being abandoned by the females when they transfer to a new male. Males gain access to females by attacking established mixed-sex groups. This can occasionally lead to there being two males in a group. This state will result in either one of the males being ousted or killed by the other. As such, it is unstable, and will usually revert back to the typical single male, multi-female formation within a short period of time (Gursky-Doyen and Supriatna 2010).

There is currently little data available on this species within the Sikundur region. *P. thomasi* is extremely vigilant, and will often disappear into the upper canopy at the slightest disturbance (Sterck 1996), making surveys challenging. Census methods which rely on visual detection (i.e. line transects) may not be the best method for this species, particularly when they are unhabituated to the presence of humans. Morning vocalisations produced by dominant males are distinct from any other species' calls (Wich and Sterck 2010). These calls can be used as an indicator of the number of groups within an area. Auditory sampling is an effective tool which has been implemented successfully in other species, primarily gibbons, *Hylobates* species' (Cheyne et al. 2008), but it has not yet been attempted with *Presbytis* species'. Developing this method could provide a faster, more efficient method of surveying *Presbytis* populations than the use of line transects, which must be intensively sampled to provide useful data.

3.2: Field Data Collection

A summary of the field methods which were employed, along with the dates on which they were sampled and their sampling effort, is given in table 3.2 below.

Table 3.2: Summary of different methods employed during data collection, along with their sampling dates and sampling effort.

				Samples collcted, N			
	Sampling date	***Number of survey points***	***Number of sampling occasions***	***Alluvial***	***Hills***	***Plains***	***Total***
Vegetation transects	15th Feb 2015 - 30th Mar 2015	30	1	400	400	400	1,200
Vegetation plots	15th Jun 2015 - 10th Jul 2015	15	1	171	149	182	502
Density transects	5th Apr 2015 - 16th May 2015	30	2	0	0	0	0
Vocal arrays	22nd May 2015 - 30th June 2015	3	4	301	257	312	870

3.2.1: Forest structural data

Structural data was collected by a team consisting of myself and two other researchers, Rosanna Consiglio and John Abernethy, along with field assistants employed by the Sumatran Orangutan Conservation Programme. Prior to data collection, the team were trained together in all data collection methods, in order to minimise inter-observer variability. The vertical structure of the forest was measured in five 25x25m plots placed randomly in each land unit (15 in total; see figure 3.2). These were each sampled once between 15th June 2015 and 10th July 2015. Within each plot, the total number of trees with a diameter at breast height (DBH) of more than 10cm was recorded, along with their DBH and position within the plot (see figure 3.3). Table 3.4 describes the measurements taken for each of these trees. Structure was also measured along ten north-south oriented line transects, each sampled once between 15th February 2015 and 30th March 2015, placed systematically throughout each land unit (30 in total; see figure 3.2). The point-centred quarter method (PCQM) adapted from Manduell et al. (2012) was employed along these transects. Sample points were made every 50m along each transect, and a line was drawn perpendicular to the transect line, creating four quadrants (see figure 3.6). In each quadrant the nearest tree with a DBH>10cm was selected and the variables described in table 3.5 were measured. For each land unit the number of trees with a top height >25m, and the number of trees within three DBH classes (10-30cm; 31-60cm; >60cm) were totalled from all plots and transects.

Table 3.3: Number classes used to estimate the number of branches in each of five diameter size classes (0-2cm, 2-4cm, 4-10cm, 10-20cm and >20cm) for all trees measured.

Class	*Estimated number of branches*	*Mid-point of class*
1	0-10	5
2	11-50	30
3	51-100	75
4	101-500	300
5	501-1,000	750
6	1,001-5,000	3,000
7	5,001-10,000	7,500
8	>10,001	10,000

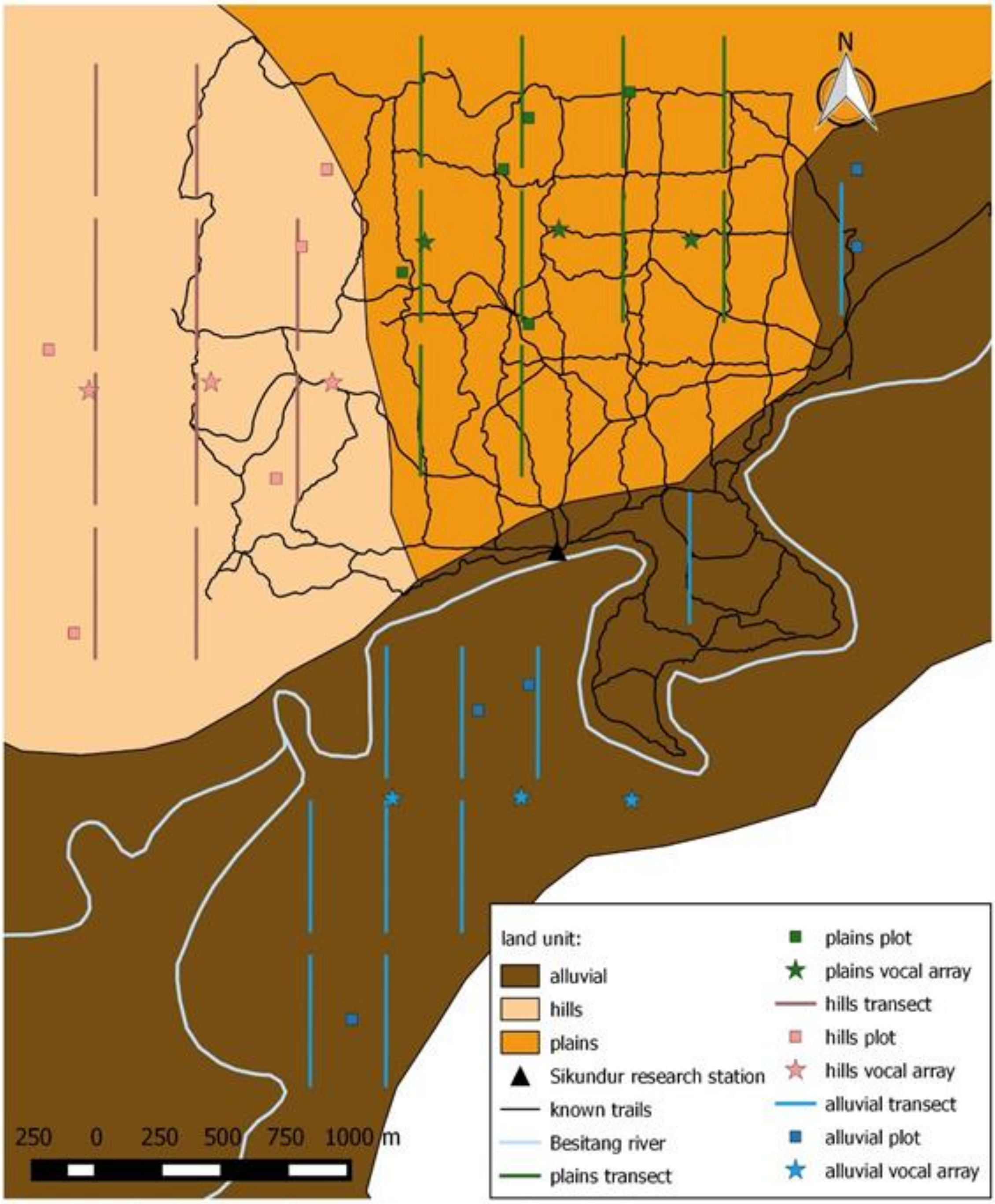

Figure 3.2: land units and survey locations in the Sikundur region.

Table 3.4: variables collected from plots.

Variable	***Units***	***Explanation***	***Method***
Per tree with DBH>10cm:			
Plot position	*m*	Distance in metres along the x and y boundary of the plot.	Measured with a tape measure on the ground (see figure 3.3).
Circumference at breast height, CBH	*cm*	Circumference of the trunk at approx. 1.3m.	Measured with a tape measure around the trunk.
Diameter at breast height, DBH	*cm*	Diameter of the trunk at approx. 1.3m.	Calculated from CBH, using the formula: $DBH = \frac{CBH}{\pi}$
Basal area, BA	cm^2	Cross-sectional area of the trunk at 1.3m.	Calculated using the formula: $BA = \pi\left(\frac{DBH}{2}\right)^2$
Top height	*m*	Distance in metres from the base of the trunk to the tallest point on the crown, measured using a laser range finder.	Measured using a laser range finder.
Bole height	*m*	Distance in metres from the base of the trunk to the underside of the first major bough, measured using a laser range finder.	Measured using a laser range finder.
Height-DBH ratio	-	Top height divided by DBH; proivdes an indication of tree age.	Calculated using the formula: $ratio = \frac{height}{DBH}$
Crown width	*m*	Distance in metres between the north and south ordinal points of the crown, and the west and east ordinal points of the crown.	Distance from the trunk to each of the four ordinal points (N, E, S and W) measured using a tape measure on the ground. The north and south measurements were added together, and then added to the DBH. The same was done for the east and west measurements (see figure 3.4).
Crown area	m^2	estimate of the crown area.	calculated using the formula: $A = \pi\left(\frac{N-S\,width}{2}\right) \text{x} \left(\frac{E-W\,width}{2}\right)$
Crown shape	-	A desrciption of the shape of the crown.	Assigned to one of six categories, shown in figure 3.5.
Crown connectivity	*%*	The connectivity of the crown in relation to neighbouring crowns.	Estimated using a four-point scale: 0-25%, 25-50%, 50-75%, 75-100%.
Number of branches	-	An estimate of the number of branches within each of five diameter classes: 0-2cm, 2-4cm, 4-10cm, 10-20cm and >20cm.	Estimated using number classes shown in table 3.2.
Per plot:			
Total number of trees	-	The total number of trees with a DBH >10cm within the plot.	N/A
Per hectare:			
Tree density	*trees / hectare*	Estimated number of trees with DBH >10cm per hectare.	Calculated by multiplying the total number of trees within each plot by 16.
Stand basal area, SBA	m^2 */ hectare*	Estimated area occupied by tree stands per hectare.	Calculated using the formula: $SBA = \Sigma(100 \text{ x } BA) \text{ x } 16$

Table 3.5: Variables collected from trees measured along transects.

Variable	***Units***	***Explanation***	***Method***
Distance from point	*m*	Distance in metres from transect point to	Measured with a tape measure on the ground (see figure 3.6).
Bearing	*degrees*	Compass bearing of trunk in relation to transect point.	Measured from transect point using a compass (see figure 3.6).
Circumference at breast height, CBH	*cm*	Circumference of the trunk at approx. 1.3m.	Measured with a tape measure around the trunk.
Diameter at breast height, DBH	*cm*	Diameter of the trunk at approx. 1.3m.	Calculated from CBH, using the formula: $DBH = \frac{CBH}{\pi}$
Top height	*m*	Distance in metres from the base of the trunk to the tallest point on the crown.	Measured using a laser range finder.
Bole height	*m*	Distance in metres from the base of the trunk to the underside of the first major bough.	Measured using a laser range finder.
Height-DBH ratio	-	Top height divided by DBH; proivdes an indication of tree age.	Calculated using the formula: $\mathrm{ratio} = \frac{height}{DBH}$
Crown width	*m*	Distance in metres between the north and south ordinal points of the crown, and the west and east ordinal points of the crown.	Distance from the trunk to each of the four ordinal points (N, E, S and W) measured using a tape measure on the ground. The north and south measurements were added together, and then added to the DBH. The same was done for the east and west measurements (see figure 3.4).
Crown area	m^2	Estimate of the crown area.	Calculated using the formula: $A = \pi \left(\frac{N - S\ width}{2}\right) \mathrm{x} \left(\frac{E - W\ width}{2}\right)$
Crown shape	-	A desrciption of the shape of the crown.	Assigned to one of six categories, shown in figure 3.5.
Crown connectivity	*%*	The connectivity of the crown in relation to neighbouring crowns.	Estimated using a four-point scale: 0-25%, 25-50%, 50-75%, 75-100%.
Number of branches	-	An estimate of the number of branches within each of five diameter classes: 0-2cm, 2-4cm, 4-10cm, 10-20cm and >20cm.	Estimated using number classes shown in table 3.2.

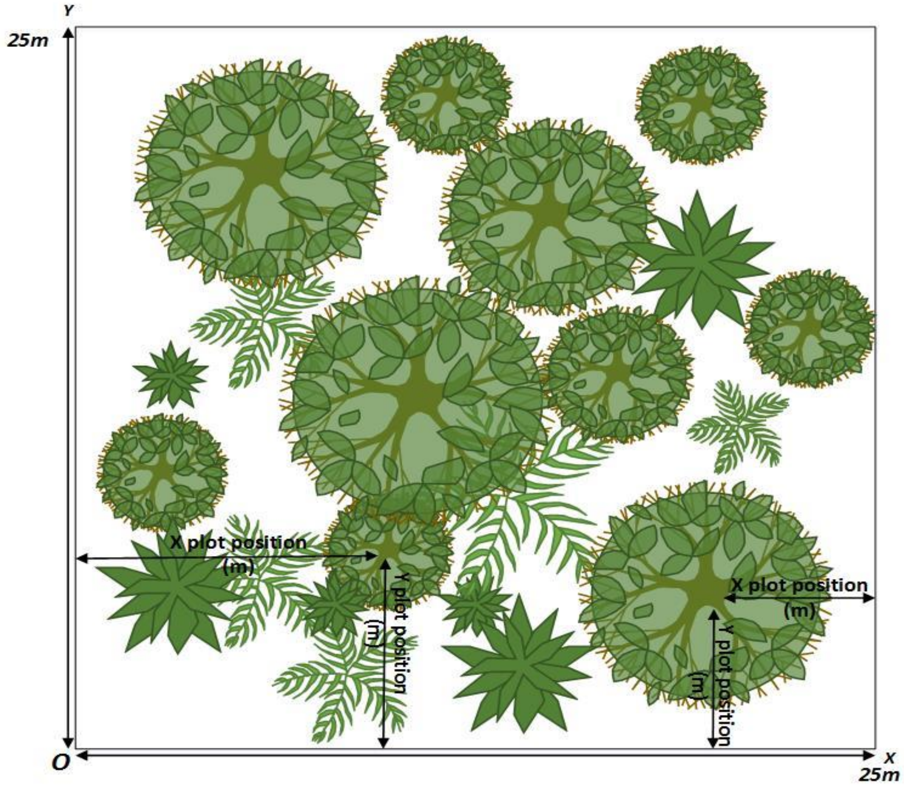

Figure 3.3: A 25x25m plot detailing the method used to measure plot position of each tree with diameter at breast height >10cm.

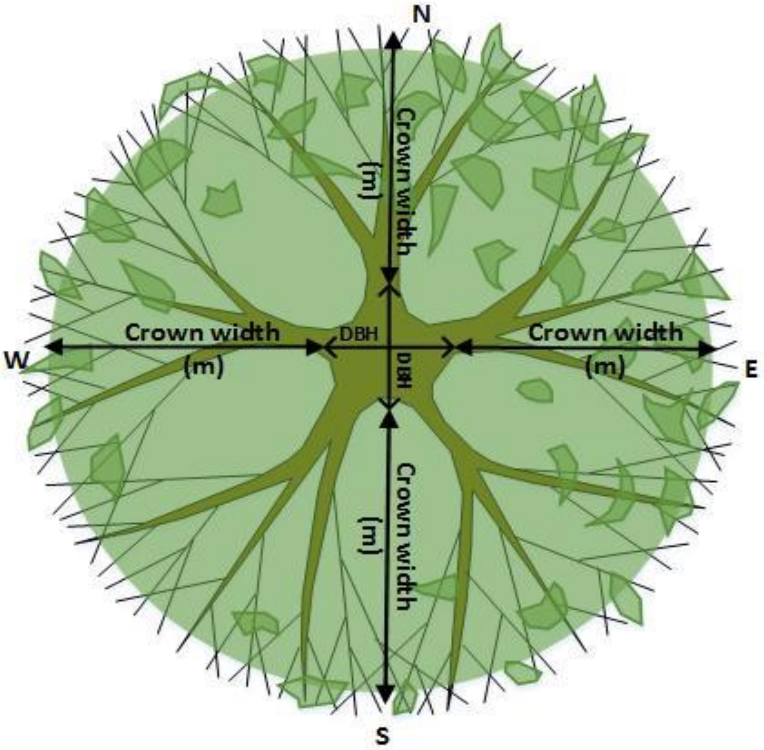

Figure 3.4: The method used to measure crown width (m) and crown area (m^2).

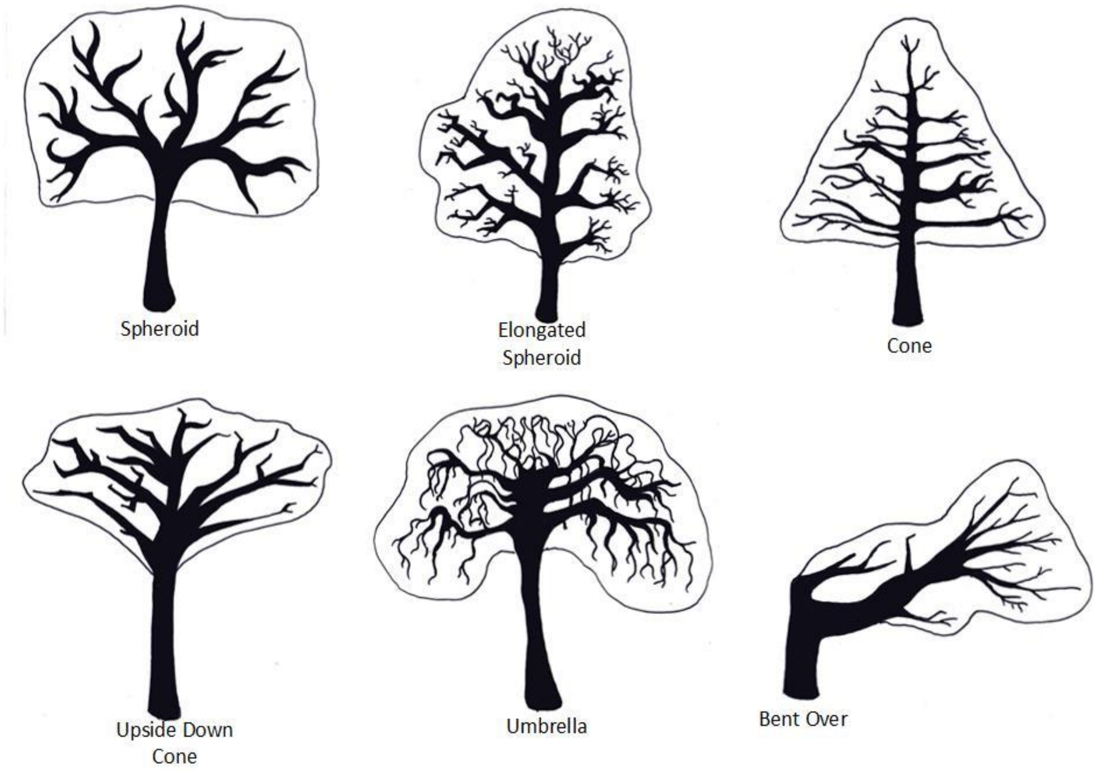

Figure 3.5: Crown shapes were placed into one of the six categories shown above.

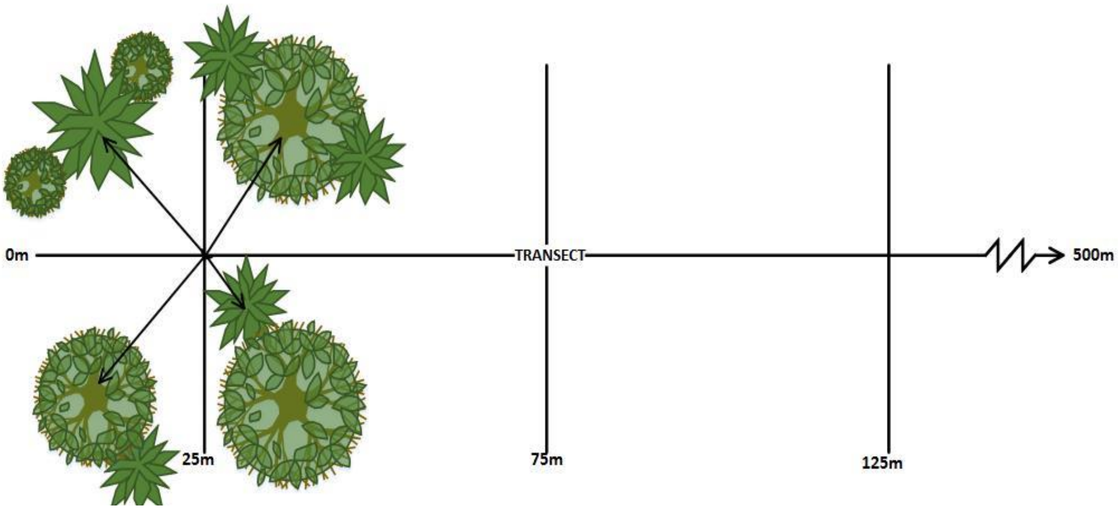

Figure 3.6: The point centre quarter method. Points were made every 50m along transects, starting at 25m and finishing at 475m. The nearest tree to the point with DBH >10cm was measured in each of the four quadrants.

3.2.2: Group density of P. Thomasi

Primate surveys were carried out by a team consisting of myself and fellow researcher, Rosanna Consiglio, along with field assistants employed by the Sumatran Orangutan Conservation Programme. Pilot surveys were carried out, prior to data collection, to allow researchers to practice the data collection methods and reduce inter-observer variability.

The density of Thomas langur monkeys was estimated using point count and line transect surveys, similar to the method employed by Lee et al. (2014) to survey agile gibbons, *Hylobates agilis*. The same transects used to survey forest structure were sampled at a constant pace of 1-2 mph on two separate occasions, between 06:30 and 09:30am, and between 14:30 and 17:30pm, between 5th April 2015 and 16th May 2015. No transect was sampled more than once per day and at least one week was allowed following cutting or surveying along each transect, to allow the animals' behaviour to return to normal. During each walk any encounters with groups of *P. thomasi* were recorded, along with the time; location on transect (recorded with a handheld Garmin GPS device); approximate group size; estimated distance from the point of first observation to both the first individual sighted and the approximate centre of the group, using a laser range finder; bearing to the first individual sighted from the point of first observation; and any other *ad hoc* behavioural notes.

Point counts were carried out using morning loud calls as a proxy for group density. Three vocal arrays were placed throughout the study region, one in each land unit. A single vocal array consists of 3 observation points arranged in a straight line approximately 500 metres apart (figure 3.7). A straight-line formation was chosen over the traditional triangular arrangement for this survey design, since a recent study by Kidney et al. (2013) demonstrated that linear arrays yield a lower variance and bias than non-linear arrays with the same spacing. All calls by *P. thomasi* were recorded, along with their start time in hh:mm:ss, compass bearing and estimated distance from the sampling point. Each location was monitored for one sampling period, consisting of four consecutive days between 22nd May 2015 and 30th June 2015. Sampling took place from 05:00am to 11:30am to ensure that all groups in the area were detected. Each listening post was plotted in ArcGIS. For each individual call a line was drawn from the post at which the call was recorded using the estimated bearing of that call and a maximum distance of 2000m, to produce a diagram, such as the one shown in figure 3.8. A distance of 2000m was chosen since calls from further than 1500m away would not be detected (Cheyne et al. 2008). Lines were categorized according to the time at which they were recorded, and labelled with the call start time. Mapping calls in this way enables the identification of individual calls detected at multiple posts at the same time, by identifying where lines from separate posts intersect. Once all individual calls had been identified and mapped, they were assigned a group. Calls mapped more than 550m apart were considered to be a separate group, since this is the average reported width of a Thomas' langur home range (Gurmaya 1986).

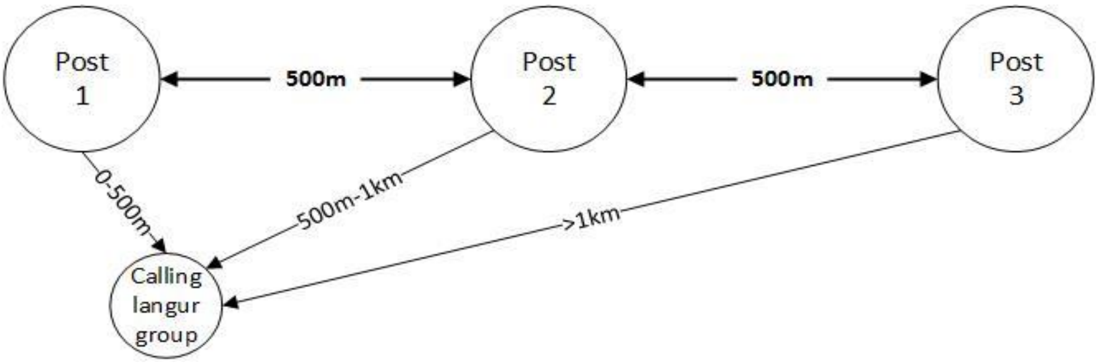

Figure 3.7: A vocal array. Three listening points are arranged in a straight line

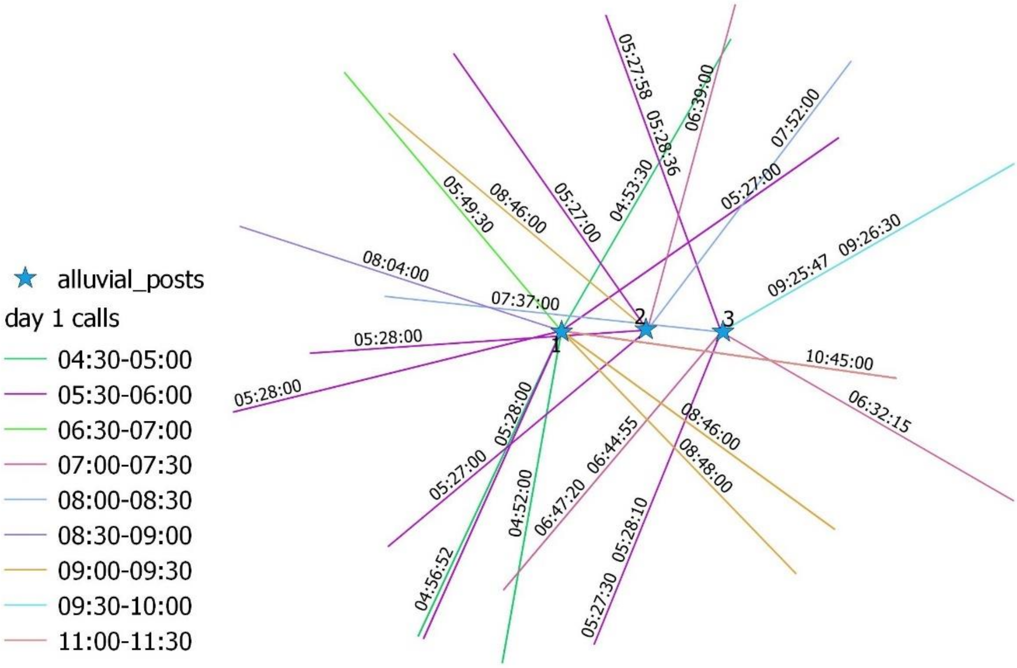

Figure 3.8: Method used in ArcGIS to triangulate calls. Each line represents a recorded call. Lines are categorized according to the time at which they were recorded and labelled with their start time to make triangulation easier. Lines from separate posts which intersect and have the same start time are considered to be the same call, which has been detected at multiple posts.

3.3: Statistical analysis

3.3.1: Forest Structure

The data collected on forest structure was tested to look for differences in the structure of the forest between the alluvial, plains and hills land units. All of the continuous variables (DBH; BA; top height; bole height; height-DBH ratio; crown area; number trees per plot; tree density per hectare; and SBA per hectare) were first tested for a normal distribution using a Shapiro-Wilkinson normality test. Variables which were collected from both plots and transects were then tested to ensure that the two methods gave data which were sampled from the same population. Non-parametric Kruskal-Wallis test, followed by post-hoc pairwise Mann-Whitney U tests, were used to test this (Fowler et al. 1998). The data from plots and transects were then combined, and a non-parametric Kruskal-Wallis, followed by post-hoc pairwise Mann-Whitney U tests, were used to test for differences between the alluvial, hills and plains land units for all of the continuous variables. Basal area, stand basal area and tree density were only calculated using data from plots, and were tested using a non-parametric Kruskal-Wallis test, followed by post-hoc pairwise Mann-Whitney U tests, in order to identify significant differences between the alluvial, hills and plains land units for these variables. Critical values for Mann-Whitney U tests were obtained by sequential Bonferroni correction. First, P-values were ranked from smallest-to-largest. The critical value, α, was divided by the number of tests, k, in a sequential order. The smallest value is considered first, and if $P_1 \leq \alpha/k$, the test was considered significant. The second smallest value is considered next, and if $P_2 \leq \alpha/k-1$, this test is considered significant. This continues until a test indicates non-significance, in which case all following tests are considered to be non-significant (Rice 1989). Crown shape and connectivity were collected as categorical variables, and so their frequency distributions were compared across the three land units using a chi-squared two-way contingency table. A chi-squared goodness-of-fit test was used to test for a difference in the proportion of trees with a top height >25m, and the proportion of trees in each of three DBH classes (10-30cm; 31-60cm; and >60cm) between the alluvial, hills and plains land units. A summary of the statistical tests used for each forest structure variable can be seen in table 3.6.

Table 3.6: Summary of statistical tests used for forest structure variables.

Variable	***Units***	***Data from***	***Statistical test used***
Per tree with DBH>10cm:			
Diameter at breast height, DBH	cm	Plots and transects	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Basal area, BA	cm^2	Plots only	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Top height	m	Plots and transects	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Bole height	m	Plots and transects	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Height-DBH ratio	-	Plots and transects	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Crown area	m^2	Plots and transects	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Crown shape	-	Plots and transects	Chi-squared two-way contingency table
Crown connectivity	%	Plots and transects	Chi-squared two-way contingency table
Number of branches	-	Plots and transects	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Per plot:			
Total number of trees	-	Plots only	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Per hectare:			
Tree density	trees / hectare	Plots only	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Stand basal area, SBA	m^2 / hectare	Plots only	Shapiro-Wilkinson normality test Kruskal-Wallis test Post-hoc pairwise Mann-Whitney U test
Per land unit:			
Number of trees with top height >25m	-	Plots and transects	Chi-squared goodness-of-fit test
Number of trees with DBH 10-20cm	-	Plots and transects	Chi-squared goodness-of-fit test
Number of trees with DBH 31-60cm	-	Plots and transects	Chi-squared goodness-of-fit test
Number of trees with DBH >60cm	-	Plots and transects	Chi-squared goodness-of-fit test

3.3.2: Group density of P. thomasi

3.3.2.1: Line transects

No statistical analyses were performed on data from line transects due to low encounter rates.

3.3.2.2: Vocal arrays

Group density from point counts based on vocal arrays was first calculated using the traditional method of triangulation. The total sampling area was estimated at each array by fitting a circular buffer of a set distance around the centre point in ArcGIS, and calculating the total area in km2. The buffer distance represents the maximum distance from which calls may be detected. This was calculated by measuring the distance to the furthest mapped call from the centre post in ArcGIS. Due to the small size of the study site, the sampling areas of each array contained other land units. This was corrected for by reducing the buffer distance until the total sampling area was comprised of at least 80% of the focal land unit. Sections of other land units which were still located within the buffer radius were excluded from the final measure of corrected sampling area, *A*, and groups which were mapped outside of this area were excluded from the analysis (see figure 3.9). The group density, *d*, was then calculated as follows: $d = \frac{n}{P(call)A}$, where *n*= number of groups, and *P(call)*= the probability of calling for any group within any given sample period, calculated as the average of the probability of calling for each group, calculated by dividing the number of days each group was heard calling by the total number of days sampled (i.e. 4 days).. Kidney et al. (2013) noted that a major limitation of this method is the assumption of uniform detection throughout the total sampling area. In reality, this assumption is unlikely to hold true, and can lead to underestimation of group density. Therefore, an alternative method of spatially explicit capture recapture (SECR) was employed and compared with the traditional method of triangulation.

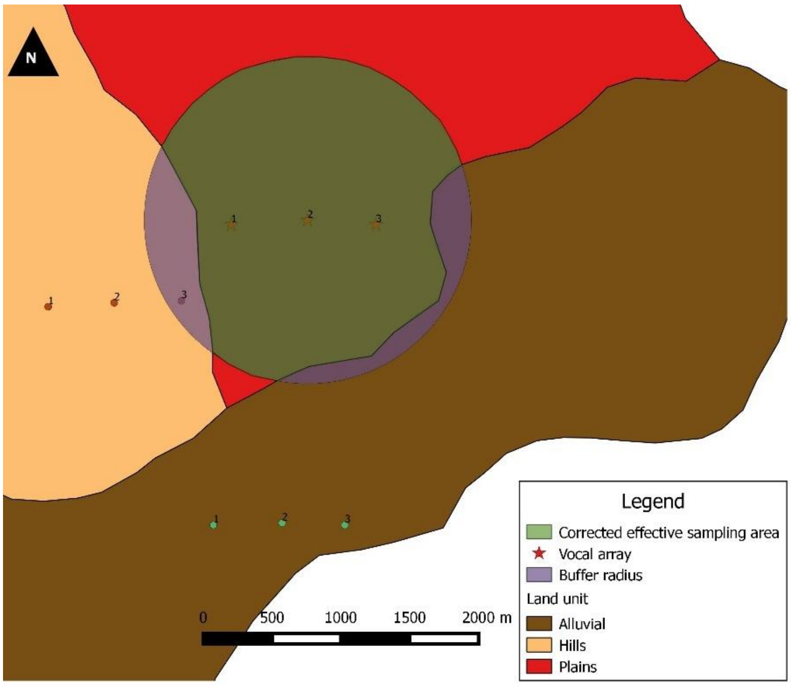

Figure 3.9: How total sampling area is calculated in the triangulation method for acoustic surveys.

The SECR model was run using the gibbonsSECR package in R (developed by Darren Kidney, University of St Andrews; available at : //github.com/dkidney/gibbonsSECR). Once groups were identified in ArcGIS, every call recorded by each group was assigned an occasion number and input into the SECR model. A buffer radius (m) was selected by increasing the buffer radius from 1000m until the Akaike Information Criterion, AIC and effective sampling area values stabilised. The SECR model uses a detection function to account for imperfect detection, providing a more reliable estimate of effective sampling area. Simultaneous captures at multiple posts are used to correct for bearing error, making it a more robust method for calculating group density than using triangulation of groups alone (Kidney et al. 2013). In this analysis, a half normal detection function was applied. This assumes that the probability of detection has a half normal distribution, starting at 1 at the sample point and exponentially decreasing as distance from the sample point increases (see figure 3.10). The half normal detection function is calculated as follows, $P_k(x;\theta) = \theta_0 exp - \left(\frac{d_k(x)^2}{2\theta_1^2}\right)$, where d_k= distance between animal and detector, k, x= animal location, and $\theta_0, \theta_1$and $\theta_2$are parameters determining the intercept, scale and shape of the detection function. θ_0 is fixed at 1, since it is assumed that animals calling from d_k=0 would be detected with certainty, meaning that the y-intercept would be at 1. θ_1 and θ_2 are computed automatically within the gibbonsSECR programme (Kidney et al. 2013).

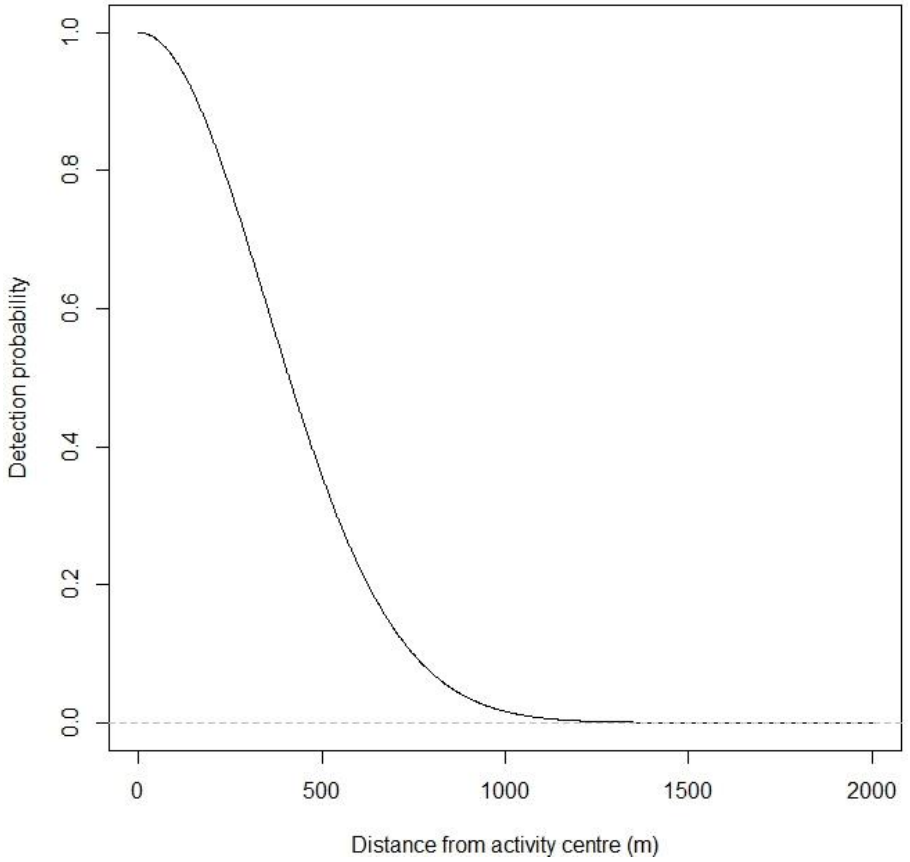

Figure 3.10: An example of the half normal detection function calculated in the SECR model.

3.4: Linking group density to forest structure

A lack of data for group density meant that it was not possible to carry out any meaningful statistical analysis to correlate density with forest structure variables. However, it was possible to identify differences in both structure and group density between the three land units. These differences can be used to infer possible links between habitat preferences of *P. thomasi* and forest structure.

Chapter 4 : Results

4.1: Forest structure

4.1.1: Normality tests

Table 4.1 shows the results of the Shapiro-Wilkinson test for normality. All tests were significant ($P<0.05$) with the only exceptions being stand basal area, SBA (m^2/ha) total trees per plot; and tree density (trees/ha), however, these all had a low sample number ($n=5$; Table 4.1). Therefore, non-parametric tests were chosen to test for significant differences in forest structure between the three land units.

4.1.2: Comparison of plots and transects

Continuous variables which were collected from both plots and transects were compared to ensure that the two methods were sampled from the same population in each land unit. A summary of the results of the Kruskal-Wallis and post-hoc Mann-Whitney pairwise tests is given in table 4.2. All of the Mann-Whitney tests between transects and plots within each land unit are non-significants after sequential Bonferroni correction. The one exception is top height (m) in hills. From these results it is reasonable to assume that plots and transects were sampled from the same population and that the data from both methods can therefore be analysed together.

Table 4.1: Results for Shapiro-Wilkinson test for normality. Significant P-values are highlighted in bold and underlined.

		N			***Shapiro-Wilkinson, W***			***p(normal)***	
	alluvial	***hills***	***plains***	***alluvial***	***hills***	***plains***	***alluvial***	***hills***	***plains***
per tree with DBH >10cm									
DBH (cm)	572	548	583	0.7584	0.05802	0.1127	**<0.001**	**<0.001**	**<0.001**
BA (cm$^{2)}$	170	148	181	0.4236	0.5468	0.3775	**<0.001**	**<0.001**	**<0.001**
BA - DBH>20cm (cm2)	67	65	58	0.5114	0.6079	0.5021	**<0.001**	**<0.001**	**<0.001**
top height (m)	571	547	582	0.9004	0.8851	0.8684	**<0.001**	**<0.001**	**<0.001**
bole height (m)	569	547	580	0.9371	0.9395	0.9429	**<0.001**	**<0.001**	**<0.001**
height-DBH ratio	571	548	582	0.9861	0.8543	0.9828	**<0.001**	**<0.001**	**<0.001**
crown area (m^{2})	571	549	582	0.6367	0.4839	0.4256	**<0.001**	**<0.001**	**<0.001**
branch counts *<2cm*	569	579	549	0.7133	0.6965	0.6719	**<0.001**	**<0.001**	**<0.001**
2-4cm	569	579	549	0.4291	0.5838	0.2985	**<0.001**	**<0.001**	**<0.001**
4-10cm	569	579	549	0.5006	0.2128	0.2349	**<0.001**	**<0.001**	**<0.001**
10-20cm	569	579	549	0.3965	0.3222	0.2772	**<0.001**	**<0.001**	**<0.001**
>20cm	569	579	549	0.26	0.2319	0.1572	**<0.001**	**<0.001**	**<0.001**
per plot									
total number of trees	5	5	5	0.9039	0.984	0.9628	0.374	0.8425	0.8274
per hectare									
tree density (trees/ha)	5	5	5	0.9719	0.9526	0.9225	0.8873	0.7558	0.546
stand basal area (m^{2}/ha)	5	5	5	0.9719	0.9526	0.9225	0.8873	0.7558	0.546

Table 4.2: Summary of results for Kruskal-Wallis and Mann-Whitney pairwise tests to compare data collected from transects with data collected from plots. Significant P-values are highlighted in bold and underlined.

		Kruskal-Wallis - all samples			***Mann-Whitney post-hoc (transects x plots)***								
					alluvial			***Hills***			***Plains***		
		N	χ^2	***P***	***N***	***U***	***P***	***N***	***U***	***P***	***N***	***U***	***P***
DBH(cm)		1703	23.84	0.000233	572	32500	0.3385	548	25300	0.005988	583	33100	0.07883
top height (m)		1700	21.83	0.000561	571	32800	0.448	547	23800	**<0.001**	582	32400	0.0325
bole height (m)		1696	17.79	0.003203	569	33600	0.83	547	25700	0.0139	580	32300	0.0306
Crown area (m^2)		1701	7.734	0.1715	571	32310	0.2946	548	28610	0.4706	582	34490	0.3087
height-DBH ratio		1702	19.36	0.001645	571	25950	0.01068	549	28640	0.5607	582	36280	0.9512
branch counts	*<2cm*	1697	8.453	0.112	569	31100	0.1196	579	29500	0.8736	549	35900	0.9053
	2-4cm	1697	10.34	0.0282	569	32350	0.3756	579	29720	0.9603	549	29720	0.1628
	4-10cm	1697	1.635	0.8363	569	32470	0.411	579	27680	0.1354	549	34470	0.3117
	10-20cm	1697	-17.04	-38.05	569	33200	0.6472	579	28290	0.1673	549	34750	0.2239
	>20cm	1697	-27.5	1	569	33710	0.9083	579	28670	0.07683	549	35790	0.6229

Table 4.3: Summary of continuous variables collected on forest structure and results of the non-parametric Kruskal-Wallis and post-hoc Mann-Whitney U tests. P-values which are significant following sequential Bonferroni correction are highlighted in bold and underlined.

		alluvial			***hills***			***plains***			***Kruskal-Wallis***		***Mann-Whitney U***		
		N	***median***	***mean***	***N***	***median***	***mean***	***N***	***median***	***mean***	***χ^2***	***P***	***alluvial x hills***	***hills x plains***	***plains x alluvial***
per tree with DBH>10cm															
	diameter at breast height, DBH (cm)	572	17.83	22.65	548	15.60	20.79	583	15.92	20.59	12.17	**<0.001**	U=140500, **P=0.002**	U=159400, P=0.95	U=14900, **P=0.002**
	basal area, BA (cm^2)	170	215.18	499.17	148	267.70	509.42	181	161.14	425.70	8.65	**0.01**	U=121900, P=0.50	U=111910, **P=0.006**	U=13450, P=0.03
	BA (cm^2) - trees with DBH>20cm	67	602.32	1033.89	65	703.15	966.43	58	616.33	1038.87	0.46	0.79	U=2113, P=0.77	U=1721, P=0.42	U=1914, P=0.89
	top height(m)	571	14.00	15.20	547	13.40	15.26	582	13.30	14.40	4.00	0.14	U=155000, P=0.85	U=151000, P=0.12	U=156000, P=0.06
	bole height (m)	569	8.40	9.32	547	9.30	10.01	580	8.60	9.34	7.29	**0.03**	U=143000, **P=0.01**	U=148000, P=0.03	U=163000, P=0.66
	height-DBH ratio	571	74.84	76.34	548	80.73	82.33	582	75.95	78.88	13.12	**<0.001**	U=136600, **P<0.001**	U=146900, P=0.02	U=158400, P=0.17
	crown area (m^2)	571	20.65	32.92	549	18.97	32.06	582	18.90	31.95	4.91	0.09	U=150600, P=0.26	U=154000, P=0.29	U=153600, P=0.03
branch counts	*<2cm*	569	750.00	2265.48	579	750.00	2081.69	549	750.00	1808.27	5.55	0.05	U=151800, P=0.41	U=150800, P=0.12	U=151700, **P=0.02**
	2-4cm	569	5.00	14.18	579	5.00	9.74	549	5.00	12.14	10.08	**<0.001**	U=136100, **P<0.001**	U=155000, P=0.42	U=147100, **P<0.001**
	4-10cm	569	5.00	5.35	579	0.00	4.09	549	0.00	4.54	2.77	0.17	U=135000, **P<0.001**	U=151600, P=0.12	U=149700, **P=0.003**
	10-20cm	569	0.00	1.32	579	0.00	1.16	549	0.00	1.18	-13.17	1.00	U=148300, P=0.04	U=153700, P=0.13	U=151000, **P<0.001**
	>20cm	569	0.00	0.32	579	0.00	0.26	549	0.00	0.28	-22.39	1.00	U=154600, P=0.45	U=158200, P=0.74	U=162300, P=0.28
per plot															
	total number of trees	5	33.00	34.20	5	31.00	29.80	5	36.00	36.40	1.81	0.40	U=11, P=0.83	U=6, P=0.21	U=8.5, P=0.46
per hectare															
	tree density (trees / ha)	5	528.00	547.20	5	496.00	476.80	5	576.00	582.40	0.32	0.85	U=10, P=0.68	U=11, P=0.83	U=11, P=0.83
	stand basal area, SBA (m^2/ha)	5	27.20	27.32	5	24.28	24.29	5	25.61	24.79	0.32	0.85	U=10, P=0.68	U=11, P=0.83	U=11, P=0.83

4.1.3: Structural differences in individual trees

There is no significant difference in top height (m) between the three land units after sequential Bonferroni correction (table 4.3; figure 4.1). There is however a significant difference in bole height (m) between the three land units (table 4.3). There is a significant difference in bole height between the hills and alluvial land units after sequential Bonferroni correction (table 4.3). Alluvial and plains appear to have similar bole heights, median= 8.4m and median= 8.6m respectively, while hills is higher, median= 9.3m (figure 4.2). DBH (cm) also differs significantly across the three land units (table 4.3). Alluvial has a significantly higher DBH, median= 17.83cm, than hills, median= 15.6cm. Plains does not differ significantly from either of the other two land units after Bonferroni correction (table 4.3), and is intermediate, median= 15.9cm (figure 4.3).

The height-DBH ratio differs significantly across the three land units (table 4.3). Alluvial and hills are the only two land units which differ significantly in their height-DBH ratio following sequential Bonferroni correction (table 4.3). Hills has the highest height-DBH ratio, mean= 82.33, while alluvial has the lowest, mean= 76.34 (figure 4.4). A Spearman's rho correlation shows a significant correlation between height (m) and DBH (m) in all land units (table 4.4; figures 4.5-7). The correlation between height (m) and DBH (m) appears to be stronger in both the plains and hills land unit, compared with the alluvial land unit.

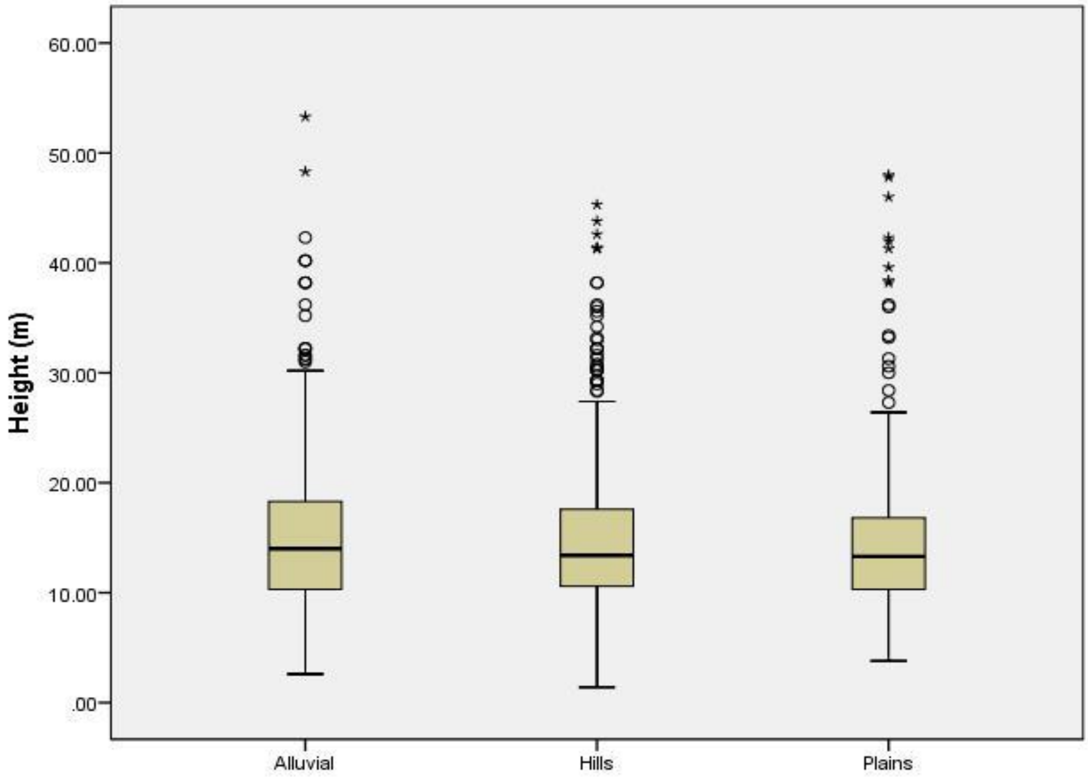

Figure 4.1: Top height (m) of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

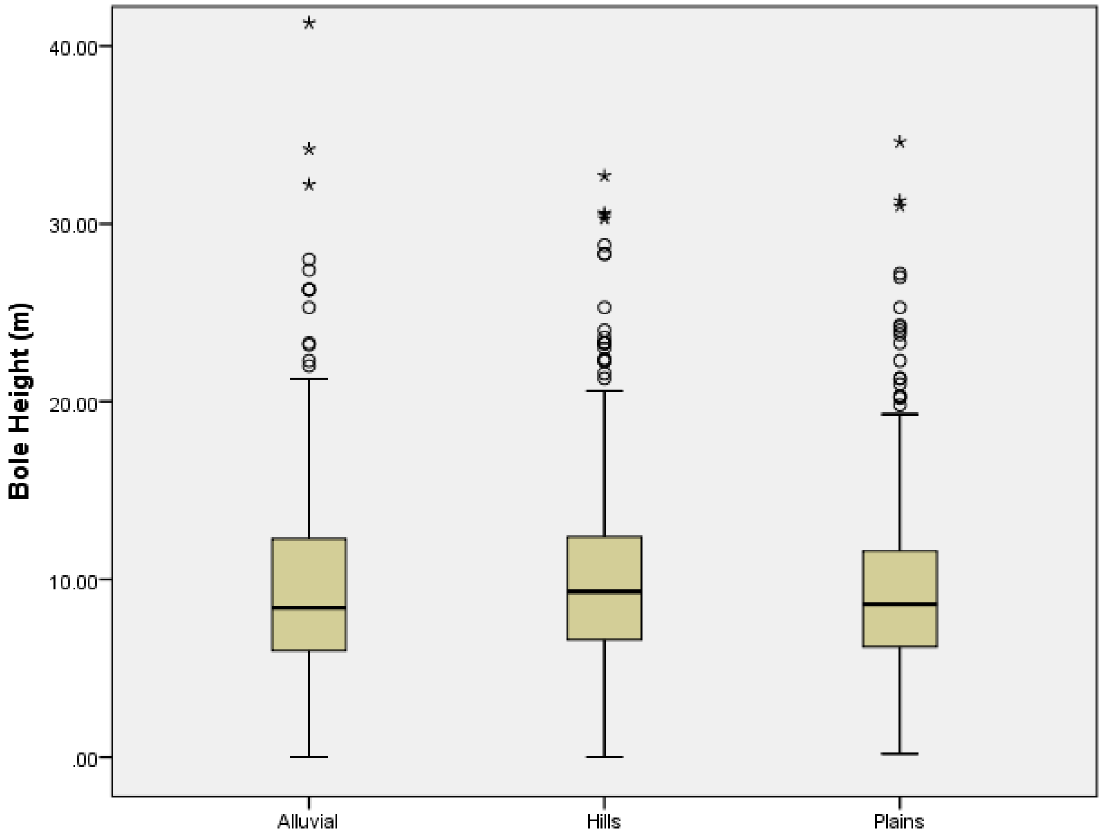

Figure 4.2: Differences between land units in bole height (m). Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

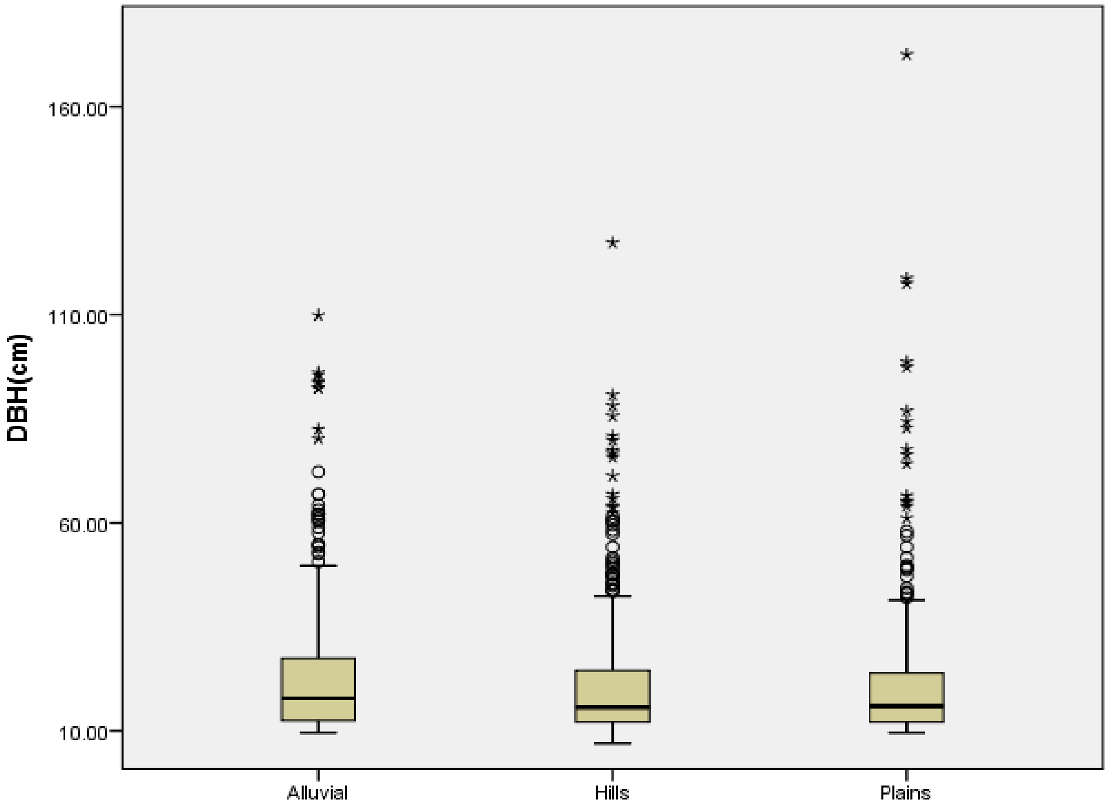

Figure 4.3: Diameter at breast height (DBH) in cm of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

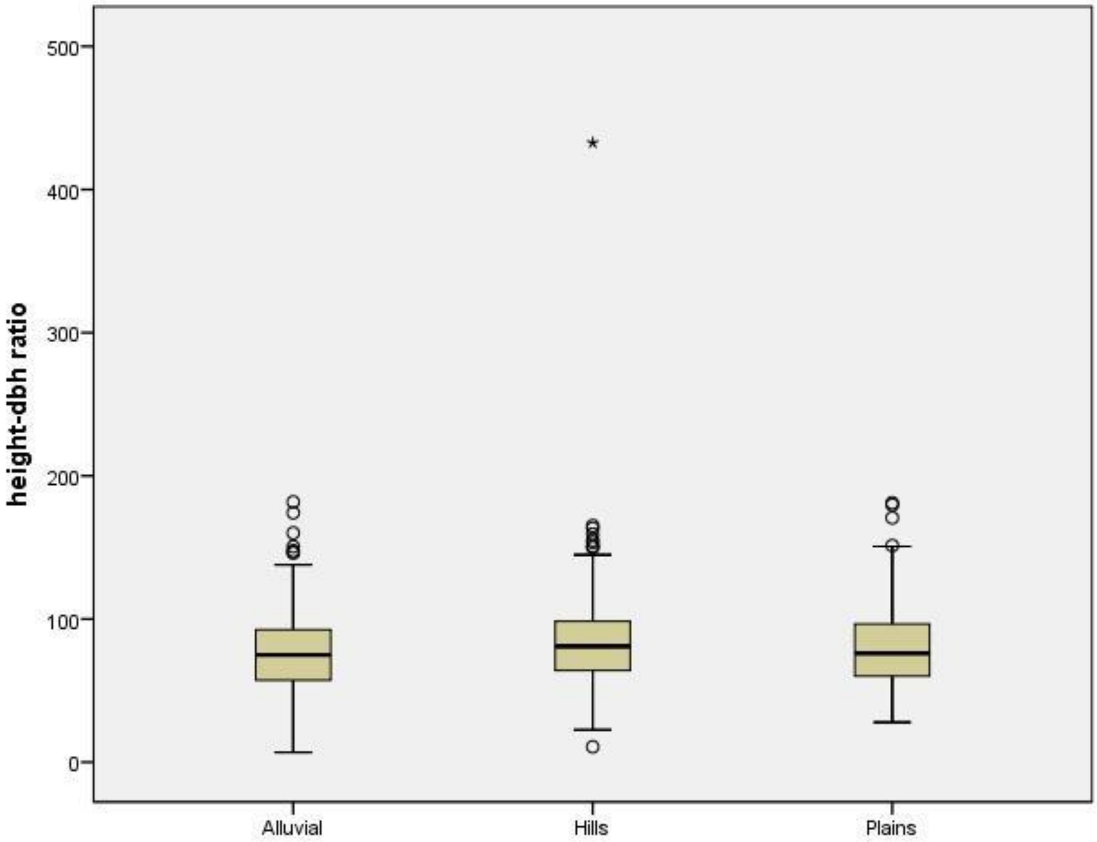

Figure 4.4: Height-DBH ratio of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

Table 4.4: Results of Spearman's rho correlation of height (m) and DBH (m) in each land unit. Significant values are indicated in bold and underlined.

	Spearman's rho correlation		
land unit	***N***	***rho***	***P***
alluvial	571	0.7326	**1.501E-93**
hills	549	0.7925	**3.87E-119**
plains	582	0.79072	**1.03E-125**

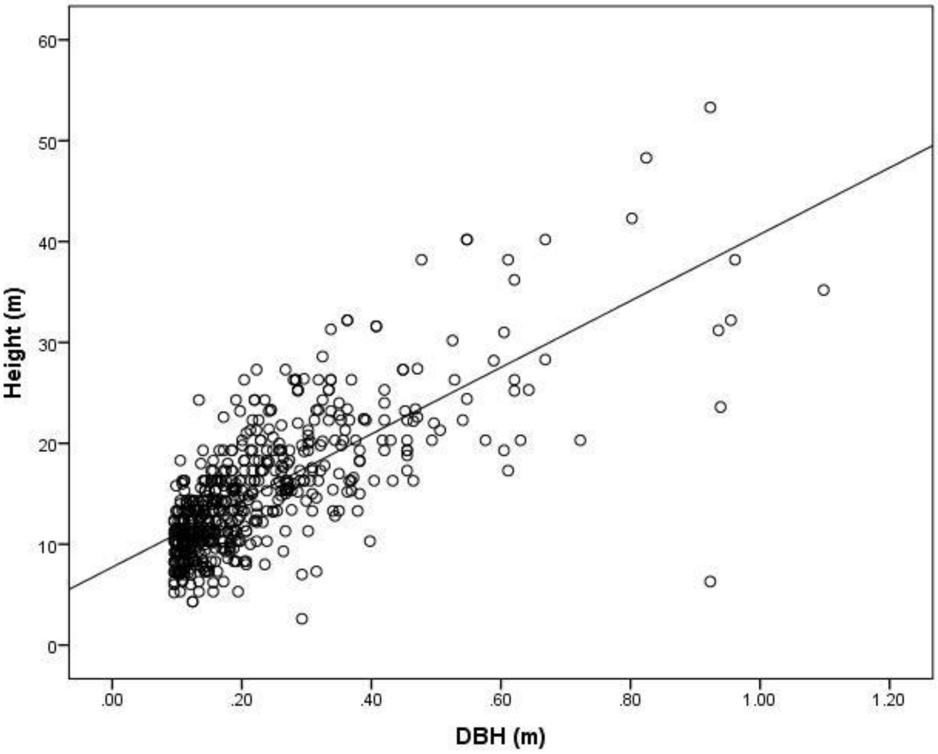

Figure 4.5: The relationship between height (m) and DBH (m) for trees in the alluvial land unit.

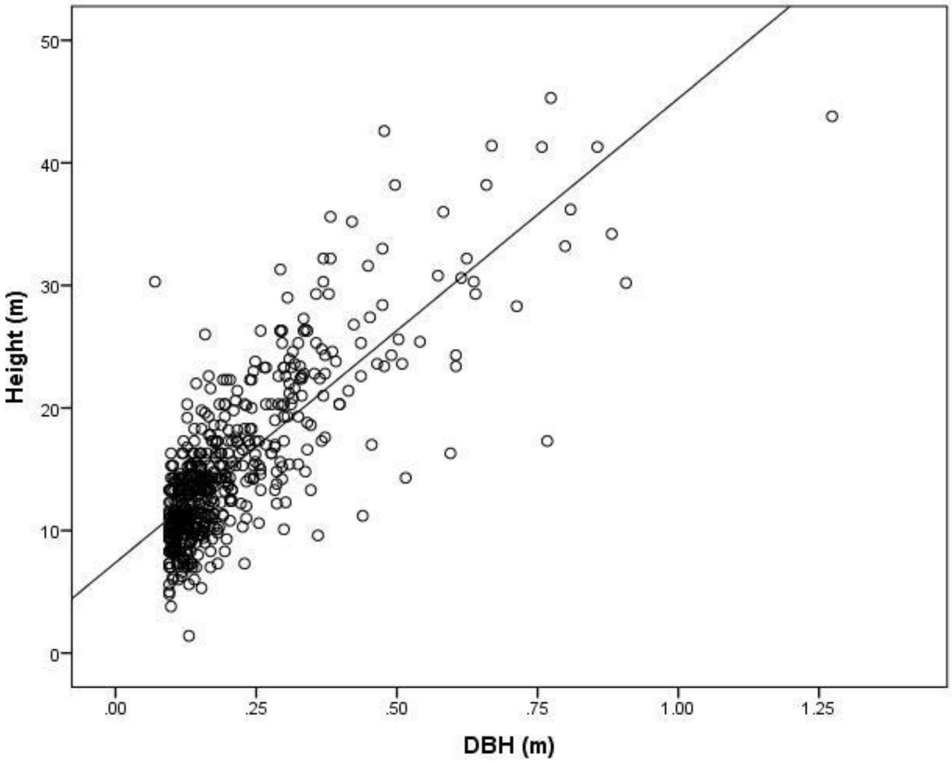

Figure 4.6: The relationship between height (m) and DBH (m) in the hills land unit.

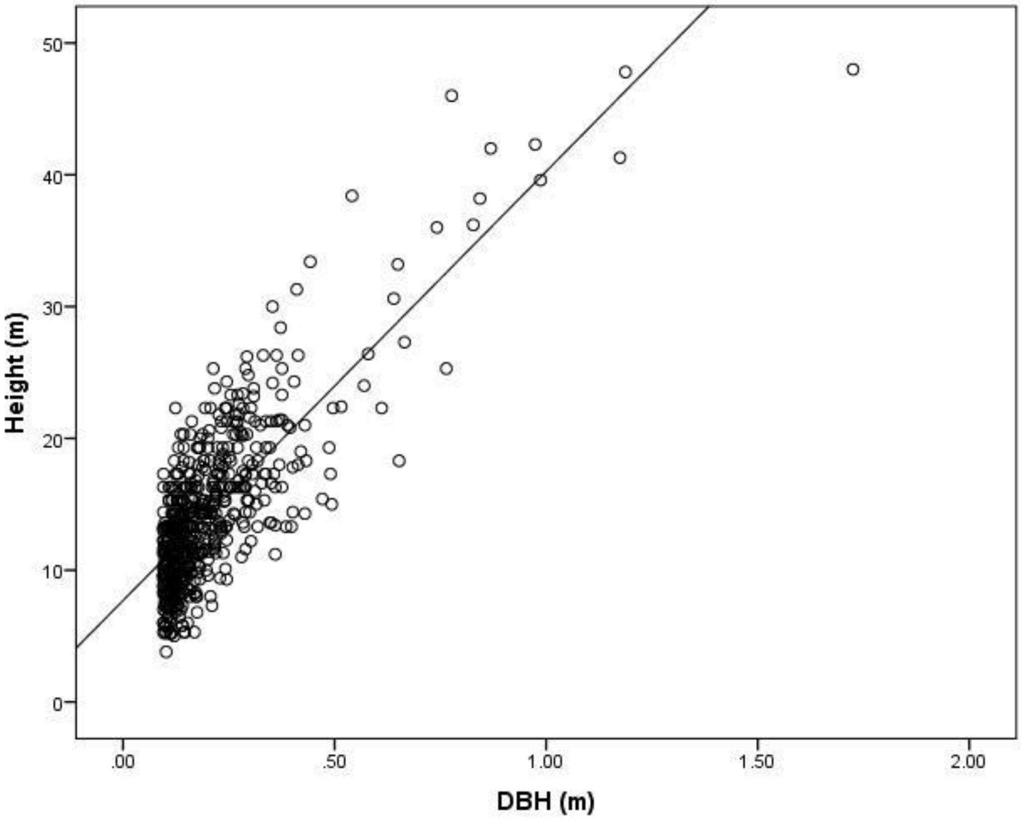

Figure 4.7: The relationship between height (m) and DBH (m) in the plains land unit.

Crown area does not differ significantly between the three land units (table 4.3). However, the median of crown area is slightly higher in alluvial, (20.65m^2, compared with 18.97m^2 and 18.9m^2 in hills and plains respectively; figure 4.8). There is no significant difference in the frequencies of crown shapes (chi-squared two-way contingency test: χ^2=7.4474, df=6, P=0.28; table 4.5; figure 4.9) and crown connectivity (chi-squared two-way contingency test: χ^2= 13.527, df=10, P=0.19; table 4.6; figure 4.10). Spheroid is by far the most common shape, accounting for 64.83% of all trees. 79.1% of all trees recorded have a connectivity above 50%.

There is a significant difference in the number of small branches (diameter 2-4cm) with a Kruskal-Wallis test (table 4.3). There is a significant difference between alluvial and plains and between alluvial and hills after sequential Bonferroni correction (table 4.3). Alluvial has the highest number of small branches, median=5 and mean=14.18, while hills has the lowest, median=5 and mean=9.74. Plains is intermediate, median=5 and mean=12.14116 (table 4.3; figure 4.12). The number of very small branches (diameter <2cm), medium branches (2-4cm), large branches (10-20cm) and very large branches (>20cm) does not differ between land units (table 4.3; figures 4.11, 13, 14 and 15). However, there is a significant difference in very small branches between alluvial and plains, even after sequential Bonferroni correction (table 4.3). Alluvial has a higher number of very small branches, median=750 and mean=2265.475; while plains has the lowest number median=750 and mean=1808.273; hills is intermediate, median=750 and mean=2081.685 (table 4.3; figure 4.11). The Mann-Whitney pairwise test also shows a significant difference in the number of medium branches between alluvial and hills and alluvial and plains, even after sequential Bonferroni correction (see table 4.3). The mean number of medium branches is highest in alluvial at 5.35, and lowest in hills at 4.09, with plains being in between at 4.54 (table 4.3; figure 4.13). There is also a significant difference in the number of large branches between alluvial and plains (table 4.3). The mean count of large branches is highest in alluvial at 1.32, with plains and hills being lower at 1.18 and 1.15 respectively (table 4.3; figure 4.14). There are no significant differences in the number of very large branches, with all land units having a very low count (table 4.3; figure 4.15).

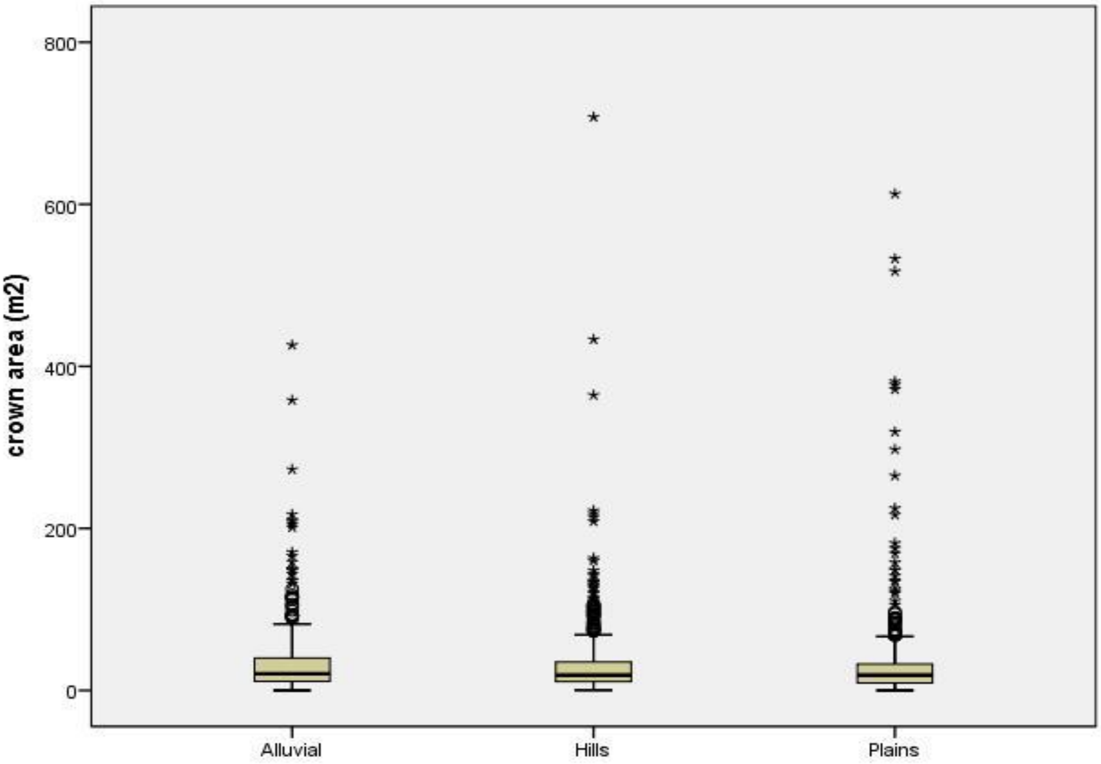

Figure 4.8: Crown area (m^2) of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

Table 4.5: Chi-squared two-way contingency table for observed connectivity of tree canopies in each land unit.

crown connectivity	***alluvial***		***hills***		***plains***	
	observed	***expected***	***observed***	***expected***	***observed***	***expected***
0-25%	20	25.83	28	24.88	29	26.29
25-50%	106	93.27	78	89.83	94	94.90
50-75%	219	213.37	212	205.51	205	217.12
75-100%	225	237.53	231	228.78	252	241.70
total	570	570	549	549	580	580

Table 4.6: Chi-squared two-way contingency table for observed shape of tree canopies in each land unit.

crown shape	***alluvial***		***hills***		***plains***	
	observed	***expected***	***observed***	***expected***	***observed***	***expected***
spheroid	354	353.99	371	375.38	359	354.63
elongated spheroid	74	60.09	56	63.72	54	60.20
cone	31	41.15	45	43.63	50	41.22
upside down cone	30	30.37	40	32.21	23	30.43
umbrella	18	19.59	23	20.78	19	19.63
bent over	39	40.82	44	43.29	42	40.89
total	546	546	579	579	547	547

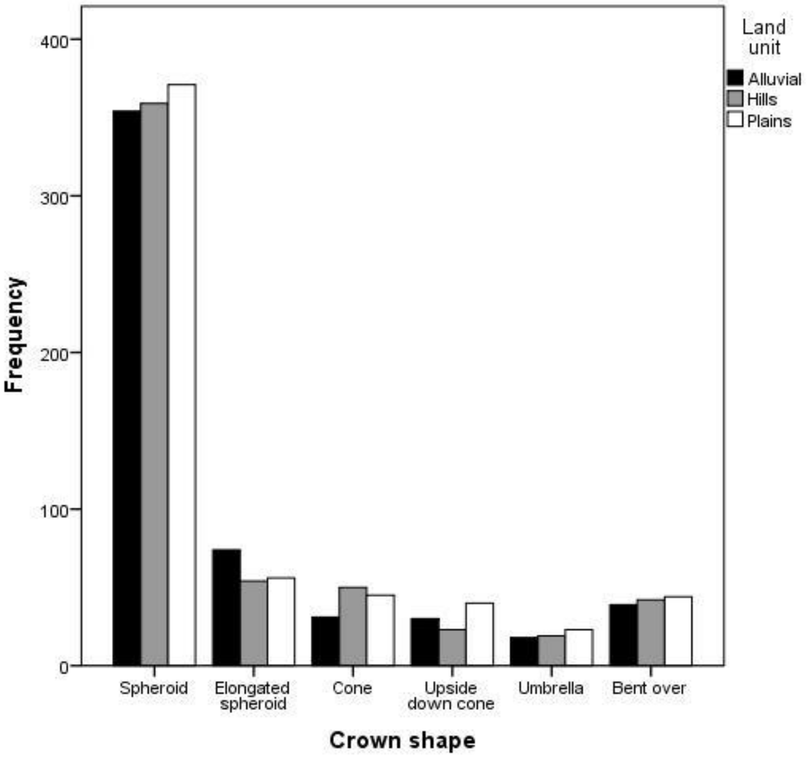

Figure 4.9: Frequencies of crown shape categories for trees in each land unit.

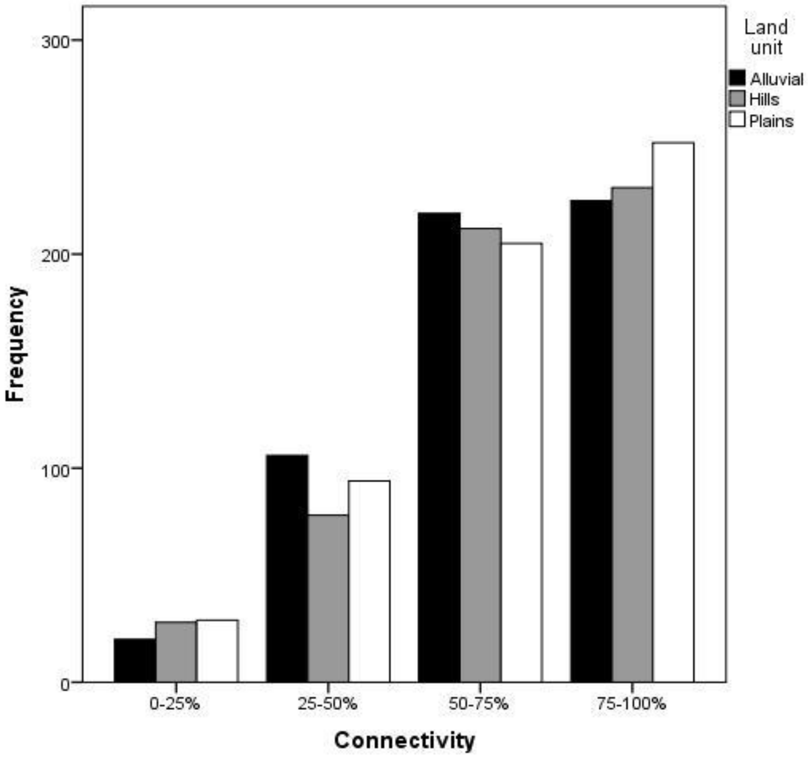

Figure 4.10: Frequencies of categories for estimated canopy connectivity of trees in each land unit.

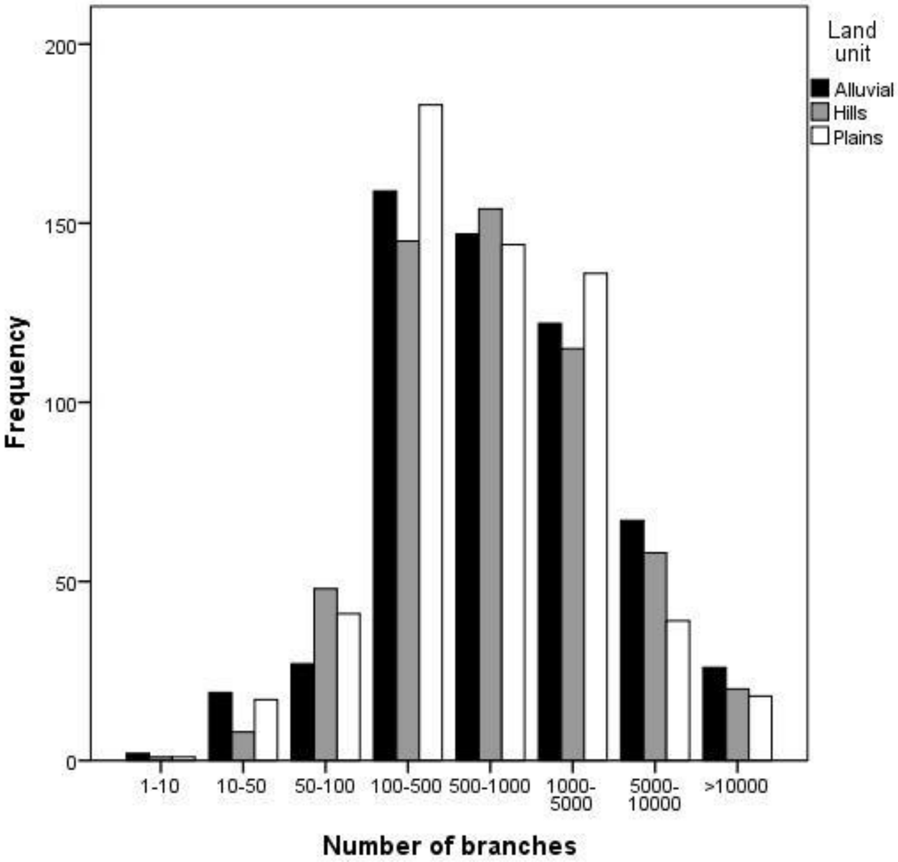

Figure 4.11: Frequencies of estimated number of branches with a diameter 0-2cm for trees in each land unit.

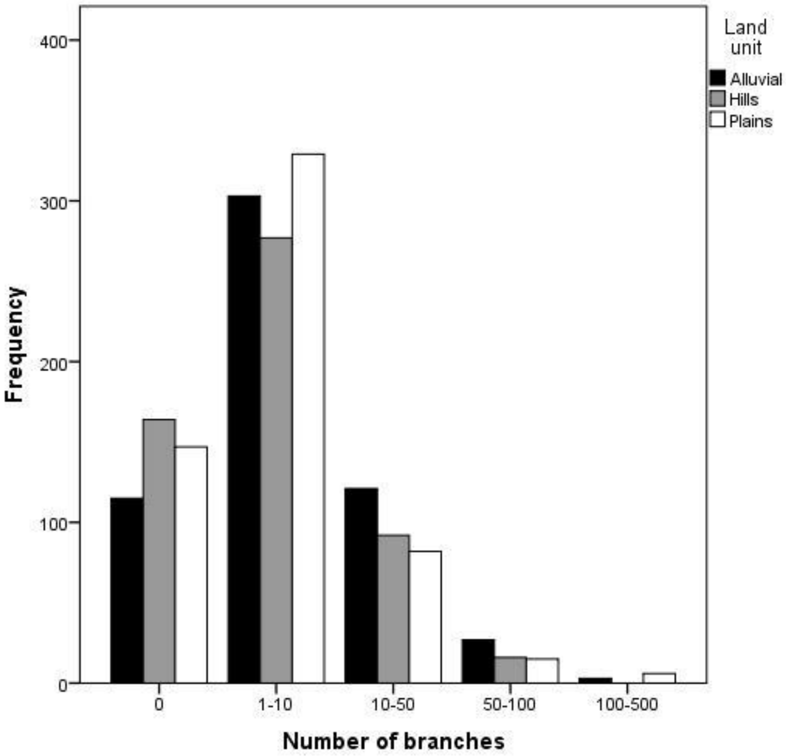

Figure 4.12: Frequencies of estimated number of branches with a diameter of 2-4cm for trees in each land unit.

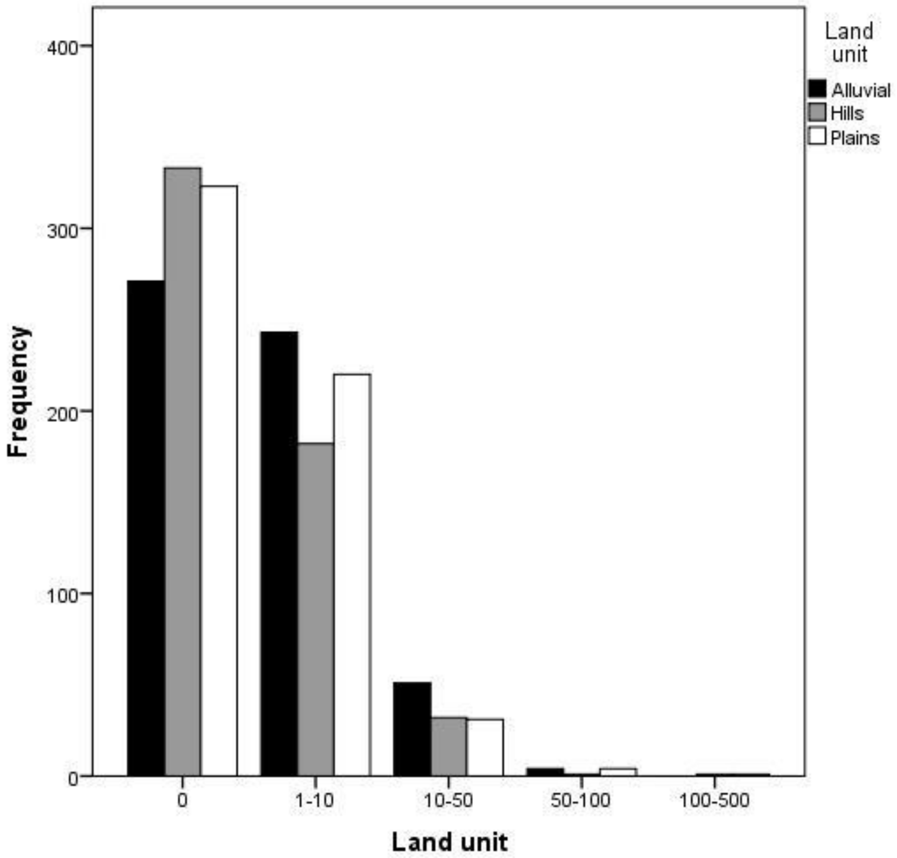

Figure 4.13: Frequencies of estimated number of branches with diameter 4-10cm for trees in each land unit.

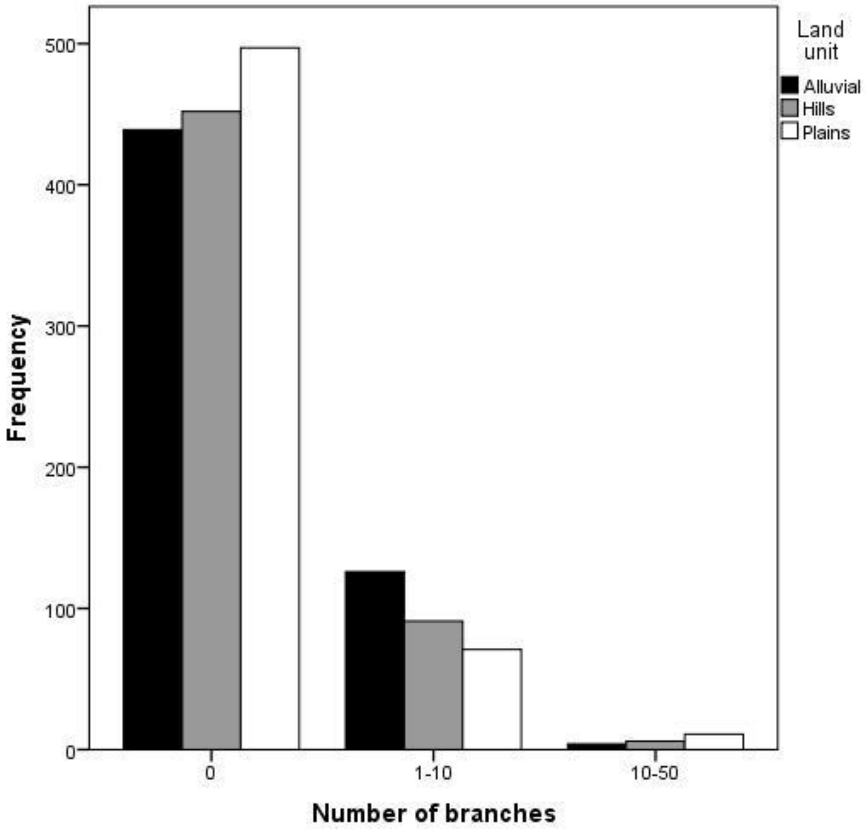

Figure 4.14: Frequencies of estimated number of branches with diameter 10-20cm.

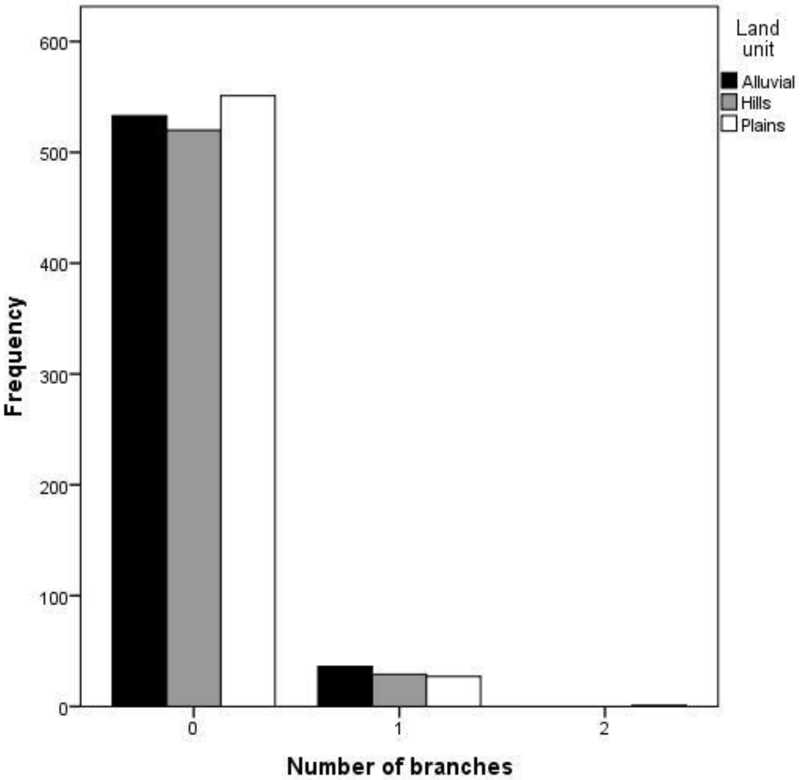

Figure 4.15: Frequencies of estimated number of branches with diameter >20cm for trees in each land unit.

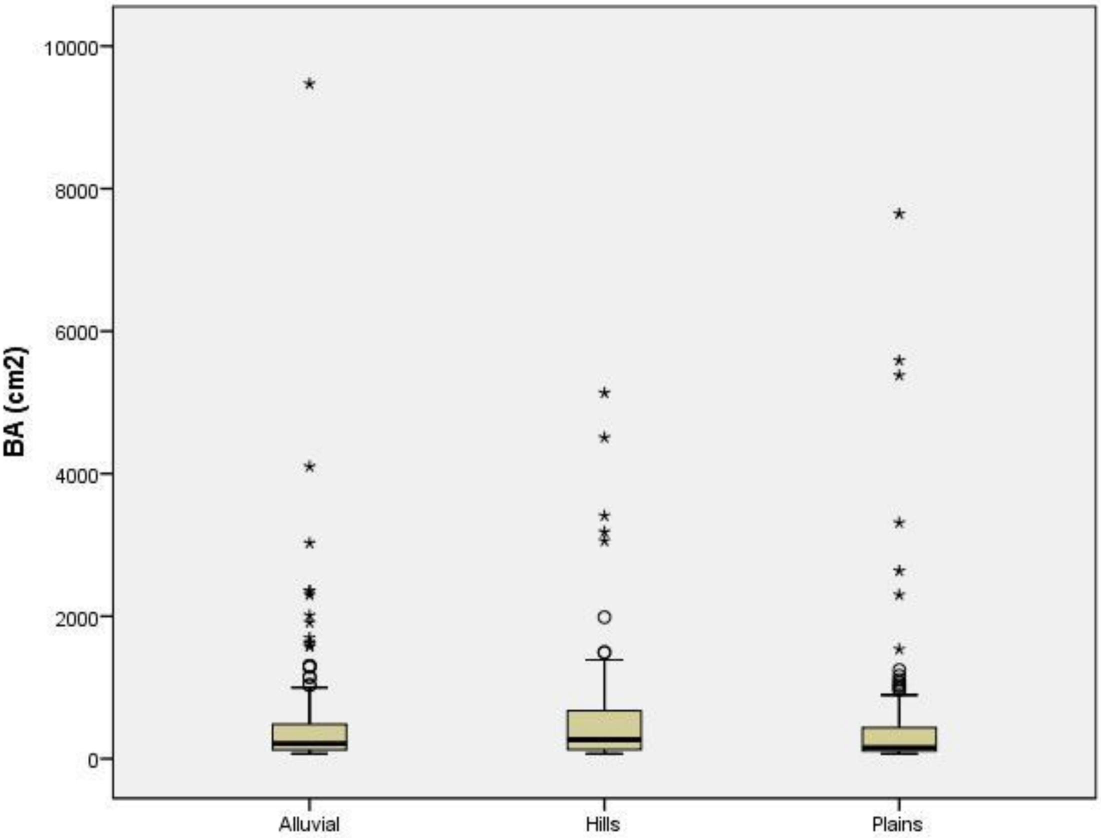

Figure 4.16: Basal area (BA) in cm^2 of trees in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

Basal area, BA, is significantly different between hills and plains (table 4.3). Plains has the lowest median BA of 161.14cm^2, while hills and alluvial are both similar, with medians of 267.7cm^2 and 215.18cm^2 respectively. Hills has the highest median BA, with plains being the lowest, and alluvial being intermediate (figure 4.16).

4.1.4: Tree densities

There is no significant difference in stand basal area (SBA) in m^2/ha between the three land units (table 4.3; figure 4.17), although the median SBA of alluvial is somewhat higher than that of plains and hills (27.2m^2/ha; 24.29m^2/ha; and 24.29m^2/ha respectively). There is no significant difference between land units for total number of trees per plot (table 4.3; figure 4.17). There is no significant difference in tree density between the three land units (table 4.3; figure 4.19). However, hills does have a much lower median tree density at 496 trees per hectare than alluvial and plains (528 trees per hectare and 576 trees per hectare respectively).

4.1.5: Sizes of tree found in each land unit

There is a significant difference in the number of trees with a top height exceeding 25m (chi-squared goodness-of-fit test χ^2=8.381, df=2, P=0.015; table 4.7). Plains has only 27 taller trees, compared with alluvial and hills, which have far more (47 and 49 respectively; figure 4.20). There is no significant difference in the number of trees with DBH 10-30cm; (chi-squared goodness-of-fit test χ^2=0.845, df=2, P=0.655; table 4.8), or in the number of trees with DBH <60cm (chi-squared goodness-of-fit test χ^2=0.7747, df=2, P=0.679; table 4.10). There is, however, a significantly higher number of trees with DBH 31-60cm (chi-squared goodness-of-fit test χ^2=6.893, df=2, P=0.032) in the alluvial land unit (88, compared with 67 in hills and 58 in plains; table 4.9; figure 4.21). All of the land units have a fairly low number of large trees (21 in alluvial, 18 in hills and 16 in plains; figure 4.21). Overall, alluvial appears to have generally larger trees than hills and plains.

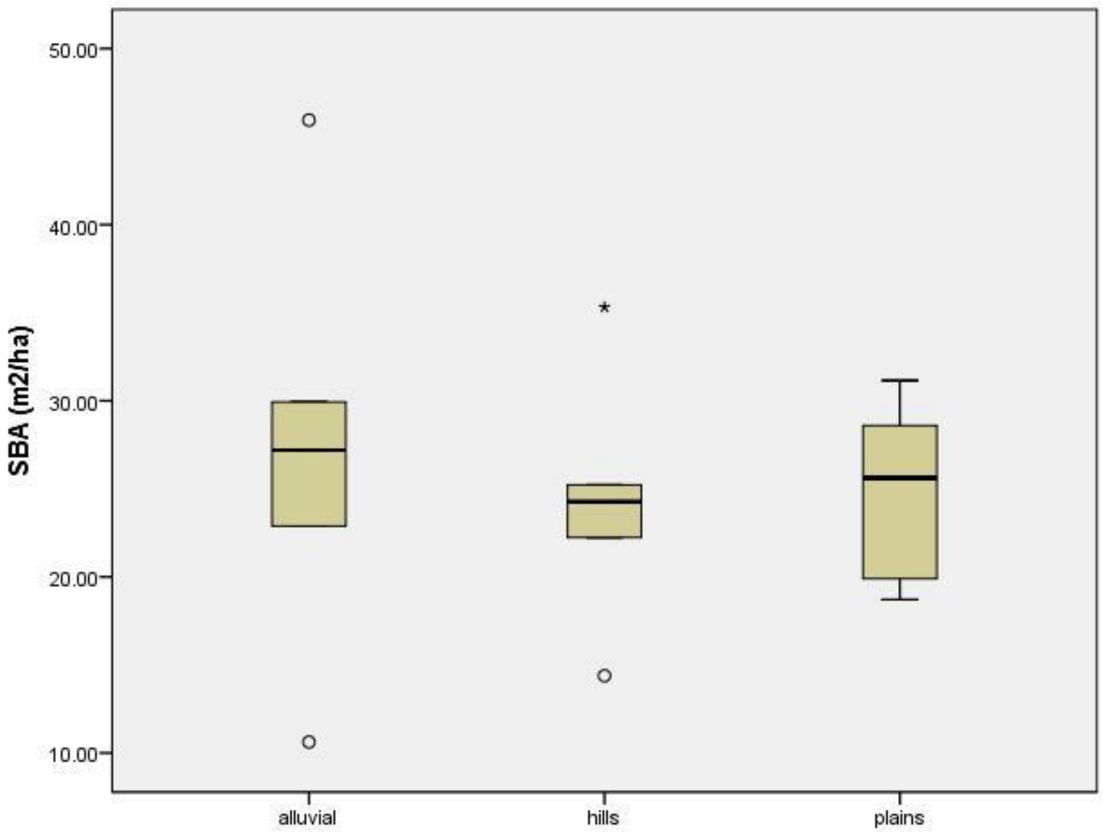

Figure 4.17: Stand basal area (SBA) in m^2/ha of trees with diameter >10cm in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

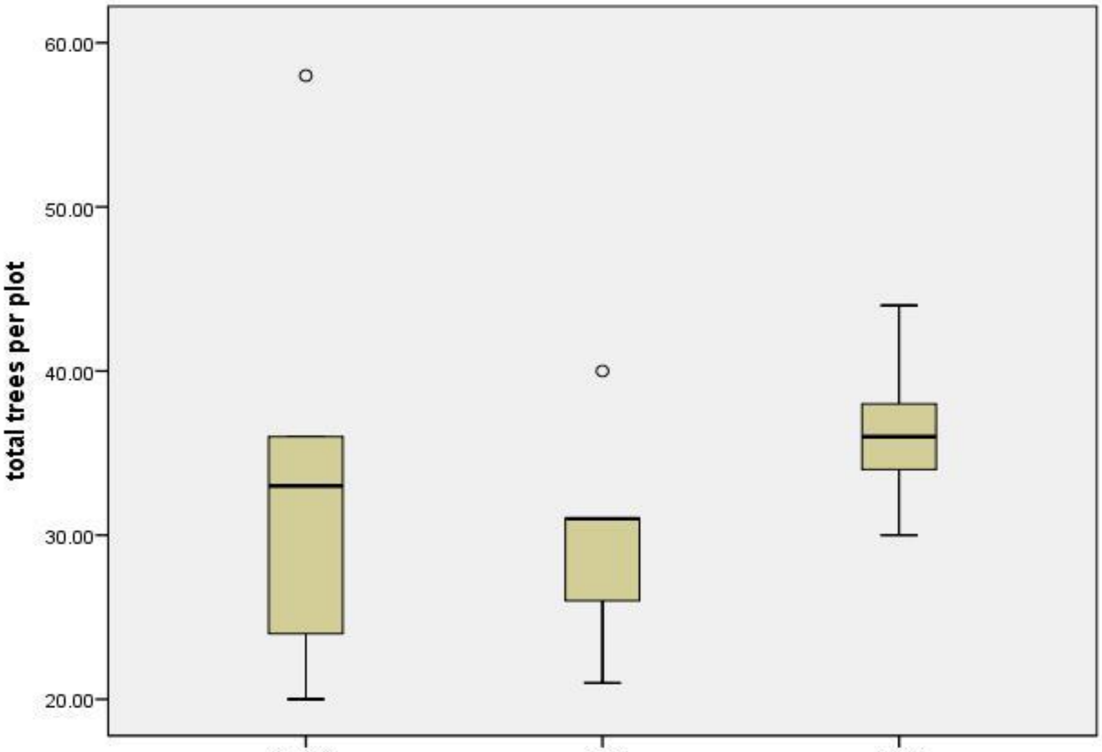

Figure 4.18: Total number of trees with DBH >10cm per plot in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

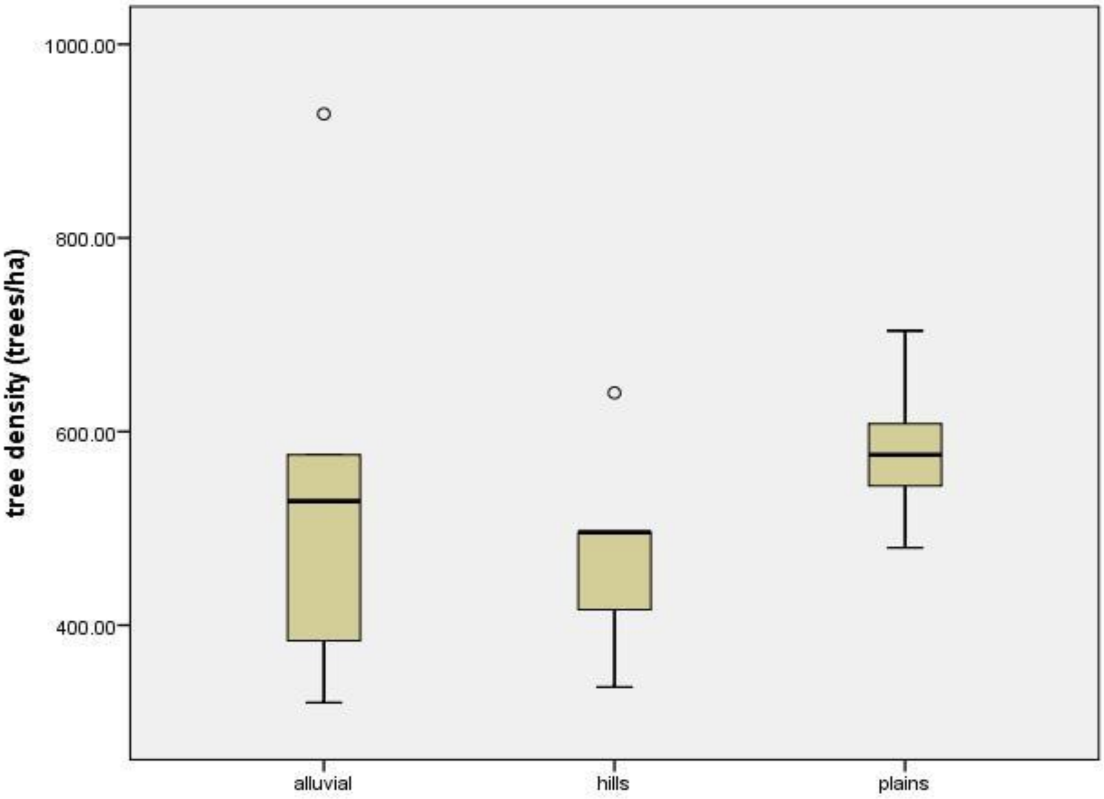

Figure 4.19: Tree density (trees/ha) calculated from plots in each land unit. Boxes represent quartiles, whiskers indicate 95 percentile values, * and ° represent the extremes and outliers respectively.

Table 4.7: Chi-squared goodness-of-fit table showing differences in the number of trees with top height >25m in each land unit.

land unit	*observed*	*total*	*expected*
Alluvial	47	571	41.2649824
Hills	49	549	39.6750881
Plains	27	582	42.0599295
Total	123	1702	123

Table 4.8: Chi-squared goodness-of-fit table showing differences in the number of trees with DBH 10-30cm in each land unit.

land unit	*observed*	*total*	*expected*
Alluvial	425	571	435.1275
Hills	413	549	418.3625
Plains	459	582	443.51
Total	1297	1702	1297

Table 4.9: Chi-squared goodness-of-fit table showing differences in the number of trees with DBH 31-60cm in each land unit.

land unit	*observed*	*total*	*expected*
Alluvial	88	571	71.45887
Hills	67	549	68.70564
Plains	58	582	72.83549
Total	213	1702	213

Table 4.10: Chi-squared goodness-of-fit table showing differences in the number of trees with DBH >60cm in each land unit.

land unit	*observed*	*total*	*expected*
Alluvial	21	571	18.45182
Hills	18	549	17.74089
Plains	16	582	18.80729
Total	55	1702	55

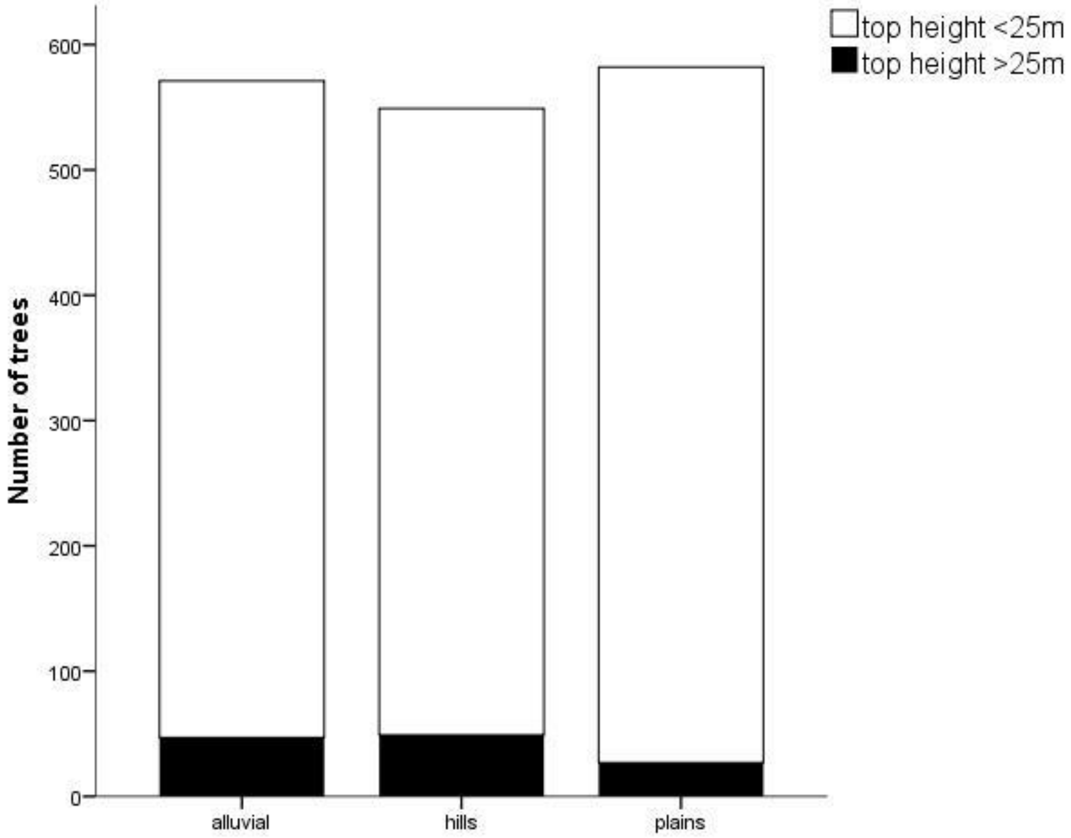

Figure 4.20: Proportion of trees with top height both above and below 25m recorded in each land unit.

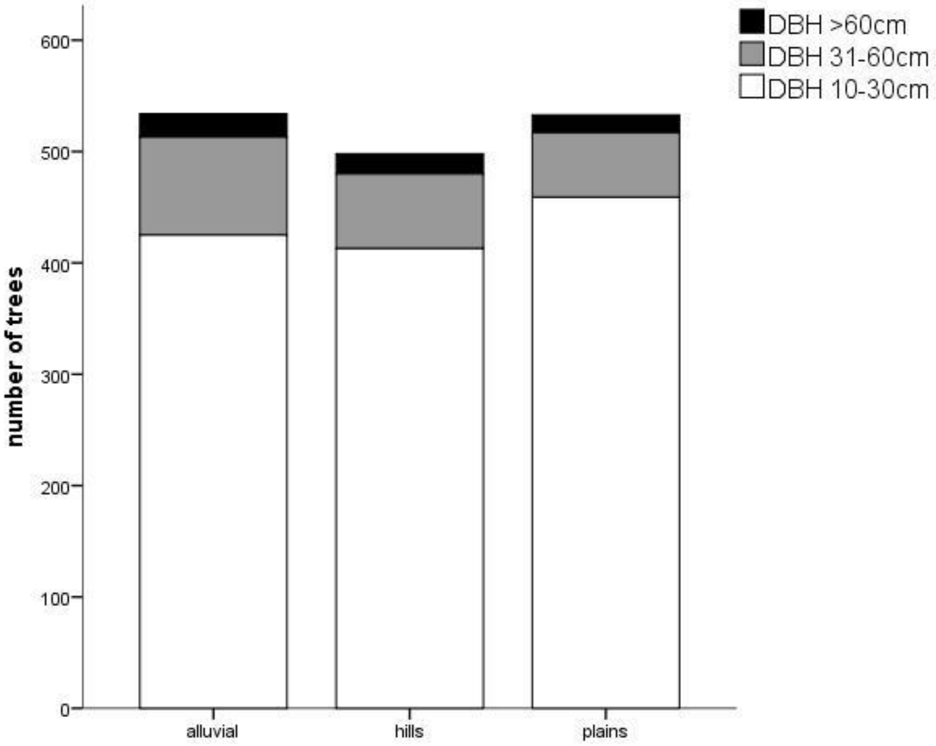

Figure 4.21: Number of trees with DBH between 10-30cm, the number of trees with DBH between 31-60cm and the number of trees with DBH>60cm recorded in each land unit.

4.1.6: Summary of structural data

Diameter at breast height (DBH) is significantly higher in alluvial forest, while height-DBH ratio is significantly lower compared with plains and hills, which do not differ. Alluvial also has a significantly higher number of trees with top height exceeding 25m, and a DBH of 31-60cm. The range of branch sizes is higher in alluvial, with this land unit having a higher count of branches with diameters 2-4cm, 4-10cm and 10-20cm than both plains and hills. Bole height is significantly higher in hills than plains and alluvial which did not differ. There is no significant difference between land units in top height; crown area, shape and connectivity; number of trees per plot; tree density per ha; stand basal area; and number of trees with DBH 10-30cm and >60cm.

4.2: *Group density of* P. thomasi

4.2.1: Line transects

In total, 30km of line transects were sampled throughout the whole study area. Throughout these surveys, there was not a single encounter with any individual or group of *P. thomasi*.

4.2.2: Vocal arrays

4.2.2.1: Triangulation of groups

Table 4.11 gives the total sampling areas before and after correction for array overlap, along with the estimated group density for each land unit, calculated following the traditional method of triangulation. Hills has a higher density of 4.45 groups/km^2, compared to alluvial and plains, with densities of 3.88 and 3.14 groups/km^2 respectively. Figures 4.22 and 4.23 show the estimated locations of groups both prior to and following correction for array overlap. The density for the whole site is 3.97 groups/km^2, with a total sampling area of 9.99km^2.

Table 4.11: Results of the traditional triangulation method for calculating total sampling area (km2) and group density at each array and for the whole study site.

land unit	***distance to furthest group (km)***	***sampling area (km^2)***	***% area in focal land unit***	***corrected buffer radius (km)***	***corrected sampling area (km^2)***	***number of groups heard***	***p(call)***	***group density (groups/km^2)***
alluvial	1.26	3.14	80%	1	2.48	8	0.83	3.88
hills	1.32	4.65	80%	1.22	3.74	11	0.66	4.45
plains	1.19	4.4	86%	1.19	3.77	8	0.675	3.14
whole site	-	-	-	-	9.99	29	0.73	3.97

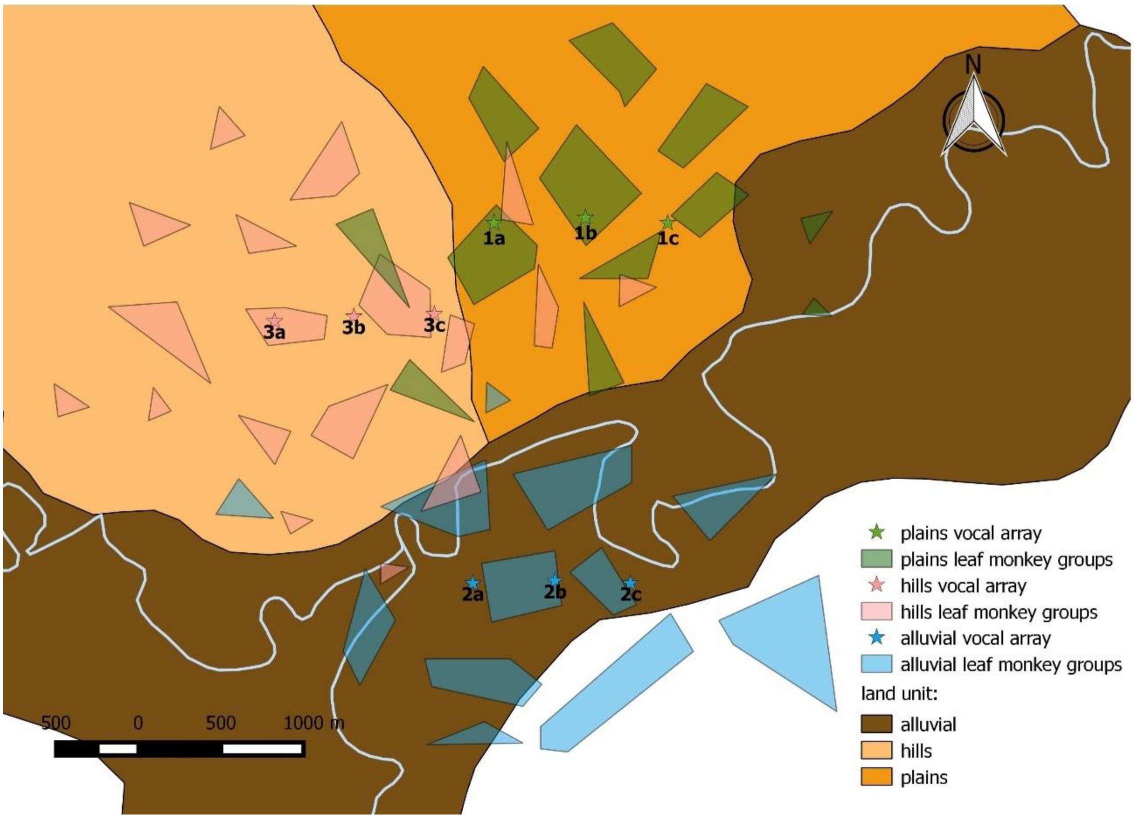

Figure 4.22: Groups detected from each vocal array before correction for array overlap.

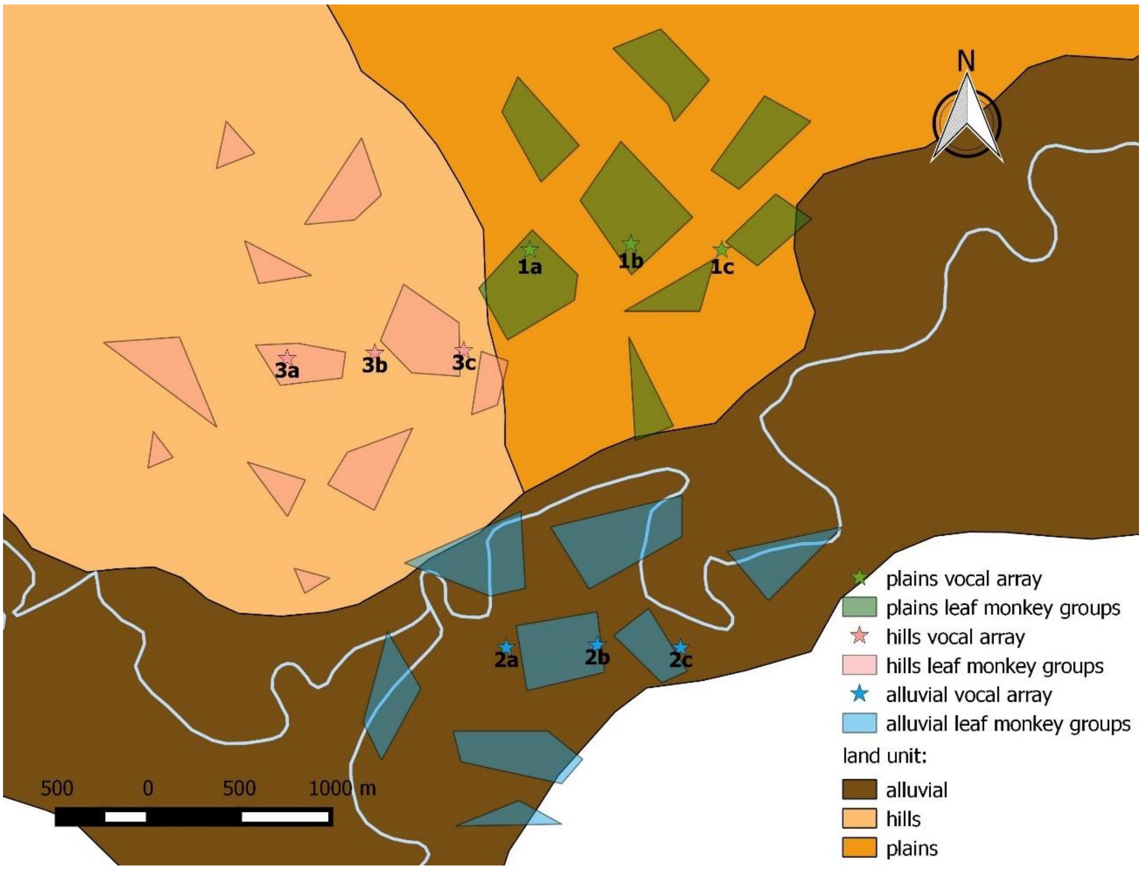

Figure 4.23: Groups detected from each vocal array following correction for array overlap.

4.2.2.2: SECR results

Table 4.12 gives the output figures from the SECR model for each array, and figures 4.24-29 show the detection functions and detection surfaces of the model for each array. The effective sampling area calculated by the SECR programme is roughly the same between all of the arrays, and in all instances, is lower than that calculated with triangulation alone. For alluvial and plains the buffer radius stabilised at 1000m, while hills required a larger buffer distance of 3000m. Hills has a notably higher group density, than plains and alluvial, both of which are fairly similar (5.25 groups/km^2, 2.72 groups/km^2 and 3.09 groups/km^2 respectively). The output of density for the whole site is 3.40 groups/km^2, with an effective sampling area of 8.7 km^2.

Table 4.12: Output results of the SECR model for each vocal array and for the whole study site.

land unit	***number of groups detected***	***buffer radius (km)***	***p(call)***	***AIC***	***effective sampling area (km^2)***	***density***		
						mean	***upper 95***	***lower 95***
alluvial	8	1	0.83	151.3121	3	2.7169	1.2657	5.8318
hills	11	1.22	0.66	208.464	6.5	1.5452	0.85068	2.8068
hills	11	3	0.66	226.0288	2.3	5.2496	2.8506	9.6677
plains	8	1	0.675	176.04	3.2	3.0852	1.5546	6.1277
whole site	29	2.5	0.73	482.7433	8.7	3.3937	2.2632	5.089

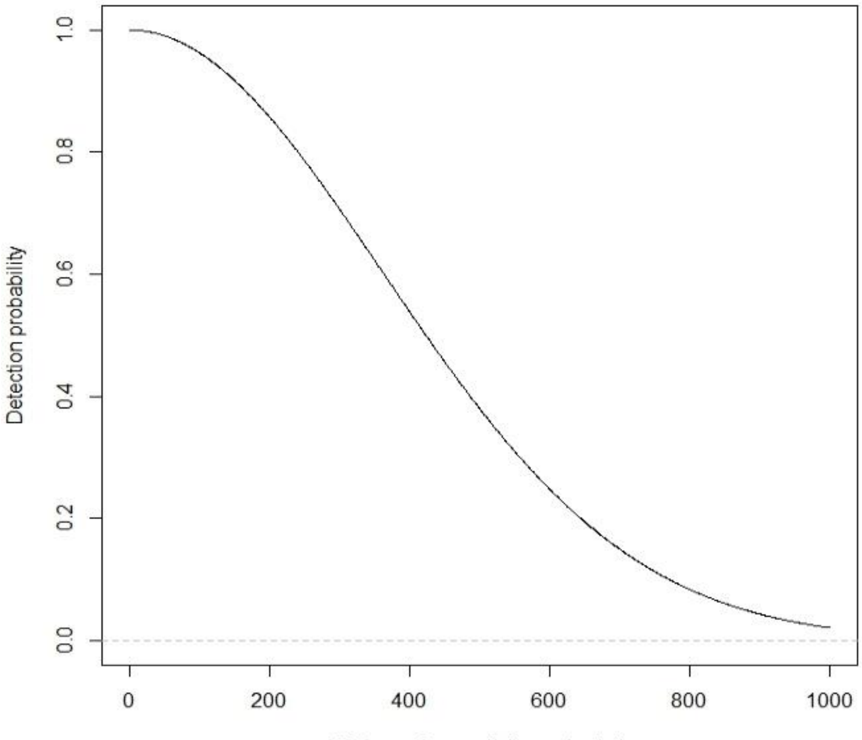

Figure 4.24: The half-normal detection function fitted to vocal array data collected in the alluvial land unit, showing the detection probability with increasing distance from the sample point.

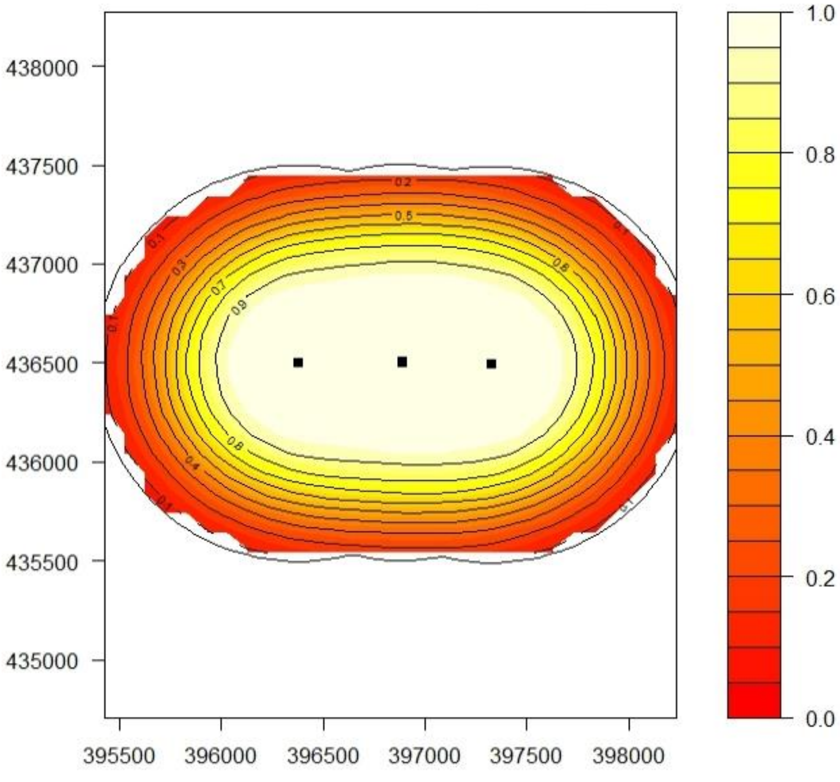

Figure 4.25: The detection surface fitted to vocal array data collected in the alluvial land unit, showing the detection probability with increasing distance from the sample point.

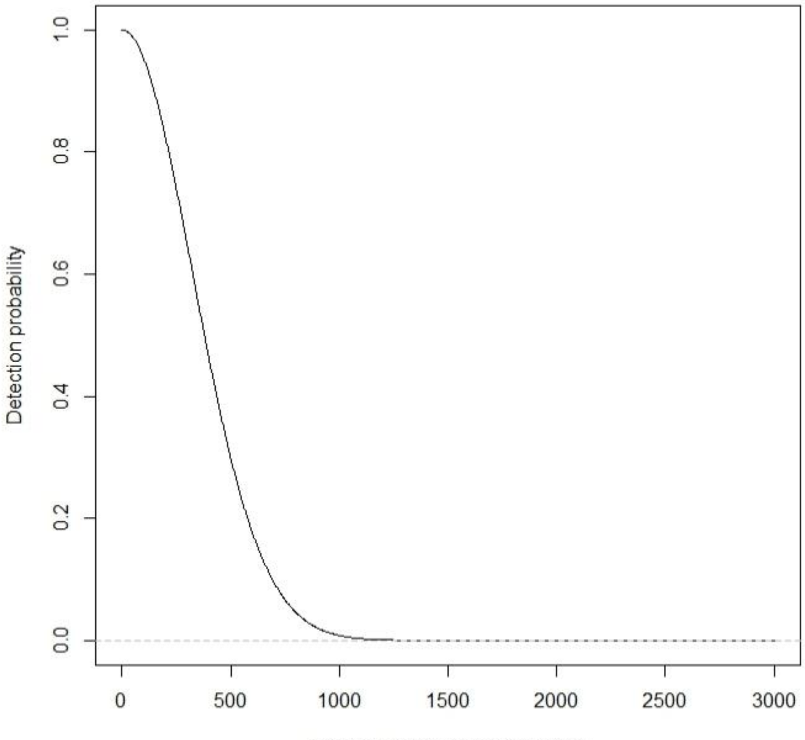

Figure 4.26: The half-normal detection function fitted to vocal array data collected in the hills land unit, showing the detection probability with increasing distance from the sample point.

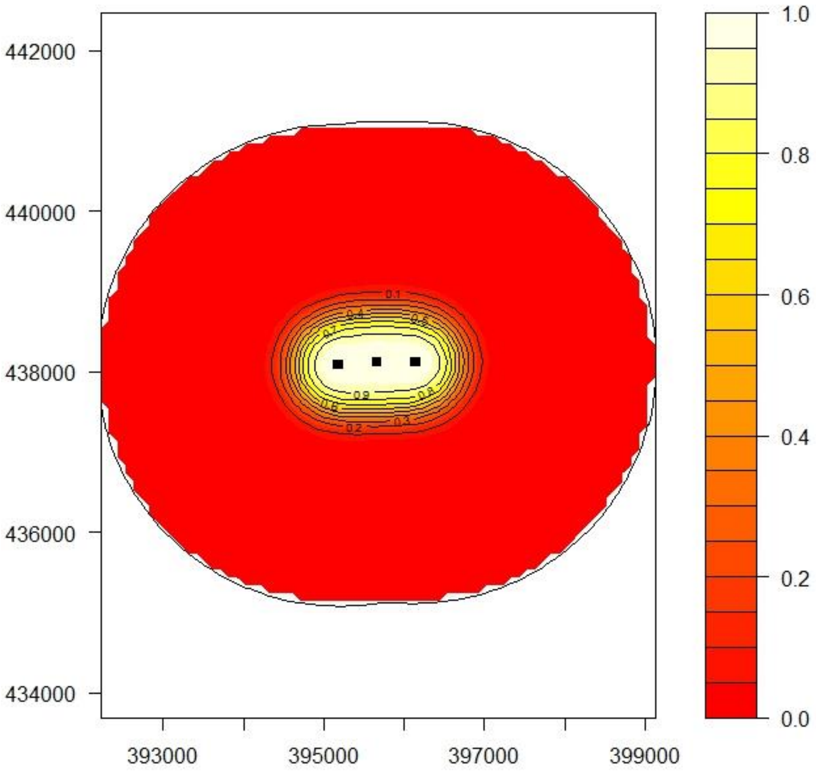

Figure 4.27: The detection surface fitted to vocal array data collected in the hills land unit, showing the detection probability with increasing distance from the sample point.

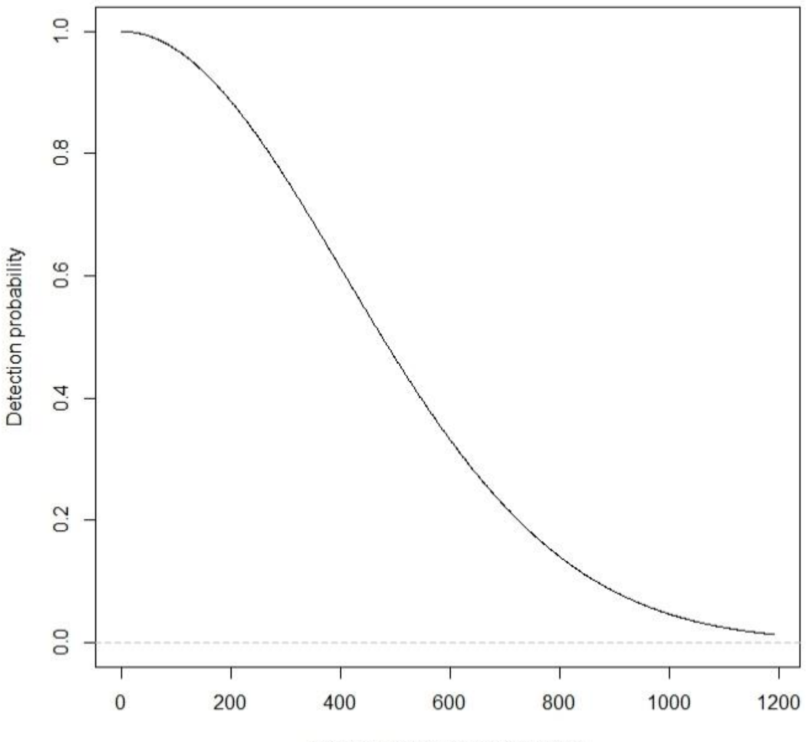

Figure 4.28: The half-normal detection function fitted to vocal array data collected in the plains land unit, showing the detection probability with increasing distance from the sample point.

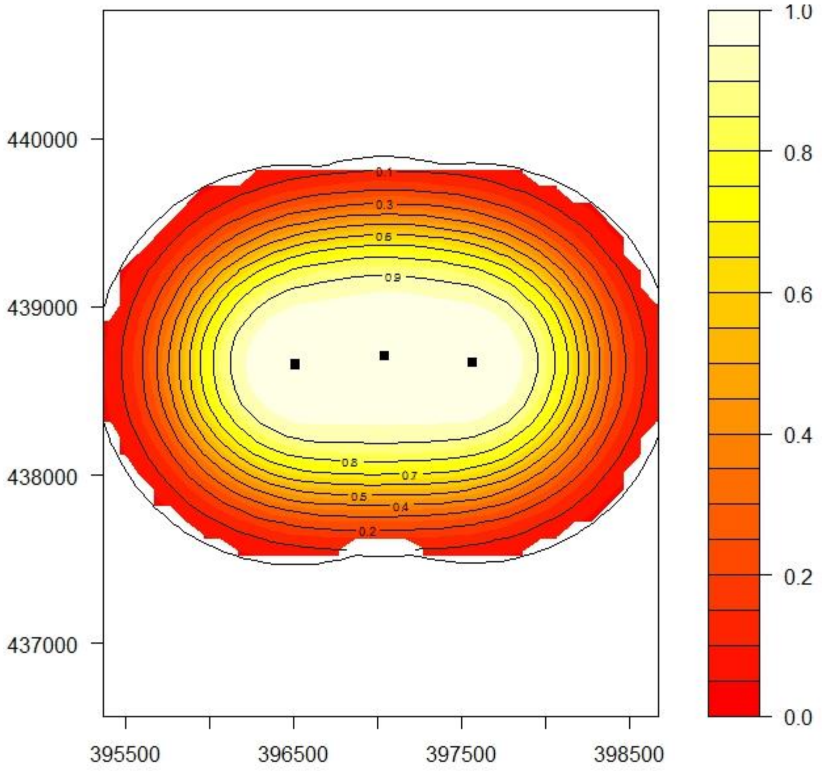

Figure 4.29: The detection surface fitted to vocal array data collected in the plains land unit, showing the detection probability with increasing distance from the sample point.

4.3: Forest structure and group density

The density of *P. thomasi* is highest in the hills land unit. This land unit has a higher bole height and basal area than both plains and hills. There is also a significantly higher proportion of trees with a top height exceeding 25m. The density of trees per hectare is lowest in the hills, although the tree canopies are still relatively well-connected. There is also a fairly high number of small-medium branches. Trees in the alluvial and plains land unit have a lower height-DBH ratio, and higher DBH. However, this does not appear to affect group density.

Chapter 5 : Discussion

The aims of this study were to establish differences in forest structure and group density of *Presbytis thomasi* between the three land units, alluvial, hills and plains, found at Sikundur, and to test the effectiveness of vocal arrays in estimating group densities of *P. thomasi*. The effects of past disturbance can be seen throughout the whole site by the lack of large, emergent trees (top height>25m, or diameter at breast height, DBH>60cm). There are still visible structural differences however, with the alluvial land unit having a generally larger DBH, suggesting that trees in alluvial are generally at a later growth stage, since DBH is an indicator of tree age (O'Brien et al. 1995). Forests in this region are still undergoing regular bouts of illegal logging, and the data indicate that this is concentrated in areas which are more easily accessible from the local village (i.e. plains and hills). Thomas' langur group density is highest in hills, and lowest in plains, negating the hypothesis that group density will be lower in areas which have been more heavily logged. The vocal array method produces results which are consistent with group density estimates reported from previous studies (Sterck 1996).

5.1: Structural differences between land units

Overall, the alluvial land unit has the most distinctive forest structure, while hills and plains are fairly similar. The most notable difference in alluvial forest is in DBH, and SBA. Both are significantly higher in alluvial, compared with plains and hills which did not differ. The alluvial forest also contains a significantly higher proportion of medium diameter trees (DBH between 10 and 30cm), and has the lowest height-DBH ratio of all three land units. This indicates that trees in the alluvial forest have a generally wider girth and are therefore at a later growth stage than those in the plains and hills forests. Despite having a higher SBA than plains, the number of trees per hectare is lower in alluvial forest. This provides additional evidence that alluvial forest is undergoing lower levels of current human interference than plains and hills. The proportion of trees with a DBH below 30cm was lower in alluvial forest, suggesting that this land unit has had more time to regenerate, since the trees here are older.

Usually in tropical forests, trees will first allocate more resources towards upward growth in order to reach the canopy and gain access to light radiation (O'Brien et al. 1995). Once they achieve this, they will then assign resources to stem and trunk growth, and therefore increase in girth; thus older trees will have a lower height-DBH ratio than younger trees. This relationship has been found to be uniform across neotropical tree species (O'Brien et al. 1995), and so it is unlikely that the difference in height-DBH ratio is due to a difference in species composition between land units. Since the establishment of Gunung Leuser National Park in 1980, the main logging road through the area has fallen into disrepair, and the bridge which connected the nearest village to the opposite side of the river has been destroyed, making much of the alluvial forest harder to access. As a result, it is likely that the alluvial forest has suffered from lower levels of more recent illegal logging than the hills and plains, and has therefore been able to regenerate more, leading to the larger proportion of trees with a wider girth. Trees in the alluvial forest also have the highest number of branches, and the most heterogeneity in terms of support availability, adding further weight to this explanation.

There are few differences in forest structure between hills and plains. Both land units have significantly lower DBHs and height-DBH ratios than alluvial forest, and both have fewer branches. Throughout the study, signs of human disturbance, including bird traps, recent camps and abandoned litter, were frequently encountered. These were more common in plains forest, which is situated most closely to the nearest village, and the boundary of the national park. This would suggest that this land unit is more susceptible to small-scale disturbances and illegal logging, and may explain the lack of tall or wide trees in this land unit. Plains forest contains significantly fewer trees with DBH >30cm than both hills and alluvial, with just 12% of trees compared with 16% and 19% respectively. Despite the protected status of the GLNP, illegal logging remains a regular occurrence, and represents one of the greatest challenges to conservation in the region (Jepson et al. 2001, McCarthy 2002, Cannon et al. 2009, Mulyani and Jepson 2013). Since the forest at Sikundur is located so close to the national park boundary, it is highly likely that this region is also experiencing frequent illegal logging, which will be hindering the forest's ability to regenerate. The differences in accessibility may therefore account for the differences in forest structure between the three land units.

The data is indicative of a gradient in recent disturbance through the three land units, with plains and hills being the most disturbed, and alluvial being the least disturbed.

There is a surprising lack of difference in top height, and in the proportion of large trees, between the three land units. In the absence of data on the extent of logging which has occurred in the region, it could be assumed that alluvial forest would be the most heavily logged due to its proximity to the river. Hills, on the other hand, is found at a higher elevation and contains more difficult terrain, such as ridges and steep slopes, therefore it would be expected to have suffered from lower levels of disturbance (Laumonier, 1997). The data collected in this study, however, shows that historical logging in this region has been uniform, with all three land units showing a low proportion of trees with top heights exceeding 25m, or diameters exceeding 60cm. The Sikundur region was a government logging concession prior to the 1980s, and so the selective logging in this area was extensive, and likely impacted all three land units equally (van Schaik and Supriatna 1996, Priatna et al. 2000, YOSL-OIC 2009). The data on forest structure indicate that differences in accessibility between land units have not determined the level of exploitation within them prior to the establishment of the GLNP. In contrast, logging which has occurred post-1980 has predominantly been in the form of small-scale illegal operations, and has therefore been concentrated towards the national park boundaries and nearest villages (i.e. within plains and hills), since these areas are much easier to access.

5.2: Group density of P. thomasi

5.2.1: Effectiveness of vocal arrays to survey group density

Vocal arrays proved to be substantially more effective in surveying unhabituated arboreal primates. A total of 30km of line transects were sampled, which yielded absolutely no data on the density of Thomas' langurs. Langurs are known to be extremely vigilant where they are not habituated to the presence of humans, even when they are not being directly hunted (Sterck 1996). Since the forest at Sikundur has been so heavily disturbed, the lower canopy is very dense, and makes the detection of animals in the upper canopy extremely difficult. It was a common occurrence during line transect sampling to hear animals moving high up in the forest canopy, but never actually see them to identify them. This is a widely encountered problem in studies of gibbons, another arboreal species which preferentially uses the upper canopy (Brockelman and Srikosamatara 1993, Cheyne et al. 2008, Kidney et al. 2013). Gibbons, similar to Thomas' langurs, have distinctive morning vocalisations which they use to reinforce pair bonds and maintain their home range boundaries. The use of vocal arrays has therefore been widely implemented in gibbon surveys to overcome the problem of poor visual detection from line transects. Prior to this study, the vocal array method had not been applied to Thomas' langurs, despite the advantages of this approach. Previous studies carried out from field stations at Ketambe and Bohorok, North Sumatra, were long-term and carried out on populations which had been habituated, making them easier to survey with visual census methods (Gurmaya 1986, Sterck 1996, Wich et al. 2007) The group densities recorded at this site are consistent with those reported from other field sites in North Sumatra (figure 5.1). This demonstrates that auditory sampling is just as reliable as visual census methods, while eliminating the problem of poor detection where populations are unhabituated.

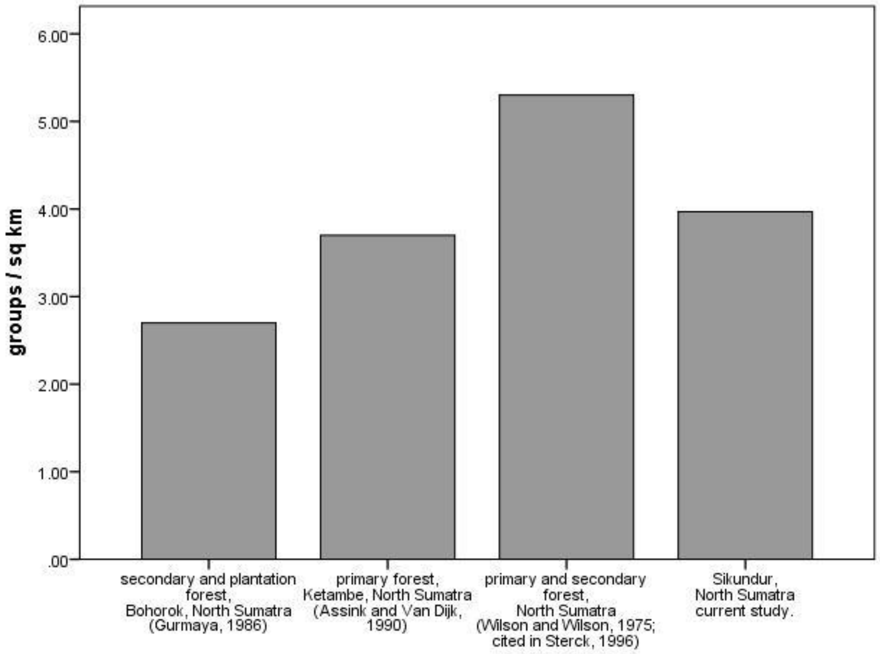

Figure 5.1: Group densities reported from previous studies using visual census methods, compared with group densities found at Sikundur using vocal arrays.

5.2.2: Spatially explicit capture-recapture versus manual triangulation of groups

Results estimated using the SECR model within gibbonsSECR were similar to those produced using manual triangulation alone (figure 5.2), although SECR still has advantages over triangulation. Previous studies using vocal arrays to survey primate density have calculated their effective sampling area using an estimated maximum distance of detection, and have assumed that all calls within this sampling area will be detected with certainty (Aldrich et al. 2008, Cheyne et al. 2008, Hamard et al. 2010). This often leads to an overestimation of effective sampling area, which in turns underestimates primate density (Kidney et al. 2013). In this study, it was necessary to reduce the effective sampling area to exclude areas of non-focal land unit sampled at each array. This explains why, in this particular study, the densities reported by SECR were not notably higher than those calculated from manual triangulation. Despite both methods producing similar results, SECR has some distinct advantages over triangulation when analysing vocal array data. SECR incorporates a detection function which removes the assumption of uniform detection within the effective sampling area, and minimises the risk of underestimating primate density (Kidney et al. 2013). There is one major limitation in using SECR for primate calls. Currently, the gibbonsSECR program is unable to account for multiple sample occasions, and so surveys which have been carried out over several days must be entered as one single sample period, creating a potential source of error. With further development, SECR is a promising tool which can be used alongside auditory sampling methods to improve the accuracy and reliability of primate density data for vocal species which are difficult to detect through visual survey methods.

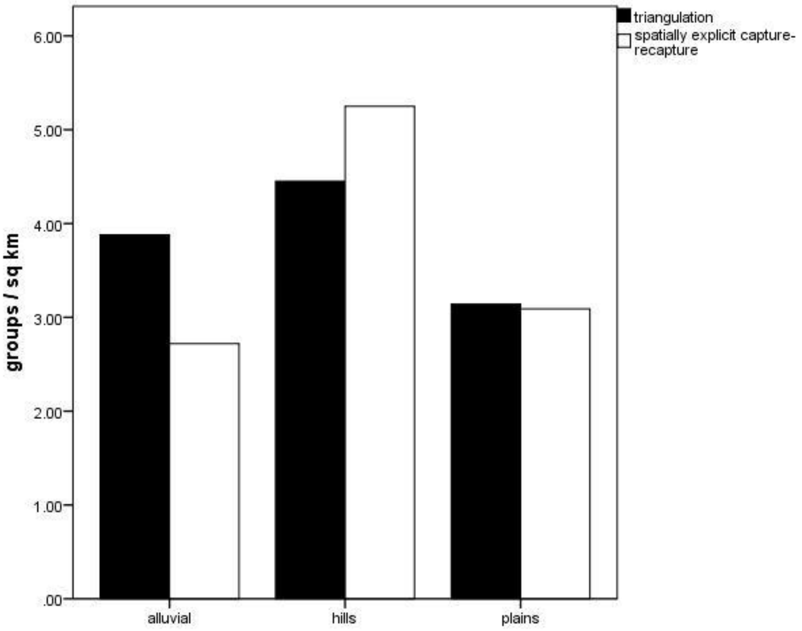

Figure 5.2: Group densities of *P. thomasi* within each land unit, obtained from both triangulation and spatially explicit capture recapture.

5.2.3: Differences in group density between land units

Hills forest has a higher group density than both alluvial and plains. This is somewhat surprising given the apparent structural impact of logging activities in this land unit. However, hills has a higher bole height than both plains and hills. Langurs prefer trees with tall, straight trunks and few branches close to the ground for sleeping sites. These provide the best protection from felids, their main predators (Sterck 2013). A higher density of these trees provides them with more choice in suitable sleeping sites, enabling them to rotate trees in order to reduce disease and parasite transmission (Wich et al. 2007). Trees in the hills generally have higher first boughs and larger basal areas than alluvial and plains, making them less accessible for ground predators, and safer sleeping sites for langurs. There is also a higher proportion of tall trees in hills compared with plains. This indicates that hills has a higher availability of suitable sleeping sites than plains and hills. Langurs may be choosing home ranges with a higher number of sleeping trees, explaining their higher density in hills forest, and meaning that bole height could be an important determinant of Thomas' langur group density. It is important to note that there are other factors which may be influencing the distribution of Thomas’ langurs, for which there is currently no available data. For example, food availability is an important determinant of many primate species distributions (Ganzhorn 2002, Knop 2004, Hamard et al. 2010). The absence of data on the composition of tree species means that the distribution of food trees cannot be discounted as a potential influence on langur distribution at this site. Competition between other primate species may also be determining their distribution. Further data on the behaviour and ecology of Thomas’ langurs at this site is required to establish which of these factors is most important in determining their distribution.

Langurs travel primarily by leaping between crowns, and are therefore able to cross small gaps in the upper canopy. High levels of connectivity are subsequently less important for this species than those which travel through suspensory behaviours (e.g. gibbons). The forest at Sikundur has been selectively logged rather than clear-felled, and retains much of its canopy connectivity, with 79.1% of trees having an estimated connectivity above 50%. Langurs are consequently still able to move between tree crowns with relative ease. At this site, canopy connectivity and support availability are not important factors influencing the density of Thomas’ langurs.

Human disturbance which is not related to logging may also be influencing group density. Langurs demonstrate extreme vigilance in the presence of humans, where they have not been habituated (Sterck 1996). If they are regularly disturbed by people within the forest, this vigilance can become maladaptive, by reducing their time spent foraging (Willems and Hill 2009, Bettridge et al. 2010, Coleman and Hill 2014). Throughout field data collection signs of human activity (i.e. litter, old campsites, sounds of cutting, and bird traps) were encountered most frequently in plains than any other land unit. Langurs may be preferentially using parts of the site which are experiencing lower levels of utilisation by local people. Although no evidence of hunting was observed at this site, Thomas’ langurs have been observed to be traded in wildlife markets in North Sumatra (Shepherd 2010). Hunting could therefore be influencing the distribution of langurs at Sikundur; more data is needed to investigate this. Despite their apparent resilience to logging practices, Thomas’ langurs could be subject to negative impacts from other forms of human disturbance.

5.3: Implications for forest conservation

Deforestation and conversion to plantation remains the biggest threat to biodiversity in Indonesia (Brun et al. 2015, Wijaya et al. 2015). As well as biodiversity loss, logging and slash-and-burn agriculture have a global impact in terms of greenhouse gas emissions and climate change. An estimated 60% of Indonesia's carbon emissions can be attributed to the forestry sector (Mulyani and Jepson 2013). Curbing the rate of forest loss will not only help to protect Indonesia's biodiversity, but will also help to reach the country's goals within the REDD+ framework to reduce greenhouse gas emissions. Despite their protected status, many forests within national parks on Sumatra are still being subjected to frequent bouts of illegal logging (Jepson et al. 2001, McCarthy 2002, Mulyani and Jepson 2013). In addition, the current network of protected areas on Sumatra does not adequately cover the island's ecosystems (Laumonier et al. 2010). Biogeographical studies are immensely useful in highlighting areas which should be prioritised for protection, and can help to refine the current network of protected areas. Improved enforcement of deforestation laws and management of protected areas will help to reduce forest and biodiversity loss, as well as lower the amount of carbon released from felled forests.

Previous published studies have reported lower group densities in secondary forest compared with primary forest (Sterck 1996), however, the densities found at Sikundur are closer to those recorded from primary forest in Ketambe (Assink & Van Dijk 1990). Other unpublished studies have reported similar densities in both logged and unlogged forest (Wich & Sterck 2010). Langurs travel by leaping between canopies, and are better able to cross gaps than other arboreal primates, such as gibbons, which move via brachiation. They are also predominantly folivorous, and demonstrate dietary flexibility, making them more resilient to changes in tree species composition than frugivorous primates (Milich et al. 2014; Schwitzer et al. 2011; Irwin et al. 2010; Ganzhorn 2002). Secondary forests have been shown to still support high densities of primate species in other parts of Indonesia and south-east Asia (Riley 2008, Sodhi et al. 2010, Lee et al. 2014). The results from this study indicate that langurs are able to persist in anthropogenically altered forests, therefore these areas are still valuable for primate populations and should remain a focus of conservation efforts, in addition to preserving remaining primary forest.

5.4: Recommendations for future research

In order to better understand habitat preferences of Thomas' langurs, it is necessary to gather more data on their distribution and behaviour at the site. Increasing the sample numbers of density data through additional vocal arrays will enable statistical correlations to be made between structural characteristics, such as top height, bole height and canopy connectivity. Habituation of langur groups at Sikundur to enable visual observation is the next step in better understanding their habitat preferences. Identifying sleeping trees and their typical canopy structure, particularly bole height and connectivity, will help to better explain their spatial distribution. If there is a correlation between the density of suitable sleeping trees and Thomas' langur density, this can then be used to predict their abundance in other forests. Day follows of groups and mapping of home range territories will enable direct conclusions on the structural characteristics which impact their habitat use, and can then be used to predict their abundance in other parts of Sumatra, and their responses to future environmental change.

Quantifying the extent of both historical and current anthropogenic disturbance should also be an objective of future research. Gathering data from primary forest, located upriver from the Sikundur region, will enable direct comparison with data collected from this site and will quantify the structural changes brought about by logging. Data from unmanned aerial vehicle (UAV) mounted photography, which has already been collected in the region, can be used to monitor the current rate of forest loss from illegal logging (PanEco 2013). Collecting quantitative data on the number of people who are utilising the forest in other ways will also be useful.

Utilising the developing technologies of remote sensing and unmanned aerial vehicles can help to improve both the accuracy and scale of the structural data collected in this study. Remote sensing techniques can provide large amounts of reliable data with relative ease, eliminating the need for laborious and time-consuming ground data collection. Until recently, high quality remote sensing data has been costly to acquire. Light detection and ranging (LiDAR) techniques and cameras mounted on unmanned aerial vehicles (UAVs) can be used to acquire reliable, high resolution data on the forest upper canopy, relatively quickly and often at low cost (Hill et al. 2011). Large scale landscape studies and more detailed research linking the landscape and habitat structure to primate ecology and behaviour will shed light on these mechanisms. Understanding this will then, in turn, help to explain species' ecological requirements and habitat preferences and identify those species or ecosystems which are most vulnerable to disturbance and highlight priority areas for conservation (Palminteri et al. 2012).

Chapter 6 : Conclusion

Forests are undergoing extensive changes as a result of human activities and this has implications for arboreal primates. Tropical forests contain a substantial portion of global biodiversity, and provide a wide range of ecosystem services, including carbon sequestration, climate and atmospheric regulation and nutrient cycling (Cardinale et al. 2012). Anthropogenic activities such as logging and agriculture alter the structure of tropical forests. Human-modified forests typically have lower structural heterogeneity and tree species diversity, along with more frequent and larger canopy gaps. This impacts on arboreal primates by altering the availability of food and suitable sleeping sites and reducing their ability to move with ease through the forest canopy. There are many studies detailing the negative impacts of anthropogenic disturbance on primate populations in tropical forests (e.g. Michalski and Peres 2005a, Gillespie and Chapman 2008, Schwitzer et al. 2011, Barelli et al. 2015), however few of these adequately explain the mechanisms behind these impacts. This study investigated the structure of disturbed forest at Sikundur, North Sumatra, Indonesia and the group density of an arboreal primate, *Presbytis thomasi*, with a view to identifying links between forest structure and density of arboreal primates.

The forest at Sikundur has been heavily disturbed by historical logging, which has been consistent throughout the whole site, although this has not had a major impact on the density of *Presbytis thomasi*. All three land units had a uniformly low canopy height, and a low proportion of trees with top height exceeding 25m, and diameter at breast height exceeding 60cm. The group densities of langurs reported from this site are not notably lower than those reported from primary forest in Ketambe (Assink and Van Dijk 1990), indicating that this species is more resilient to habitat degradation than previously thought. Langurs are folivorous and travel predominantly through leaping between crowns, and so food availability and connectivity are less important for this species than other arboreal primates, such as gibbons and orangutans, which rely on suspensory locomotion and feed mainly on fruits. Habitat preference in langurs could be related to the availability of suitable sleeping sites. This is important both for predator avoidance and to reduce disease transmission and build-up of parasites. Hills forest has a significantly higher bole height than alluvial and plains, indicating that there are generally more trees with the type of structure that langurs prefer to sleep in; this land unit also had the highest group density. Despite the clear impacts of past logging at Sikundur, this has not impacted on the distribution of Thomas' langurs.

The forest at Sikundur is located within the boundaries of the Gunung Leuser national park, and as such is a protected area, however, parts of this forest still suffer from regular bouts of illegal logging and other forms of exploitation. This exploitation is now dependent on the levels of accessibility of the forest, and is more concentrated towards the national park boundaries and the nearest village. Trees in alluvial forest generally have a higher DBH, and lower height-DBH ratio than those in plains and hills, indicating that they are generally more mature, and the alluvial forest has therefore been able to regenerate to a greater extent (O'Brien et al. 1995). While plains and hills forest can be accessed with ease from the local village, access to the alluvial land unit is now only possible via boat, since the bridge which once traversed the river has been destroyed. Signs of human activity were most commonly encountered within the plains land unit during field data collection. This will also influence the behaviour of Thomas' langurs, since they are extremely vigilant when not habituated to humans. The increased human traffic in the plains land unit may therefore account for the lower density recorded in this area. This forest is still undergoing regular disturbance, which is linked to accessibility and is having unknown impacts on primate populations within the area.

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