Avifauna and anthropogenic forest disturbance in two biodiversity hotspots

Thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

by

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Submitted 16/10/09

I, Thomas Martin, declare that the research presented in this thesis represents my own work, and this body of work has not been submitted elsewhere for the award of higher degree.

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Abstract

The primary objective of this thesis is to examine the impact of anthropogenic forest disturbance on avifaunal communities in two biodiversity hotspots- lowland tropical forest in the Lambusango Forest Reserve within the Wallacean archipelago and Neotropical cloud forest in Cusuco National Park, Mesoamerica. Both these study areas possess diverse bird communities with high rates of endemism, yet are under severe pressure from anthropogenic activity. The research also evaluates the optimal methodologies for surveying bird communities in these poorly studied ecosystems and examines the extent to which under-managed protected areas can be successful in preserving bird species with high conservational importance, and the habitat associations of these avifaunal communities. Results demonstrate that point count methods are more effective than mist-nets for describing cloud forest bird communities. Research also shows that many Wallacean species are tolerant of moderate habitat disturbance, although endemic species are sensitive to heavy disturbance. Cloud forest endemics appear to be sensitive to moderate disturbance, although protected areas can be effective in preserving these species even where severely undermanaged. Endemic birds in the two hotspots display different responses to habitat disturbance; this may be due to differential community compositions, niche competition and biogeography. Research has also demonstrated that richness and composition of Wallacean bird communities have strong associations with a range of habitat variables which can be used to provide proxy data for identifying priority conservation areas when appropriate scales of data aggregation are used. The findings of this thesis demonstrate the value of using multiple research perspectives to fully investigate geographical problems.

Acknowledgements

This thesis could not have been produced without the assistance and support of a great many people from Lancaster University and Operation Wallacea, as well as from friends and family. I would like to thank the following people for the help, kindness and patience shown towards me during the last three years. Many others have also shown me great support and kindness and apologies are given to those whose names are omitted here.

At Lancaster University I would first and foremost like to thank my supervisor, Dr Alan Blackburn, for his sound advice, unwavering support and seemingly endless patience. I would also like to thank Dr Jos Barlow for advice offered at numerous junctures during the course of producing this thesis. I would additionaly like to thank my fellow postgraduate students for their tolerance of pestering questions and moaning.

From the Lambusango I would firstly like to thank Mr Dani Heriyadi, Mr Henry Singh and Mr Tasman for their help and great enthusiasm in conducting bird surveys in the Lambusango. I would also like to thank my guide, Mr Kasima, Arthur Arfion and Dr Phil Wheeler for his advice and logistical support.

In Cusuco I would like to thank most of all Wilf Simcox for his advice, support and unrivalled mist-netting skill. I would also like to thank the 2007 ornithology team; Martin Meads, Chris Hill, Ernesto Reyes and Sarah Rustage. I would additionally like to thank Dr Tim Coles and Jose Nunez-Mino of Operation Wallacea for making the fieldwork this thesis is based on possible.

Finally, I would like to thank my friends and family for their amazing patience and support, especially mum – my proof-reader extraordinaire.

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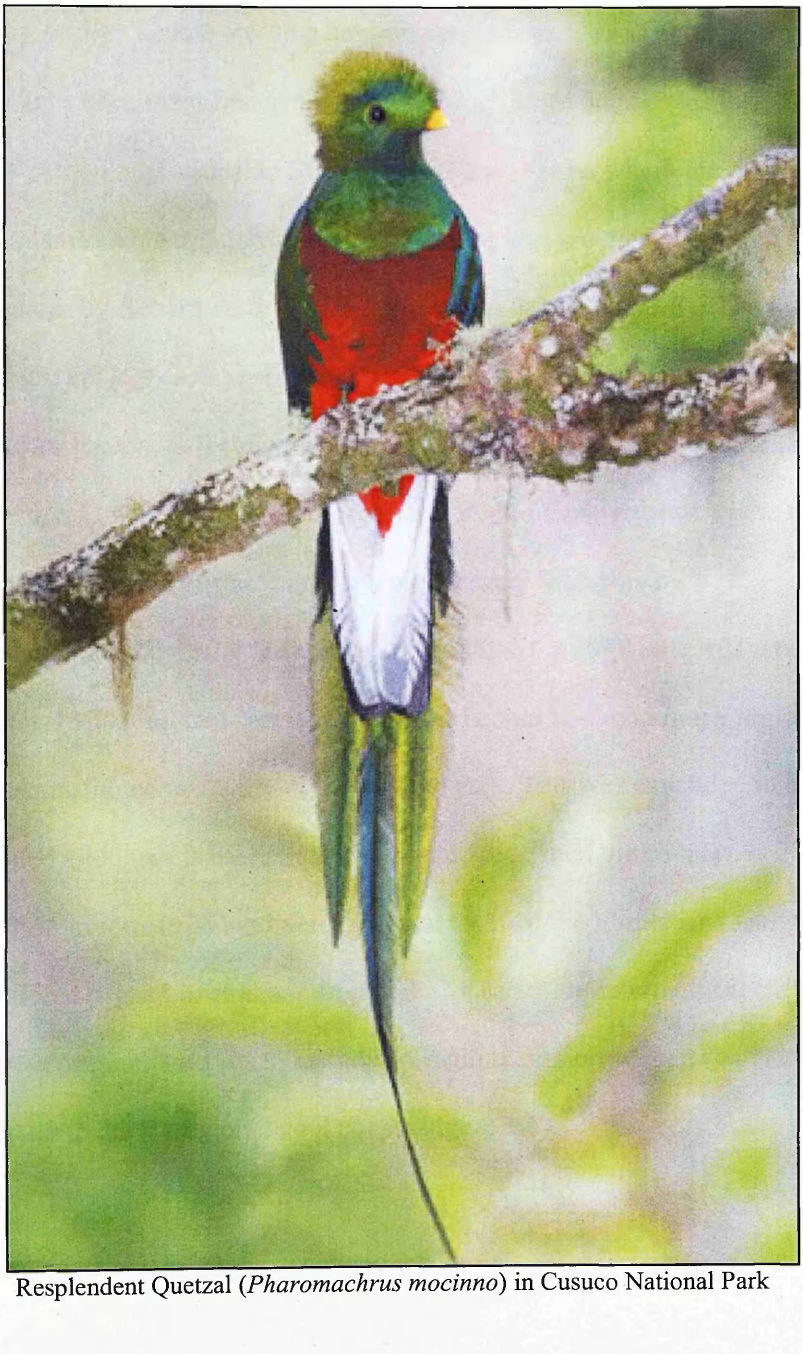
CHAPTER 1 - INTRODUCTION



Resplendent Quetzal (*Pharomachrus mocinno*) in Cusuco National Park

1.1 - OVERVIEW

The predicted loss of biodiversity on a global scale is widely regarded as one of contemporary society's most pressing environmental issues, and habitat destruction and degradation have been identified as the main driving forces behind this loss (Sala *et al.* 2000). This issue is particularly critical in tropical forest ecosystems where the majority of the Earth's organisms are distributed and rates of habitat loss are greatest (Sodhi *et al.* 2004). Recent estimates by Achard *et al.* (2002) suggest that as much as 5.8 ± 1.4 million hectares of tropical forest were lost each year during the 1990s. If these patterns of habitat destruction continue the consequences for global biodiversity are predicted to be severe (Sodhi *et al.* 2004, Leaky and Lewin 1996). This is especially true of those regions where the greatest concentrations of species can be found; the biodiversity 'hotspots'.

The concept of biodiversity hotspots was introduced in 1988, when Myers (1988) described how 13% of all tree species in the world could be found in ten regions of tropical forest which constituted just 0.2% of global land area. This was expanded in a later study which included all higher taxonomical groups, and redefined the concept as 20 regions containing 35% of terrestrial biodiversity in just 1.4% of the Earths land area (Myers 2000). A later revision designed in collaboration with Conservation International (Myers 2003) extended these original hotspots to include 34 regions supporting approximately 50% of global diversity in 2.3% of global land cover (Figure 1.1).

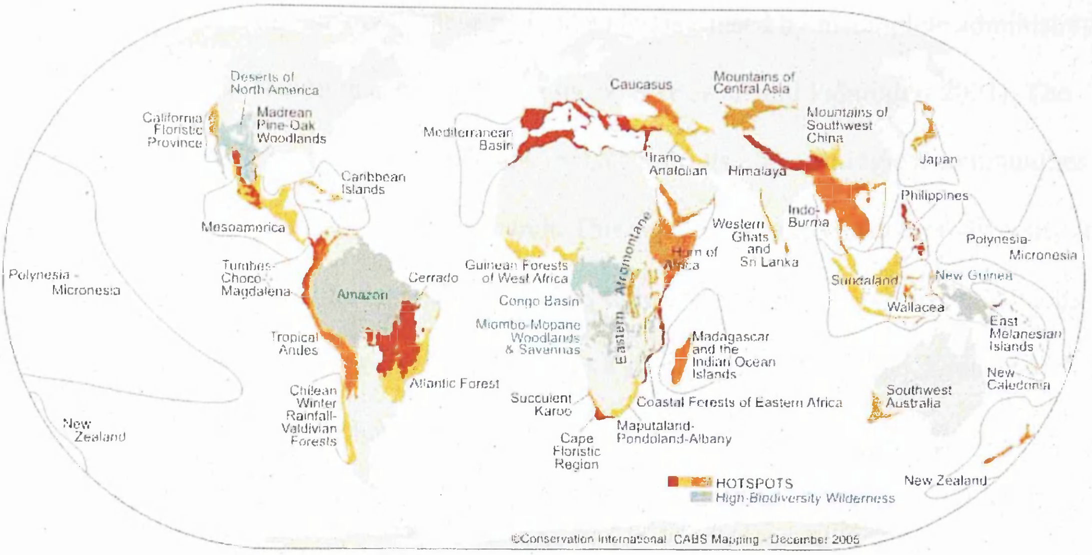


Figure 1.1. Global biodiversity hotspots (Conservation International 2005).

The hotspots shown in Figure 1.1 not only support a high representation of total global biodiversity, but also possess a disproportionate concentration of range-restricted species which are inherently at the greatest risk of extinction from habitat destruction; 50% of all plant species and 42% of terrestrial vertebrates are endemic to hotspots (Conservation International 2007).

Despite an elevated ecological importance, biodiversity hotspots are experiencing some of the highest rates of habitat loss of all terrestrial ecosystems. Conservation International (2007) estimate that all hotspots have lost at least 70% of their natural vegetation cover, with severe consequences for their biota. Over 200 known vertebrate extinctions have already occurred within the hotspots, and 59% of all IUCN-listed critically endangered mammals and 78% of critically endangered birds are restricted to these areas (Conservation International 2007).

Mitigating the impacts of further anthropogenic disturbance is therefore essential if the long-term integrity of these regions' exceptional biodiversity is to be maintained. However, the implementation of effective conservation strategies has frequently proved problematic, particularly within tropical forest hotspots, due to an imperfect understanding of the extent of habitat disturbance in many of these regions which is caused by incomplete administrative records and the inherent inaccessibility of the sites (Powell and Palminteri 2001). The understanding of how anthropogenic disturbance impacts upon ecological communities here is also poor, owing to insufficient research. This results partially because biodiversity surveys are often restricted by the inevitably complex, time-consuming and expensive methods necessary to survey changes in biodiversity as a whole (Sutherland 2000, Kremen 1992). A lack of consensus as to which methodological approaches are most effective for surveying different taxa in these regions also contributes to this problem (Whitman *et al.* 1997). Furthermore, even where sufficient baseline biodiversity data exist to implement conservation strategies in these regions, lack of adequate funding often means that conservation initiatives are chronically under-managed and under-resourced. There has been little research evaluating how valuable these under-resourced conservation efforts have been, which has inhibited the effective implementation of conservation policies which need to be based on understandings of the successes or failures of previous strategies (Bruner *et al.* 2001). Two biodiversity hotspots which are commonly subject to these research problems are the Wallacean archipelago and Mesoamerica.

1.2 –WALLACEA

The Wallacean hotspot is an archipelago of approximately 13,500 islands located between the Greater Sunda island group and New Guinea (Coates and Bishop 1997) (Figure 1.2). It consists of three main island groupings; Sulawesi (by far the largest landmass in Wallacea) and its attendant islands, the Moluccas and the Lesser Sundas, in addition to numerous smaller island clusters (Whitten *et al.* 2002). This region lies almost entirely within the borders of Indonesia, with the exception of the nation of East Timor in the Lesser Sundas.

The geographical position and geological history of these islands have facilitated a unique biogeographical region which has attracted the attention of biologists, geologists and geographers for nearly 200 years.

Figure 1.2. The Indonesian archipelago, with boundaries of the Wallacean region shown . Adapted from Indonesian embassy (2009).

The Wallacean region is named after the 19th century zoologist, biogeographer and evolutionary theorist Alfred Russell Wallace, who was the first to describe many of the unique organisms found on the islands and to notice the unusual overlap of faunal families displaying characteristics similar to those of both mainland Asia and Australasia (Wallace 1869). Indeed, Wallacea is one of the few biological hotspots which span two of the world's great zoogeographical realms; in this case the Oriental and the Australasian (Cox and Moore 2002). Wallace initially hypothesised that a sharp break occurred in the geographical affinities of fauna across an imaginary line running between 'Asian' Borneo and Bali in the West and 'Australian' Sulawesi and Lombok in the East, which was later coined 'Wallace's line' by Thomas Huxley (1868). Later revisions determined that biogeographical divides in the Wallacea region are not quite so well-defined, and represent more of a transitional gradient between the two zoogeographical zones (Darlington 1964). Wallace's line is now used to demark the Eastern limit of the Oriental zone, while a further boundary hypothesised by Richard Lydekker in 1895 to mark the Western extent of the Australian zone runs between New Guinea and the Moluccas (Whitten 2002). Wallacea lies between these lines and possesses a transitional fauna that has species representative of both zones. A third theoretical boundary running between Sulawesi and the Moluccas, Weber's line, marks the divide between Eastern Wallacean islands which are dominated by species with Australasian origins and Western Wallacea where a majority of species are Asian in character (Whitten 2002) (Figure 1.3).

Figure 1.3. Biogeographical boundaries in the Wallacea region. Wallace's line (1) demarks the Eastern boundary of the Oriental zoogeographical zone. Lydekker's line (3) demarks the Western boundary of the Australasian zoogeographical zone. Wallacea lies between and possesses a transitional fauna, with Weber's line (2) demarking the boundary between dominance of Oriental and Australasian dominated species assemblages. Adapted from Indonesian embassy (2009).

The global importance of Wallacean biodiversity lies primarily with the very high rates of endemism exhibited here in almost all taxonomical groups. This is the result of a complex geological history involving the collision of ancient terrane plate fragments of both Asian and

Australasian origin between the mid-Miocene and early Pliocene (Villeneuve *et al.* 2001, White and Bruce 1986). These collisions of continental crust were followed by long subsequent periods of geological isolation caused by the archipelago's insular nature and by the deep ocean trenches which surround the island group. These have prevented land-bridges forming during glacial periods, such as have frequently occurred between the Greater Sundas island groups and the Asian mainland (Whitten *et al.* 2002, Kinnaird 1995). As a result, almost 50% of the region's terrestrial vertebrate species are restricted entirely to the hotspot, including 68% of reptiles, 88% of mammals (excluding bats) and 40% (249 species) of birds; a proportion greater than any other hotspot aside from the Tropical Andes (Myers 2000). The avifauna of Wallacea is also remarkably taxonomically distinct; Sulawesi alone possesses 14 endemic bird genera, the highest number of any of Birdlife International's 218 recognised endemic bird areas (Stattersfield *et al.* 1998). A further nine endemic bird areas are located within the Wallacean hotspot, which together encompass almost every sizeable island in the region (Stattersfield *et al.* 1998). The conservational importance of Sulawesi in particular is reflected by its inclusion in other assessments of the world's most diverse and distinctive biological regions; all three terrestrial and freshwater Sulawesian ecosystems were included in the World Wildlife Fund's 'Global 200' assessment of priority eco-regions, for example (Olson and Dinerstein 1998).

As with all hotspots, the biodiversity of Wallacea is under intense pressure from anthropogenic activities, but threats to the archipelago are especially severe due to the scale of habitat destruction. Expanding agricultural activities and unsustainable logging practices have facilitated a relative rate of habitat destruction in South-East Asia greater than any other tropical region: around 1.4% per annum (Sodhi *et al.* 2004). This is cause enough for great concern in mainland South-East Asia and the large islands of the Greater Sundas, where predictive extinction models estimate that continued habitat alterations on this scale could result in the loss of up to 42% of flora and fauna species across the region by 2100 (Sodhi *et al.* 2004). However the implications for Wallacea may be even greater, given the archipelago's insular nature. Wallacea is comprised entirely of oceanic islands unconnected to continental shelves which (with the exception of mainland Sulawesi) represent small, isolated ecosystems which are inherently more fragile than continental landscapes, as theorised by Macarthur and Wilson (1967). Spatially limited habitats on these islands mean any disturbance is likely to destroy a proportionally higher ratio of the total area of habitat available. Pimm *et al.* (1995) describe this as the 'cookie cutter' effect, in that if a cookie-cutter shaped area the size of a small island is deforested in a large landscape biodiversity will be locally reduced, but species lost to that area will continue to exist in other surrounding areas and can later recolonise the area. If, however, this 'cookie cutter' swathe of destruction is placed on a small island of the same size, all the species on that island will be lost, and recovery will not occur as endemic species will be extinct. The vulnerability of island endemics has been well-described; Trevino *et al.* (2007) describes how island birds are over 40 times more likely to become extinct than continental species, with Trainor (2007), Birdlife International (2004), Fuller (2000) and Pimm (1998) further relating the vulnerabilities of island species. Mainland Sulawesi is the only Wallacean landmass that could not be considered a small island ecosystem, with an area of >180,000km² (Kinnaird 1995). However, its unusual physical geography has been hypothesised to make it more vulnerable to deforestation processes than other landmasses of a comparable size. The island is comprised of four elongated 'arms' and as such no part is located more than 100km from the coast (Cannon *et al.* 2007). As such Sulawesi possesses no significant interior core, meaning that its remaining forest ecosystems have high edge/area ratios and are prone to fragmentation and edge effects.

An estimated 55% of original vegetation cover and 85% of original pristine rainforest within Wallacea has already been lost or modified (Conservation International 2007, Global Forest Watch 2002). Effective conservation strategies are required to safeguard remaining habitats; Wilson *et al.* (2006) argue that Sulawesi should be the highest priority for conservation resources in the whole of Insular South-East Asia. However, conservation policies have often proved difficult to implement here due to a poor understanding of precisely how habitat modification impacts upon biodiversity; this results from a chronic lack of biological research in the region. Aside from a few recent surveys (Coates and Bishop 1997, White and Bruce 1986), the most reliable accounts of bird communities on many Wallacean islands date back to collectors' reports from the late 19th century (Trainor 2007), and species inventories for most areas are poor (Cannon *et al.* 2007). Furthermore, most research conducted in recent years has focussed on low-lying areas on larger islands, chiefly mainland Sulawesi (Waltert *et al.* 2004, Sodhi *et al.* 2005, Thiollay *et al.* 1997) and the major islands of the Moluccas group (Poulsen and Lambert 2000, Marsden and Fielding 1999). This has led to montane regions and smaller islands, which are more ecologically fragile and where many endemic species are located, being comparatively neglected by ecological research. This lack of scientific information has seriously impeded efforts for establishing optimal conservation management in these areas.

1.3 - MESOAMERICA

The second study area examined in this thesis is located within Mesoamerica; a continental biodiversity hotspot.

The forest habitats of the Central American tropics extend over 1,130,000km^2 and eight countries, forming the third largest biodiversity hotspot (Conservation International 2007)

(Figure 1.4). The region supports an extremely rich flora and fauna; almost 1200 bird species have been recorded here, the second highest of any hotspot, with 251 (20.9%) of these being regionally endemic (Myers *et al.* 2000). Mesoamerica supports more endemic mammal (210) and reptile (391) species than any other hotspot, and possesses the second highest total of endemic amphibian species (307) (Myers *et al.* 2000). The region was classified as one of the ten 'hottest' hotspots by Myers *et al.* (2000) with regard to diversity of endemic vertebrates, and contains three of Olsen and Dinerstein's (1998) 'Global 200' priority ecoregions.

The biological richness of this region is a function not only of the high productivity inherent in most low-latitude terrestrial ecosystems, but also of the overlapping of Nearctic and Neotropical zoogeographical regions enabled by the rise of the Panamanian isthmus in the late Pliocene. Thus occured the 'Great American Interchange' of species from both continents (Webb 1991). The influence of the region's numerous mountain ranges has also had a powerful isolating effect on biological populations, creating a great diversity of altitudinal microhabitats which have facilitated speciation (Morrone 2006, Cox 2000, Cox and Moore 2000). It is these mountainous areas, particularly cloud forest, where the majority of the regions endemic species are concentrated (Holwell and Webb 2005, Bubb *et al.* 2004, Stattersfield *et al.* 1998).

Figure 1.4. The Mesoamerican hotspot (Conservation International 2005).

As with most tropical ecosystems, the forests of Mesoamerica are being subject to heavy anthropogenic pressures and consequential environmental degradation. While the region has a long and complex history of environmental disturbance, from the emergence of complex agrarian societies 5000 BP to the influence of advanced civilisations such as the classical Maya (Bray and Klepeis 2005, Goman and Byrne 1998, Abrams and Rue 1988), the rate and scale of this disturbance have increased exponentially over the last century, with rapid population growth, the expansion of extensive agriculture and commercial plantations and, since the mid 20th century, mechanised forestry and the expansion of modern transport infrastructure (Bray and Klepeis 2005). It has been estimated that approximately 80% of the region's original vegetation has now been lost or substantially modified (Conservation International 2007) while remaining fragments of primary forest continue to be lost at a rate of 0.8-1.5% per annum (Brooks *et al.* 2002, Achard *et al.* 2002). Effective conservation policies are needed to maintain the long-term integrity of this region, but these have also proved problematic to implement here due to incomplete inventories of local organisms and knowledge of their response to habitat modification, as well as a limited understanding of how effective current conservation strategies have been. The majority of protected areas within the hotspot are severely undermanaged and understaffed to the extent that many have been labelled 'paper parks' which possess very little conservation-related infrastructure and the existence of which is largely theoretical (Global Environment Facility 2005, Bonta 2005, Reyes and Cruz 1994). The effectiveness of these 'paper parks' has been explored in other tropical regions (Struhsaker *et al.* 2005, Curran *et al.* 2004, Peres and Terborgh 1995), although no research of this kind has ever been undertaken in Mesoamerica.

As in the case of Wallacea, research into relationships between biodiversity, habitat disturbance and conservation policy has been scarce, and the limited research which has been conducted has focussed on lowland forests which usually represent the most accessible ecosystems for researchers. This is highly significant as some of the region's most pristine and biologically diverse remaining habitats are found in mountainous areas, in particular within tropical cloud forest ecosystems (Powell and Palminteri 2001). Cloud forests are a rare habitat comprising only 2.5% of all global forest ecosystems (Cayuela *et al.* 2006), yet provide habitats for over 10% of all range-restricted bird species (Stattersfield *et al.* 1998), as well as being centres of endemism for plants (Bubb *et al.* 2004), herpetofauna (Wilson and McCranie 2003) and invertebrates (Anderson and Ashe 2000). However, these ecosystems are rapidly disappearing, and have been considered the most threatened of all tropical habitats on a global scale (Williams-Linera 2002). Mesoamerican cloud forests are currently experiencing a deforestation rate greater than that of the region's lowland forest, and remaining pockets of this habitat are highly fragmented and ecologically vulnerable (Cayuela *et al.* 2006, Solorzano *et al.* 2003). It has been estimated that if current rates of habitat loss continue, virtually all remaining cloud forest could be lost by 2021 (Mejia *et al.* 2001). This ecosystem therefore represents a high conservation research priority.

1.4 - RESEARCH OBJECTIVES

The study areas examined in this thesis are of global biological significance, yet are under severe anthropogenic pressure and further research is required in order to implement effective conservation strategies. Research examining ecosystem diversity as a whole has, however, often proved expensive, highly complex and time-consuming, particularly when researchers attempt to monitor a broad range of taxonomical groups which require specialist knowledge or laboratory analysis (Gardner *et al.* 2007, Lawton *et al.* 1998).

Birds are one taxonomical grouping where researchers are less limited by these issues. This class of vertebrates is comparatively well known in the tropics and can be surveyed quickly and efficiently using methods which preclude the need to make time-consuming, specialist-dependent, expensive and potentially ecologically damaging physical sampling efforts (Stotz *et al.* 1996). Research also suggests that avifaunal assemblages may, to a certain extent, be utilised as an indicator taxon to estimate population dynamics in other, more cryptic, taxonomical groups (Blair 1999, Rappole *et al.* 1998, Howard *et al.* 1998, Furness and Greenwood 1994). This makes avifaunal studies a potentially powerful tool in future biodiversity monitoring strategies. However, knowledge of avifaunal communities and their relationship to environmental disturbance is incomplete, as is an understanding of the best methods to survey these communities, the effectiveness of current conservation areas and the habitat associations of these communities.

With consideration to these research issues, the overall aim of this thesis is to examine relationships between bird communities, the environment, and habitat disturbance in two biologically important but poorly studied ecosystems, with a view to providing practical recommendations for conservation efforts in these regions. A broad range of issues will be addresses, being defined by five main research objectives:

1) To critically assess the effectiveness of methodologies currently used to survey avifaunal communities in these study sites.

2) To examine the relationships between anthropogenic disturbance and the composition of avian biodiversity in the Wallacean and Mesoamerican biological hotspots, looking at large-scale comprehensive bird communities as well as focussing on key range-restricted, endemic and threatened species with a high conservation value.

3) To critically assess the effectiveness of current conservation strategies in the study areas.

4) To explore the habitat associations of avifaunal communities in the study areas with a view to determining how best to identify priority areas for conservation.

5) To examine differential responses of Wallacean and Mesoamerican endemic avifauna to anthropogenic disturbance, and to discuss possible ecological and biogeographical reasons for any differential response.

These research objectives were examined in two field sites: the Lambusango forest reserve on Buton Island, South East Sulawesi, and Cusuco National Park, Honduras. Research was conducted in conjunction with the scientific research organisation Operation Wallacea.

1.5 -OPERATION WALLACEA

Operation Wallacea is an international conservation organisation that coordinates biological and social science research projects in tropical and sub-tropical ecosystems. The company was founded in 1995 with a single research site in South-East Sulawesi, and has since expanded to run expeditions in seven countries across four continents (Operation Wallacea 2008). Operation Wallacea aims to conduct large-scale, long-term monitoring biodiversity surveys in each of its expedition sites, with a view to inform conservation policy in these areas and produce an output of scientific research articles. The author has had a five-year working relationship with the organisation, and the field data forming the basis of this thesis was collected while participating in these expeditions, with Operation Wallacea providing the requisite logistical and staffing support.

1.6 -THE LAMBUSANGO FOREST

The Lambusango Forest Reserve (5°10'S, 122°24' E) is a 65,000 hectare expanse of uninhabited tropical monsoon forest located on the Island of Buton, the largest attendant island of Sulawesi in the Indonesian archipelago (Figure 1.5).

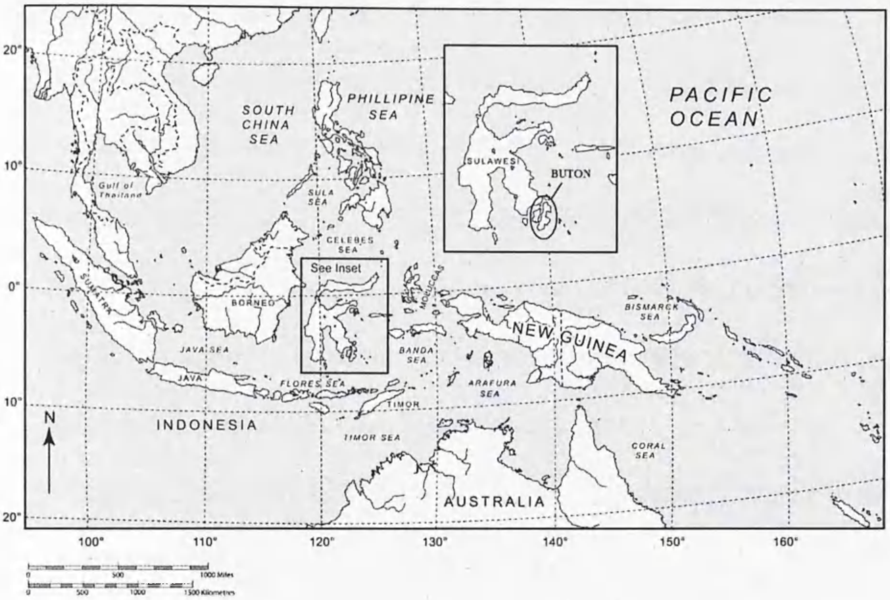


Figure 1.5. The Indonesian archipelago. Inset displays location of Sulawesi and Buton island.

The island experiences a tropical monsoon climate with a June-September dry season and a November-April wet season. Mean annual rainfall ranges between 1500 – 2000mm, peaking between April and June (Whitten *et al.* 2002), with mean annual temperatures of 25 ºC - 27 ºC (Figure 1.6).

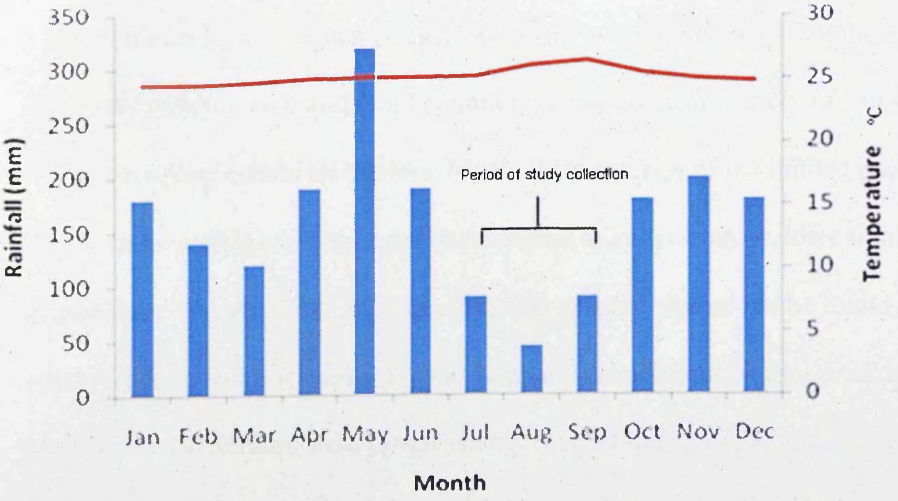


Figure 1.6. Monthly mean rainfall and temperature data for Buton Island, South East Sulawesi. Adapted from Singer and Purwanto (2006).

Much of Buton has been identified as being of high conservational value (Cannon *et al.* 2007), possessing a diverse flora and fauna. Catterall (1998) reported the presence on the island of at least 231 bird species including 52 Sulawesi endemics. It is also a stronghold for two species of endangered endemic bovid; the Lowland (*Bubalus depressicornis*) and Mountain (*Bubalus quarlesi*) anoa; this is one of only two locations where the ranges of both species are known to overlap, with approximately 10% of the global population of both species occurring on the island (Burton *et al.* 2005).

Forest cover on the islands has undergone significant clearance in recent years; Seymour (2004) describes how agricultural expansion, logging and mining activities have led to the loss of over 13% (27,809 hectares) of remaining forested areas between 1991 and 2002.

The Lambusango forest reserve was established in 1982 as part of a nationwide policy by the Suharto administration to found new national parks and reserves across Indonesia. The Lambusango was selected as one of these new reserves based on its 'potency of flora and fauna' and now occupies a large part of south-central Buton. Its area is divided into a 28,510 hectare strict forest reserve where all commercial, recreational and agricultural activities are nominally prohibited, and a 35,000 hectare production forest where some sustainable activity is allowed (Singer and Purwanto 2006).

The Lambusango provides an excellent study site for investigating the aims of this thesis due to its endemic-rich avifaunal community and the wide variety of forest successional stages occurring within its borders. Much of the interior of the limited production zone is highly inaccessible and has never been subject to cultivation or other significant human disturbance. Consequently high quality, near-primary forest can be found here. Much of the strict reserve's interior, however, was settled and under cultivation prior to designation as a protected area. Settlers were progressively evicted in the 1980s and the vegetation here has had over 25 years to regenerate, providing a good example of well-regenerated secondary forest. While the strict reserve's interior has been left largely intact since the declaration of the reserve, much of the peripherary has been inadequately regulated and there has been much encroachment from shifting cultivation and logging activities, creating a belt of heavily disturbed secondary forest. Surrounding the reserve is a matrix of cleared mixed agricultural land. Photographic examples of these habitat types are shown in Appendix 3. This variation of habitats provides a well-defined disturbance gradient to investigate the impacts of anthropogenic activities on a unique avifaunal community (Figure 1.7).

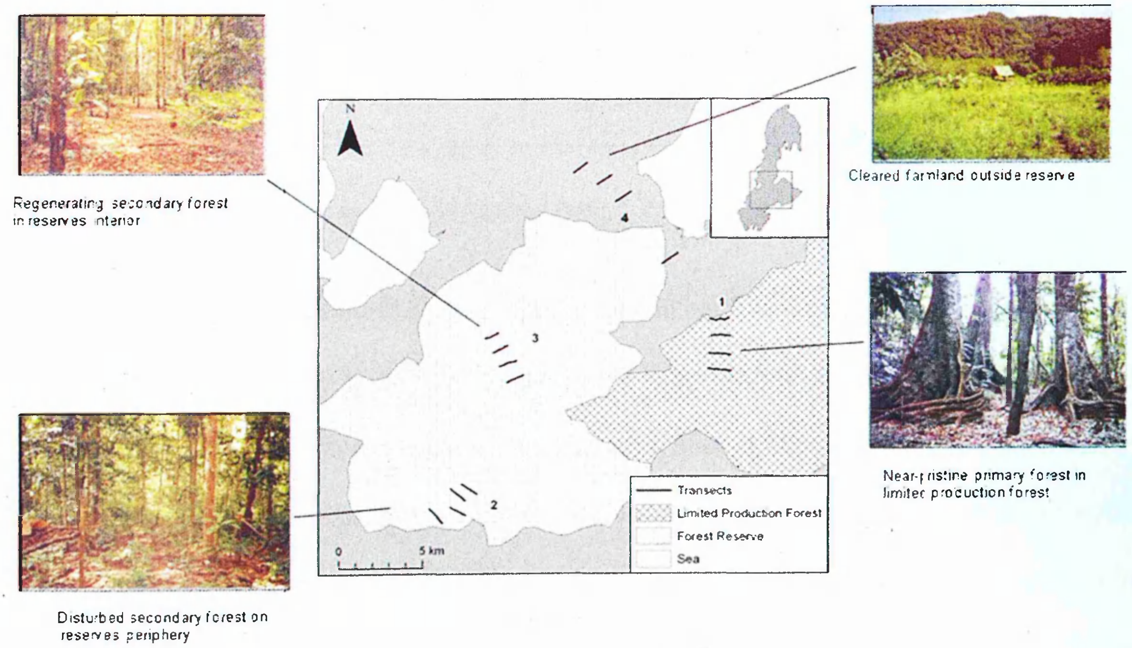


Figure 1.7. Forest categories and study sites within the Lambusango reserve.

1.7 - CUSUCO NATIONAL PARK

The second study site examined in this thesis is Cusuco National Park (15°29.8'-15°32'N / 88°13 - 88°26' W); a 23,440 hectare region of tropical montane cloud forest located in Cortez province, North-West Honduras, near the Guatemalan border (Figure 1.8).

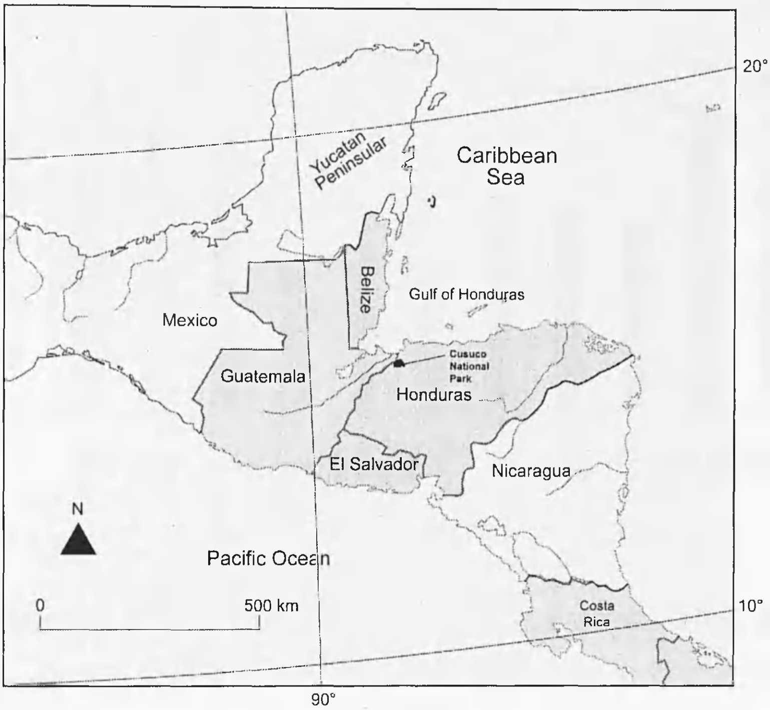


Figure 1.8. Central America and Cusuco National Park.

The park occupies the central peaks of the Merendón cordillero at altitudes between 500 m – 2,242 m above sea level (Lenkh 2005). These are fairly low elevations for the occurrence of cloud forest, which is more typically found between 2000-3500m (Bubb *et al.* 2006). The habitat occurs here due to its proximity to the Caribbean and the effect of the Westernly Alize trade winds, which bring moisture-bearing air up the mountain slopes where it condenses into cloud banks (Bubb *et al.* 2006). Mean annual precipitation in the Park ranges from 2,995 mm in the core zone and 2,580 mm in the buffer zone, with heaviest rainfall occurring between October – December. Mean monthly temperatures range from 12.9°C in December to 20.2°C in April, with a mean of 16.7°C in the core and 20.6°C in the buffer zone (Fundación Ecologista 1994) (Figure 1.9).

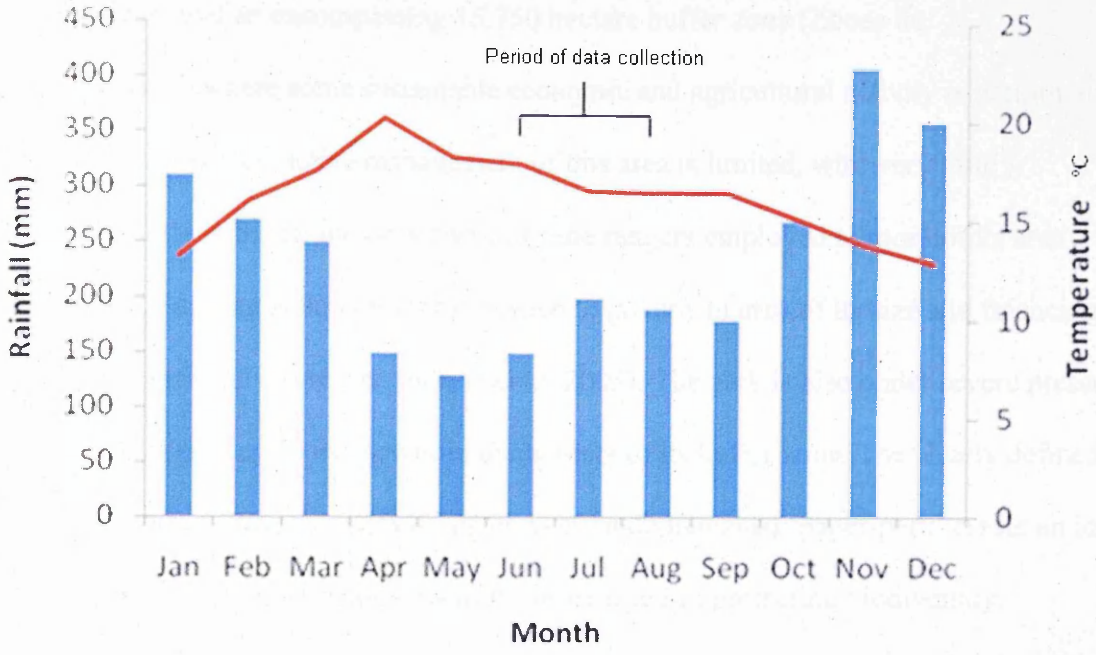


Figure 1.9. Monthly mean rainfall and temperature data for Cusuco National Park, Honduras. Adapted from Fundación Ecologista (1994).

Vegetation classifications within the park vary from cleared agricultural land and *Pinus oocarpa* pine forest at lower elevations to hardwood cloud forest and Bosque enano dwarf forest at altitudes above 2000m (Lenkh 2005) (See Figure 1.10 and Appendix 3).

The park supports a rich avifauna with over 270 species having been recorded (Martin 2007) including several species of a high conservation value such as the Resplendent Quetzal (*Pharomachrus mocinno*) and Highland Guan (*Penelopina nigra*). Cusuco also provides habitat for many other rare and endangered species, including at least six species of endangered or critically endangered herpetofauna, four of which are endemic to the park (Townsend *et al*. 2006), and small populations of threatened large mammals, including Jaguar (*Panthera onca*) and Baird's Tapir (*Tapirus bairdii*) (Operation Wallacea 2008).

Cusuco National Park was established in 1993 following the Honduran government passing the Cloud Forest Act (1987) and General Environment Law (1993) as one of 37 new high altitude forest reserves. The park is divided into a nominally inviolate 7,690 hectare core zone

(Zonas nucleos) and an encompassing 15,750 hectare buffer zone (Zonas de amortiguamiento) where some sustainable economic and agricultural activity is permitted (Figure 1.10). However, active management of this area is limited, with very little conservation infrastructure and only five full-time rangers employed to monitor its area (Lenkh 2005). Funding is far below that needed to govern an area of its size and financing has decreased markedly in recent years (Lenkh 2005). The park is also under severe pressure from the 30-40,000 people living within the borders of its buffer zone. The clearly defined zonation of the park, together with its status as an undermanaged 'paper-park' create an ideal opportunity to assess the effectiveness of these areas are in protecting biodiversity.

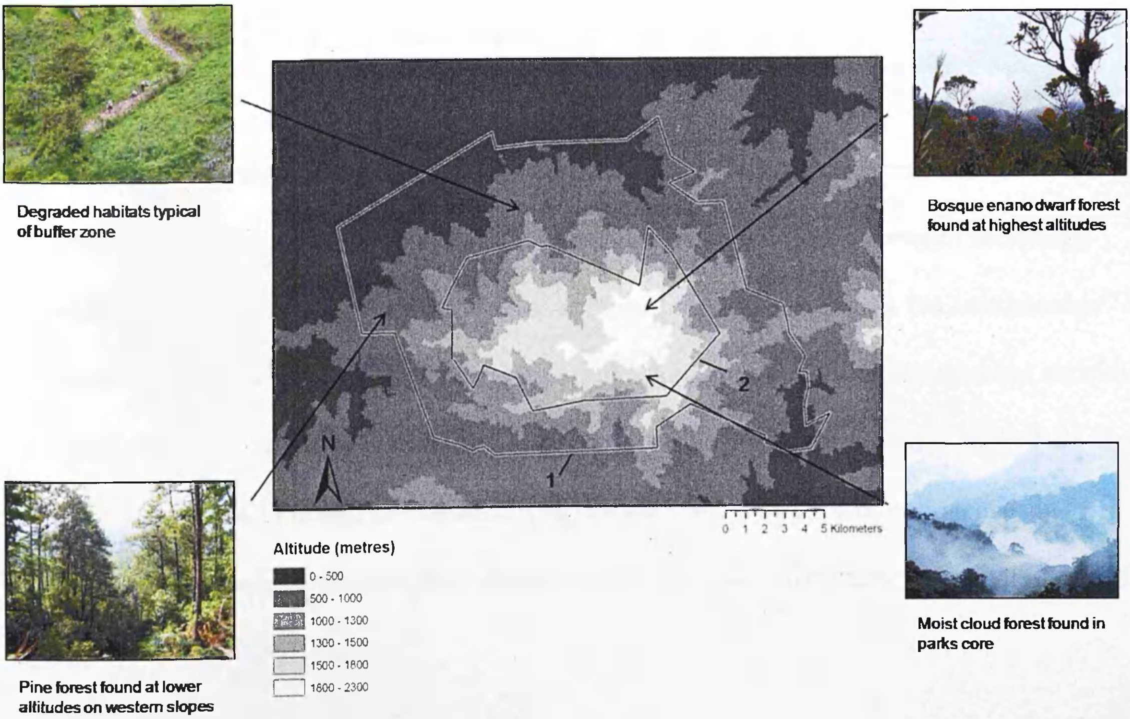


Figure 1.10. Forest categories and study sites within Cusuco National Park. Notation 1 indicates park boundary. Notation 2 indicates the park's buffer/core boundary.

1.8 - THESIS STRUCTURE

This thesis follows the structure of 'submission by paper'. The first two chapters are represented by this introduction and a literature review. Each of the subsequent five chapters was initially written in the format of a peer reviewed publication corresponding to one of the four research aims previously stated, although the structure of each has been standardised into a uniform 'thesis' style for ease and consistency of reading.

Chapter 3: 'Assessment of the effectiveness of two different methodological techniques for surveying cloud forest bird communities' compares and contrasts the effectiveness of two different census techniques, point counts and mist netting, in surveying bird communities in cloud forest; a distinctive ecosystem where little methodological research has been conducted previously. It forms an important part of the thesis by determining the most effective way to conduct avifaunal surveys in this environment as well as providing justification for the methodologies utilised elsewhere in the thesis.

Chapter 4: 'Impacts of tropical forest disturbance upon avifauna on a small island with high endemism: implications for conservation' describes the relationship between increasing anthropogenic disturbance and patterns of avifaunal biodiversity within the Lambusango forest reserve. It examines avifaunal communities in their entirety, range-restricted endemic species and certain key species with a high conservational importance, such as the Red-knobbed Hornbill *Rhyticeros cassidix*. It represents a key component of the thesis by providing a detailed overview of avifaunal response across a disturbance gradient in one of the two study sites.

Chapter 5: 'An assessment of the effectiveness of a Mesoamerican 'paper park' in conserving a cloud forest avifauna' examines the effectiveness of an under-managed Mesoamerican National Park in conserving cloud forest bird species. It examines how the composition of avifaunal communities varies between the core and buffer zones of Cusuco National Park, with a strong emphasis on range-restricted and threatened species of a high conservational importance, and uses variations in bird populations to assess the park's effectiveness in conserving biodiversity to a species level. This chapter is of significance to the thesis as it further explores the relationship between avifaunal communities and environmental disturbance, and represents one of the few extant studies evaluating the effectiveness of 'paper-parks' in the region.

Chapter 6: 'Habitat associations of an insular Wallacean avifauna: a multi-scale approach for biodiversity proxies' builds upon the research described in Chapter 3, examining relationships between avifaunal communities and habitat structure at several spatial scales. The chapter aims to determine how best to utilise remote sensing and *in-situ* habitat measurements to provide useful proxy estimates of bird community composition, with a view to facilitating the identification of priority conservation areas.

Chapter 7: 'Differential vulnerabilities of range-restricted avifauna on a Wallacean Island and in Mesoamerican cloud forest: the influence of ecological and biogeographical factors?' This chapter synthesis the findings of data collected across both study sites, comparing sensitivity of range restricted avifauna in these areas to habitat disturbance and providing hypothetical arguments for any differences identified.

Chapter 8 provides a conclusion summarising the findings of the thesis as well as evaluating the research methods used in its production. It discusses potential further studies and research questions generated by our results.

The structure of this thesis, along with a demonstration of how each chapter and research topic is interlinked, is displayed in the conceptual model in Figure 1.11.

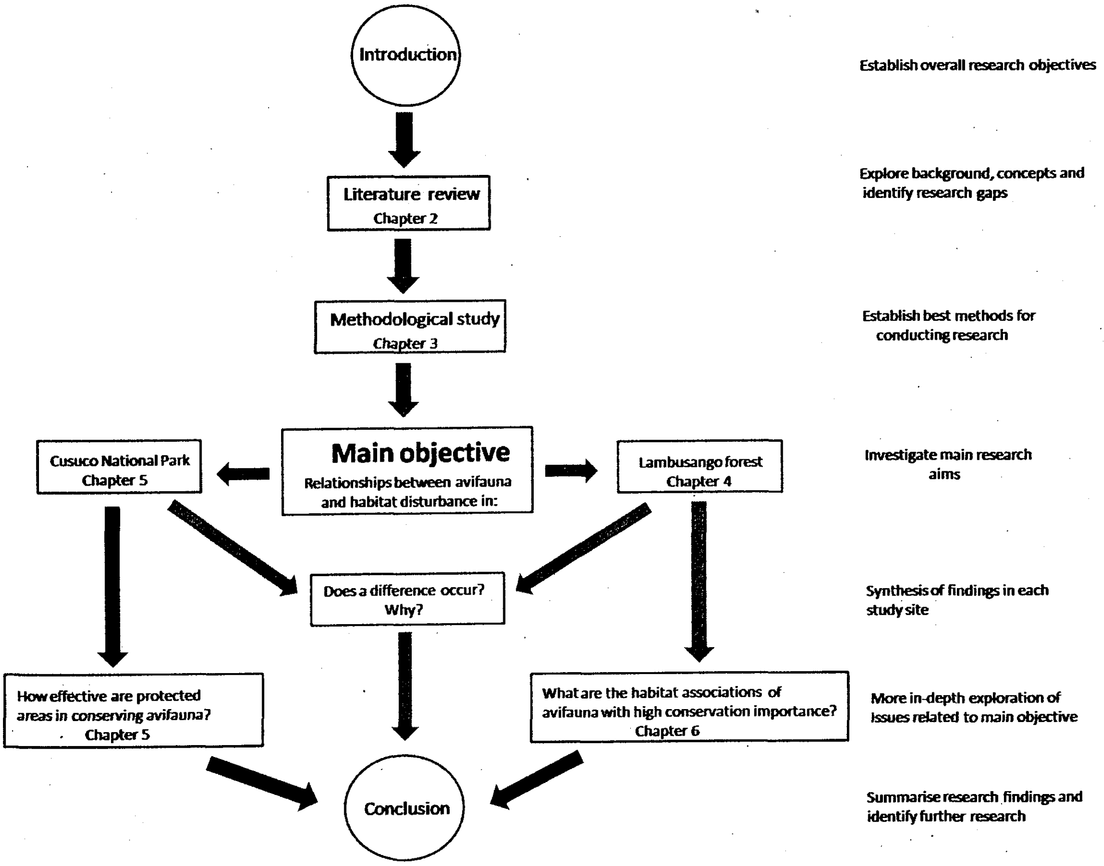


Figure 1.11- Conceptual diagram identifying research objectives, thesis structure and relationships between chapters.

Two appendix chapters summarise additional research conducted in the course of this thesis:

Appendix 1 provides an overview of the avifauna of the Lambusango Forest Reserve and its environs, including a systematic checklist of species recorded there. This provides important base-line data for this previously undescribed area.

Appendix 2 details morphometric measurements of >1500 birds captured by mist-netting surveys in Cusuco National Park between 2004-2008, which include previously unpublished, valuable data on many poorly described cloud forest species

Two further appendicies provide photographic examples of the study sites examined in this thesis, and summarise the progress of papers submitted for peer-review at the time of thesis acceptance, including details of journal titles, submission dates and publication dates.

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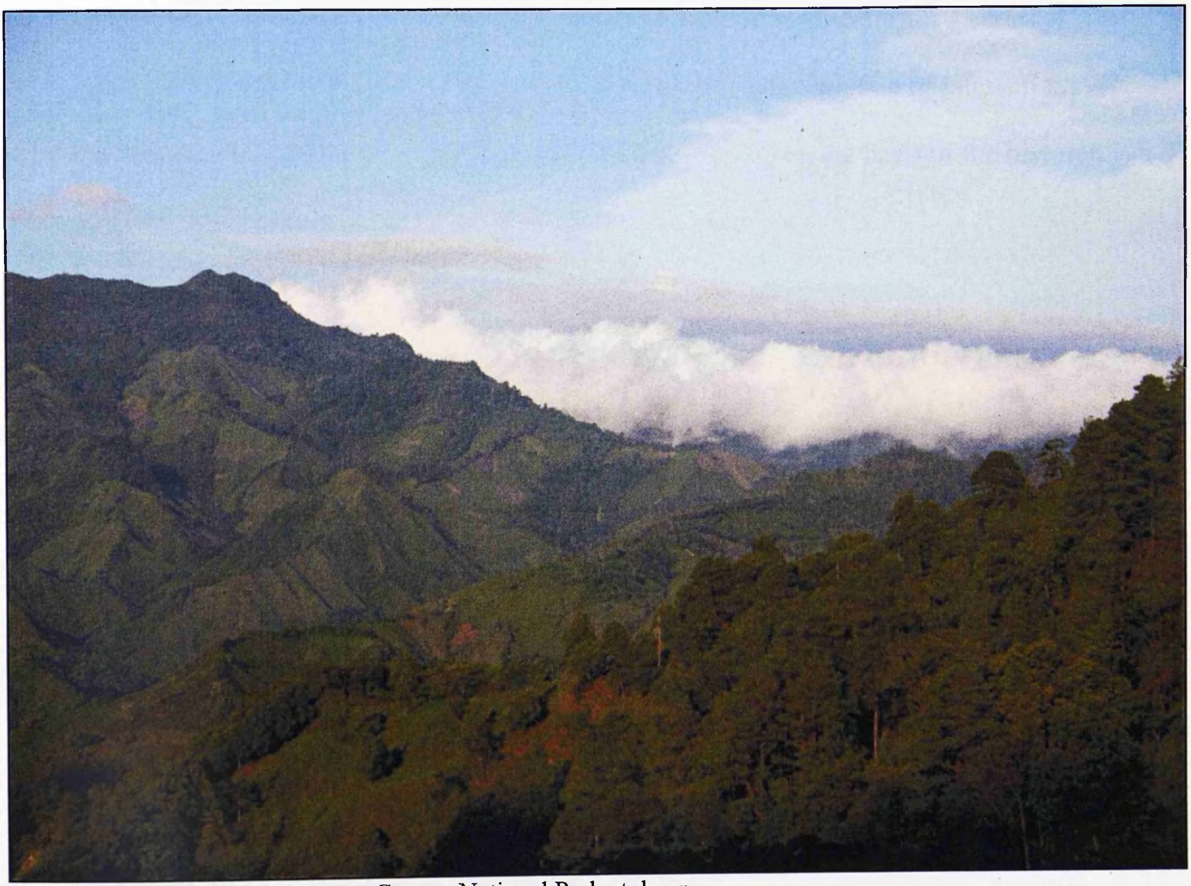
CHAPTER 2 - LITERATURE REVIEW - HABITAT LOSS AND AVIFAUNA: RESEARCH PROBLEMS AND OPPORTUNITIES



Cusuco National Park at dawn

2.1 – OVERVIEW

This literature review chapter is divided into three sections. The first of these provides an overview of tropical deforestation patterns, biodiversity loss and the relevance of this to society. The second section discusses the problems associated with attempting to research relationships between biodiversity and habitat modification, and how bird community analysis can be a useful tool in addressing these. The last section identifies a series of opportunities for research that could improve the current understanding of interactions between bird communities and habitat modification which form the basis of the research presented in this thesis.

2.2 -TROPICAL FORESTS, HABITAT DESTRUCTION AND BIODIVERSITY: AN OVERVIEW

The research themes presented in this thesis are based largely around one of the most critical environmental issues facing our global society: the destruction of tropical forest ecosystems and the ensuing loss of biodiversity predicted to occur as a result of this.

2.2.1 - Tropical forests

Tropical forest ecosystems are broadly defined as any area of forest located between 30° North and 30° South, although in some cases these extend beyond the southern limits of the Tropic of Capricorn (Whitmore 1998). These forests are generally classified as belonging to one of three major geographical zones. The Neotropics contain the most extensive remaining tracts of tropical forest; approximately half the global total (Primack and Corlett 2005). These are subdivided into three main blocks: the Amazon/Orinoco Basin, which forms the largest expanse of tropical forest in the world, the Andean forests of North-West South America which stretch into Mesoamerica as far as Southern Mexico, and the Atlantic forest of South-East Brazil (Whitmore 1998). South-East Asia holds the second-largest expanse of tropical forest. This is centred on the Indonesian archipelago and stretches north across the Malay Peninsula, Indo-China, Thailand and Indo-Burma, and east into New Guinea. These forests also extend into Northern Queensland in Australia, which is frequently classified as part of the Asian tropical zone, despite possessing many unique biological characteristics (Bowman 2000). Outliers of Asian tropical forest can also be found in India's Western Ghats and Sri Lanka (Whitmore 1998). The last major region of tropical forest occurs in Equatorial Africa, which is largely confined to western and central areas of the continent, with smaller fragments, mostly centred on mountain ranges, occurring in parts of East Africa (Whitmore 1998). Smaller areas of tropical forest can also be found in Madagascar and several Caribbean and Indo-Pacific Islands (Primack and Corlett 2005, Whitmore 1998) (Figure 2.1).

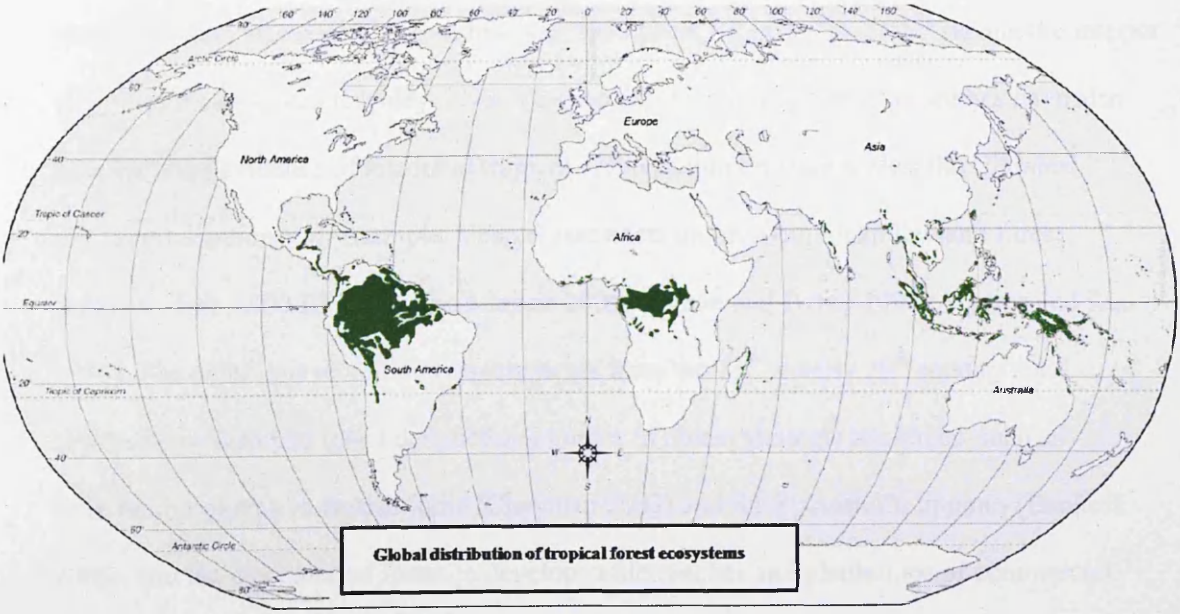


Figure 2.1. Global distribution of tropical forest ecosystems. (Based on United Nations Environment Programme World Conservation Monitoring Centre 2009).

Ecosystems at these latitudes generally experience a warm year-round climate, although most other environmental factors here are highly variable, leading to the existence of many different categories of tropical forest, from lowland rainforest with perennial heavy precipitation to tropical dry or seasonally dry forest and high-altitude montane cloud forest (Moran 2006, Goldsmith 1998).

Tropical forest ecosystems at present cover between 6-8% of the world's land surface (Moran 2006), which is an exponential reduction of the 50-66% cover which is believed to have been the extent of these forests at the start of the Holocene (Pimm and Raven 1999, Terborgh 1992) and anthropogenic activity is continuing to destroy remaining areas at a rapid pace. The continued destruction of remaining tropical forest is considered by many to be among the foremost contemporary global environmental issues (Wilson 1999).

2.2.2 -Tropical deforestation – causality and consequences

Deforestation in the tropics is by no means a uniquely modern phenomenon. There is evidence of forest clearance for agriculture dating back at least 3000 years BP in Africa, 7000 years BP in the Neotropics, and as much as 9000 years BP in South-East Asia and the interior valleys of New Guinea (Flenley 1979). Archaeological and palaeobotany studies have also demonstrated evidence of historical tropical deforestation on large scales; the Classical Mayan civilisations, for example, cleared vast tracts on Mesoamerican lowland forest between 1500 – 900 BP (Bray and Klepeis 2005, Goman and Byrne 1998, Abrams and Rue 1988). The ambitions of colonial governments from the 17th to early 20th century also facilitated widespread forest destruction in order to obtain strategic resources, such as exploitation of teak in British India (Chapman 2003) and the Spanish Philippines (Bankoff 2006), and the clearance of forest to develop cattle ranches and plantations of commercial crops in Latin America (Park 1992). Modern deforestation patterns are hypothesised to differ markedly, however, in the exponentially greater scope of their scale. Recent well-researched estimates by Achard *et al.* (2002) predict global deforestation rates in the tropics during the 1990s at 0.52% per annum, which represents a total loss of 5.8 ± 1.4 million hectares each year throughout the last decade, with a further 2.3 ± 0.7 million hectares being visibly degraded. This equates to an area of tropical forest the size of the nation of Belize being lost daily (Moran 2006). More recent estimates by the Food and Agriculture Organisation (2005) estimate global forest loss at between 2000 – 2005 at 7.3 million hectares per year, although these figures have been criticised by some sources as poorly researched and inaccurate (Rainforest Alliance 2005). While deforestation rates undoubtedly remain high on a global scale, this forest loss has not been distributed evenly across the tropics. Achard *et al.* (2002) estimates Latin America to have experienced the heaviest deforestation rates on a large spatial scale (-2.2 ± 1.2 million hectares per annum), followed by South-East Asia (-2.0 ± 0.8 million hectares per annum) and Tropical Africa (-0.71 ± 0.31 million hectares per annum), although South-East Asia has lost the highest percentage of its total forest cover (Sodhi *et al.* 2004b). The causes of this deforestation are diverse. Myers (1996) identified the three major driving factors as commercial exploitation of timber, clearance of land for agriculture and biomass fuel, and clearance for cattle ranching, especially in the Neotropics. A range of other important causalities has also been identified, however, including mining activities (Park 1992), expansion of road networks, and the implementation of large hydro-electric dam projects (Laurence *et al.* 2004). Political resettlements of populations in forested areas, such as in Indonesia (Fearnside 1997) and Brazil (Park 1992), have also been important factors. The multitude of processes driving deforestation in the tropics today is, however, believed by several prominent authors (eg. Wilson 1999, Pullin 1992) to stem from a single root cause: rapid demographic growth globally, and especially within the tropics. The United Nations

Department of Economic and Social Affairs (UNDES 2009) estimates that the population of the planet has increased by over 400% since 1900, from a population of approximately 1.65 billion to around 6.78 billion today, and projects global populations to reach 9.2 billion by 2050. Population growth is currently occurring at an average rate of 1.19% per annum, with around 98% of this growth occurring in developing countries (UNEDS 2009) which is also where the great majority of the world's tropical forests are located (see Figure 2.2).

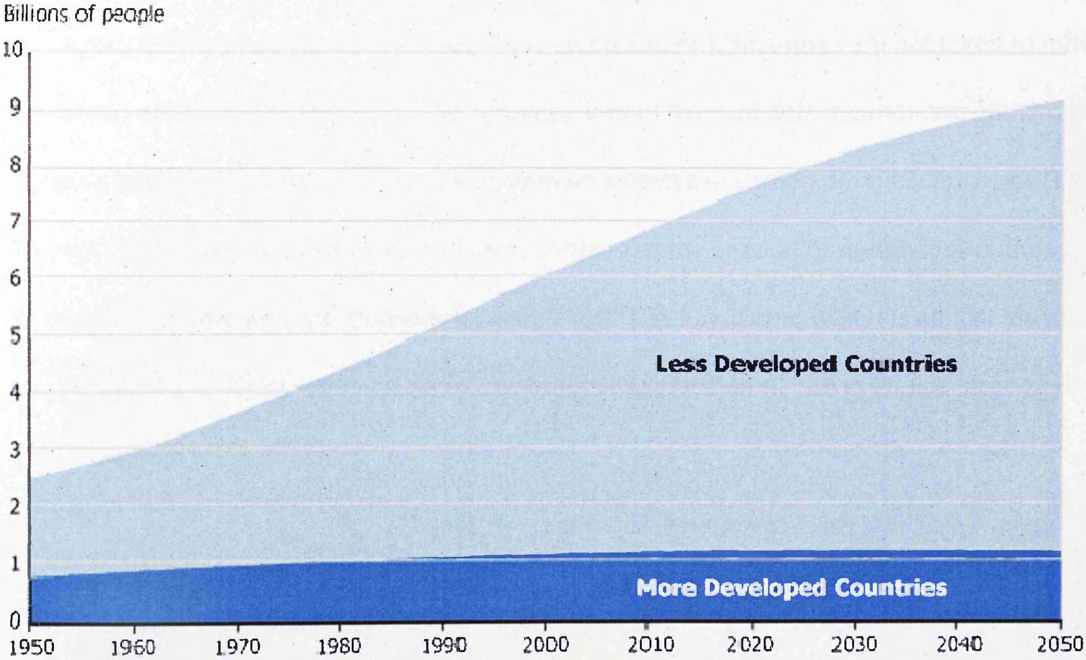


Figure 2.2. Global population projections 1950 – 2050 (Population Reference Bureau 2009).

Growing populations within the tropics are creating increasing pressures on living space and agricultural land, and this is exacerbated by the rising demand from an increasingly affluent global population for natural resources, in particular for hardwoods, minerals, fossil fuels and energy (Wilson 1999, Whitmore 1998). This demand has been further facilitated by expanding infrastructure and mechanised technology that has provided both access to previously remote tropical forest ecosystems and also the means to fell trees on an industrial scale (Whitmore 1998). The result of this has been the rapid and widespread destruction of tropical forest ecosystems as quantified by Achard *et al.* (2002).

The current tropical deforestation crisis has been described by many authors as representing environmental degradation on an unprecedented scale (Kauffman *et al.* 2002 Fearnside 1997, Bierregaard 1990). This is debatable; comparable rates of deforestation are believed to have occurred in the forests of Eastern North America during the 18th and 19th century (Pimm and Askins 1995) and in Europe during the High Middle Ages (1000-1300 AD) (Rackham 1986). It is universally accepted, though, that continued deforestation in the tropics will have serious and irreversible consequences if measures are not taken to mitigate further ecosystem destruction. The consequences of tropical deforestation are numerous and have been widely discussed; issues include an increase in carbon dioxide emissions (Defries *et al.* 2002), degradation of soils (Torras 2000), and the erosion of indigenous cultures (Centre for International Forestry Research 2005). A key theme which is almost always identified as a foremost consequence of tropical deforestation, however, is a large-scale loss of biodiversity.

2.2.3 - Biodiversity – richness, distribution, importance and loss

Biodiversity is an abbreviated term for biological diversity, a multi-faceted phrase of which the exact definition has been applied widely (Table 2.1) although generally it can be described as the measurement of the variety of life in a given area.

Source	Definition
International Council of Bird Preservation (2009)	The total variety of life in an area, including all genes, species and ecosystems
Myers *et al.* (2000)	The total number and variability of species and genes within a region
Heywood (1995)	The total variability of life in a given area
Groombridge (1992)	The number, variety and variability of living organisms in an ecosystem

Table 2.1. Select definitions of the term 'biodiversity'. Adapted from Primack (2008).

Tropical forest ecosystems are exceptionally rich reservoirs of biodiversity, harbouring more species of higher taxa than any other ecosystem on Earth. While tropical forests cover just 6-8% of the Earth's land surface (Moran 2006), they are predicted to support more than 50% of all terrestrial species (Plotkin *et al.* 2000, Wilson 1986), although these predictions represent highly approximate estimates due to the difficulties and conflicting conclusions encountered when attempting to calculating the number of species on Earth (Convention on Biological Diversity 2007, Pullin 2002, Stork 1993).

The spatial distribution of the majority of the Earth's species within the tropics, particularly in tropical forests, with progressively less diverse ecosystems occurring with increasing latitude, is described as the Species Gradient, and can be applied to nearly all taxonomical groups (Willig *et al.* 2003). The existence of this gradient has been widely recognised from at least the time of Alfred Wallace (1876) and Alexander von Humbolt (1808). The primary mechanisms responsible for this concentration of biodiversity in the tropics, however, remain contentious; Rohde (2002) lists as many as 28 hypotheses for a 'primary causality', none of which have been universally accepted as a definitive leading factor. While the mechanisms responsible are diverse, factors commonly cited in the literature include high primary productivity (Moran 2006), a wide variety of ecological niches with organisms adapting to spatial and temporal niche separation (Whitmore 1998), a heterogeneous landscape providing many habitat types and breeding sites (Bourliere 1996), and extensive periods of geological stability facilitating speciation (Moran 2006).

While the diversity of life in tropical forest ecosystems is prolific, current trends of habitat destruction are having severe impacts on this richness. There are concerns that the current global rate of species extinction is of such magnitude that it could be precipitating a sixth mass extinction event (Leaky and Lewin 1996). Current extinction rates are estimated to be 100 – 1000 times higher than naturally occurring background rates (Lawton and May 1995), with species estimated to be disappearing at a rate of 27,000 – 30,000 per year (Wilson 1999, Eldredge 1998). While this loss is a global phenomenon, extinction rates are far greater in the tropics where most diversity is concentrated (Wilson 1999), and within the tropics the potential for highest extinction rates lies in a discreet number of spatially restricted areas where biological diversity is highest: the 'biodiversity hotspots' defined by Myers (2000).

The concept of biodiversity 'hotspots' has been discussed in Chapter 1, with their global distribution shown in Figure 1.1. While these hotspots are widely dispersed globally, they are dominated by tropical forest ecosystems. All eight of what Myers (2000) termed the 'hottest' hotspots - those that possessed not only the richest diversity, but also the highest concentration of endemic species - were tropical forest ecosystems.

Some criticism has been made of the use of biological hotspots as a means of quantifying areas of conservational value. Lombard (1995) described how congruence between different taxonomical groups often varies greatly between hotspots, and Orme *et al.* (2005) argue further that species richness hotspots do not necessarily have high congruence with hotspots of endemism or threatened species. Pullin (2002) describes how hotspots are generally based on analysis of a discreet number of taxonomical groups rather than total diversity, and Mittermeir *et al.* (2008) describes how focussing on small, often degraded areas of hotspot habitat can lead to the neglect of large areas of intact wilderness. The concept has, however, become something of a paradigm for defining areas of high biological importance, being utilised by many conservation organisation such as Conservation International (2007), the International Union of Conservation and Nature (2009), and Flora and Fauna International (2009).

Despite possessing an elevated conservational importance, tropical forests located in these biodiversity 'hotspots' are expected to experience the greatest number of species extinctions of all global ecosystems over the next few decades (Conservation International 2007). This is partly because this is where the greatest concentrations of species lie, so there are more species to be lost, but also because all tropical hotspots are under severe anthropogenic pressure. All have suffered extensive habitat clearance and none have more than 25% of their original pristine vegetation remaining (Mittermeir 2008). Brooks *et al.* (2002) describes how between half and two-thirds of all globally threatened plants and 57% of globally threatened mammals are endemic to hotspots, the majority in tropical forest hotspots.

It has been demonstrated that tropical forest ecosystems and tropical forests in biodiversity hotspots in particular stand to lose a very substantial proportion of their rich biodiversity if current trends of habitat disturbance continue. There is also evidence that habitat destruction is the dominant factor driving this extinction loss. Sala *et al* (2000) estimate forest destruction to account for 90% of extinction risk in the tropics over the next 100 years, with the second most important factor, climate change, accounting for just 5% of future extinction risk.

Biodiversity loss on the scale estimated by current predictions will undoubtedly have severe consequences for society. Kunin and Lawton (1996) identified three main consequences of biodiversity loss. The first, most utilitarian reason is a loss of marketable commodities; biodiversity provides society with exploitable resources such as timber, food and pharmaceuticals. Additionally, the properties of many exploitable species have been poorly researched and the extinction of these could deprive society of valuable sources of medicine or nutrition of which we are not even aware (Park 1992). Second, and of potentially greater importance, are the non-marketable 'ecosystem services' that biodiversity provides, such as flood prevention, waste recycling, crop pollination and improving water quality. It has been estimated that around one-in-six rainforest species possesses a non-economic utilitarian value (Park 1992). Costanza *et al.* (1997) estimated the total value of these functions to be as much as $33 trillion per annum. It has been estimated that the economic cost-benefit ratio for conserving biodiversity for these direct and indirect utilitarian reasons is at least 100:1 (Balmford *et al.* 2002). Finally, there is a large literature describing the intrinsic value of biodiversity. Chapin *et al.* (2000) describes the intangible cultural, intellectual and aesthetic value that biodiversity possesses, while Park (1992) argues that there is a widespread belief, rooted in moral principles, that biodiversity simply deserves to exist for its own sake and is our responsibility to protect. These ideas relate to Wilson's (1984) 'Biophilia' hypothesis; that there exists a deep-rooted instinctive bond between humans and the environment, based in our evolutionary past, which drives a non-utilitarian desire to protect the ecosystems in which we live.

2.3 - CONSERVATION POLICY AND AVIFAUNA – PROBLEMS AND OPPORTUNITIES

2.3.1 - Monitoring biodiversity: limitations of the 'data vacuum'

The consequences of biodiversity loss in the tropics are now widely recognised. As such, conservation measures to prevent this loss are becoming an increasingly important, if still highly under-prioritised and underfunded, global focus. James *et al.* (1999) estimated at the turn of the century that an annual global budget of up to $6 billion had become available for conservation of biodiversity. The majority of these funds (approximately 90%) are spent in industrialised OECD countries where most of this capital is raised, although this still leaves hundreds of millions of dollars available for conservation in the tropics through multilateral organisations such as the Global Environment Facility (GEF), bi-lateral aid, and private funds (Brooks *et al.* 2006). The GEF alone invested >$1 billion in tropical conservation projects between 1992 and 1999 (James *et al.* 1999). While far below the optimal sum necessary to effectively preserve biodiversity in the tropics, equating to an investment of just \$93 per km^2 (James *et al.* 1999), this still provides a vital source of funding for conservation initiatives, particularly in hotspots where biodiversity conservation projects are becoming increasingly concentrated due to escalating awareness of the richness and irreplaceability of the organisms they support (Brooks *et al.* 2006).

Although support for conservation projects in biodiversity hotspots is increasing, success of proposed schemes often depends on an understanding of habitat disturbance patterns in ecological systems and the ways in which organisms react to this disturbance (Canterbury *et al.* 2000, Ludeke *et al.* 1990). This understanding is frequently lacking in the tropics for most taxonomic groups (Balmford 2005, Lawton *et al.* 1998), which inhibits the successful application of conservation schemes (Brooks *et al.* 2004).

An understanding of how biodiversity as a whole reacts to environmental disturbance nominally requires in-depth knowledge of the response patterns of all taxonomical groups. This has proved unattainable in tropical ecosystems due to incomplete taxonomical inventories and limited financial, labour and scientific resources. Surveying the response to disturbance of every species in a given tropical ecosystem is virtually impossible, given the extremely high diversity of these ecosystems. It is not even known how many species inhabit these ecosystems. While there is general consensus that >50% of global biodiversity can be found in tropical forests, estimates as to how many species global biodiversity constitutes vary widely. Most estimates range between 5-15 million species (Primack 2008, Pullin 2002), with higher estimates predicting that as many as 30 million species could exist on the planet (Stork 1993). Currently around 1.5 million species are scientifically described, with an additional 20,000 being discovered each year (Primack 2008). Even if this discovery rate is maintained, it will take >500 years for species inventories comprehensively to include even the lowest global biodiversity estimates. This makes an understanding of how biodiversity in its entirety responds to environmental disturbance logistically unfeasible. Lawton *et al.* (1998) estimated that an all-taxa biological inventory of a single hectare of tropical rainforest would have to be conducted on a scale 1-2 times greater than anything attempted by ecologists by the end of the 1990s, and would require the input of 10-20% of the entire global workforce of taxonomists.

Monitoring the response of biodiversity to habitat modification has also proved difficult when only a select range of taxonomical groups are analysed. Gardner *et al.* (2008) conducted a study of 14 higher taxa in 15 medium-sized study sites in the Amazonian rainforest. The resultant effort totalled 8.1 person years of labour and cost approximately $145,000; a fairly substantial sum considering that the income for some protected areas in the Neotropics is <$27,000 (Lenkh 2005). Gardner *et al.* (2008) also demonstrated how certain taxonomical groups, particularly cryptic invertebrates, are particularly expensive to survey and require an input of highly specialised equipment and taxonomical knowledge.

Assessing the impact of habitat modification on biodiversity based on surveys of just higher taxonomical groups is therefore also problematic; limitations restricting these studies are not only financial, but also technical. Lee (2000) describes how there is a serious and increasing shortage of the taxonomical expertise required to monitor biodiversity change. This shortage is also temporal; the speed of habitat change in many tropical areas could mean that forest areas are degraded before survey efforts are even complete, let alone enabling conservation policies based on their results to be put into place (Kremen 1992).

2.3.2 - Indicator taxa

The difficulties of examining the response of biodiversity to habitat modification on a multi-taxa scale have led conservationists to attempt other approaches, perhaps the most frequent of which is the use of indicator groups. Indicators are a grouping of organisms, usually a taxonomical group but sometimes smaller taxonomical sub-groups, which can be surveyed with relative simplicity and utilised to provide useful estimates of absolute biodiversity under the assumption that ecological characteristics of certain groupings will be representative of sympatric species within the same ecosystem (Caro and Doherty 2001, Canterbury *et al.* 2000). There are several important limitations associated with the use of indicator taxa in this way. Research has shown that although certain groups are effective in providing proxy indications of forest quality, they still only represent a small proportion of total biodiversity and are not always effective in determining change in all organisms (Gardner *et al.* 2008) or representing responses in rare or endangered species of high conservational importance (Su *et al.* 2004). There are also concerns that the increasing use of indicators as a methodological paradigm could lead to the neglect of many more cryptic groups of organisms, in a form of 'taxonomical chauvinism' (Pawar 2003). However, indicators have also been shown to be effective in identifying areas of high species biodiversity (Caro and Doherty 2001) and in reflecting habitat structural and functional diversity (Duelli and Obrist 2003), and are often regarded as the most practical way of determining the extent to which biodiversity responds to habitat disturbance in highly complex and diverse tropical ecosystems (Canterbury *et al.* 2000). There are several taxonomical groups which have been identified as potentially high-performance indicator groups in tropical forest ecosystems, including butterflies (Gardner *et al.* 2008, Schultze *et al.* 2004, Howard *et al.* 1998) and dung beetles (Davies *et al.* 2001). However, perhaps the most commonly applied indicator group occurring in the literature are bird communities.

2.3.3 - The value of birds

Birds are considered effective bio-indicators for assessing the impact of habitat modification upon biodiversity in its entirety for several reasons. They are considered the most simple of all taxonomical groups to census, as they are among the most well-known and researched of all taxa (Pimm 1998), and nearly all species can be identified in the field, either by sight or by vocalisation, which precludes the need to employ complex survey methodologies (Sutherland 2000) or to rely on taking physical specimens, which can raise logistical and ethical issues (Donegan 2000). Gardner *et al.* (2008) found bird communities cheaper and faster to survey than any other vertebrate group and many invertebrate groups, including other commonly used indicator taxon such as butterflies. Additionally, variations in bird communities have often been shown to be effective in predicting changes in other taxonomical groups, displaying good congruence on local scales (Schulze *et al.* 2004, Canterbury *et al.* 2000, Blair 1999, Lawton *et al.* 1998) and also on larger landscape scales; for example the global endemic bird areas defined by Stattersfield *et al.* (1998), which are sympatric with concentrations of endemism in other taxa. Further, it has been argued that birds represent a high profile 'flagship' group (Lawton *et al.* 1998) and the response of avifauna to habitat disturbance may have a disproportionate impact on public perception and conservation policy compared to most other taxonomical groups, at least from a Western perspective. This idea relates to sociological research by Schulz (1987), who found that people in Western countries displayed a more positive attitude towards birds than any other wildlife group, concluding that many people in society display a 'special affection' towards birds. This is reflected tangibly by the proliferation of many large national and international organisations directed towards the conservation of birds (Royal Society for Protection of Birds, International Council of Bird Preservation, Birdlife International etc.), equivalents of which do not exist for most other taxonomical groups.

Studies examining the relationship between avifauna and environmental disturbance are therefore of potentially high value, providing a proxy understanding of how biodiversity as a whole may respond to habitat modification and influencing conservation strategy to an extent that many less charismatic taxonomical groups may not be able to equal. However, these studies also have a more direct value related more intrinsically to the conservation of avifauna specifically. Bird species are among the most globally threatened higher taxa, with research showing them to be vulnerable to habitat modification due to their relatively small population sizes, poor dispersal potential and possessing high habitat specificity (Sodhi *et al.* 2004b, Turner 1996). If patterns of tropical deforestation persist, high incidences of avian extinctions are predicted. The International Council of Bird Preservation (2005) estimates that 11% of bird species are now threatened with extinction, and Birdlife International (2000) has made predictions that one in eight species of bird could be extinct by 2100, with the vast majority of these (93% of threatened forest birds) occurring in the tropics. Human activity is considered the primary causality for extinction risk for >99% of these species. It is therefore important to obtain a greater understanding of the relationships between bird communities and habitat modification for the sake of conserving bird communities at a taxa scale, as well as providing a tool for understanding biodiversity on a wider basis (Sodhi *et al.* 2004a).

2.4 - RESEARCH OPPORTUNITIES

While it has been shown that studies examining the relationships between habitat disturbance and avifaunal communities are important for biodiversity conservation, there are several areas where further research would be valuable. A series of research gaps meriting further investigation are described below:

2.4.1 – Poor records of base-line avifaunal data

One of the most basic limitations concerning the understanding of how bird communities in the poorly researched study sites examined in this thesis respond to habitat modification relates to the lack of base-line information relating to the bird species themselves. As discussed, birds represent one of the best understood and widely studied of all taxonomical groups, although basic information concerning species distributions in tropical ecosystems remains extremely limited. This is important, as an appreciation of the species present in a study area is essential for determining an overall understanding of species richness and community structure. It is also important for preparing researchers for the species they can expect to encounter during fieldwork (Bibby 2002). Detailed species inventories exist for some areas of the tropics; Brace (2007) has produced an excellent account of species records in Cusuco National Park, although an equivalent for the Lambusango forest is non-existent. A lack of species inventories in protected areas is very common in Wallacea, which remains one of the least-explored ornithological regions on Earth (Coates and Bishop 1997). Some islands here have not been surveyed for over 100 years, with current knowledge being based on the reports of Victorian-era specimen collectors (Trainor 2007). The only modern survey of Buton is a preliminary atlas survey conducted by Catterall (1997), and no account of avifauna in the Lambusango Forest specifically has ever been produced.

Basic information is also lacking for other aspects of avifaunal communities. A review of the most comprehensive field-guides available for species in Mesoamerican cloud forest (Howell and Webb 2005, Stiles *et al.* 1990) and Wallacean island avifauna (Coates and Bishop 1997, White and Bruce 1987) as well as species databases such as those produced by Birdlife International (2009) reveal that there is a lack of accessible, published data concerning very basic morphometric data for most of these regions' endemic bird species, such as the *Selasphorus ellioti* specimen shown in Plate 2.1. Typically the only information readily available for most species is body-length; accounts of other simple morphometric measurements such as mass and wing-length do not appear anywhere in accessible literature. This is of high significance, firstly as it is difficult to implement effective conservation management schemes if there is no understanding of the basic characteristics of the species to be conserved, and also because morphometric measurements have been shown to have strong links with a species' vulnerability to habitat modification. Numerous studies have demonstrated relationships between bird species' body mass and risk of local extirpation, ie: Boyer (2008), Sodhi *et al.* (2004a), Mckinney (1999). Description of basic morphometric data on poorly researched endemic species would therefore be of conservation value.

Plate 2.1: The Wine-throated Hummingbird ***Selasphorus ellioti****, endemic to cloud forest habitats in Northern Central America. Very little basic morphometric data has been published for this species, as is the case for many endemic cloud forest birds.*

2.4.2 – Insufficient methodological research

Related to the lack of understanding of basic descriptive data concerning endemic bird species in poorly researched forest types is a lack of understanding of how best to survey avifauna communities in these habitat types. Research into optimal methods for monitoring birds has been ongoing for over 50 years (Bibby *et al.* 2002) and two main methodological approaches have now attained predominance: mist-netting and point-counting (Bibby *et al.* 2002, Sutherland *et al.* 2000, Whitman *et al.* 1997). Mist-netting involves the capture of birds in fine mesh nets (Plate 2a) and began to be developed as a systematic methodology in the 1970s (Macarthur and Macarthur 1974, Ralph and Dunn 2004). Until the last few decades this was a preferred approach to monitoring bird populations due to ease of identification and lack of observer bias (Derlindati and Caziani 2005, Herzog *et al.* 2002). However in recent years point count methodology, a remote sampling technique that involves surveying a series of points and censoring avifaunal assemblages present based on birds seen and heard by the observer (Plate 2b), has become increasingly utilised as understanding of bird vocalisations has improved. This approach is now more widely used by ornithologists due to its greater time efficiency, higher rate of detection and ability to record birds occurring in a wider range of habitats than mist nets (O'Dea *et al.* 2004, Bibby *et al.* 2002, Whitman 1997).

Plate 2.2a: A mist-net line. (Author 2006).

Plate 2.2b: Surveyor conducting an acoustical point count (Author 2003).

Both these methods are subject to limitations based on the physical environment in which they are used, and while there have been several studies which compare the effectiveness of these two techniques in lowland tropical forest (Derlindati and Caziani 2005, Wang and Finch 2002, Blake and Loiselle 2001, Whitman *et al.* 1997) there has been no published research examining the comparative effectiveness of methodologies in many less-explored forest ecosystems with markedly different habitat structures. Tropical cloud forest is one such ecosystem. The structural form of these high altitude forests differs visibly from lowland tropical forests due to the unique biogeographical influences to which they are subject. Different precipitation patterns, reduced temperatures, steeper topography and impoverished soil types have facilitated the development of a floral structure highly distinct from that found in lowland forest (Letts and Mulligan 2005, Hamilton 1994). Trees here are on average shorter and possess higher stem density, and a higher proportion of the ecosystems biomass is found at low stratigraphic levels, with a typically dense undergrowth and high abundance of low-level epiphytes and bryophytes (Nadkarni 1995, Reyes and Cruz 1994, Hamilton 1994). This distinct floristic structure may influence the relative effectiveness of the two primary methods utilised to survey bird communities, as the thicker understorey and reduced canopy level may increase the proportion of species likely to be captured in mist-nets, while simultaneously limiting observer visibility and inhibiting the effectiveness of point-counts. Thus while point-counts have become increasingly prescribed as the optimal way to monitor bird communities, they may not necessarily be the most effective method of surveying cloud forest birds, and this merits further research.

2.4.3 - Lack of understanding of relationships between habitat disturbance and bird communities in poorly studied forest habitats

Further research also needs to be completed in examining the response of bird communities to anthropogenic disturbance on broader spatial scales, and in a wider range of tropical forest ecosystems than has been conducted so far. Although numerous studies have examined this research issue, they have largely been confined to areas of continental lowland forest (Barlow *et al.* 2007, Peh *et al.* 2005 Thiollay *et al.* 1997) or large island ecosystems (Lee *et al.* 2007, Sodhi *et al.* 2005, Waltert *et al.* 2004). This is of high importance, as so far very little research has been conducted on more spatially restricted, ecologically fragile forest ecosystems such as Mesoamerican cloud forest and small Wallacean islands. These poorly studied regions may display different response patterns to those described in other studies due to the higher incidence of endemism among avifaunal communities in these ecosystems, and more complex community interaction due to overlapping of zoogeographic zones (the Oriental and Australasian zones in Wallacea and Nearctic and Neotropical zones in Mesoamerica). Bird communities in these habitats are also subject to a theoretically increased vulnerability to disturbance due to their inhabiting small, isolated and fragmented ecosystems in concordance with Macarthur and Wilson's (1967) theory of island biogeography. Little research has also been conducted examining how endemic species in particular respond to disturbance in these biodiversity hotspots. This is highly relevant, as it has been theorised that endemic species possess greater vulnerability to habitat modification than wide-ranging species due to their possessing narrower ecological tolerances, such species being adapted to highly specialised, local habitat types (Jankowski & Rabenold 2007) and inhabiting spatially smaller and hence more vulnerable habitat ranges (Sutherland 2000, Pimm and Raven 1999). While the assumed vulnerability of endemic species has been discussed extensively in the literature, few studies have examined this quantitatively in the Wallacean or Mesoamerican hotspots, and none of which we are aware of have compared how the response of endemic bird species differ in these widely separated and biogeographically distinct regions.

2.4.4 – Insufficient research evaluating the success of undermanaged conservation schemes in poorly studied forest ecosystems

In addition to a limited understanding of how bird communities react to habitat disturbance in these poorly studied forest ecosystems, there also is a notable lack of research examining how successful existing conservation schemes have been in protecting these bird communities. Protected areas in the tropics, while increasingly numerous, have a noted tendency to be severely under-managed, even to the extent where their presence is purely theoretical, existing on paper but providing very little biodiversity protection in reality (Struhsaker *et al.* 2005). Virtually all parks and reserves protecting cloud forest ecosystems in Honduras possess characteristics of these 'paper parks', being severely under-staffed, under-funded entities lacking almost any kind of conservation-related infrastructure (Bonta 2005, Reyes and Cruz 2004, Powell and Palminteri 2001). The extent of 'paper parks' and their effectiveness in preserving biodiversity has been examined in several studies, some of which suggest they offer significant protection despite their non-managed status (Struhsaker *et al.* 2005, Bruner *et al.* 2001, Myers *et al.* 2000), while others indicate that their presence is no better or even worse than having no official protection at all (Curran *et al.* 2004, Liu *et al.* 2001, Kramer *et al.* 1997). While conclusions differ, these existing studies all show similar methodological characteristics. Each employs a broad-scale approach, examining a large number of parks on a regional or global scale primarily focussing on lowland forest sites, and each estimates the managemental effectiveness of these parks by indirect analysis, either through remote sensing data of forest cover change (Joppa *et al.* 2008, Struhstaker *et al.* 2005, Curran *et al.* 2004) or sociological questionnaire data (Bruner *et al.* 2001). There appears to be no existing research which has examined the effectiveness of paper parks utilising a single, detailed case study, or has utilised species-level data to assess this effectiveness. There also appears to have been no research examining the efficacy of paper parks are in conserving cloud forest species specifically. This is of high importance, as it has been proposed that the existing protected area network of cloud forest parks be expanded as part of the planned Mesoamerican biological corridor (Bubb *et al.* 2004). A study examining how effective these parks actually are in conserving biodiversity to a species level would therefore be valuable in assessing the viability of this proposed expansion.

2.4.5 - Poor understanding of habitat associations of birds in the study areas, and the role of spatial scale in understanding these associations

A final research gap involves examining the associations of these avifaunal communities with habitat structure at multiple spatial scales. Understanding the environmental variables which determine spatial distributions of bird species can be highly valuable in identifying priority areas for the focussing of conservation efforts. However, while several studies have demonstrated that spatially extensive analysis of habitat types can successfully predict broad, landscape-scale patterns of avian diversity (Gillespie and Walter 2001, Johnson *et al.* 1998), few studies have examined how habitat variations on smaller ecosystem scales are associated with bird community composition at an α-diversity level (Cleary *et al.* 2005), particularly within the study areas examined within this thesis. This lack of understanding may inhibit the effectiveness of current conservation strategies within these regions, as several studies have suggested that local variation in habitat can be of equal or greater importance as landscape scale habitat patterns in governing spatial distribution of species (Herrando and Brotons 2002, Potts *et al.* 2002). There is also an unclear appreciation of how spatial scales of data aggregations should best be used to ensure accurate representation of avian habitat associations. While it has long been recognised that spatial scales of analysis have an important influence on how researchers view environmental responses in ecological communities (Jansson 2002, Hamer and Hill 2001, Noss 1990), there has been almost no research examining how this affects congruence between bird communities and habitat variables within the biological 'hotspots' examined in this thesis.

2.5 - Summary

This literature review has detailed a series of research gaps that merit further investigation, and each of the subsequent analysis chapters will examine one or more of these research gaps:

- Baseline descriptive data providing species inventories and morphometric measurements are presented in Appendix 1 'The avifauna of the Lambusango Reserve and vicinity' and Appendix 2 'Morphometric data for Mesoamerican cloud forest bird species'.

- The effectiveness of different methodological techniques is explored in Chapter 3 'An assessment of the effectiveness of two methods in describing a Neotropical cloud forest bird community'.

- Responses of bird communities in Wallacea and Mesoamerica are examined in Chapter 4 'Impacts of tropical forest disturbance upon avifauna on a small island with high endemism: implications for conservation' and Chapter 5 'The effectiveness of a Mesoamerican 'Paper park' in conserving cloud forest avifauna'. Differential responses observed in these communities are examined and considered in Chapter 7 'Differential vulnerabilities of range-restricted avifauna on a Wallacean Island and in Mesoamerican cloud forest: the influence of ecological and biogeographical factors?'

- The extent to which an undermanaged protected area can effectively conserve avifauna is evaluated in Chapter 5.

- Habitat associations of a poorly described avifauna, and the influence of spatial scale on assessing these associations, are examined in Chapter 6 'Habitat associations of an insular Wallacean avifauna: a multi-scale approach for biodiversity proxies'.

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CHAPTER 3 - AN ASSESSMENT OF THE EFFECTIVENESS OF TWO METHODS IN DESCRIBING A NEOTROPICAL CLOUD FOREST BIRD COMMUNITY

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Orange-billed Sparrow (*Arremon aurantiirostris)* netted in Cusuco National Park

3.1 - SUMMARY

Mist-netting and point-counting are the two most commonly used techniques for surveying Neotropical avifauna communities, although their effectiveness remains poorly understood in tropical montane cloud forest. This paper seeks to determine how best to conduct bird surveys in this distinctive ecosystem by comparing the effectiveness of these two methodologies in the Parque Nacional Cusuco, North-West Honduras. Mist netting was conducted at 26 sites, with point counts being conducted at 126 sites. Neither technique succeeded in providing a wholly accurate description of avifaunal assemblages, with mist netting and point counts detecting 37.5% and 59.3% of all avian species respectively, in comparison with our preliminary checklist of the area. However, results indicate point-counts as more effective overall, detecting a greater sum of species (124 species compared to 78), being markedly more time-efficient and detecting a wider range of avian sub-groups. Both methods in conjunction still failed to detect 27.8% of species on the preliminary checklist. Any survey aiming to accurately survey all cloud forest species would therefore need to incorporate a wide range of integrated methodological techniques.

Key words: Cloud forest, mist nets, point counts

3.2 - INTRODUCTION

The need for effective survey methods in monitoring Mesoamerican bird communities has become increasingly important as growing anthropogenic pressures cause greater conservation challenges. Nearly 80% of original vegetation cover within the Mesoamerican biodiversity 'hotspot' (Myers *et al.* 2000) has been lost or modified and remaining intact forest continues to be lost at an estimated rate of 0.8 – 1.5% per annum (Food and Agriculture Organisation 2006, Achard *et al.* 2002). If current disturbance patterns continue high extinction rates in bird species are predicted (Conservation International 2007, Brooks *et al.* 2002, Stattersfield *et al.* 1998). Effective conservation schemes are needed to safeguard regional avifauna, but to implement these extensive monitoring is required to ascertain how bird communities respond to environmental disturbance. At present, however, a full understanding of the effectiveness of different survey methods available to ornithologists is incomplete.

Mist netting and point-counts represent the most frequently utilised techniques for surveying avifaunal communities in the Neotropics (Sutherland *et al.* 2004, Whitman *et al.* 1997). Mist netting involves the sampling of avifaunal communities by capturing birds in fine mesh nets, and has been developed as a systematic methodology for over 30 years (Ralph and Dunn 2004, MacArthur and MacArthur 1974). Point-counting is a sampling technique that involves surveying a series of points and taking a census of avifaunal assemblages based on birds seen and heard by the observer and has become increasingly viable as a methodology through a better understanding of bird vocalizations.

These two methodological approaches are subject to well-defined limitations. Mist netting is restricted by poor time-efficiency, reliance on external factors such as time of day, weather, and the behavioural characteristics of different bird species, and its limited capacity to survey components of avifaunal communities rarely found beyond the nets' capture range of 3-5m above ground (Wang and Finch 2002, Rappole *et al.* 1998, Remsen and Good 1996). Point counts are similarly limited by external environmental factors, as well as from a necessarily heavy reliance on the skill and experience of individual observers, the increased probability of recording individual birds multiple times, and an ineffectiveness in recording the presence of rare species. Furtive birds which rarely vocalise and certain other avifaunal groupings such as nocturnal species, raptors and swifts (Shiu and Lee 2003, Blake and Loiselle 2001, Bibby *et al.* 2002, Remsen and Good 1996) are also poorly recorded by point count surveys.

Several studies have attempted to compare and assess the relative effectiveness of these two methodologies (Derlindati and Caziani 2005, Wang and Finch 2002, Blake and Loiselle 2001, Whitman *et al.* 1997). However, these have largely focussed on lowland forest ecosystems and there remains a poor appreciation of how best to employ survey methods in less explored areas such as tropical cloud forest.

Tropical montane cloud forest is a rare ecosystem of high conservation importance due to it supporting a rich biodiversity and a high prevalence of endemic organisms, in addition to the provision of a range of ecological services (UNEP 2006, Powell and Palminteri 2001). Bird communities in particular are characterised by a high prevalence of endemic species; 10% of all globally range restricted species can be found in cloud forest ecosystems (Stattersfield *et al.* 1998). Cloud forests also provide an important refugia habitat for many endangered species marginalised by destruction of lowland forest habitats (Aldrich *et al.* 1997).

Until recently the relative inaccessibility of most cloud forest ecosystems ensured their ecological integrity, but these habitats are now becoming increasingly vulnerable to exploitation due to expanding regional infrastructure, demographic pressures and inadequate governmental protection (Powell and Palminteri 2001, Aldrich *et al.* 1997). Cloud forest is now disappearing with greater rapidity than the region's remaining lowland forests

(Solorzano *et al.* 2003) which has severe implications for local avifauna.

Extensive monitoring of cloud forest avifaunal communities is required to inform future conservation policy. However few studies have been conducted here to determine the most appropriate survey methods. This is important, as cloud forests possess characteristics which may influence the relative effectiveness of point counts and mist nets beyond that described in previous studies.

Tropical cloud forest occurs in an altitudinal band ranging from between 1000—4000m (Powell and Palminteri 2001) and the geographical conditions at these altitudes have created an ecosystem with very distinct structural form. Precipitation is high, averaging 2000—4000mm per year (Powell and Palminteri 2001) with most of this precipitation supplied by enveloping cloud banks. This persistent cloud cover leads to heavy saturation of all vegetation strata from canopy to forest floor, reducing solar radiation and creating an almost permanently saturated canopy, which suppresses evapotranspiration, giving rise to a very moist, humid environment (Letts and Mulligan 2005, Hamilton 1995). This, in combination with reduced temperatures, steeper topography, nutrient-poor soils and higher exposure, has given rise to a very distinct floral structure. Canopy level trees are reduced in stature, with more compact crowns and higher stem density than those found in lowland forest. There is also a greater proportion of biomass at lower levels in the ecosystem, with heavier undergrowth and greater abundance of bryophytes, lichens, bromeliads and other epiphytes (Nadkarni *et al.* 1995, Hamilton 1995, Reyes and Cruz 1994). This distinctive vegetation structure has given rise to an equally distinguished avifaunal community which differs significantly from lowland bird assemblages in trophic and taxonomic composition (Renjifo *et al.* 1997). These communities may therefore be expected to respond differently to survey efforts than has been described in other forest ecosystems; specifically, denser undergrowth and reduced tree stature may increase the proportion of species within mist net capture range, while simultaneously limiting visibility which could inhibit the effectiveness of point counts. Thus the comparative effectiveness of mist netting to point counts may be greater than described in other ecosystems.

In this paper we aim to critically assess the effectiveness of these two commonly employed methodologies in surveying bird communities in this poorly understood ecosystem, testing the hypothesis that mist netting will prove to be comparatively more effective than described by studies in lowland forest sites. The findings of this assessment will then be used to prescribe the most effective approach for monitoring cloud forest avifauna communities.

3.3 - METHODS

3.3.1 - Study area

Research was conducted over an eight week period between June – August 2007 in the Parque Nacional Cusuco, Departamento Cortez, North-West Honduras (15°29.8'—15°32.1'N / 88°13.0—88°26.3' W) (See Figure 1.7 in Introduction). The park represents a 23,440 ha area of tropical montane cloud forest divided into a 7,690 ha core zone with extensive protective legislation and an encompassing 15,750 ha buffer area where land-use is controlled (Figure 3.1). Elevation ranges used in this study sites varied from 700 m—2,200 m above sea level (Lenkh 2005); these elevations occupy the lower altitudinal bands of montane cloud forest as described by Powell and Palminteri (2001). This altitudinal range is a high research priority because avian species richness is higher and anthropogenic pressures are greater here than in montane forests of higher elevation (Navarro and Aldolfo 1993). Climatic data for the park can be found in Figure 1.9 in the Introduction.

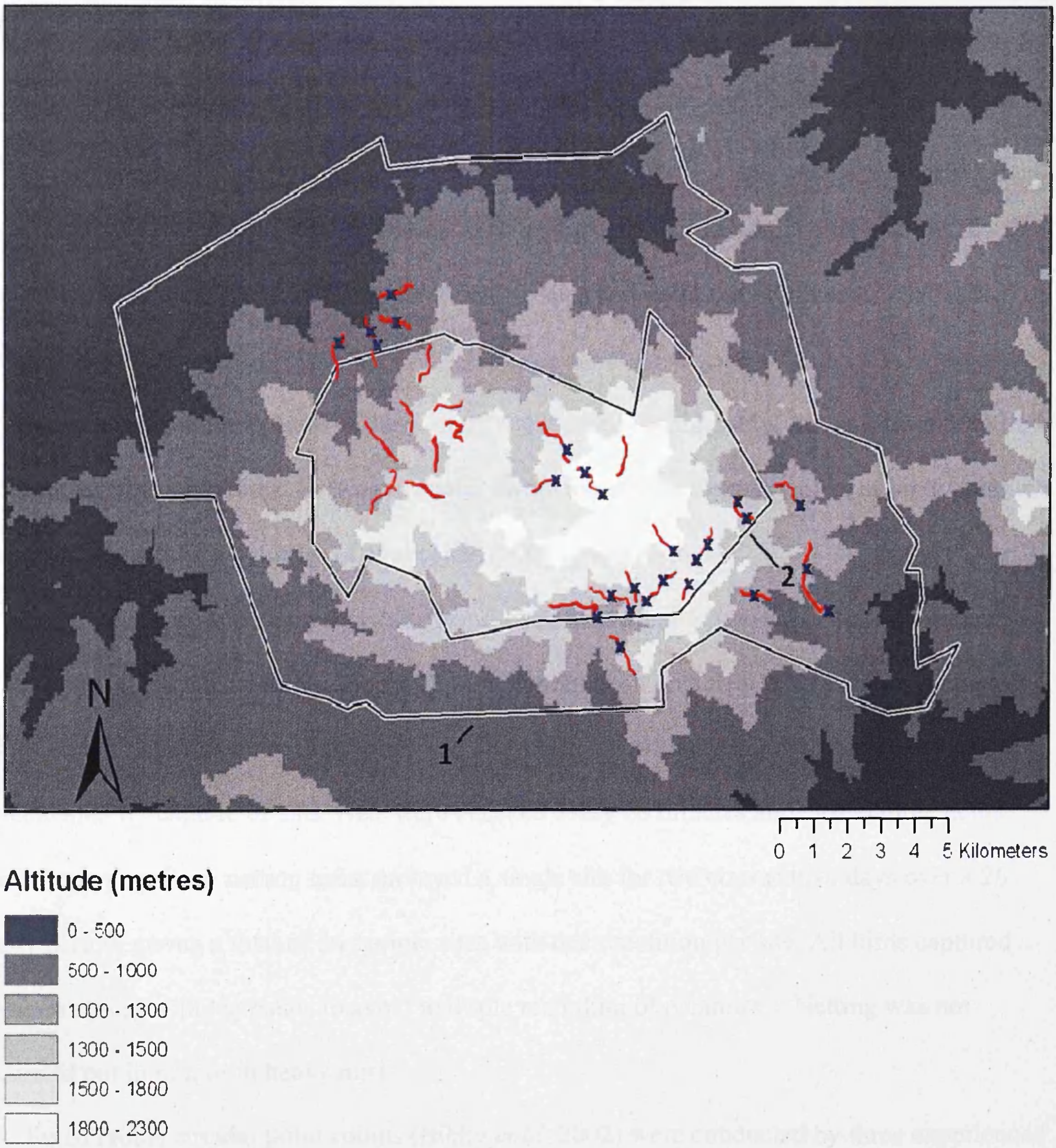

Figure 3.1 – Location of point-count and mist-net study sites within the border of Cusuco National Park, Honduras. Point-count transects are represented by red lines. Mist-netting sites are represented by blue crosses.

3.3.2 - Bird surveys

Bird surveys were conducted along 28 linear transects throughout the park; twelve located in core zone primary forest, eight in the edge forest ecosystems of the buffer zone and eight on the transitional zone between the buffer and core. Each transect contained between four and seven study sites with a distance of at least 200 m separating each site. All sites along each transect were used for point counts, with a single site per transect being sampled by the mist netting teams. The location of mist-netting sites and point-count transects are detailed on Figure 3.1.

Vegetation structure at each of these study sites varied considerably, ranging from 30m high *Pinus oocarpa* pine forest to Bosque enano dwarf forest with a canopy of <2m high, although canopy height at the majority of study sites (> 80%) was <15m.

Mist netting was conducted by two teams, each consisting of two experienced banders. These teams each used three 2.6 m x 20 m x 36 mm mesh mist nets. Mist nets were opened half an hour after dawn each morning (05:30 h). This half-hour delay was imposed to reduce accidental by-capture of bats. Nets were checked every 20 minutes and closed three hours after opening. Each netting team surveyed a single site for two consecutive days over a 26 day period, giving a total of 26 sample sites with one repetition per site. All birds captured were marked with leg bands to avoid multiple recording of recaptures. Netting was not carried out in rain or in heavy mist.

Fixed radius circular point counts (Bibby *et al.* 2002) were conducted by three experienced ornithologists familiar with Neotropical avifauna vocalisations, with each observer working independently across three different transects. Between four and seven sites were surveyed along each transect, and each transect was repeated three times on consecutive days, giving a total of 377 samples across 126 sites. Sampling was conducted each morning from dawn (05:30 h) to 09:30 h, this being the most efficient time-period for conducting point counts due to bird detectability being high and most species being fairly sedentary (Marsden 1999, Wunderle 1994, Blake 1992). Surveying commenced immediately upon reaching each sample site with no settling-in period, allowing the recording of birds which had been disturbed by the surveyors and thus increasing the number of contacts made at each point (Lee and Marsden 2008). Each point count lasted for 10 minutes as sampling periods of this length have a lower chance of recording individuals multiple times than longer counts while still detecting a high percentage of species present at the points. (Lynch 1995, Waide and Wunderle 1987). All species seen and heard within a 50 m radius were recorded, excluding those flying above the canopy as these may wandering or passage birds not associated with cloud forest habitats. A 50 m radius was used to prevent overlap with other count points and to reduce bias against smaller species, which are inaudible beyond this distance.

In addition to these two methodological approaches, a checklist of species recorded in the park consisting of all species detected by either systematic methodology or sighted opportunistically was also kept for the 8-week study period. This checklist of species represents 280 person days (> 2240 person hours) compared to 26 mornings spent netting (468 netting hours or 416 person hours, including an hour each morning to raise and take down nets) and 63 person hours point-counting. It should be acknowledged that this checklist, although based on a survey effort much greater than either standardised methodology, must be regarded as a preliminary list. The survey effort represented by our checklist is fairly small compared with comprehensive surveys in better-studied areas of the Neotropics (Whitman *et al.* 1997, Bierregard 1990) and, being confined to a single season, will in likelihood under-represent certain groups of birds such as latitudinal and altitudinal migrants and uncommon 'wandering' species (Remsen 1994).

3.3.3 - Statistical analysis

Statistical analyses largely follow those employed by Whitman *et al.* (1997) to ensure consistency of results and allow meaningful comparisons between our study area and a lowland forest site. The total number of species detected by each method was compared using a Sign test (Zar 1999). Three non-parametric species estimators (ACE, Chao 2, and MMMeans) were also calculated for each method using the software package EstimateS (Colwell 2006), these being considered appropriate estimators for tropical bird community richness (Herzog *et al.* 2002). These estimators were based on data aggregations from all sampling points together and calculated using 50 randomization runs. The mean value of these estimators was taken as an estimation of the total number of species present predicted by each sampling technique, which was compared to the checklist. Mean values of the three estimators were used as the effectiveness of different estimators varies between data sets (Walther and Moran 1998).

The efficiency of each method in detecting species was evaluated by the construction of species effort curves, comparing the number of person hours with the number of species detected for each method. The effectiveness of both methods in detecting different sub-groups of the avifaunal community was also examined. Groupings categories were designated after Whitman *et al.* (1997) and were based on family, abundance, body-size categories, diet, height strata, feeding guilds and habitat. Family status was based on Clements (2007). Abundance categories were based on those described by Desante and Pyle (1986) and Whitman *et al.* (1997). These categories were: very rare (detected <1% of days): rare (1—10% of days): uncommon (10—50% of days): common (1—90%) and abundant (detected > 90% of days). Body size categories were based on those utilised by Whitman *et al.* (1997) with bird species being grouped into small (<22.5g), medium (22.5 – 51g) and large (>51g) categories based on Stiles *et al.* (1989) and our own field measurements. Birds were assigned to diet, height strata, feeding guild and forest type categories after Howell and Webb (2005), Karr *et al.* (1990), Stiles *et al.* (1989) and the authors' own field observations. Differences in grouping were statistically compared using a χ^2 squared test.

Compositions of avifauna were also examined at an individual point level in order to take into account different sample sizes and allow a direct comparison of methods. All netting sites were statistically compared with corresponding point-counts conducted at those sites. The numbers of species found at individual points were compared using a paired t-test (Zar 1999). The numbers of species in each of the previously defined grouping categories were also compared using a series of paired t-tests. Differences in community compositions were compared using a Jacard's Index, calculated by dividing the number of species detected at each point by both techniques with the number of species at each point detected by either technique (Whitman *et al.* 1997). Where appropriate, standard deviations were expressed as ± values of averages.

3.4 - RESULTS

A total of 3028 individual birds were recorded in the sampling effort, with 513 individual birds of 78 species being captured in mist nets and 2515 individuals from 124 different species being recorded by the point counts. The majority of point count contacts were detected by sound (88%), with 12% being detected visually. A total of 209 species were recorded on the checklist. 7.9% of contacts in the point count surveys were unidentified and excluded from analysis. 58% of these unidentified contacts were hummingbird species. 100% of birds caught in the mist nets were identified.

Although a substantial overlap of species detected occurred between the two approaches, each method managed to record a substantial number of species that the other failed to detect. Mist netting recorded 25 species which were not recorded by point counts, including two families which were absent from the counts, while point counts recorded 71 species which were not detected by mist nets, including 13 families (Table 3.1). Both methodologies failed to detect all species recorded on the total checklist, with nets and points detecting 37.5% and 59.33% of species respectively. However, point counts detected significantly more species than mist nets (Sign test $p = <0.05$). Non-parametric species estimators also predict point-counts to detect a greater number of the total species checklist than mist nets; 157 species compared to 99 (Table 3.2).

Table 3.1 - Summary of families and number of species detected by mist netting and point counts, as well as both or neither methodologies, in Cusuco National Park, North-West Honduras. Families based on Clements (2007).

Family	**Common name**	**Number of species only captured in nets**	**Number of species only recorded on counts**	**Number of species recorded by both methods**	**Number of species recorded by neither method**
Tinamidae	Tinamous	0	3	0	0
Cathartidae	New-World vultures	0	0	0	3
Accipitridae	Raptors	0	2	0	7
Falconidae	Falcons	0	1	1	3
Cracidae	Cracids	0	4	0	0
Eurypygidae	Sun-bittern	0	0	0	1
Phasianidae	Gamebirds	0	2	0	0
Columbidae	Pigeons	1	5	1	2
Psittacidae	Parrots	0	4	0	0
Cuculidae	Cuckoos	0	1	0	3
Strigidae	Owls	0	2	0	2
Caprimulgidae	Nightjars	0	0	0	1
Apodidae	Swifts	0	2	0	2
Trochilidae	Hummingbirds	9	0	9	1
Trogonidae	Trogons	0	3	0	1
Alcedinidae	Kingfishers	0	0	0	1
Motmotidae	Motmots	1	2	1	0
Ramphastidae	Toucans	0	2	0	1
Picidae	Woodpeckers	0	5	1	3
Dendrocolaptidae	Woodcreepers	1	2	2	3
Furnariidae	Ovenbirds	1	0	5	1
Formicariidae	Antbirds	0	2	1	0
Tyrannidae	Tyrant-Flycatchers	1	4	4	5
Cotingidae	Cotingas	0	1	0	2
Pipridae	Manakins	1	0	1	0
Troglodytidae	Wrens	0	0	5	2
Turdidae	Thrushes	0	2	4	0
Cinclidae	Dippers	1	0	0	0
Corvidae	Crows	0	3	0	0
Sylviidae	Old World warblers	1	0	0	0
Coerebinae	Bananaquit	0	0	1	0
Thraupinae	Tanagers	3	5	4	7
Emberizinae	American Sparrows	1	3	5	0
Cardinalinae	Grosbeaks	1	2	1	0
Parulinae	New-World warblers	1	2	4	2
Vireonidae	Vireos	1	1	1	1
Fringillidae	Finches	0	0	0	1
Icteridae	Blackbirds	0	5	0	3

Table 3.2 - Non-parametric species estimators for mist-netting and point count survey efforts in Cusuco National Park, North-West Honduras. ACE, CHAO2, and MMMeans are non-parametric species estimators (Colwell 2006).

Parameters	Mist nets	Point counts
Sample size	26	377
Species observed	78	124
Individuals observed	504	2515
ACE	93	165
Chao2	91	173.3
MMMeans	111.6	131.8
Average of species richness estimates	**99**	**157**

Point-counting proved to be a significantly more efficient method of detecting bird species than mist netting (Figure 3.2). For nets, the accumulation of new species detected began to level off at around 70 species after 250 person hours, with very few new species yielded in the next 200 person hours. Point counts, in contrast, recorded 125 species after just 50 person hours, and while the accumulation curve had begun to level out after this, it is likely that further survey effort would yield further species detections.

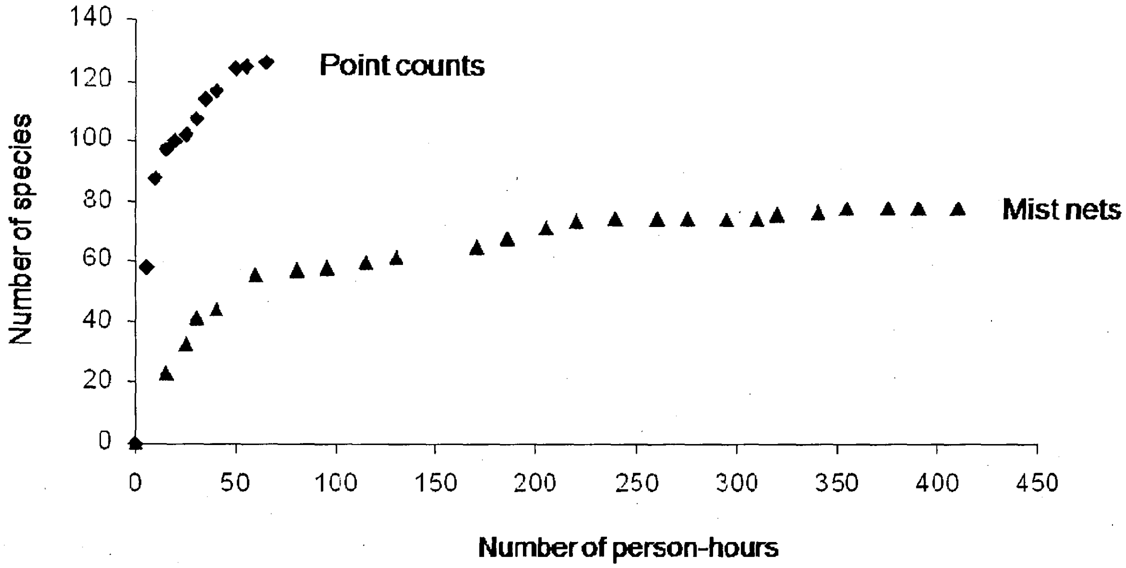

Figure 3.2 - Cumulative number of species detected by mist netting and point counts with increasing survey effort.

Point counts were more effective overall in surveying most avifaunal grouping (Table 3.3), detecting a greater proportion of bird families than netting (84.2% compared to 55.3%) as well as identifying significantly higher proportions of common and uncommon species, large birds, canopy-level species and all dietary groups except nectarivores. Point counts were also significantly more effective at detecting five of the seven feeding substrate groupings. Mist nets were considerably more limited in their efficacy, being significantly better at detecting only nectarivores and water feeders, and marginally more effective at detecting rare and very rare species, small birds and species primarily occurring at shrub level. Netting was entirely unsuccessful in recording aerial and canopy level birds (0% detected) as well as all large birds, raptors (defined in this study to include the families Accipitridae, Falconidae, Cathartidae and Strigidae) and ground-level species (each group < 10% detected).

Table 3.3 - Proportion of species in different categories detected by mist netting, point counting, both methods and neither method at all points in comparison to the preliminary check-list of birds of Cusuco National Park, North-West Honduras. Bracketed figures show actual species counts.

	Group	**Mist netting**	**Point-counting**	**Both**	**Neither**	**Checklist**
Family	Proportion detected	(21) 55.3%	(32) 84.2%	(18) 92.1%	(4) 10.5%	38
Abundance ($\chi^2 = 5.6, p = 0.2$)	Abundant	(10) 76.9%	(13) 100%	(13) 100%	(0) 0%	13
	Common	(23) 41.8 %	(46) 83.6%	(49) 89.1%	(7) 12.7%	55
	Uncommon	(20) 33.3%	(39) 65 %	(49) 81.7%	(13) 21.6%	60
	Rare	(18) 37.5%	(17) 35.4%	(28) 58.3%	(20) 40.4%	48
	Very rare	(5) 16.6%	(4) 13.3%	(9) 33.3%	(20) 66.6%	30
Body size ($\chi^2 = 25.8,\ p = <0.05$)	Large	(7) 8.5%	(51) 62.2 %	(56) 68.3%	(28) 34.1%	82
	Medium	(21) 38.9%	(28) 51.9%	(36) 66.6%	(18) 33.3%	54
	Small	(45) 63.4%	(41) 57.8%	(56) 78.9%	(15) 21.1%	71
Height strata ($\chi^2 = 26.4, p = <0.05$)	Air	(0) 0%	(2) 50	(2) 50	(2) 50	4
	Canopy	(0) 0%	(25) 59.5%	(25) 59.5%	(17) 40.5%	42
	Mid-storey	(22) 32.8%	(40) 59.7%	(46) 68.7%	(21) 31.3%	67
	Shrub	(53) 61.6%	(51) 59.3%	(70) 81.4%	(16) 18.6	86
	Ground	(1) 11.1%	(7) 77.8%	(8) 88.9%	(1) 11.1%	9
Diet ($\chi^2 = 18.9, p = <0.05$)	Carnivore/Carrion	(1) 4.4%	(5) 21.7%	(7) 30.4%	(20) 87%	23
	Fruit/seeds	(6) 20%	(23) 76.7%	(26) 86.7%	(5) 16.7%	30
	Insectivores	(31) 45.6%	(40) 58.8%	(48) 70.6%	(20) 29.4%	68
	Insects and fruits	(17) 33.3%	(31) 60.8%	(12) 70.6%	(15) 29.4%	51
	Nectarivores	(20) 87%	(11) 47.8%	(21) 91.3%	(2) 8.7%	23
	All foods	(2) 18.2%	(10) 90.9%	(11) 100%	(0) 0%	11
Feeding substrate ($\chi^2 = 17.2. p = <0.05$)	Water	(1) 33%	(0) 0%	(1) 33%	(1) 33%	3
	Air	(0) 0%	(3) 37.5%	(3) 62.5%	(5) 62.5%	8
	Branch	(12) 19.7%	(40) 65.6%	(44) 72.1%	(17) 27.9%	61
	Trunk	(6) 31.6%	(11) 57.9%	(13) 68.4%	(6) 31.6%	19
	Live foliage	(45) 60%	(46) 61.3%	(64) 85.3%	(11) 14.7%	75
	Dead foliage	(11) 61.1%	(14) 77.8%	(15) 83.3%	(3) 16.7%	18
	Ground	(1) 4.5%	(9) 40.9%	(9) 40.9%	(13) 59.1%	22
Forest type ($\chi^2 = 4.4, p = 0.112$)	Core	(23) 40.4%	(44) 77.2%	(51) 95.5%	(7) 12.3%	57
	Edge	(17) 21.3%	(35) 43.8%	(44) 55%	(38) 47.5%	80
	Both	(37) 53.6%	(41) 59.4	(54) 78.3%	(15) 21.7	69

While results demonstrate that point-counting is the more time-efficient methodology overall, detecting a wider range of species in considerably less time, the use of both methods combined proved more effective than either technique in isolation. Both methods together detected > 92% of all avian families, compared to just 84.2% by point-counting alone, and 23 of the 29 avian subgroups yielded a higher proportion of species when both methods were used in conjunction. Both methods combined also achieved a > 80% detection rate of species in 11 sub-groups, with similar proportions being obtained in just three groups for point counting alone and only a single group for mist netting alone. This combination of methods still failed to detect 27.8% of species on the preliminary checklist. Neither technique was effectual in detecting scarce species, with 40.4% of rare and 66.6% of very rare species on the checklist remaining undetected by both methods. Both techniques were also ineffective at detecting raptors (75% of species undetected) as well as aerial and water feeders (62.5% and 66% undetected respectively). The proportion of total species detected in edge forest environments was also poor (47.5% undetected).

Individual points. Point counts detected significantly more species than mist nets at individual points, with a mean of 9.3 ± 6 std species being recorded per point for nets, in comparison to 12.9 ± 3.9 std species per point for counts (paired t-test $t = -2.785$, $p < 0.05$).

The mean proportion of species in each category detected at each of the 26 individual points (Table 3.4) indicates again that point counting is the more effective methodology overall, although the differences in efficacy were not as pronounced as in the sum of points analysis. Point counting still detected marginally more species per point and category than mist netting (5.6 species compared to 4.4 species) but detected a substantially higher proportion of species in only 10 sub-groups, compared to 19 in the sum of points analysis. At an individual points scale, mist netting proved significantly more effective in detecting very rare species, small birds, shrub-level species, nectarivorous birds and species dependent on live foliage feeding substrates; a more successful performance in five sub-groups, compared to only two groupings from the sum of points analysis.

As with the sum of points, a combination of both methods together was more successful in describing avian communities than either method alone, with 16 of the 29 sub-groups detecting a substantially higher proportion of species than either method in isolation, and another nine sub-groups showing minor increases in detection rates. The rate of detection per point for abundant species, small birds, shrub-level species, species which feed on live and dead foliage and species restricted to mature forest was particularly improved by combining both methods. Neither method, nor both methods together, were particularly successful in surveying the same avian sub-groups defined as poorly represented by the sum of points analysis, such as rare species, raptors and aerial and water feeders. The mean similarity (Jacard's index) between points was low ($t_{25} = 2.373$, $P < 0.05$) with both techniques sharing only a mean of 9.6% ± 8.9 of total species caught. This indicates only a small overlap in the species being detected by the two methods.

Table 3.4 - Mean proportion of species in different categories detected per individual point for mist netting, point counts and both methods in Cusuco National Park, North-West Honduras. ± represents 1 standard deviation. Underlined values indicate a significantly higher mean for species detected by that method (paired t-test p = <0.05).

		Mean ± SD number of species		
Group		**Mist netting**	**Point counting**	**Both**
Total		4.42 ± 2.81	5.64 ± 1.63	9.17 ± 3.1
Abundance	Abundant	18.04 ± 14.74	**32.54 ± 17.17**	42.89 ± 20.31
	Common	6.72 ± 6.17	9.73 ± 6.98	15.47 ± 10.14
	Uncommon	3.15 ± 3.04	2.96 ± 2.13	5.72 ± 3.17
	Rare	2.32 ± 3.01	0.56 ± 1.11	2.88 ± 3.33
	Very rare	**1.41 ± 2.14**	0 ± 0	1.41 ± 2.14
Body Size	Large	0.74 ± 1.10	**7.16 ± 3.69**	7.66 ± 3.77
	Medium	3.63 ± 2.38	4.45 ± 2.53	7.06 ± 3.25
	Small	**8.72 ± 6.23**	4.75 ± 2.51	11.91 ± 6.41
Height strata	Air	0 ± 0	0.96 ± 5	0.96 ± 5
	Canopy	0 ± 0	**6.41 ± 2.76**	6.41 ± 2.76
	Mid-storey	2.06 ± 2.31	**5.67 ± 2.11**	7.16 ± 2.76
	Shrub	**8.79 ± 5.41**	5.44 ± 3.22	12.67 ± 6.22
	Ground	0.43 ± 2.18	4.27 ± 6.35	4.7 ± 6.42
Diet	Carnivore/carrion	0.17 ± 0.85	1 ± 1.86	1.17 ± 1.97
	Fruit and seeds	1.54 ± 2.7	**7.43 ± 5.75**	8.58 ± 6.54
	Insectivorous	4.58 ± 3.15	5.1 ± 2.13	8.48 ± 3.67
	Insects and fruits	3.78 ± 2.97	**7.62 ± 3.41**	10.02 ± 3.74
	Nectarivorous	**14.18 ± 11.42**	1.29 ± 2.65	14.66 ± 12.07
	All	1.4 ± 3.35	**12.94 ± 10.96**	13.64 ± 10.98
Foraging substrate	Water	1.27 ± 6.47	0 ± 0	1.27 ± 6.47
	Air	0 ± 0	0.96 ± 3.4	0.96 ± 3.4
	Branch	1.34 ± 1.93	**8.02 ± 2.7**	9.1 ± 3.16
	Trunk	0.81 ± 1.94	3.24 ± 3.96	3.84 ± 4.35
	Live foliage	**8.75 ± 5.84**	5.17 ± 3.18	12.33 ± 6.41
	Dead foliage	8.13 ± 6.53	8.34 ± 5.72	14.11 ± 7.9
	Ground	0.34 ± 1.21	2.02 ± 3.42	2.19 ± 3.65
Habitat	Mature	4.44 ± 3.75	**9.02 ± 4.36**	12.65 ± 6.86
	Edge	2.02 ± 2.9	**3.75 ± 3.91**	5.29 ± 5.67
	All	7.14 ± 4.87	6.02 ± 4.28	11.66 ± 5.69

3.5 – DISCUSSION

The results of this study demonstrate that point counts can be generally regarded as more effective and efficient than mist-nets for describing cloud forest avifaunal communities; a similar finding to that concluded by studies in other forest ecosystems (Stiles and Rosselli 1998, Whitman *et al.* 1997). The aggregate analysis of the sum of points demonstrated that mist netting was found to be highly limited in the number of species caught, and species that were detected tended to be weighted towards discreet avian groupings, such as small understorey birds. Entire body-size and feeding-guild groupings were virtually absent from the netting surveys. Analysis of individual points suggested a less marked difference in the effectiveness of both techniques, most likely because of the smaller survey effort of the point counts, although point counting still managed to detect significantly more species in 10 of the 30 defined categories, with high netting effectiveness being limited to the same sub-categories as those described by the sum of points analysis. This is in concordance with the limitations of netting described by Gram and Faaborg (1997), Whitman *et al.* (1997), and Karr (1981). These results would therefore suggest that mist netting alone cannot be considered an appropriate method of surveying avifaunal communities. Indeed, the results of this study would concur with Bibby *et al* (2002), Stiles and Rosselli (1998), Bierregard (1990), and MacArthur and MacArthur (1974), who predict that netting surveys will usually be restricted to detecting around 40–50% of total bird species in a forest ecosystem.

The discrepancy in effectiveness between the two methodologies in cloud forest ecosystems is even greater than that found by studies in lowland forest sites. Blake & Loiselle (2001), for example, found mist-nets detected 62% of species on their checklist, compared to 68% by point-counts, and reported 34 species caught in nets but not detected by counts, compared to 53 species observed in counts that were not caught: a much smaller discrepancy in favour of nets than our results suggest. A less evident divide between the effectiveness of the two methodologies was also reported by Derlindati & Caziani (2005), Wang and Finch (2002), Pagen *et al.* (2002), and Rappole *et al.* (1998), although it should be noted that this last study focussed on migrant birds which may be more susceptible to mist-net capture than forest bird communities in their entirety (Wallace *et al* 1996).

Results therefore suggest that the denser vegetation and reduced canopy height inherent in cloud forest do not increase the relative effectiveness of mist-netting as hypothesised. However, although mist netting may not show an improvement in effectiveness when compared to point counts, the proportion of the avifaunal community captured was higher than studies in lowland ecosystems have reported, capturing 78 species (37.5% of checklist) compared to the 58 species (28.6% of checklist) described by Whitman *et al.* (1997). This disparity could result from the differential habitat structure inherent in cloud forest ecosystems as discussed. It should also be noted that, despite detecting fewer species overall, netting was shown to be more effective for monitoring certain sub-groups of cloud forest bird communities. The small overlap in species detected by both techniques, as demonstrated by the Jacard's index community comparison, indicates that mist netting regularly captures species that point-counting fails to detect.

While this study indicates point counts to be a more time-efficient methodology than nets, the person-hours calculated to demonstrate this assumed that two people were needed for running each line of mist nets compared to just a single observer needed for point counts. Two banders per netting line were considered necessary in this study to carry equipment, set nets up quickly, and ensure captured birds were extracted as fast as possible to minimise stress - particularly important when large numbers of birds were caught in a short period of time (North American Banding Council 2001, Gaunt and Oring 1999). Two banders were also needed to deal with difficult extractions and to allow simultaneous sample processing and data recording. It might have been possible, however, for a single skilled bander to run each netting line, which would considerably reduce the disparity in time-efficiency between the two methods. However, this would make the field-work considerably more difficult, could increase stress and mortality among captured birds, and, even with person-hours halved, mist-netting would still be markedly less time-efficient in detecting species than point counts.

An additional consideration for the time efficiency curves is that the results do not take into account that the high level of observer skill required to use this method reliably takes at least several months of local experience to attain, an issue that is not applicable to mist-nets (although banders also must invest in months or even years of training before they are competent to undertake mist-netting surveys). Furthermore, even with experienced surveyors, misidentified or unidentified contacts can still occur when conducting point counts, especially in complex ecosystems such as cloud forest where species richness is high and many birds have regional vocalisations. This may explain the low rate of detection of hummingbird (Trochilidae) species in the point-counts.

A further finding of the mist netting survey worthy of comment was the methodologies' high degree of variance between study sites. While point counting yielded a similar rate of species detection across all sites along transects, the number of species and individual birds caught by nets was highly dependent on local environmental factors such as topography and terrain features. For instance, netting sites located on steep inclines captured comparatively fewer species and individual birds than areas with more level topography (Table 3.5). Indeed some of these sloping sites yielded an average of < 1 catch per morning. By contrast, netting sites located along ridges at the crests of topographical features achieved by far the highest capture rates for both species and individual birds. This is probably due to these ridges having the effect of 'funnelling' birds into the traps. One such ridge site yielded 98 captures: > 19%

of the entire survey effort. These findings suggest that the placement of mist nets requires careful and selective positioning by the surveyor to yield the best capture rates, although the systematic sampling necessary in most ecological surveys may not always allow this.

Table 3.5 - Mean number of species and individual birds captured at sites of differing topography within Cusuco National Park, North-West Honduras. Bracketed numbers show number of sites in each category. ± represents 1 standard deviation.

	Mean species captured	Mean individuals captured
Ridge (6)	15.83 ± 8.08	45.33 ± 28.63
Flat ground 0°—30° (11)	9.27 ± 3.23	16.27 ± 5.83
Incline > 30° (9)	5 ± 1.94	6.89 ± 3.22

Results demonstrate that using both methods in conjunction is considerably more effective than either method in isolation, with the proportion of species detected by both techniques being higher than either technique alone in 79% and 83% of groups for points and nets respectively (Tables 3.3 and 3.4). The significant improvement of effectiveness by using a combination of both methodologies concurs with the findings of previous studies in other forest sites (Rappole *et al.* 1998, Whitman *et al.* 1997). The use of this combined method approach in cloud forest appears to yield a higher detection rate of all known species (73.3%) than with similar studies in lowland sites; Whitman *et al.* (1997), for example, described a detection rate of 61.1%. This could partly result from the increased rate of netting captures discussed previously.

While a combined methods approach appears to be reasonably successful in cloud forest ecosystems, it still leaves a large component of the avifaunal community (27.8% of the preliminary checklist) unaccounted for. A large proportion of these undetected species are found in a discrete range of avian groups, such as raptors (75% undetected) and nocturnal birds (60% undetected) as well as aerial and aquatic feeders (50% and 66% undetected respectively). This can be partially attributed to species of these groupings having peak activity times that do not correspond to the timing of mist net and point count surveys (Bibby *et al.* 2002). In addition these species can be inherently difficult to monitor using the evaluated methodologies due to non-vocalisation and/or occurring primarily above canopy level, where both capture and visual observation are difficult (Thiollay 1989). This is a significant limitation of the assessed methodologies, as these groups fulfil roles of high ecological importance, being either top predators in the avifaunal community (raptors) or based on a food chain totally separate from other avian groups which would otherwise be unconsidered (aquatic birds). Further, raptors in particular have been considered a valuable indicator of ecosystem integrity due to their predations strongly influencing the community structures of other avifaunal groups. Decline in populations of top level predators such as raptors are also often indicative of dysfunctional ecosystems, particularly in tropical forest ecosystems (Rodríguez-Estrella *et al.* 1998, Thiollay 1996, Terborgh 1992).

The inability to effectively detect important avian groupings would suggest that both point counts and mist nets, either individually or in conjunction, are insufficient to make full descriptions of avifaunal communities in cloud forest ecosystems, and that other techniques may be required if an observer wishes to make a complete census of bird communities in these habitats. Raptors, for example, could be more effectively monitored by conducting observations of soaring birds in clearings during optimal hours (09:00–13:00 h) (Thiollay and Rahman 2002, Thiollay 1989). Point-counts might also be more effective in detecting raptors if birds observed flying above canopy level were included in analysis. However, due to the necessary systematic design of survey sites, point-count sites rarely corresponded with forest clearings, and thick canopy usually obscured vision. This, combined with survey times occurring before peak raptor activity, meant that few birds observed above canopy level were excluded from analysis and no species were excluded which were not also recorded at or below canopy level. Nocturnal birds could be more accurately surveyed by returning to study sites at night to conduct point-counts and mist-netting. This proved difficult to achieve in this study, however, due to large by-catches of bats in the nets, and because reaching the far point-count sites, which were often located across very difficult terrain, was logistically difficult. Play-back calls and spot-mapping during crepuscular periods might also be effective alternative methodologies for describing nocturnal bird communities (Kavanagh and Bamkin 1995, Terbourgh *et al.* 1990). Further methods could also be employed to better represent groups of birds under-recorded by point-counts and mist-nets, such as using line transects to survey small, soft-vocalising canopy species and rare species (Terbourgh *et al.* 1990).

In conclusion, the results of this study have demonstrated that the unique structural characteristics of tropical montane cloud forest do not significantly influence the relative effectiveness of point-counting and mist netting beyond that described by other studies as hypothesised. Findings indicate point counting as the more effective and efficient methodology for surveying cloud forest bird communities, which is in concordance with comparative studies in lowland ecosystems, and where time and resources are limited it is this approach that should be prioritised. The study has also demonstrated that a greater proportion of species can be detected if mist netting is used to supplement point count surveys, and this combined methods approach is recommended wherever possible. However, these two methods alone are still insufficient if a surveyor wishes to describe cloud forest avifauna communities in their entirety, and the inclusion of all avifaunal groups would require a more integrated approach involving multiple methodological techniques.

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CHAPTER 4 - Impacts of tropical forest disturbance upon avifauna on a small island with high endemism: implications for conservation

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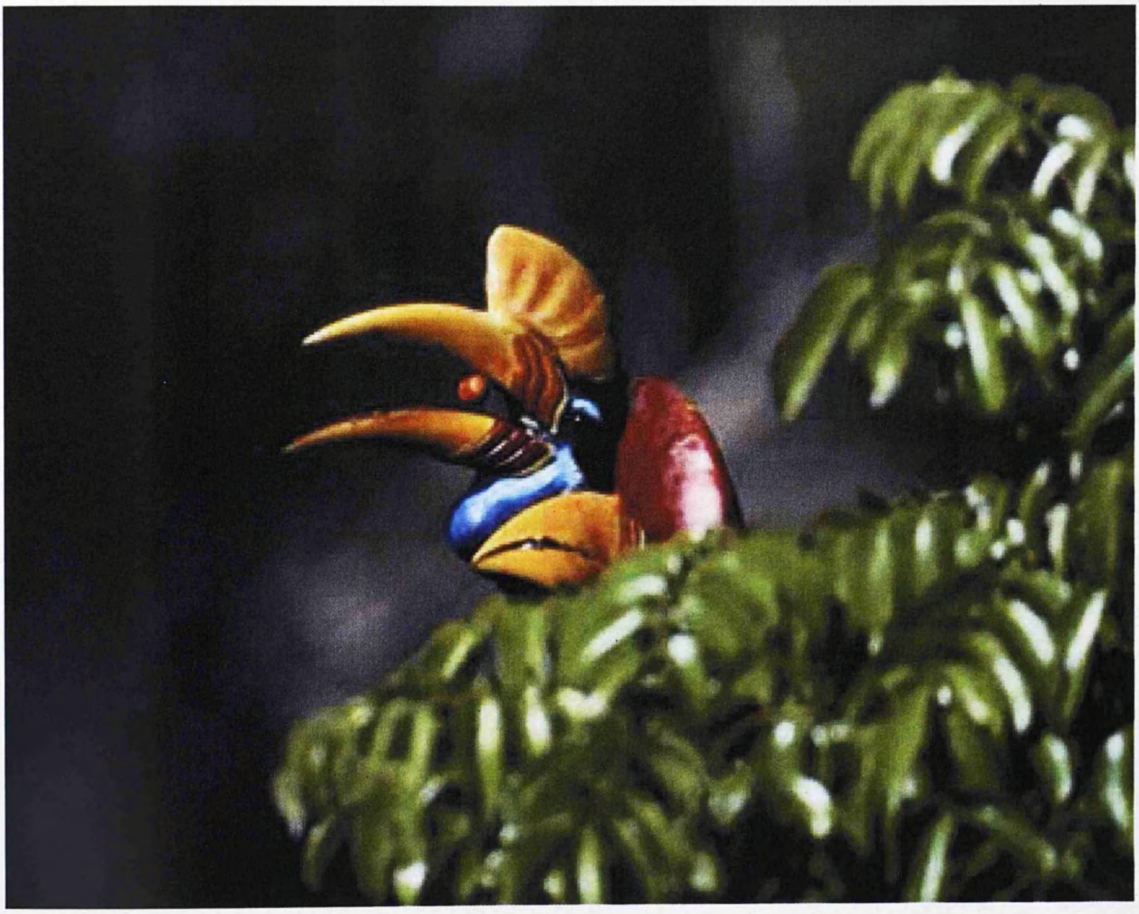

Pair of Red-knobbed Hornbills (*Rhyticeros cassidix*) eating figs in the Lambusango forest

4.1 – SUMMARY

Tropical forests are rapidly being lost across South East Asia and this is predicted to have severe implications for many of the region's bird species. However, relationships between forest disturbance and avifaunal assemblages remain poorly understood, particularly on small island ecosystems such as those found in the biodiversity 'hotspot' of Wallacea. This study examines how avifaunal richness varies across a disturbance gradient in a forest reserve on Buton Island, South-East Sulawesi. Particular emphasis is placed upon examining responses in endemic and red-listed species with high conservation importance. Results indicate that overall avian richness increases between primary and regenerating secondary forest and then decreases through disturbed secondary forest, but is highest in cleared farmland. However, high species richness in farmland does not signify high conservation importance; bird community composition here differs significantly from that found in forest sites, and is poor in supporting forest specialists and endemic species. Certain large-bodied endemic species such as the Red-knobbed Hornbill (*Rhyticeros cassidix*) appear to be sensitive to moderate disturbance, with populations occurring at greatest density within primary forest. However, overall endemic species richness is similar in primary and secondary forest ecosystems. Results indicate that well-established secondary forest in particular has an important role in supporting species with high conservational importance, possessing community composition similar to that found in primary forest and supporting a high richness of endemic species.

Key words: Anthropogenic disturbance; Bird communities; Island endemics; Tropical rainforest; Wallacea

4.2 – INTRODUCTION

South-East Asia's rainforests are facing the highest relative rates of habitat destruction of any major tropical area (Mayaux *et al.* 2005, Achard *et al.* 2002) and this has been identified as the major driving force of potential biodiversity loss across the region (Sodhi *et al.* 2004). This has severe implication for the biodiversity 'hotspot' of Wallacea, a biogeographical region where a complex geological history has facilitated a high prevalence of endemic fauna (Whitten *et al.* 2002, Myers *et al.* 2000, Kinnaird 1995). Over 46% of resident vertebrates are restricted entirely to the hotspot, including >35% of bird species (Myers *et al.* 2000), while Sulawesi, the region's largest island, supports 14 endemic bird genera, the highest of all globally identified endemic bird areas (Stattersfield *et al.* 1998). As with much of Indonesia, Wallacean forests are being subjected to heavy clearance, primarily from expanding agricultural activities related to population growth and socio-economic factors (Trainor 2007, Sodhi 2005a), but also from unsustainable logging practices (Marsden 1998). An estimated 55% of original vegetation cover and 85% of original pristine rainforest within the region has been lost or modified (Global Forest Watch 2002). Predictive extinction models estimate that continued habitat alterations on this scale could result in the loss of up to 42% of flora and fauna species across South East Asia by 2100 (Sodhi *et al.* 2004), although consequences could be more severe still in the Wallacea region due to its insular nature, being comprised of 13,500 oceanic islands (Coates and Bishop 1997). Island birds have been estimated to possess extinction risks up to 40 times greater than continental species due to their small ranges and population sizes, and consequently are highly vulnerable to habitat destruction (Trevino *et al.* 2007, Pimm *et al.* 1995). Indeed, over 90% of recent (post AD 1600) bird extinctions have been island endemics (Trainor 2007, Birdlife International 2004).

Safeguarding the unique biodiversity of this important region is therefore a high conservation priority, and extensive research is required to determine more precisely how habitat loss and change impacts upon biodiversity so that effective measures may be taken to mitigate these impacts. However, current understanding of the ecological associations of avifaunal communities in this area remains poor. Aside from a few recent surveys (Coates and Bishop 1997, White and Bruce 1987), the most reliable accounts of bird communities on many Wallacean islands date back to collectors' reports from the late 19th century (Trainor 2007) while the bulk of more recent research has focussed on lowland areas or on larger islands (Lee *et al.* 2007, Sodhi *et al.* 2005b, Waltert *et al.* 2004, Thiollay *et al.* 2002). Few studies have examined bird communities on small island or montane ecosystems, which are often highly endemic and potentially more ecologically fragile (Macarthur and Wilson 1967). This paper seeks to address this by examining variations in avifaunal communities across a disturbance gradient on a small Wallacean island. Bird communities were chosen as a study focus for their own intrinsic value and also because they can to a certain extent be utilised as ecological indicators for overall biodiversity, due to a high ecological congruity with other taxonomical groups (Gardner *et al.* 2008, Howard *et al.* 1998, Furness *et al.* 1994).

The study focuses on Buton, an attendant island of Sulawesi, which is representative of a small, sub-montane island ecosystem with a highly endemic avifauna assemblage. Recent work on these islands focussing on herpetofauna (Gillespie *et al.* 2005) and butterflies (Fermon *et al.* 2005) has demonstrated the complex nature of the relationships between forest disturbance and the distributions of endemic and habitat-specialist taxa. It has also highlighted the urgent need for more extensive research on the human impact on biodiversity in this region. The study also examines how a select key species, the Red-knobbed Hornbill *Rhyticeros cassidix*, responds to environmental disturbance. This species was chosen due to its potential as a flagship species, being a highly distinctive, charismatic bird which is widely recognised locally, and the faunal symbol of South Sulawesi province. The relationship between environmental disturbance and the populations of several other large-bodied Sulawesi endemic species is also examined, as is the ecological response of forest specialist species and regional endemic avifauna overall.

4.3 - METHODS

4.3.1 - Study site

The study focuses on Buton Island, the largest (5,600km^2) attendant island of Sulawesi in the Indonesian archipelago (See Figure 1.5 in Introduction). The island is approximately 100km long and 42km wide at its widest point. Altitude ranges from 0-200m in coastal areas to 400m along the island's central spine, with isolated peaks reaching up to 1000m (Whitten *et al.* 2002, O'Donovan 2001). Detailed climatic data for Buton is provided in section 1.6 of the introduction chapter. Recent work using remotely-sensed and GIS data has identified much of the island as being of high conservation value (Cannon *et al.* 2007). Buton has been shown to support a rich avifauna, with at least 231 bird species including 52 Sulawesi endemics being reported (Catterall 1997). However, the island's forest habitats have undergone significant clearance in recent years. Between 1991–2002 over 13% of land in Southern Buton (27,809 hectares) was converted from forest to non-forest land use (Seymour 2004). The primary cause of this deforestation is considered to be agricultural expansion, with further clearance resulting from selective logging, rattan collection and asphalt mining (Seymour 2004).

Research was conducted in and around the Lambusango Forest (5°10'S, 122°24' E), a 65,000 hectare area of uninhabited lowland and sub-montane tropical forest divided into a 28,510 hectare strict forest reserve and a 35,000 hectare production forest (Singer and Purwanto 2006) (Figure 4.1). A great diversity of tree species occurs within the reserve, with no single family being predominant. The underlying geology of the area is Quaternary karst coral limestone (O'Donovan 2001).

4.3.2 - Sample sites

Sampling was conducted in three forest areas located throughout the reserve. Analysis of habitat structure (see below), supported by visual observations and research into local ecological history, suggests that these three forest areas correspond approximately to areas of near-pristine primary forest; well-regenerated secondary forest subjected to agricultural clearance and logging until the Lambusango conservation area was set up in 1975, and heavily-disturbed secondary forest in the reserve's periphery which has been recently subjected to intermittent logging, shifting cultivation and rattan extraction. The underlying environmental parameters of these last two categories (geology, topography etc) is expected be similar to the primary forest sites, with disturbance being the only significant cause of difference in vegetation structure. Additionally, an area of recently-cleared mixed farmland consisting of cassava (*Manihot esculenta*), papaya (*Carica papaya*) and rice (*Oryza sp.*) plantations was surveyed. Four 900m linear transects spaced at least 1km apart were used in each area (Figure 4.1). Each transect contained seven sample sites, with each site being spaced 150m apart. This gave a total of 112 study sites with 28 sites located in each habitat category. The elevation of primary and disturbed secondary forest sites varied between 300 – 400m, while elevation of the regenerating secondary forest sites varied between 650 – 700m. These altitudinal variations are not expected to be great enough to cause significant systematic changes in vegetation structure. Farmland sites were located at elevations between 100 - 150m.

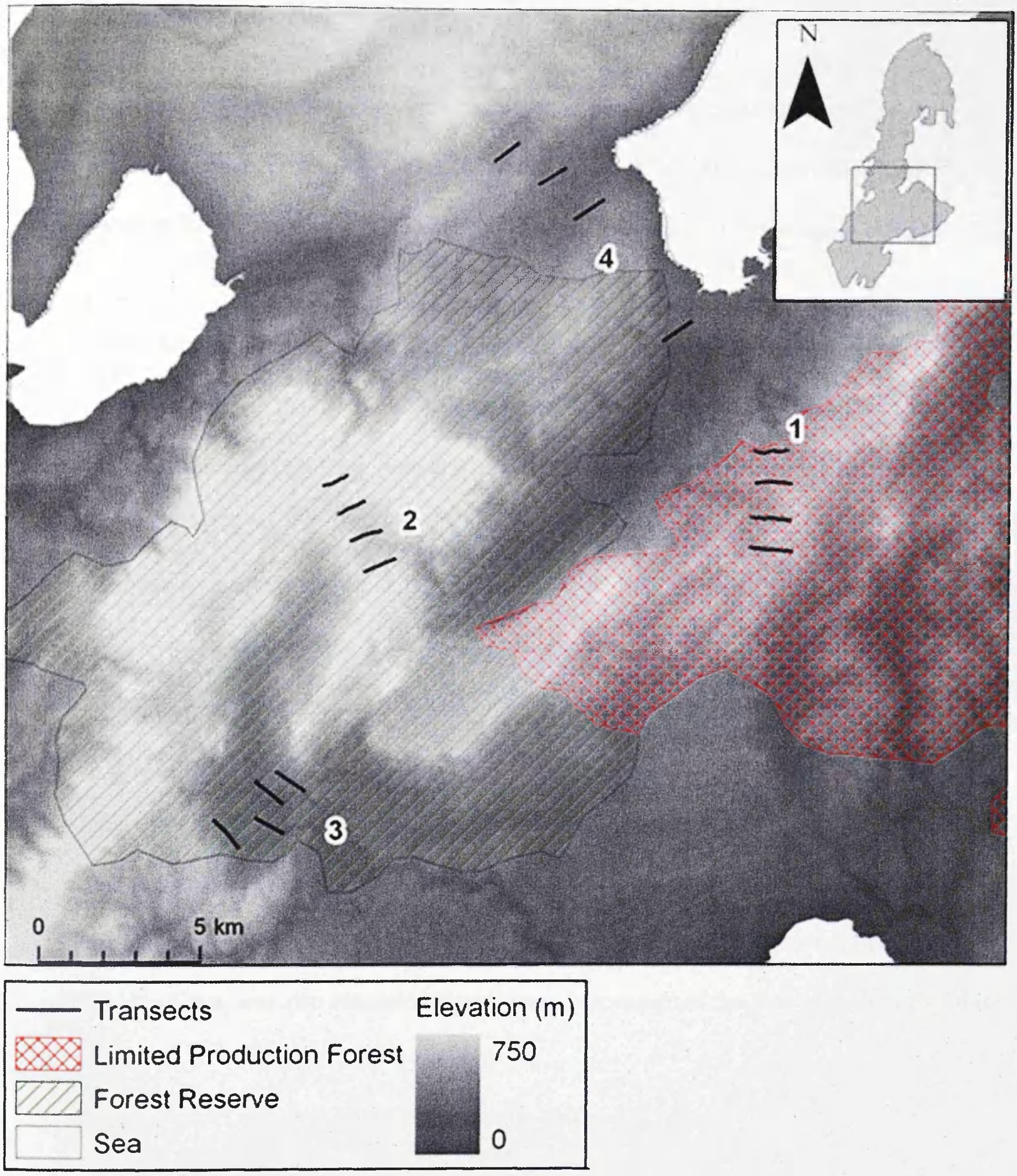

Figure 4.1 - The Lambusango Forest reserve and relative locations of study transects. Inset shows study area's location within Buton Island. Transects located within areas of primary forest, regenerating secondary forest, disturbed secondary forest and farmland are notated 1, 2, 3 and 4 respectively

4.3.3 - Vegetation sampling

A series of vegetation variables were measured within a 20m radius of each forest study site to provide evidence for differences in habitat structure. Vegetation variables were not measured in farmland sites, as differences in habitat structure here were clearly evident.

The sum total of large trees with a diameter at breast height (dbh) of >50 cm was counted within each plot, with the mean dbh of large trees also being recorded at each site. Canopy cover was evaluated at each plot utilising a canopy scope constructed from a perspex square marked with a 5X5 grid of dots separated by 3cm (Brown *et al.* 2000). At each site five measurements were taken, with density assessed by holding the scope 10cm away from an observer's eye-level and towards the largest visible canopy gap, with the number of dots unobscured by vegetation being recorded. Relative understorey densities were estimated utilising a 1.5m measuring pole marked with 50 black bands. A consistent observer counted the number of bands visible at 10m at four points within each quadrat, which was then doubled to a proxy percentage value density estimate. Coverage of rattan (*Calamus* sp.), which can be gauged as an indicator of forest quality due to its invasive nature in recently disturbed habitats, was also estimated visually as a percentage of the area of each plot (Table 4.1).

Table 4.1 - Vegetation analysis summary for primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi. ± indicates variance to 1 standard deviation.

	Mean canopy score (0-25)	Mean frequency of large trees (>50cm dbh diameter)	Mean dbh of large trees (cm)	Undergrowth density (%)	Rattan cover (%)
Primary forest	4.02 ± 1.27	4.8 ± 1.89	83.9 ± 35.2	17.17 ±5.1	21 ± 14.1
Regenerating secondary forest	4.66 ± 1.3	2.1 ± 0.9	68.77 ± 18.32	2.4.4 ± 0.7	22.5 ± 12.3
Disturbed secondary forest	6.36 ± 1.73	2.3 ± 1.1	61.763 ± 15.2	7.8 ± 1.6	52.1 ± 27.5
Farmland	n/a	0	n/a	0	0

4.3.4 - Bird sampling

Bird communities were surveyed at each study site using 50m fixed-radius circular plot point counts (Bibby *et al.* 2002). Each point count was repeated once, with the total number of species detected after both counts being recorded. Point count surveys were led by the first author and Mr Dani Heryadi of Operation Wallacea, who both had several months' field experience with avifauna in the Lambusango, in addition to several years experience working with tropical birds. The data collection period corresponded to the breeding season for most local bird species.

Sampling was conducted each morning between 06:00 – 08:00, this being the period where bird detectibility is highest and mobility is low, reducing the chance of recording contacts multiple times (Marsden 1999, Wunderle 1994). Point count samples were begun on immediate arrival at each study site, with no 'settling in' period being used. This has been shown to allow the recording of any birds disturbed by the surveyors, thereby increasing the number of contacts made per count (Lee and Marsden 2008). A 10 minute sampling period was used, as counts of this length have a reduced likelihood of multiple contact recording, while still being capable of detecting >80% of bird species present in an area (Lynch 1995, Waide and Wunderle 1987).

4.3.5 - Statistical analysis

The mean number of species detected at sample sites after one repetition was calculated and compared for each habitat category using non-parametric Kruskal-Wallis one-way ANOVA analysis (Zar 1999). The mean number of endemic and forest specialist species per site (identified after Coates and Bishop 1997), were also compared using Kruskal-Wallis one-way ANOVA analysis.

Sample-based rarefaction curves plotting numbers of individuals recorded against number of species detected were calculated utilising the software package EstimateS (Colwell 2006). A further series of nonparametric species richness estimators were calculated utilising EstimateS; the mean value of these being utilised as an overall species richness estimate, as the effectiveness of different estimators is expected to vary with different data sets (Walther and Moran 1998). This was included to corroborate the results of the accumulation curve, as information in larger samples may be lost when 'rarefied' to the size of the smallest sample in the analysis (Lee *et al.* 2007, Sodhi *et al.* 2005a).

Comparisons of community structure between habitat categories were examined by constructing similarity matrices using PC-ORD version 5.0 and comparing congruence using a series of Mantel tests. Significance of these tests was determined by a Monte-Carlo procedure utilising 999 permutations (McCune and Grace 2002).

Kruskal-Wallis one-way ANOVA analysis was also utilised to compare mean abundance of *R. cassidix* individuals per study site in each habitat category, along with two other selected large-bodied endemic species; the insectivorous Pied Cuckoo Shrike (*Coracina bicolor*), classifying as Near-Threatened by the IUCN (2009), and the frugivorous Golden-mantled Racquet-tail Parrot (*Prioniturus platurus*).

4.4 - RESULTS

A total of 67 species and 1701 individual birds were recorded in the point count surveys. Most contacts (90%) were detected by sound, with 10% being detected visually. <1% of contacts were unidentified and these were excluded from analysis. Table 4.2 summarises species detected within each habitat category.

*Table 4.2 - Mean number of individuals per point count sample of each recorded species in primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi. Species ranked in taxonomical order after Wells (1998). Scientific and common names follow Coates and Bishop (1997) Species in bold are endemic to the Sulawesi sub-region. Species marked † are classified as forest species after Coates and Bishop (1997). Species marked * have significantly different population densities across habitat types (Kruskal-Wallis $p < 0.05$).*

Species name	English name	Primary	Reg. Sec	Dist. Sec	Farm
Ardea purpurea	Purple Heron	0	0	0	0.036
Egretta alba	Great Egret	0	0	0	0.036
*Egretta garzetta**	Little Heron	0	0	0	0.071
Haliastur indus	Brahminy Kite	0	0.036	0	0
Spilornis rufipectus†	**Sulawesi Serpent Eagle**	**0.034**	**0.036**	**0.036**	**0**
Accipiter trinotatus†*	**Spot-tailed Goshawk**	**0.125**	**0.143**	**0.018**	**0.821**
Ictinaetus malayensis†	Black Eagle	0	0	0	0.036
Dendrocygna arcuata	Wandering Whistling Duck	0	0	0	0.036
Gallus gallus†	Red Junglefowl	0	0.054	0.036	0
Amaurornis isabellina	**Isabelline Waterhen**	**0**	**0**	**0**	**0.018**
*Ducula aenea**	Green Imperial Pigeon	0.21	0.554	0.286	0.25
Ducula forsteni†*	**White-bellied Imperial Pigeon**	**0.09**	**0.196**	**0**	**0**
Ducula luctaosa	**Silver-tipped Imperial Pigeon**	**0**	**0.036**	**0**	**0.018**
Macropygia amboinensis	Brown Cuckoo-dove	0	0.036	0.018	0
Treron griseicauda	Grey-cheeked Green Pigeon	0	0	0.018	0
*Ptilinopus melanospila**	Black-naped Fruit-dove	0.107	0.232	0.232	0.018
*Streptopelia chinensis**	Spotted Dove	0	0	0	0.482
Turacoena manadensis	**Sulawesi Black Pigeon**	**0.018**	**0.018**	**0.071**	**0**
Trichoglossus ornatus	**Ornate Lorikeet**	**0**	**0**	**0.079**	**0**
Prioniturus platurus†*	**Golden-mantled Racquet-tail**	**1.304**	**0.339**	**0.089**	**0**
Tanygnathus sumatranus	Blue-backed Parrot	0.018	0.054	0.018	0.018
Loriculus stigmatus†	**Sulawesi Large Hanging Parrot**	**0.089**	**0.036**	**0.161**	**0**
Cacomantis merulinus	Plaintive Cuckoo	0	0	0	0.018
Surniculus lugubris†	Drongo-cuckoo	0	0.036	0.054	0.036
Phaenicophaetus calyorhynchus	**Yellow-billed Malkoa**	**0**	**0**	**0.036**	**0.054**
Centropus bengalensis	Lesser Coucal	0	0	0	0.304
Centropus celebensis†*	**Bay Coucal**	**0.286**	**0.375**	**0.304**	**0**
Collocalia esculenta	Glossy Swiftlet	0	0	0	0.018
Hemiprocne longipennis	Grey-rumped Tree-swift	0	0	0.054	0.071
Halcyon coromanda	Ruddy Kingfisher	0	0	0	0.018
*Halcyon chloris**	Collared Kingfisher	0.018	0	0	0.039

Penelopides exhartus*†	**Sulawesi Dwarf Hornbill**	**0.107**	**0.25**	**0.196**	**0**
Rhyticeros cassidix*†	**Red-knobbed Hornbill**	**0.232**	**0.196**	**0.036**	**0.036**
Mulleripicus fulvus*†	**Ashy Woodpecker**	**0.286**	**0.143**	**0.071**	**0**
Pitta erythrogaster†	Blue-breasted Pitta	0	0.036	0.054	0
*Hirundo tahitica**	Pacific Swallow	0	0	0	0.089
Coracina bicolor*†	**Pied Cuckoo-shrike**	**0.393**	**0.679**	**0.142**	**0**
Coracina leucopygia	**White-rumped Cuckoo-shrike**	**0.107**	**0**	**0**	**0**
Coracina morio*†	**Sulawesi Cicadabird**	**0.286**	**0.286**	**0.232**	**0.018**
Dicrurus hottentotus	Hair-crested Drongo	0.5	0.875	0.536	0.392
Oriolus chinensis†	Black-naped Oriole	0.411	0.429	0.393	0.339
Corvus enca	Slender-billed Crow	0	0	0.036	0.054
Corvus typicus*†	**Piping Crow**	**0.054**	**0.196**	**0**	**0**
Trichastoma celebense	**Sulawesi Babbler**	**0.643**	**0.679**	**0.982**	**0.82**
*Gerygone sulphurea**	Flyeater	0	0	0	0.089
Culicicapa helianthea	**Citrine Flycatcher**	**0.25**	**0.268**	**0.357**	**0.018**
Hypothymis azurea	Black-naped Monarch	0.43	0.554	0.571	0.571
*Artamus leucorhynchus**	White-breasted Wood-swallow	0	0	0	0.357
Aplonis panayensis	Asian Glossy Starling	0	0.268	0	0.304
Scissirostrum dubium	**Grosbeak Starling**	**0.107**	**0**	**0.375**	**0**
***Basilornis celebensis*†**	**Sulawesi Crested Myna**	**0.018**	**0.018**	**0**	**0**
***Streptocitta albicollis*†**	**White-necked Myna**	**0.125**	**0.054**	**0.125**	**0.018**
Myzomela sanguinolenta	Scarlet Honeyeater	0	0	0	0.036
Anthreptes malacensis	Brown-throated Sunbird	0	0	0	0.054
*Nectarina aspasia**	Black Sunbird	0.857	1.107	0.446	0.232
Nectarina jugularis	Olive-backed Sunbird	0	0.054	0.017	0.071
*Aethopyga siparaja**	Crimson Sunbird	0	0	0	0.071
***Dicaeum aureolimbatum*†**	**Yellow-sided Flowerpecker**	**0.018**	**0.071**	**0.089**	**0.053**
***Dicaeum celebicum*†**	**Grey-sided Flowerpecker**	**0**	**0.018**	**0.071**	**0.036**
Zosterops celebense	**Sulawesi White-eye**	**0.25**	**0.396**	**0.339**	**0**
*Zosterops consobrinorum**	Lemon-bellied White-eye	0	0	0.054	0.554
*Passer montanus**	Tree Sparrow	0	0	0	0.393
*Lonchura molucca**	Black-faced Muniah	0	0	0	0.056
*Lonchura punctulata**	Scaly-breasted Muniah	0	0	0	1.196
*Lonchura malacca**	Chestnut Muniah	0	0	0	0.125

Figure 4.2 demonstrates that mean species richness per study site increases between the primary forest and regenerating secondary forest sites, rising from a mean of 7.17 ± 1.24 to 9.25 ± 1.41 species per site. As anthropogenic disturbance levels increase further, however, richness decreases linearly, with a drop in mean species per site to 7.2 ± 1.12 in disturbed secondary forest and 6.29 ± 0.95 in cleared agricultural land.

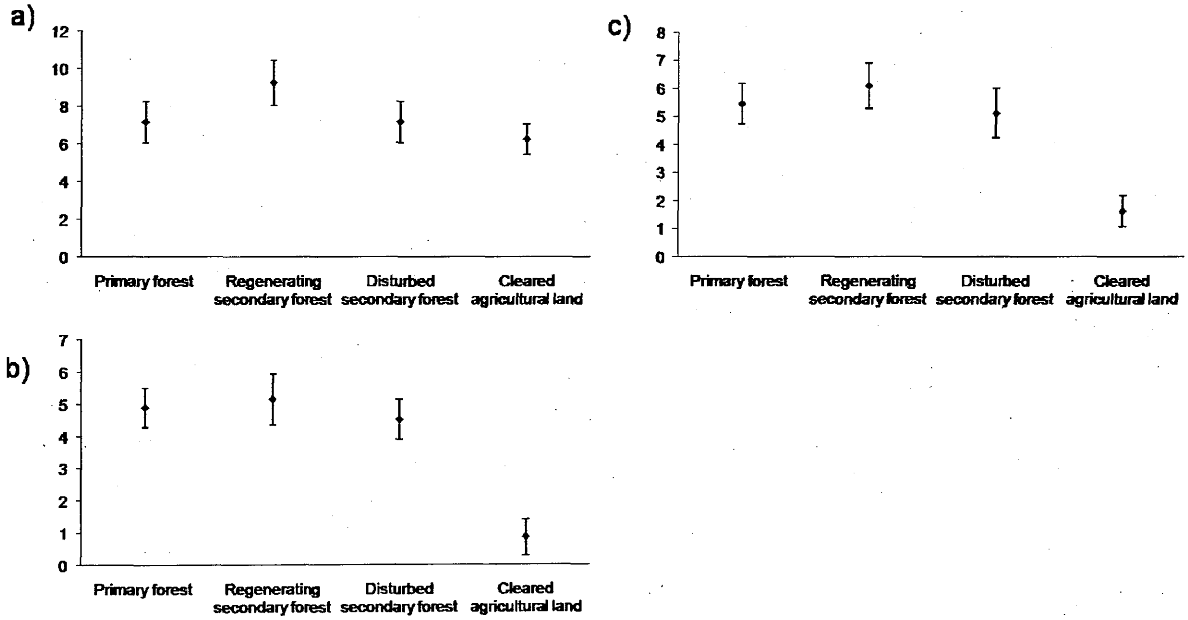

*Figure 4.2 - Mean number of **a)** avifaunal species Kruskal-Wallis H = 14.852, p <0.001) **b)** endemic avifaunal species (Kruskal-Wallis H = 73.996, p <0.001) and **c)** forest species (Kruskal-Wallis H = 47.57, p <0.001) detected per sample in primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi. Error bars represent 95% confidence intervals. Endemic and forest birds identified utilising Coates and Bishop (1997).*

While mean aggregations of species per site suggest a relatively impoverished avifaunal assemblage in cleared farmland, other statistical analyses provide an alternative view. Average species richness estimates displayed in Table 4.3 were calculated as 33.2 (95%

confidence interval) for primary forest, 38.256 for regenerating secondary forest, 40.45 for disturbed secondary forest and 56.78 for farmland. This would suggest a trend in our study sites of increasing species richness with greater anthropogenically induced habitat heterogeniety, with areas of mixed farmland near forest edge possessing the highest richness estimates. Rarefaction curves in Figure 4.3 support this, predicting primary forest to have the most impoverished avifauna, with farmland having the highest number of species and species density. Regenerating secondary forest displays similar predicted overall species richness to disturbed secondary forest, which again implies that no simple linear relationship exists between richness and level of disturbance exists.

Table 4.3 - Non-parametric species estimators for primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi. n represents sample size. Sp obs and Ind obs represent total number of species and individuals observed, respectively. ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, Bootstrap, MMRuns and MMMeans are non-parametric species estimators (Colwell and Coddington, 1994).

Parameters	**Primary Forest**	**Regenerating secondary forest**	**Disturbed secondary forest**	**Farm**
N	28	28	28	28
Sp obs	29	35	35	46
Ind obs	417	472	359	452
ACE	31.83	37.21	37.68	51.71
ICE	33.61	39.05	42.88	60.98
Chao1	34	35.37	37	50.5
Chao2	32.68	37.45	40.05	55.37
Jack1	34.89	40.89	43.83	55
Jack2	37.83	41.94	46.83	60.73
Bootstrap	31.74	38.04	39.3	65.72
MMRuns	31.25	37.02	38.09	55.39
MMMeans	30.99	37.33	38.35	55.51
Average species estimate	33.2	38.256	40.45	56.78

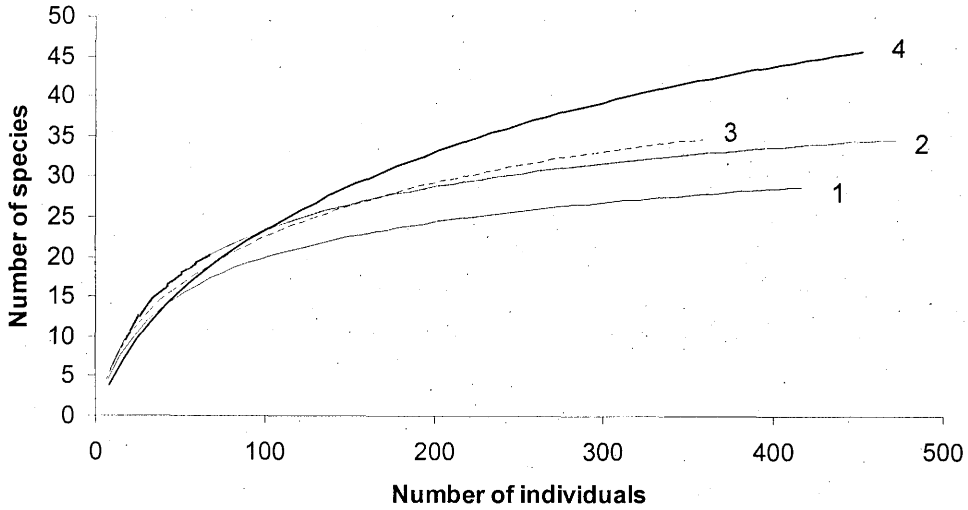

Figure 4.3 - Sample-based rarefaction curves displaying number of individuals against number of species recorded in primary forest (notated as 1), regenerating secondary forest (notated at 2), disturbed secondary forest (notated as 3) and cleared agricultural land (notated as 4) sample sites within the Lambusango forest reserve, Buton Island, South-East Sulawesi.

Mantel test r-values shown in Table 4.4 indicate that, although R-values are low, significant congruence occurs between bird community structure in primary forest and regenerating secondary forest ($r = 0.154$). Community structure in regenerating secondary forest and disturbed secondary forest also displayed significant similarity ($r = 0.161$). Community structure in farmland sites was not significantly correlated with community structure in any forest sites.

*Table 4.4 - Mantel test r-values comparing community similarity of bird assemblages between primary forest, regenerating secondary forest, disturbed secondary forest and cleared farmland in the Lambusango Forest Reserve, Buton Island, South-East Sulawesi. Bold figures indicate statistically significant correlations. * indicates significance at a 95% confidence interval. ** indicates significance to a 99% confidence interval.*

	Regenerating secondary forest	Disturbed secondary forest	Farmland
Primary forest	**0.154****	0.07	0.065
Regenerating secondary forest	X	**0.161***	0.012
Disturbed secondary forest	X	X	0.001

Mean species per sample analysis in Figure 4.2 also demonstrates that richness of endemic species increases slightly between primary forest (4.89 ± 0.98 species per sample site) and regenerating secondary forest (5.14 ± 1.12 species per sample site). Disturbed secondary forest has a similar mean number of endemic species per sample site to primary forest (4.52 ± 0.98), while in cleared farmland this falls to just 0.86 ± 0.42 species per sample. Forest species show a similar pattern of response.

Figure 4.4 demonstrates that abundance of *R. cassidix* decreases rapidly with increasing disturbance, falling from a mean abundance of 0.57 individuals per sample in primary forest to 0.39 individuals per sample in regenerating secondary forest, and levelling off at a value of virtual absence in disturbed secondary forest and farmland. The decline of *R. cassidix* across the four habitat categories shares a strong linear relationship with the number of large trees per plot at each site ($r^2 = 0.87$). Similar trends of decline are also found in other selected large-bodied Sulawesi endemics; *P. platurus* and *C. bicolor.*

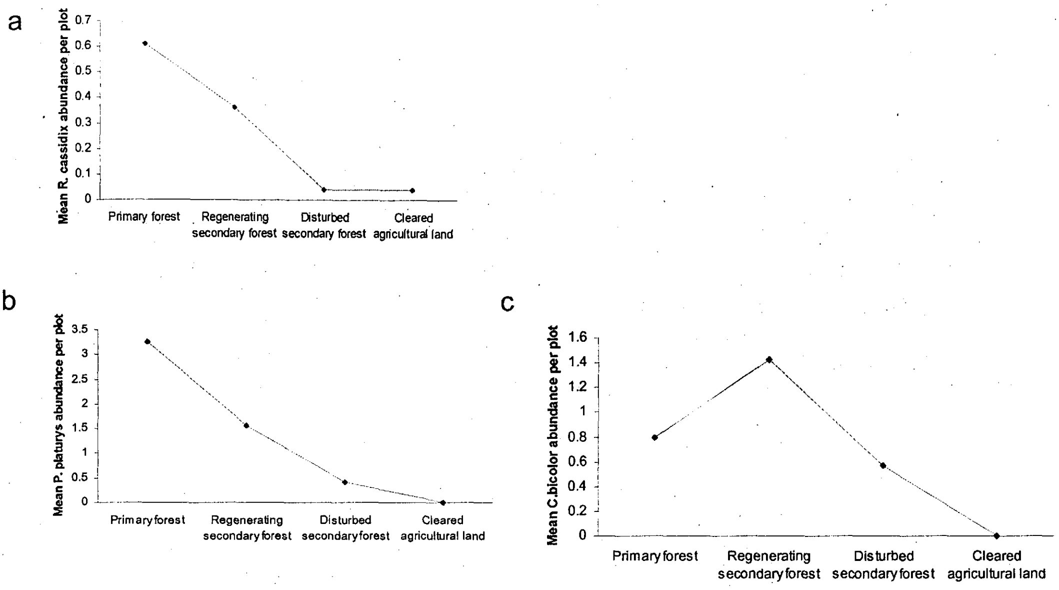

Figure 4.4 - Mean abundance of select Sulawesi endemic species detected per plot in primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi. ***a)*** *Rhyticeros cassidix (Kruskal-Wallis H = 20.231, p <0.001,* ***b)*** *Prioniturus platurus (Kruskal-Wallis H = 39.538, p <0.001,* ***c)*** *Coracina bicolor (Kruskal-Wallis H = 28.092, p <0.001).*

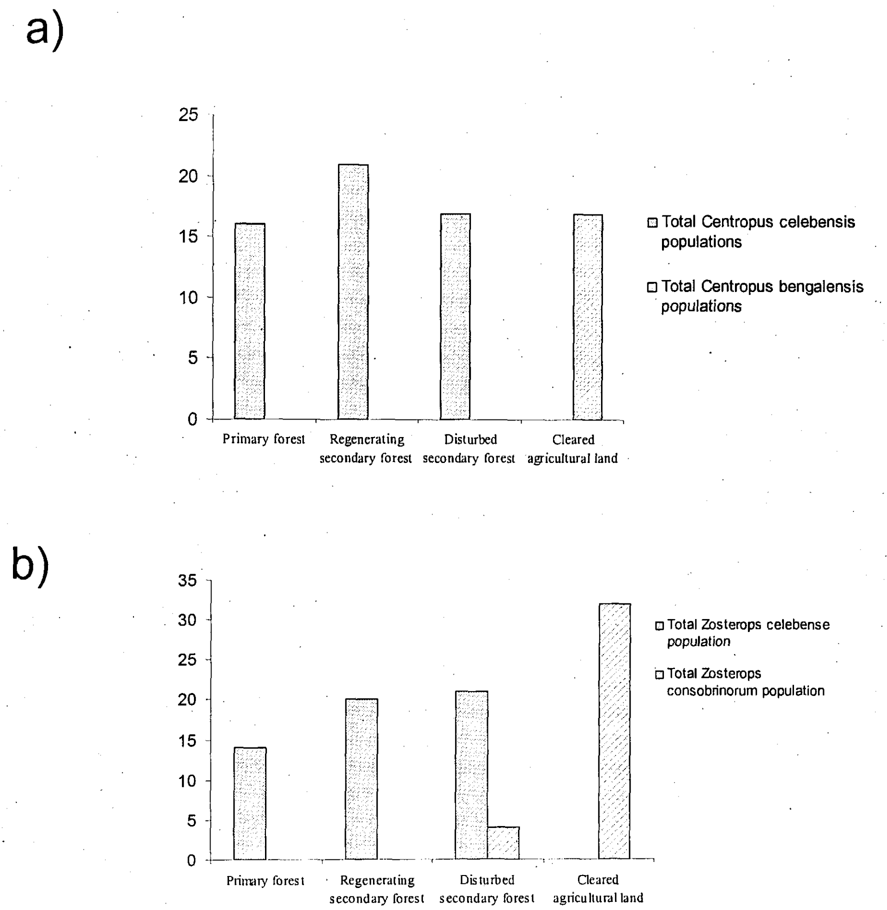

Figure 4.5- Mean abundance per plot of: ***a)*** *Coucal species* ***Centropus celebensis*** *and* ***Centropus bengalensis****, and* ***b)*** *White-eye species* ***Zosterops consobrinorum*** *and* ***Zosterops chloris*** *in primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi.*

4.5 - DISCUSSION

While mean species richness per sample demonstrates a general pattern of decline with increasing environmental disturbance, this is not a simple linear relationship as has been found in other studies (Sodhi *et al.* 2005a, Thiollay *et al.* 2002), with richness rising between primary and regenerating secondary forest before declining in the more disturbed sites. The rise in species richness between primary and regenerating secondary forest could perhaps be explained by the ecological history of the latter. These sites have been subjected to heavy disturbance in the past, but subsequently left undisturbed for over 25 years. Past disturbance would have led to major disruption of ecological niches, and while it is likely that a decline in the total diversity of avifaunal assemblages would have occurred due to local deterministic loss of specialist rainforest species (Pullin 2002), previous studies have shown that smaller numbers of generalist species are often able to colonise new niches created by disturbance that did not previously exist in the area (Sodhi *et al.* 2005a). Over time and with regeneration of the forest, niches may again have appeared which accommodate forest specialists, but it is possible that certain generalist species have become established and remain; hence the higher species richness. This is in concordance with Connell's (1978) intermediate disturbance hypothesis.

Species richness in disturbed secondary forest is somewhat higher than could be expected from findings of previous studies (Sodhi *et al.* 2005a). This, again, could possibly occur because of an overlap of opportunistic, generalist species with specialist forest species returning to the forest as it regenerates, as hypothesised for the regenerating secondary forest. However, the vegetation survey indicates that the disturbed secondary forest has not recovered so extensively, so it could be that fewer niches have become re-available for forest species, thus accounting for differences in richness between the two types of secondary forests. The present findings would appear to support the conclusions of Veddeler *et al.* (2005) who, in their work on butterflies in central Sulawesi, recognised the significance of secondary forests, especially in older successional stages, in the conservation of tropical biodiversity.

The results indicating a low mean number of species per sample in the farmland result from habitat structure. The farmland sites were largely cleared land with no significant tree growth, canopy or understorey, thus representing a heavily modified ecosystem to which forest species have not adapted, therefore creating deterministic extinctions as described by Sutherland (2000) and Pullin (2002). Further, it could be argued that as the farmland consists largely of monoculture crops, plant diversity in any given area would be comparatively low in relation to the mosaic of microhabitats represented in any pristine forest ecosystem. This lack of niches would limit the number of generalist species that could exploit the habitat change, and hence species richness is low. These results are in concordance with the findings of Sodhi *et al.* (2005a), who recorded mean avifaunal species numbers in farmed plantations as 15.67 ± 1.07 in contrast to a mean species richness of 31.99 ± 1.38 in primary forest, and of Trainor (2007), who reported comparable results. However, species estimates obtained from the non-parametric tests and the rarefaction curves predict cleared farmland to contain the highest total number of species, and primary forest the lowest. This could result from the heterogeneous nature of the cleared farmland. While the mean number of species per sampling point was low in the farmland, the high species richness predicted to occur across the entire agricultural area could result from the high spatial variability in vegetation and land-use; this would create a broad range of habitat niches on a larger spatial scale which in turn could support a more diverse avifauna than the more spatially contiguous primary forest. The high number of species predicted in the cleared farmland could also be a function of its proximity to more intact forest environments; this could result in forest specialists not typically found in agricultural land occurring as foragers based in roosts in adjacent forest habitats. Despite this proximity, the cleared farmland shows a general decline in the richness of endemics and birds classified by Coates and Bishop (1997) as forest species. This decline is in concordance with the findings of Peh *et al.* (2005), who reported only 28%-32% of birds found in primary forest as also found in mixed-rural habitats, with estimates of species richness in agricultural land being even lower. These findings support the arguments noted by Fermon *et al.* (2005); that higher overall species richness does not imply higher conservation value and that the contribution of land-use systems to global biodiversity should be evaluated with caution, even when high species richness estimates are found. This is further demonstrated by the Mantel test cross-similarity community comparisons, which indicate that no significant similarity exists between the compositions of farmland and forest bird assemblages. Species summaries show that community structures in these farmland sites are dominated by wide-ranging generalist species, including representatives from several families that were completely absent in forest habitats (i.e.; Ardeiidae, Rallidae, Hirundinidae). This persistence of generalist species in these habitats over specialist insectivores and frugivores is concurrent with the findings of Sodhi *et al.* (2005a), while the apparent high vulnerability of regional endemics to heavy disturbance is concomitant with studies by Trainor (2007) and Posa & Sodhi (2006). Indeed, our results would appear to suggest that the specialisation of many of these endemic species is extremely fine, as in the areas of heavy disturbance certain endemic species are replaced by very similar generalist species which fulfil a comparable ecological role. Examples of this effect can be seen in population comparisons of endemics and widespread generalist species in the same genus: the Bay Coucal (*Centropus celebensis*) and Lesser Coucal (*Centropus bengalensis*), and the Sulawesi White-eye (*Zosterops celebense*) with the Lemon-bellied White-eye (*Zosterops consobrinorum*) (Figure 4.5). These results are in accordance with those for the abundance of endemics overall, which suggest that while many endemic species are abundant in both primary and secondary forests, they are virtually absent from the areas of heaviest disturbance, being replaced by generalist species not found in naturally vegetated areas. This further demonstrates the vulnerability to heavy anthropogenic disturbance of Buton's endemic avifauna and highlights the critical differences between the effects of intermittent logging and shifting cultivation which permit the regeneration of secondary forest and clearance for agriculture which largely eliminates the forest habitat.

Results indicating *R. cassidix* as highly vulnerable to even moderate environmental disturbance conflict with findings in certain other studies. Sodhi *et al.* (2005a), for example, found that high numbers of the species could be found even in degraded mixed-rural habitats, and Cahill (2003), while acknowledging the reliance of hornbill populations on large trees, describes *R. cassidix* as being fairly catholic in habitat preference. However, the negative correlation between large tree and *R. cassidix* abundance found in this study is conclusively powerful, and similar trends, at least in cleared farmland, have been found in the population dynamics of similar species such as Blyth's Hornbill (*Rhyticeros plicatus*) and Rhinoceros Hornbill (*Buceros rhinoceros*) (Marsden and Pilgrim 2003, Anggraini *et al.* 2001). Similar patterns of decline have also been found in other large-bodied Sulawesi endemics.

Strong negative relationships between abundance of large-bodied forest birds and increasing disturbance have been reported and discussed in numerous other studies. Suggestions for the apparent extirpation vulnerability of these species include occurrence at naturally low densities, large habitat patch requirements, low reproductive rates and increased vulnerability to hunting (Boyer 2008, Sodhi *et al.* 2004, Gaston and Blackburn 1995). In the case of *R. cassidix,* a likely explanation may relate to deterministic extinction processes. Cahill (2003), Anggraini *et al.* (2000) and Coates and Bishop (1997) describe how hornbill species are dependent on large, mature fruit-bearing trees to provide perennial feeding grounds and roosts, thus as habitat disturbance reduces the availability of these large trees, so the abundance of *R. cassidix* declines correspondingly. Findings here accord with those from previous work in Central Sulawesi that has demonstrated the importance of trees in structuring tropical forest habitats and in providing resources (Kessler *et al.* 2005).

4.6 - CONCLUSION

This study has demonstrated that the response of avifaunal assemblages to anthropogenic disturbance in the Lambusango reserve is subject to considerable complexity. Overall, avian species richness per study site increases between primary and secondary forest and then decreases through disturbed secondary forest. Such variations may be attributable to temporal dynamics and relative abundances of endemics and generalists throughout the phases of initial forest disturbance, establishment and maturation of secondary forest. Further work is needed to examine such dynamics in greater detail and this will benefit from the ongoing long-term monitoring programme in Buton.

This research suggests that forest species and many specialist endemic species with a high conservation priority are intolerant of heavy disturbance, although many species persist in moderately disturbed forest ecosystems. Such responses have also been found for other faunal group such as herpetofauna in this region (Gillespie *et al.* 2005). This suggests that secondary forest ecosystems can have an important role in supporting endemics as well as overall avian diversity, although disturbed secondary forest is shown to be ineffective in conserving some of the region's larger-bodied endemic species with lower ecological tolerance. Secondary forest in later successional stages is indicated to have a particularly high conservational value, possessing a community structure similar to that found in primary forest and supporting high numbers of endemics as well as sizable populations of the large-bodied species evaluated. This is encouraging, given the large areas of disturbed forest ecosystems remaining on Sulawesi (Cannon *et al.* 2007). These findings therefore suggest the importance of allowing adequate regeneration of disturbed areas. However, further work is needed to determine the extent to which populations within the secondary forest are dependent upon continual recruitment from adjacent primary forest refugia, and whether critical proportions of primary and secondary forests are needed for sustainability at the landscape scale. Hence, given the biological vulnerability of islands such as Buton, which are small in size and separated from the larger land masses, strong protection of the regions remaining primary forest should be a focus for conservation efforts if viable populations of these range-restricted endemics are to be successfully maintained in Wallacea.

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CHAPTER 5 - THE EFFECTIVENESS OF A MESOAMERICAN 'PAPER PARK' IN CONSERVING CLOUD FOREST AVIFAUNA

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Entrance to Cusuco National Park

5.1 - SUMMARY

Mesoamerican cloud forests are important centres of biodiversity, but are under severe pressure from anthropogenic activities. Protected areas have been established to conserve remaining areas of this habitat, but it is debatable how effective these under-resourced 'paper parks' are in preserving biodiversity. This study investigates this issue utilising species-level data, examining composition of avifaunal communities within an undermanaged cloud forest park. Research was conducted in the Parque Nacional Cusuco, North-West Honduras. Results indicate that overall avian species richness is greater in the less heavily protected buffer zone than the nominally inviolate core zone. However, core zone areas are shown to be effective in preserving threatened and range-restricted species. Results therefore demonstrate that buffer zone forest has a comparably reduced conservation value, but the overall park system appears to be effective in conserving the core zone. These findings should be taken into account when considering extensions to protected area networks in Mesoamerica.

Key Words: Avifauna, Biodiversity Cloud forest, Protected areas

5.2 - INTRODUCTION

The forests of Mesoamerica are experiencing some of the highest rates of habitat loss globally, with an estimated 80% of original vegetation cover having already been lost or modified (Brooks *et al.* 2002, Achard *et al.* 2002, Laurance, 1999). Continued habitat destruction will have severe conservation implications for this globally important biodiversity 'hotspot' (Brooks *et al.* 2002, Myers *et al.* 2000), including local avifaunal communities. More than 1000 bird species have been recorded in Mesoamerica, including 208 regional endemics (19% of total species), although high species extinction rates are expected if current deforestation patterns continue (Conservation International 2007, Brooks *et al.* 2002, Stattersfield *et al.* 1998). Concerns of impending biodiversity loss are especially valid with regard to montane cloud forest, an ecosystem where unique biogeographical characteristics have facilitated a highly specialised bird community which is both diverse and displays a high rate of endemism (Bubb *et al.* 2004, Powell and Palminteri 2001, Jankowski and Rabenold 2007, Eisermann and Schulz 2005, Renjifo 1997). Despite comprising only 2.5% of global forest ecosystems (Bubb *et al.* 2004), cloud forests provide habitats for 10% of all range-restricted bird species (Stattersfield *et al.* 1998) as well as being centres of endemism for plants (Bubb *et al.* 2004), reptiles and amphibians (Wilson and McCranie 2003), and invertebrates (Anderson and Ashe 2000). Cloud forests also represent valuable refugia habitats for many endangered species marginalised by destruction of lowland forest habitats (Aldrich 1997).

Despite globally significant ecological importance, Central American cloud forests are a critically endangered ecosystem. For much of the early-mid 20th century the integrity of these forests remained relatively intact due to their inaccessible nature, but they are now becoming increasingly vulnerable to exploitation due to expanding regional infrastructure and demographic pressures (Powell and Palminteri 2001, Aldrich 1997) and are disappearing with greater rapidity than the region's remaining lowland forests (Solorzano *et al.* 2003). Remaining pockets of Mesoamerican cloud forest are now restricted to small scattered fragments (Cayuela *et al.* 2006) and as such are highly vulnerable; Mejia *et al.* (2001) estimated that if current deforestation trends continue, all Honduran cloud forest could be lost by 2021. Further habitat degradation would have profound consequences for the region's biodiversity, as many cloud forest species have restricted geographical ranges and narrow ecological tolerance, thus are highly vulnerable to local extinction by landscape modification (Jankowski and Rabenold 2007, Mckinney 1997, Renjifo 1997).

In response to the threat of impending biodiversity loss, extensive governmental action was taken in the 1980s and 1990s to establish a protected area network for remaining cloud forest areas (Bonta 2005). In Honduras the national system of protected areas (Sistema Nacional de Areas Protegidas en Honduras – SINAPH) was developed following the Cloud Forest Act (1987) and the General Environment Law (1993). By 2001 almost 100 protected areas had been established, including 37 high altitude montane forest habitats colloquially referred to as 'cloud forest' (Vreugdenhill *et al.* 2002, Pfeffer *et al.* 2001, Cruz 1993). These SINAPH areas largely followed the structural blue-print defined by UNESCO's Biosphere Reserve concept, consisting of a nominally inviolate core zone (Zonas nucleos) encircled by a buffer zone (Zonas de amortiguamiento) where some sustainable economic and agricultural activity is permitted. The latter theoretically provides a reconciliation of the needs of local people and the safeguarding of biodiversity with an aim of minimising human activities in the core (Li *et al.* 1999). The SINAPH system remains the central strategy for biodiversity conservation in Honduras and current management policies propose the extension of the existing network by expanding present reserves (Bubb *et al.* 2004) and by establishing up to 41 new protected areas (Pfeffer *et al.* 2001).

While in theory the SINAPH system represents a sound solution towards mitigating biodiversity loss, in practice applied management action has been minimal, leading to criticisms that the region's protected areas are little more than 'paper parks' with limited realised protection. The Global Environment Facility (2005) describes how most Honduran parks are not actively managed entities, lacking any kind of conservation-related infrastructure. Bonta (2005), Reyes and Cruz (2004) and Powell and Palminteri (2001) also describe how the vast majority of protected areas are chronically under-staffed, under-funded and lacking any kind of management or facilities. The phenomenon of paper parks has been reported widely across the tropics (Struhsaker *et al.* 2005, Curran *et al.* 2004, Peres and Terborgh 1995) and concerns have been raised that the continuation of these non-managed entities is no better or perhaps even worse than having no protective legislation at all (Liu *et al.* 2001). Frequent problems associated with paper parks include the incapacity to prevent forest clearance and extraction of natural resources (Curran *et al.* 2004) and an inability to regulate activities in the buffer to provide protection for the core (Kramer *et al.* 1997).

While the establishment of paper parks has been heavily criticised as being ineffective and unsustainable, counter-arguments suggest that a considerable amount of nominal protection can be granted solely by designating an area as 'protected', even if active management is scarce or non-existent (Struhsaker *et al.* 2005, Bruner *et al.* 2001, Myers *et al.* 2001). Most existing research examining the effectiveness of paper parks has been applied on broad, regional or global scales with analysis being based on satellite sensing imagery of forest cover (Joppa *et al.* 2008, Curran *et al.* 2004) or questionnaire data (Bruner *et al.* 2001). We know of few studies which have conducted a focussed study on a single case-study park, or assessed the effectiveness of paper parks in protecting biodiversity utilising species-level compositions of a taxonomical group.

This study seeks to address this by examining the composition of avifaunal communities in a single Honduran cloud forest reserve with minimal active management. Avifaunal groupings were utilised, as birds are a comparatively well-understood taxonomical group (Stotz *et al.* 1996) that can be surveyed quickly and efficiently via indirect methods and have good ecological congruence with other taxa (Schulze *et al.* 2004, Howard *et al.* 1998). The study analyses species richness estimates and finer-scale species assemblages of avifaunal communities in different spatial regions of the park, with different levels of protection. Particular emphasis is placed upon species with a high conservational importance, such as IUCN red-listed species and range restricted species dependent on high quality cloud forest habitat, as well as groupings of species considered to be good indicators of anthropogenic influence. The research tests the hypothesis that the relative densities of the species of high conservation importance will be low across the park if the protective status of the park is ineffectual, with comparatively high densities of these species occurring, particularly in the core zone, if the park is successfully preserving the area. This will enable an evaluation of how effective a paper park can be in protecting cloud forest avifaunal communities.

5.3 - METHODS

5.3.1 - Study Site

Research was undertaken in Parque Nacional Cusuco; a 23,440 hectare area of tropical montane cloud forest located in the Departamento Cortez, North-West Honduras (15° 29.8’- 15° 32.1’N / 88° 13.0- 88° 26.3’ W) (See Figure 1.7 in Introduction). The park is divided into a 7,690 hectare core zone and an encompassing 15,750 hectare buffer zone. Elevation of the park ranges from 500 – 2242m above sea level (Lenkh 2005). The middle and higher elevations of the park correspond with the mid-lower band of the altitudinal range of cloud forest located on coastal mountains, as defined by Bubb *et al.* (2004). The core zone occupies the higher elevations of the park (>circa 1500m) with the encircling buffer zone located on the immediately surrounding lower slopes. Climatic information for the park is provided in Figure 1.9 in the Introduction Chapter. Cusuco displays a lack of administration typical of a 'paper park'. It has minimal active management with little infrastructure and only five rangers are employed to monitor the entire entity. These ranger patrols cover only 60% of the park's area (Lenkh 2005). Funding is far below that needed to govern an area of its size and financing has dropped markedly in recent years, from approximately $132, 000 in 1999/2000 to $40,000 in 2001/2002 (Operation Wallacea 2007, Lenkh 2005). The park is under considerable environmental pressure, with an estimated 30 – 40,000 people living in 30 communities within the borders of the protected area and with new roads providing access to many previously inaccessible areas of forest (Lenkh 2005).

5.3.2 - **Habitat surveys**

Vegetation surveys were conducted at each sample point in order to examine whether variations in avifaunal assemblages across park zones are related to habitat structural properties. 20m x 20m plots divided into four quadrants were set up around the centre of each point. Canopy density was assessed at each of these plots utilising a Perspex canopy scope with 25 light-sensitive holes. An observer viewed the canopy through this scope and counted the number of visible holes; this value was then converted to a proxy percentage value (Brown *et al.* 2000). Five of these measurements were taken per plot; one in each quadrant and one in the plot centre. The number of large (diameter at breast height >50cm) trees were counted at each plot, with the number and mean circumference of large trees being recorded. Undergrowth density was assessed by placing a 0.5m pole vertically and counting the number of times any vegetation made contact with it. This was repeated 32 times at each plot. Slope was also calculated at each sample point using a clinometer to measure the angle between the highest and lowest point in the plot.

5.3.3 - Bird surveys

Field work was conducted over an eight week period between June – August 2007. Sampling was conducted at 126 points across three zones of the park; 59 points in the centre of the core zone, at altitudes between 1450 – 2200m (subsequently referred to as ‘deep core’), 39 points within transitional core zone areas close the to the buffer/core boundary between 1350 – 1700m (‘boundary core’) and 28 points in the buffer zone at altitudes of 700 – 1450m (‘buffer’). A distance of >200m was kept between points to ensure independence of samples. Fixed-radius point count surveys (Bibby 2002) were conducted at each point by a team of four experienced ornithologists familiar with neotropical avifauna vocalisations. Point-count methodologies were identical to those previously described in Chapter 3. Details can be found in section 3.3.2 of this chapter. Locations of point-count transects within the park are identical to those displayed previously in Figure 3.1.

5.3.4 - Statistical analysis

Species richness estimates were made for each park zone using a series of non-parametric species richness estimators calculated utilising the software package EstimateS (Colwell 2006), with the mean value of these being utilised as an approximate species richness estimate. Richness estimates were also made utilising a sample-based rarefaction curve comparing number of individual contacts against numbers of species recorded. This was constructed utilising PC-ORD Version 5.0. These analyses were used as they can account for differences in sampling effort among study sites and for natural levels of sample heterogeneity in the data (Walther and Moran 1998). Non-parametric species estimators provide a corroboration of the results of the rarefaction curves, which is important because information in larger samples may be lost when they are 'rarefied' to the size of the smallest sample in the analysis (Sodhi *et al.* 2005). Rarefaction curves and non-parametric species estimators were also constructed to estimate richness of species defined by Howell and Webb (2005) as being restricted to highland forest habitats >1000m, thus discounting endemic species found at lower altitude sites of the buffer zone associated with non-cloud forest ecosystems. This analysis excluded species defined as having a maximal altitudinal range of <1000m ± 100m and those whose minimal altitudinal range was >1000m ± 100m; thus reducing altitudinal influence as all species altitudinal ranges overlap. All sites in the buffer zone with an altitude of <1000m were also discounted from analysis.

The 1700m altitudinal range of our study points is not as wide as those used by previous studies to exemplify avian species turnovers (Navarro 1992), but it is still necessary to establish whether any variations between the different park zones are genuine and not primarily due to the elevation gradient. This was done by analysing the variations in the total number of bird species detected at each point after three repetitions with respect to the altitude of each point and park zone using an ANCOVA test (Zar 1999).

Kruskal-Wallis one-way ANOVA (Zar 1999) was used to compare across the three park zones the densities of a discreet number of key species with a high conservational importance, and Galliform (game bird) species, as this family has been considered a good bio-indicator of forest quality (Price 2006, Borges 1999). Suitable high priority species identified were the Resplendent Quetzal (*Pharomachrus mocinno*), a Near-Threatened species widely considered a flagship species for neotropical cloud forest ecosystems (IUCN

2007, Birdlife International 2009), and the Highland Guan (*Penelopina nigra*), a cracid species classified as vulnerable by the IUCN (2007). Galliform species indentified were *Penelopina nigra*, Crested Guan (*Penelope purpurascens*), Plain Chachalaca (*Ortalis vetula*), Buffy-crowned Wood Partridge (*Dendrortyx leucophrys*) and Spotted Wood-quail (*Odontophorus guttatus*).

The five most abundant bird species detected in each of the park zones were also calculated and compared. Compositions of three avian families, Turdidae, Troglodytidae and Corvidae were also examined to determine whether any difference in the constitute species of these families occurred between the park zones. All species detected from these families were researched using Howell and Webb (2005) and Stiles *et al.* (1990) to determine spatial range and habitat preferences and hence relative conservational value, with relative densities of each of these species being plotted and compared. The total number of species spatially restricted to the Mesoamerican hotspot detected at each site was compared utilising Kruskal-Wallis one-way ANOVA.

5.4 - RESULTS

A total of 2515 individual birds from 124 species were recorded by the point count surveys. Unidentified contacts constituted 7.9% of all recordings, and these were excluded from analysis. Most contacts (88%) were detected by sound, with 12% being detected visually.

Vegetation surveys (Table 5.1) demonstrate that considerable variation in habitat structure exists across the park, with large trees being less frequent in the buffer zone compared to core zone areas (Mean of 7.85 per site in buffer compared to 17.61 per site in boundary core) and possessing a smaller DBH (83cm mean in buffer sites compared to 108.56 in deep core).

Table 5.1 - Vegetation properties for deep core, boundary core and buffer zone points within Cusuco National Park, Honduras. ± indicates variance to 1 standard deviation.

	Deep core zone		Boundary core zone		Buffer zone	
Vegetation property	Mean	St.dev	Mean	St.dev	Mean	St.dev
Mean canopy cover (%)	89.5	5.85	90.4	6.34	88.59	8.95
Mean frequency of large trees (>50cm circum)	14.4	7.69	17.61	7.06	7.85	4.4
Mean breast height diameter of large trees (cm)	108.56	22.62	105	28.7	83	18.01
Undergrowth density	1.4	0.64	1.72	0.41	1.6	0.59
Number of Saplings	3.49	1.9	2.55	1.91	3.68	2.95
Slope angle (°)	32.97	12.33	30.18	14.67	34.29	13.83

Species accumulation curves (Figure 5.1) demonstrate clear differences in species richness between deep core, boundary core and buffer zone points. Based on the non-parametric species estimators (Table 5.2a), deep core points (average species estimate = 67.42) are predicted to have the lowest species richness, followed by boundary core points (average species estimate = 109.14), with buffer zones having the highest predicted richness of all points (average species estimate = 111.64).

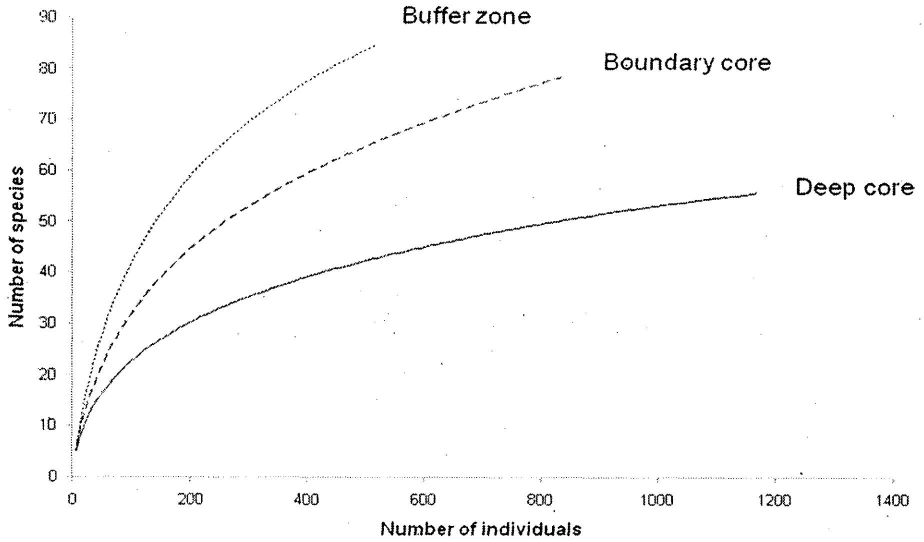

Figure 5.1 - Sample-based rarefaction curves comparing number of individuals against number of species detected in deep core, boundary core and buffer points within Cusuco National Park, Honduras.

Figure 5.2 illustrates how mean species richness of avifaunal assemblages in buffer, boundary and deep core zone points vary in relation to elevation. The graph displays a general pattern of decline in diversity with increasing altitude, from a mean species richness of 17.71 at points with an altitude of 600 – 800m to just 7.86 species detected per point at altitudes of 2100 – 2250m. This trend is consistent with findings of previous studies (Peterson *et al.* 1993, Navarro 1992). However, the graph also demonstrates a clear difference in species richness of core and buffer zone points at around 1300-1500m, the altitudinal zone where the core-buffer zone boundary occurs. Mean species richness detected at buffer zone points within the 1400-1500m boundary is 9.6, while in the boundary core zone this rises to 13.22. This is further demonstrated in the offset of regression lines 1 and 2, (ANCOVA $p = <0.05$ for zone variable) implying a real difference in richness of avifaunal groupings in core and buffer zone points for reasons independent of altitude.

*Table 5.2 – Non-parametric species richness estimates for **a)** all bird species, and **b)** highland species at altitudes of >1000m in deep core, boundary core and buffer points within Cusuco National Park, Honduras. N represents sample size. Sp obs and Ind obs represent total number of species and individuals observed, respectively. ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, Bootstrap, MMRuns and MMMeans are non-parametric species estimators (Colwell and Coddington 1994).*

a)

Parameters	Deep core	Boundary core	Buffer zone
N	59	39	28
Sp obs	56	79	85
Ind obs	1168	834	515
ACE	76.39	116.34	116.49
ICE	76.39	117.74	113.9
Chao1	66.9	124.11	116.23
Chao2	66.84	126.91	113.65
Jack1	71.91	108.74	113.65
Jack2	77.89	130.43	129.41
Bootstrap	63.44	91.5	97.87
MMRuns	52.89	83.76	102.22
MMMeans	54.13	82.77	101.31
Average species estimate	**67.42**	**109.14**	**111.64**

b)

Parameters	Deep Core	Boundary Core	Buffer zone >1000m
n	59	39	28
Sp obs	23	23	11
Ind obs	880	539	106
ACE	24.27	29.17	11
ICE	24.25	29.02	11
Chao1	23.16	24.66	11
Chao2	23.16	24.65	11
Jack1	24.98	27.95	11
Jack2	24.05	27.99	11
Bootstrap	24.55	25.51	11.47
MMRuns	23.07	23.09	14.08
MMMeans	23.12	23.99	13.73
Average species estimate	**23.85**	**26.22**	**11.69**

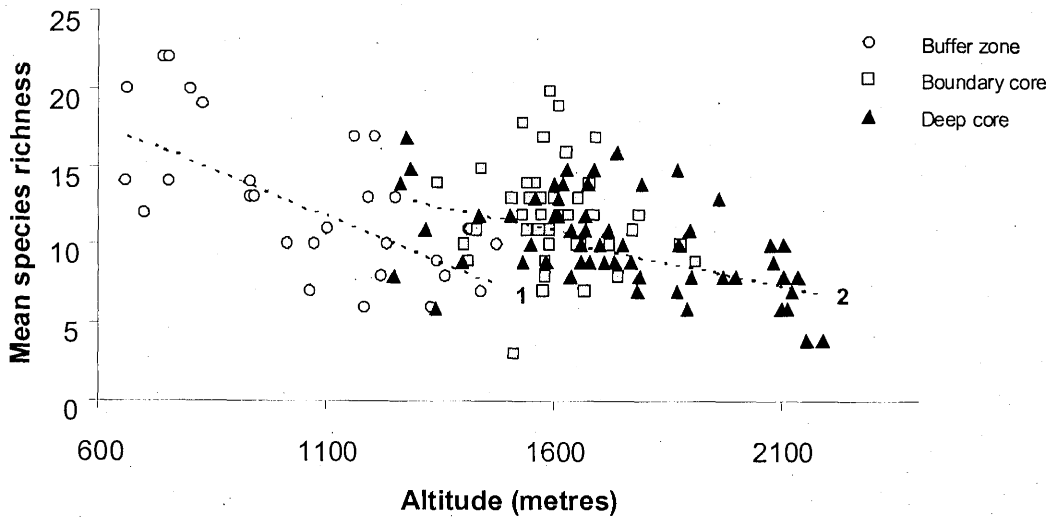

Figure 5.2 - Variation in species per sample with altitude for buffer, boundary core and deep core zone points within Cusuco National Park, Honduras. Lines 1 and 2 represent best-fit lines for buffer and deep core zone points respectively (ANCOVA altitude variable F = 30.286, p <0.05. ANCOVA zone variable F = 10.325, p <0.05).

While overall species richness of avian communities appears to decline with increasing protective legislation, more fine-scaled analysis of specific avian species and families display contrasting patterns. Figures 5.3a and 5.3b demonstrate variations occurring in the population of IUCN Red-listed species between the different park zones. Population density of *P. mocinno* is shown as relatively high in both deep and boundary core points, with a mean density of 0.19 birds per sample in areas deep within the core zone and 0.17 birds per sample in boundary zones. However, this drops to a value of near absence (0.01 birds per sample) in buffer zone areas. Similar patterns are demonstrated in population variations of *P. nigra*, which is most abundant within the deep core (0.35 birds per sample), occurs at slightly lower densities in boundary core points (0.29 birds per sample) and is extremely scarce (0.12 birds per sample) in the buffer zone. Figure 5.3c shows that variations in density of Galliformes follow those of *P. nigra*, falling from 0.382 birds per sample in deep core points to just 0.145

in the buffer. However, relative density of Galliformes peaked in boundary core points rather than in the deep core.

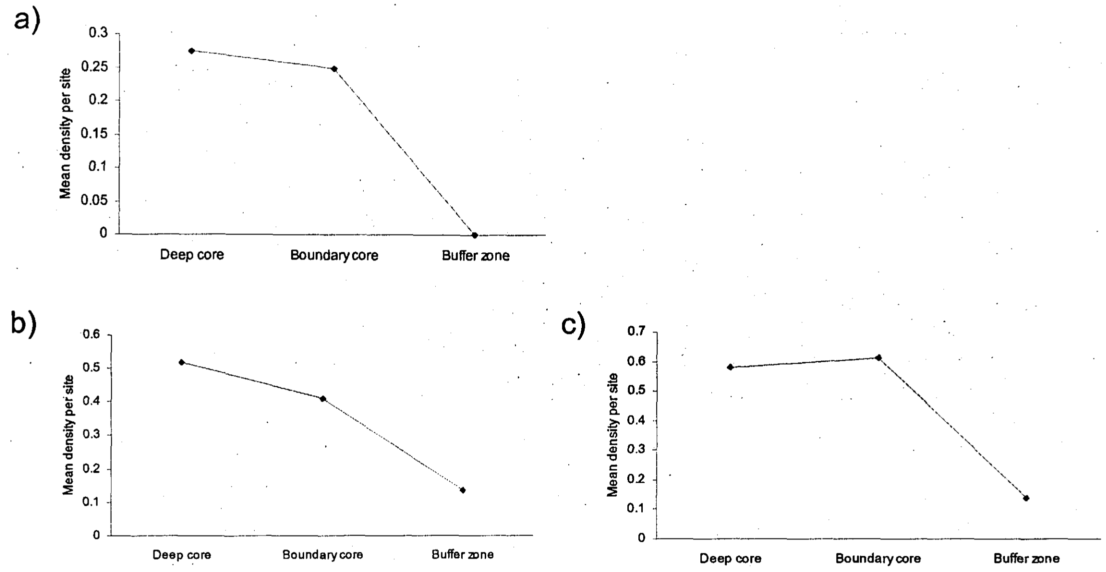

*Figure 5.3 - a: Mean Resplendent Quetzal (**Pharomachrus mocinno**) (Kruskal-Wallis H = 6.16, p = 0.046), b: Highland Guan (**Penelopina nigra**) (Kruskal-Wallis H = 8.309, p= 0.016) and c: Galliform (Kruskal-Wallis H = 18.391, p = <0.005) contacts per sample in deep core, boundary core and buffer points within Cusuco National Park, Honduras.*

Table 5.3 indicates that substantial differences occur in the most frequently detected species between deep and boundary core and buffer points. Sampling in the core and boundary yielded the same five most frequently detected species in identical hierarchy; Slate-colored Solitaire (*Myadestes unicolor),* Common Bush-Tanager (*Chlorospingus ophthalmicus),* Gray-breasted Wood-Wren (*Hemicorhina leucophrys*), Black-headed Nightingale Thrush (*Catharus mexicanus*) and Slate-throated Redstart (*Myioborus miniatus).* All five of these species are confined to highland forest habitats, with one being restricted to Northern Mesoamerica, one being confined within Mesoamerica and three being found in montane forests across a wider spatial scale. There was little overlap between these species and the most common birds detected in the buffer zone. Two species – *C. ophthalmicus* and *M. unicolor* were shared with the core zone points. The three most common species, White-throated Thrush (*Turdus assimilis*), Brown Jay (*Cyanocorax mori*) and Clay-colored Thrush (*Turdus grayi*), are all species found at a variety of elevations and are widely distributed across the Neotropics (Howell and Webb 2005).

Table 5.3 - Five most commonly occurring species in deep core, boundary core and buffer points within Cusuco National Park, Honduras. Numeration reflects spatial range of species. [1] Highland species restricted to Northern Mesoamerica [2] Highland species restricted to Mesoamerica. [3] Highland species distributed widely across the Neotropics. [4] Species found at a variety of altitudes and with a wide distribution across the Neotropics. Based on Howell and Webb (2005) and Stiles et al. (1990).

	Deep core	**Boundary core**	**Buffer zone**
1	*Myadestes unicolor* [1]	*Myadestes unicolor* [1]	*Turdus assimilis* [4]
2	*Chlorospingus ophthalmicus* [3]	*Chlorospingus ophthalmicus* [3]	*Cyanocorax morio* [4]
3	*Hemicorhina leucophrys* [3]	*Hemicorhina leucophrys* [3]	*Turdus grayi* [4]
4	*Catharus mexicanus* [2]	*Catharus mexicanus* [2]	*Chlorospingus ophthalmicus* [3]
5	*Myioborus miniatus* [3]	*Myioborus miniatus* [3]	*Myadestes unicolor* [1]

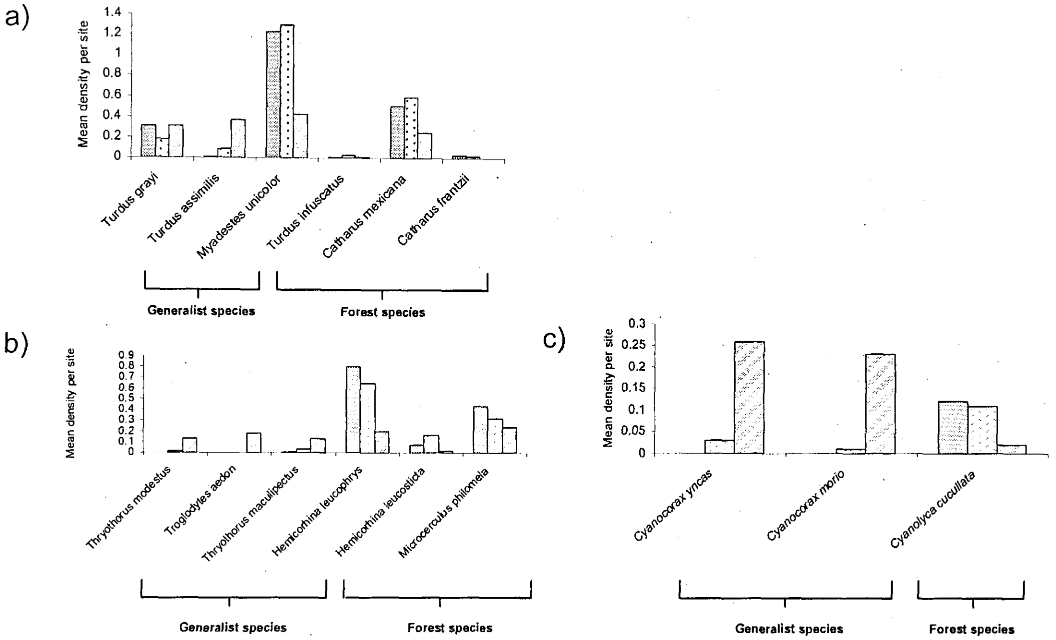

Figure 5.4 - Mean relative density of a: Turdidae b: Troglodytidae and c: Corvidae species detected by point count samples in deep core, boundary core and buffer points within Cusuco National Park, Honduras. Plain bars represent mean richness in core zone points. Spotted and striped bars represent boundary and buffer points respectively. Generalist species are defined as species with wide spatial distributions and habitat associations. Forest species are defined as those confined to montane forest habitats >1000m by Howell and Webb (2005).

Figure 5.4 demonstrates variations in the species compositions of three avian families (Turdidae, Troglodytidae, Corvidae) between deep core, boundary core and buffer zone points. Figure 5.4a shows how the most abundant species of thrush in buffer zone points are *M. unicolor* with 0.43 birds per sample, *T. assimilis* with 0.37 birds per sample, and *T. grayi* with 0.31 birds per sample. While *M. unicolor* is a species restricted to montane habitats in Northern Central America, *T. assimilis* and *T. grayi* are both generalist species found in a wide range of habitats across the Neotropics. These generalist species occur at low densities within core zone areas of forest, particularly *T. assimilis* which has a mean density of just

0.01 birds per sample in deep core points. While the relative density of generalist species appears to be low within both deep and boundary core zones, cloud-forest specialists with restricted spatial distribution appear to be considerably more abundant. *M. unicolor* occurs at densities far higher than in the buffer zone (1.3 birds per sample in boundary core points), as does *C. mexicana,* (0.6 birds per sample in boundary core points). The rare, range-restricted Black Thrush (*Turdus infuscatus*) and Ruddy-capped Nightingale thrush (*Catharus frantzii*), which were totally absent from the buffer zone also occur at low densities in core zone points.

The pattern of generalist species occurring in the buffer zone and species with narrower habitat requirements being found in the core is also displayed in other avian families. Figure 5.4b shows how five of the six species of wren recorded in the study can be found at relatively low densities (0.13 – 0.2 birds per sample) in buffer zone points. However, three species, the Plain Wren (*Thryothorus modestus*), House Wren (*Troglodytes aedon*) and Spot-breasted Wren (*Thryothorus maculipectus*) are almost entirely absent from both deep and boundary core zone points; each of these are generalist species found in a wide variety of forest and non-forest habitat types. Montane forest specialists such as the Gray-breasted and White-breasted Woodwren (*Hemicorhina leucophrys* and *Hemicorhina leucosticta*) are found at considerably higher densities than in buffer zone points. Figure 5.4c indicates that this trend can also be found in corvid species. The Green Jay and Brown Jay (*Cyanocorax yncas and Cyanocorax morio*) are both generalist species found at relatively high densities in the buffer zone while being nearly absent from both core zone categories. In contrast, the Azure-hooded Jay (*Cyanolyca cucullata*) is a range-restricted montane forest specialist found in some abundance in both deep and boundary core zone areas but occurring only at very low densities in the buffer zone.

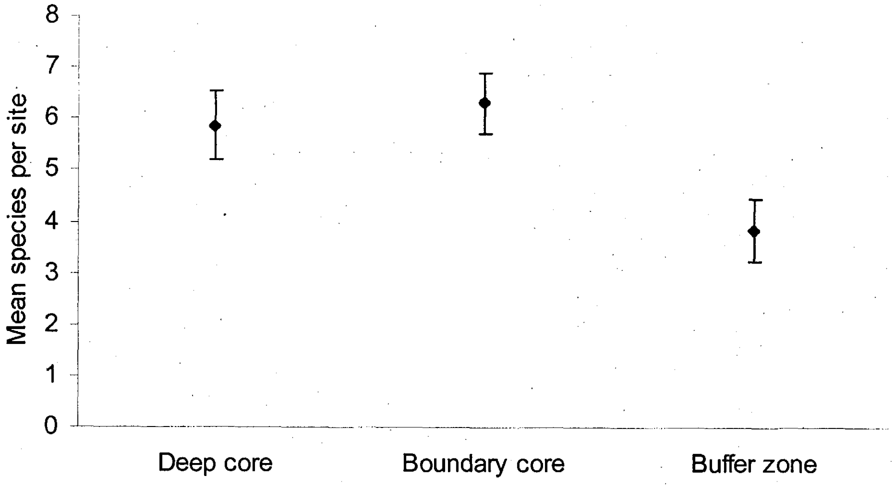

Figure 5.5 - Mean relative density of bird species restricted to the Mesoamerican hotspot per sample in deep core, boundary core and buffer points within Cusuco National Park, Honduras (Kruskal-Wallis $H = 14.04$, $p = <0.05$).

The discussed spatial pattern of generalist and cloud forest bird species within the park is further highlighted in Figures 5.5 and 5.6. Figure 5.5 demonstrates that significantly greater species richness per sample of bird species restricted to the Mesoamerican hotspot occurs in deep and boundary core zone points (5.89 and 6.34 species per sample respectively) than in the buffer zone (3.86 species per sample) (Kruskal-Wallis $p = <0.05$). Figure 5.6 and Table 5.2b show that significantly higher richness of species restricted to highland forest habitats occurs in core-zone habitats than in buffer-zone habitats which are also in their altitudinal range.

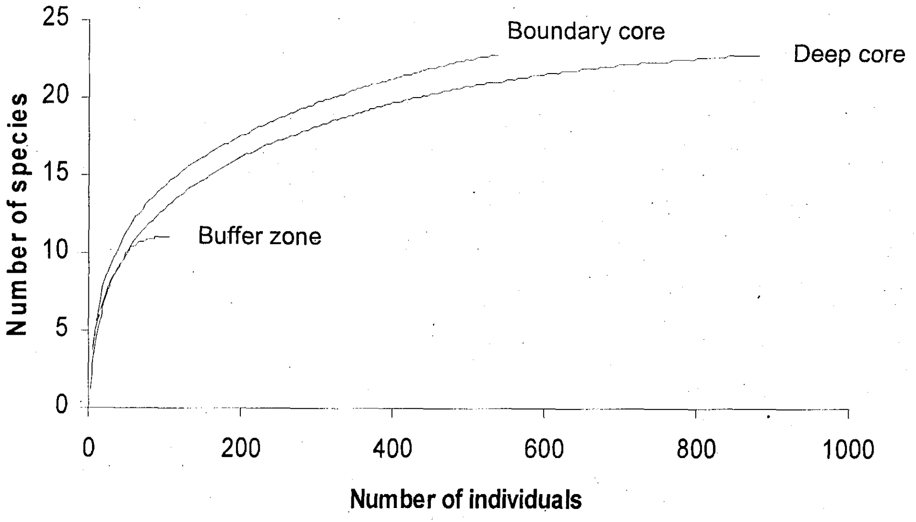

Figure 5.6 - Sample-based rarefaction curves displaying number of individuals birds detected against number of highland forest species detected in deep core, boundary core and buffer sites at altitudes of>1000m in Cusuco National Park, Honduras.

5.5 – DISCUSSION

Results demonstrate that while buffer zone habitats possess a richer avifauna than core zone habitats, high species richness does not necessarily correspond to high conservation value, as range-restricted and IUCN-listed species are largely concentrated in core zone sites.

The increase in overall avian species richness with increasing distance from the central deep core of the park could appear anomalous when viewed in the context of other research. Numerous studies (Barlow *et al.* 2007, Waltert *et al.* 2004, Blake and Loiselle 2001) have found avian communities in disturbed, mixed-rural and secondary forest type habitats similar to those of Cusuco's buffer zone to be considerably more depauperate in species than natural primary forest vegetation, such as that found in the park's core. There are several potential explanations for this. Altitudinal variation is likely to be a key control in species richness variations, as numerous studies have demonstrated strong negative correlations between diversity and increasing elevation (Sanchez-Gonzalez and Lopez-Mata 2005, Peterson *et al.* 1993, Navarro 1992). It could also be possible that buffer-type habitats could support a richer avian diversity than core zone forest due to possessing a more heterogeneous landscape. The high spatial variation in vegetation, land-use and the influence of edge effects may have created a broader range of habitat niches on a larger spatial scale which is capable of supporting a more diverse avifauna than more spatially contiguous primary forest in the deep core. This is especially valid if these edge and secondary habitats occur in close proximity to primary forest landscapes, or retain substantial patches of forest, as is the case in Cusuco (Sodhi *et al.* 2005, Hughes *et al.* 2002, Greenberg *et al.* 1997).

Finer scale analyses of selected avian sub-groups, families and individual species with a high conservational value display a different trend to species richness. Results demonstrate that significantly more species endemic to the Mesoamerican hotspot and species restricted to highland forest habitats are found in core zone habitats compared to buffer zone habitats, even for species which share similar altitudinal ranges. Results also show that the two IUCN red-listed species detected by the point-count surveys, *P. mocinno* and *P. nigra,* are both almost exclusively confined to the core zone, with populations being highest within the deep core, decreasing slightly in boundary core points before dropping to almost negligible levels within the buffer. This may again be partially explicable due to altitudinal variations between the points. *P. mocinno*, for example, typically occurs at altitudes of 1400m> (Howell and Webb, 2005) so might not be found in the buffer zone regardless of land-use policies. However, the second half of the data collection period of this study coincided with the Quetzal's annual August – October altitudinal migration to elevations as low as 700m (Powell and Bjork, 2005, Solorzano *et al.*, 2000, Wheelwright, 1983), so the buffer zone should be within the species' altitudinal range at this time. *P. nigra* is also known to occur from altitudes of >900m (Howell and Webb, 2005, Renner, 2005[a]), which would incorporate a substantial proportion of the buffer zone. This suggests these species are largely confined to core zones for reasons of differential levels of anthropogenic disturbance, and hence degrees of protection afforded by the park, rather than altitude. Indeed Renner (2005[b]) and Solorzano *et al.* (2003) describe how forest quality is a prime limiting factor for quetzal abundance, as the species requires large, mature trees to provide sufficiently large nesting holes. This was demonstrated by Wheelwright (1983), who found that 74% of quetzal nesting points in a cloud forest occurred within core zone primary forest. The vegetation survey summary in Table 5.1 would seem to support this possibility, showing large trees (>50cm dbh) in the buffer zone to be less numerous and on average considerably smaller than in the adjacent core zone.

Vegetation structure and the density and average size of large trees may also explain the low abundance of *P. nigra* populations in the buffer zone. The Cracid Specialist Group (2007) and Brooks (2006) describe how most cracid species depend on undisturbed primary forest habitats with numerous large, mature trees, and Renner's (2005) study found that 86% of *P. nigra* observations were made in primary forest.

The pattern displayed in spatial variation of *P. nigra* population density also applies for galliform species as a whole, with mean density per sample falling dramatically between core and buffer zone. This is indicative of clear differentiation in management effectiveness in different areas of the park, as Galliformes are widely regarded as good indicators of forest disturbance, with populations being not only vulnerable to habitat modification but also heavily correlated with hunting intensity (Peres and Palacios 2007, Nawaz *et al.* 2001, Borges 1999).

This study has therefore shown that core zone avifaunal assemblages are dominated by cloud forest specialist species with relatively restricted ranges and narrow habitat tolerances, while buffer zone communities are largely comprised of generalist species with wide spatial distributions and broad habitat tolerances. Previous research has reported similar findings (Martin and Blackburn 2009), although other studies have shown that areas experiencing significant levels of anthropogenic land use can retain bird communities of equal importance to inviolate core zones (Bhagawar *et al.* 2005, Gillison *et al.* 1996). Variation in bird assemblages in this study could occur due to several factors. Altitude again may be a significant factor in determining relative density of range restricted species; Peterson *et al.* (1993) describes that, while species richness has a negative correlation with increasing altitude, proportions of endemism follow a reverse pattern, citing the example of Mexico where 5.6% of birds in montane forest were endemic compared to just 1.7% in lowland areas. However, the buffer zone points sampled within the present study were well within the recognized altitudinal ranges for most of these range-restricted species (Howell and Webb 2005, Stiles *et al.* 1990), and a highly significant turnover of range-restricted to generalist species occurred between buffer and boundary zone points both located between 1300 – 1500m. This therefore implies that differences in the proportions of range-restricted species are again in likelihood due to different levels of anthropogenic disturbance and associated park protection rather than altitude. Wijesinghe and Brooke (2004) explain that this could be because range-restricted species tend to be highly specialized, adapted to narrow habitat and dietary requirements due to the unique conditions created by their localized environment. Therefore they are unable to persist in buffer zone environments where edge effects significantly alter environmental characteristics. While most of these species are not currently listed by the IUCN as being under immediate threat of extinction, the threats to many range-restricted birds, particularly montane species, are believed to be underestimated (Harris and Pimm 2008, Brooks *et al.* 1999), and inherent narrow geographical range and ecological niches could make these species increasingly vulnerable if degradation of cloud forest ecosystems progresses. Therefore the range-restricted avifaunal communities of the core can be considered to be of significantly greater conservation priority than the widely distributed generalist species that dominate bird assemblages in the buffer.

The dominance of cloud forest specialists and persistence of IUCN red-listed species in the core zone suggests that, despite a lack of active management, the national park appears to be providing a certain degree of protection to avifaunal biodiversity at least within the park nucleus, and while the buffer seems to be depauperate in range-restricted specialist species, it does seem to be succeeding in its primary function of protecting the core. It could be argued that the higher altitude core zones have retained higher quality habitat types due to being more inaccessible and possessing topography that limits its potential for conversion to other land-uses. However Table 5.1 demonstrates that both deep and boundary core have an overall gentler relief than the encompassing buffer. The results of this study therefore support the findings of Bruner *et al.* (2007), Struhsaker *et al.* (2005) and Southworth *et al.* (2004) that paper parks can serve a function in preserving biodiversity. As this study has shown that disturbed buffer zone environments are currently fairly ineffectual in conserving high priority cloud forest species, plans for extending existing park boundaries, as noted by Bubb *et al.* (2004), may not be the most appropriate strategy, as any expansion would likely only encompass lower-slope areas which are unlikely to support the threatened or range-restricted cloud forest species absent in existing buffer zones. A better decision may be to concentrate on protecting the 70% of remaining Central American primary cloud forest that currently has no protective legislation (Aldrich 1997). Another key conservation objective may be to attempt to rehabilitate buffer zones to improve their conservation value, possibly by increasing the ratio of existing core: buffer zone areas. This could prove effective as buffers frequently make up a significant proportion of total park areas, often comprising >50% (see Table 5.4). Research has demonstrated that rehabilitation of disturbed forest habitats typically found in buffer zones is possible, particularly when located in close proximity to core zone primary forest (Guariguata and Ostertag 2001) and the conservation value of well-regulated buffers can be high (Lee *et al.* 2007). However, this could prove problematic as densely populated areas of buffers will probably continue to be degraded as local communities have been shown to make land-use decisions based largely on economic rationales rather than environmental legislation (Duffy *et al.* 2001). Rehabilitation could therefore be prioritised in buffer areas with low population densities of >2 people per hectare (Pfeffer *et al.* 2005) with efforts to improve the sustainability of land-use activities in the more densely settled buffer areas. Increased monetary investment for administration and management could also strongly improve the conservational effectiveness of buffer zones, as it has been shown that even modest increases in park funding can dramatically boost the effectiveness of its protective legislation, particularly when finances are invested in demarking boundaries and recruiting guards and rangers to enforce park policy (Rodriguez and Rodriguez-Clark, 2001, Bruner *et al.* 2001).

Table 5.4 - Size in hectares of total park area, core zone size, buffer zone size and % of park as buffer for a selection of protected cloud forest areas in Central America. Statistics adapted from Rainforest Alliance 2008, Munroe et al. 2007, Lenkh 2005, Zahawi 2005, Kestenbaum 2002 and Pfeffer et al. 2001.

Park Name	Total size	Core size	Buffer size	% of Park as buffer
Parque Nacional Cusuco	31,130	7,690	23,440	75.30%
Parque Nacional Celaque	26,500	15,700	10,800	40.76%
Parque Nacional Montana de Comayagua	30,094	12,570	17,524	58.23%
Parque Nacional Pico Bonito	107,300	80,000	27,300	25.44%
Parque Nacional Cerro Azul	31,376	10,019	21,357	68.1%
Parque Nacional El Imposible	5,773	3,599	2,205	38.2%

5.6 – CONCLUSION

This study has demonstrated that Honduran cloud forest parks can be effective in safeguarding cloud forest avifaunal communities, even when chronically under-managed. However, the meaningful protection afforded by the park seems to be largely confined to the core zone, with a sharp divide in composition of avifaunal communities occurring across the core-buffer boundary. Increased commitment is required in buffer zones if these areas, which often comprise large proportions of total protected areas, are to effectively contribute to actively preserving cloud forest avifauna.

This study has been successful in demonstrating that so called 'paper parks' can be effective in preserving biodiversity in montane forest, but further work remains to be completed. One important avenue of research would be to compare avifaunal communities in a region of unprotected Honduran cloud forest with this study site, allowing a greater understanding of the extent to which nominal protection correlates to conservationally valuable bird communities. This could be difficult to achieve in Honduras, however, as the 1993 General Environment Forest Act has placed all the country's cloud forest ecosystems under at least nominal protection. Likewise, the effectiveness of buffer zones could be further evaluated by examining avian community structure in wholly unprotected areas beyond the park's limits. This study does, however, provide encouraging evidence that even undermanaged 'paper parks' can still be effective in preserving biodiversity on a species level.

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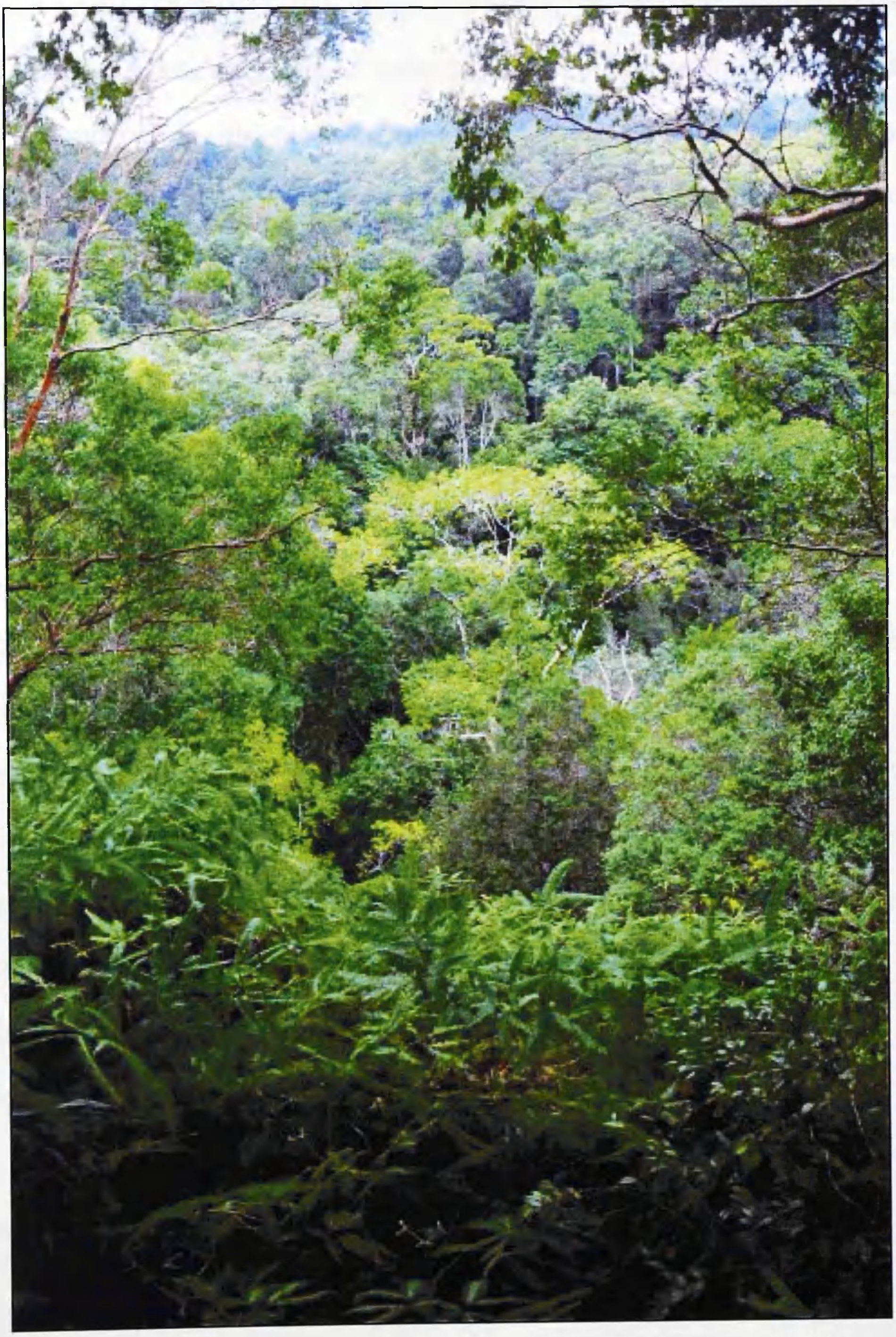
CHAPTER 6 - HABITAT ASSOCIATIONS OF AN INSULAR WALLACEAN AVIFAUNA: A MULTI-SCALE APPROACH FOR BIODIVERSITY PROXIES



Viewpoint over the Lambusango forest

6.1 – SUMMARY

The endemic avifauna of Wallacea is of high conservation significance, but remains poorly studied. The need to identify priority areas for conservation requires a greater understanding of the associations of these bird communities with habitat variables. The influence of spatial scale in analysing habitat associations of these birds is also poorly understood. This study aims to determine which proxy habitat measures, at which spatial scales of analysis, can provide useful inferential data on the composition of Wallacean forest avifauna. Research was conducted within the Lambusango forest reserve, South-East Sulawesi, where avifauna were sampled using point count surveys. Habitat properties were characterized in three ways: broad classification of forest type, canopy remotely-sensed response derived from optical satellite imagery, and *in situ* measures of vegetation composition and structure. Furthermore, we examined avifauna-habitat relationships at three spatial scale: area (c.400ha per sample site), transect (c10ha) and point (c.0.2ha). Results demonstrate that broad forest type classifications at an area scale can be useful in determining conservation value, indicating that primary and old secondary forests are important for supporting high densities of large-bodied frugivores. At transect-scale significant congruence occurs between bird community composition and several habitat variables derived from vegetation sampling and satellite imagery. Normalized Difference Vegetation Index (NDVI) values in particular displayed significant correlations with avian richness. Analysis at point-scale was ineffective in providing proxy indications for avifauna.These findings should be considered when determining priority conservation areas for Wallacean avifauna in the future.

Key words: Avifauna, Habitat associations, Scale, Wallacea

6.2 - INTRODUCTION

South-East Asian rainforests are experiencing the highest relative rates of habitat loss and modification of all major tropical forest ecosystems (Mayaux *et al.* 2005, Achard *et al.* 2002), and this is considered the principal driving factor of biodiversity loss across the region (Sodhi *et al.* 2004a). This is of high concern within the biodiversity 'hotspot' (Myers *et al.* 2000) of Wallacea, a biogeographical region within the Indonesian archipelago where a complex geological history has facilitated a high prevalence of endemic organisms; almost 50% of resident vertebrates are restricted entirely to the hotspot (Whitten *et al.* 2002, Myers *et al.* 2000, Kinnaird 1995). This taxonomical distinctiveness is well-represented in the region's avifauna; 40% (249 species) of Wallacean birds are regionally endemic, the second highest rate of endemism of all hotspots (Myers *et al.* 2000). Sulawesi, the largest island in the Wallacea region, alone possesses 14 endemic bird genera, the most of any of Birdlife International's 218 recognised endemic bird areas (Stattersfield *et al.* 1998). A further nine endemic bird areas are located within the Wallacea hotspot, which together encompass almost every sizeable island in the region (Stattersfield *et al.* 1998).

Despite high ecological importance, many Wallacean bird species are under threat from habitat loss related to expanding agricultural activities, logging, population growth and other socio-economic factors (Trainor 2007, Sodhi 2005) as well as from unsustainable logging practices (Marsden 1998). An estimated 55% of original vegetation cover and 85% of original primary rainforest within Wallacea has been lost or modified (Global Forest Watch 2002). Predictive extinction models estimate that continued habitat alterations on this scale could result in the loss of up to 42% of flora and fauna species across South East Asia by 2100 (Sodhi *et al.* 2004a). In Wallacea, which is comprised of 13,500 islands, consequences could be more severe still as islands are inherently vulnerable to habitat loss and modification

(Macarthur and Wilson 1967), and island birds may be as much as 40 times more prone to extinction than continental species (Trevino *et al.* 2007).

Safeguarding the avifauna of this unique region is therefore a high conservation concern. However, identifying priority areas for conservation efforts to focus using extensive ornithological surveys can be difficult, given the intensive input of resources that would be needed, the high level of taxonomical expertise required, and the time these surveys require in rapidly changing landscapes (Gardner *et al.* 2008, Kati *et al.* 2004, Lawton *et al.* 1998). This is especially true in Wallacea, which remains one of the least ornithologically explored areas on Earth (Trainor 2007, Coates and Bishop 1997). Understanding the environmental factors determining the spatial distributions of these species would provide the possibility of identifying suitable conservation areas using proxy assessments of ecosystem structure, providing a useful tool for prioritising areas in which to concentrate survey work. Acquiring an understanding of the habitat associations of bird communities here would therefore be valuable, particularly with regard to endemic and threatened species of high conservation importance.

While several spatially-extensive studies have been successful in predicting landscape-scale patterns of avian diversity (Gillespie and Walter 2001, Johnson *et al.* 1998), there remains an incomplete understanding of how habitat variables on smaller ecosystem scales are associated with community composition and α-diversity of bird communities (Cleary *et al.* 2005). This is important, as several studies have suggested that local forest structure can be at least as important as landscape-scale characteristics in governing patterns of species diversity (Herrando and Brotons 2002, Potts *et al.* 2002), and that this lack of understanding could be inhibiting the effectiveness of conservation strategies (Pearman 2002). Some research examining the relationships between ecosystem-scale landscape structure and avifaunal diversity has been conducted in the Neotropics (Pearman 2002), and other parts of

South-East Asia (Cleary *et al.* 2005, Shankar-Raman *et al.* 2005, Shankar Raman and Sukumar 2002), although these relationships have never been explored in detail with regard to Wallacean avifaunal communities. This is significant as bird assemblages here possess distinct characteristics, such as high rates of endemism, low species richness, a low diversity of understorey birds, and a high contribution of frugivores to community composition (Coates and Bishop 1997), which may facilitate responses differing from those reported in other studies. Additionally, most current research examining relationships between bird communities and habitat variables has focussed on species composition of avian communities in their entirety; few studies have compared these coarse-filter aggregations with fine-filtered data based on taxonomical sub-groups such as feeding guilds or species of high conservation importance such as red-listed or endemic species, as recognised by Su *et al.* (2004).

There is also a lack of understanding concerning the influence of spatial scale on determining associations of habitat variables and bird communities. While it has been well-established that scale aggregations have an important influence on examining responses of ecological communities (Jansson 2002, Hamer and Hill 2001, Noss 1990), few studies have examined how this specifically affects congruence between bird communities and habitat variables, and which scales are most appropriate for analysis of species-habitat relationships, particularly in South-East Asia and the Wallacea region.

This study aims to address these research gaps by examining relationships between bird community and sub-community compositions and habitat variables in a Wallacean rainforest ecosystem on three spatial scales. From this we attempt to determine which proxy habitat measurements, at which spatial scales, can provide useful inferential indicators of bird community composition. Bird communities were chosen for analysis both for their own intrinsic value and because they are frequently regarded as a 'flagship' taxon for biodiversity, being a relatively well-understood group which is comparatively simple to sample (Stotz *et* *al.* 1996, Furness and Greenwood 1994). They are also regarded as high-performance indicators in themselves, being potentially effective in predicting diversity and composition across land-uses and in other taxonomical groups (Gardner *et al.* 2008, Schultze *et al.* 2004, Canterbury *et al.* 2000, Lawton *et al.* 1998, Blair 1997). Therefore habitat associations of birds could possibly be extrapolated to reflect distribution of biodiversity on a broader basis.

Habitat variables were assessed in three ways: broad forest type classifications, *in situ* measurements of vegetation variables and analysis of remotely sensed imagery. Forest type classifications were used as previous research within Wallacea has shown that different bird assemblages can occur within different forest classes (Martin and Blackburn 2009). *In situ* measurements of vegetation variables were used as previous studies have shown forest structure to be strongly linked to biodiversity; a higher structural diversity may support a wider range of ecological niches, or certain structural features may be indicative of habitat quality (Cleary *et al.* 2005, Duelli and Obrist 2003). Remotely sensed imagery were analysed as this has been shown to provide useful, comprehensive, repeatable and cost effective data for mapping vegetation properties and modelling biodiversity over spatially-continuous areas (Duro *et al.* 2007, Stoms and Estes 1993). While remote sensing techniques are limited to indirect measures of biodiversity (Leyequien *et al.* 2007), numerous studies have empirically demonstrated the value of this tool for assessing biodiversity (Turner *et al.* 2003, Foody and Cutler 2003, Gould 2000, Hepinstall and Sader 1997). The results of this study will focus on suggesting key habitat variables and optimal spatial scales for using such variables when attempting to identify key areas for the conservation of Wallacean avifauna.

6.3 - METHODS

6.3.1 - Study site

Research was conducted on Buton island, the largest (5,600km^2) attendant island of Sulawesi in the Indonesian archipelago (See Figure 1.5 in Introduction). Geographical and climatic data for the island is provided in Chapter 1 (section 1.6) and Chapter 4 (section 4.3.1). Fieldwork was conducted in the Lambusango Forest Reserve (5°10'S, 122°24' E). Details of the Lambusango's geography, management and conservation issues have been detailed in Chapter 1 (Section 1.6) and Chapter 4 (Section 4.3.1).

6.3.2 - Sample sites

Sampling was conducted in five forest areas located throughout the reserve. Analysis of habitat structure based on the mean value of a discrete number of variables (Table 6.1), backed up by visual observations and research into local ecological history, suggested that three forest areas corresponded approximately to near-pristine primary forest, regenerating 30-year old secondary forest and disturbed secondary forest type classes, with the remaining two being comprised of intermediate and highly heterogeneous forest types (Table 6.1).

Table 6.1 – Vegetation analysis summary for study areas within the Lambusango forest reserve, Buton Island, South-East Sulawesi.

Site	Mean canopy score (0-25)	Mean frequency of large trees (>50cm dbh diameter)	Mean dbh of large trees (cm)	Undergrowth density (%)	Rattan cover (%)	Classification
1	4.02 ± 1.27	4.8 ± 1.89	83.9 ± 35.2	17.17 ±5.1	21 ± 14.1	Primary forest
2	4.66 ± 1.3	2.1 ± 0.9	68.77 ± 18.32	2.4.4 ± 0.7	22.5 ± 12.3	Regenerating secondary forest
3	6.36 ± 1.73	2.3 ± 1.1	61.763 ± 15.2	7.8 ± 1.6	52.1 ± 27.5	Disturbed secondary forest
4	5.8 + 3.23	2.79 ± 2.6	60.47 ± 28.3	13.43 ± 5.98	31.75 ± 28.8	Mixed 1
5	5.1 ± 6.2	3.14 ± 1.96	68.13 ± 38.5	21.71 ± 7.19	9.85 ± 14.06	Mixed 2

Four 900m linear transects spaced at least 1km apart were used in each area (Figure 6.1). Each transect contained seven sample points, with each point being spaced 150m apart. This gave a total of 140 study points spread across 20 transects. The elevation of these study points varied from 100 – 700 metres above sea level. These altitudinal variations are not expected to be great enough to cause significant systematic changes in vegetation structure, all being below the altitudinal limits of lowland forest (Whitten *et al.* 2002). Field data was collected over an eight week period in the dry season between June and August 2008.

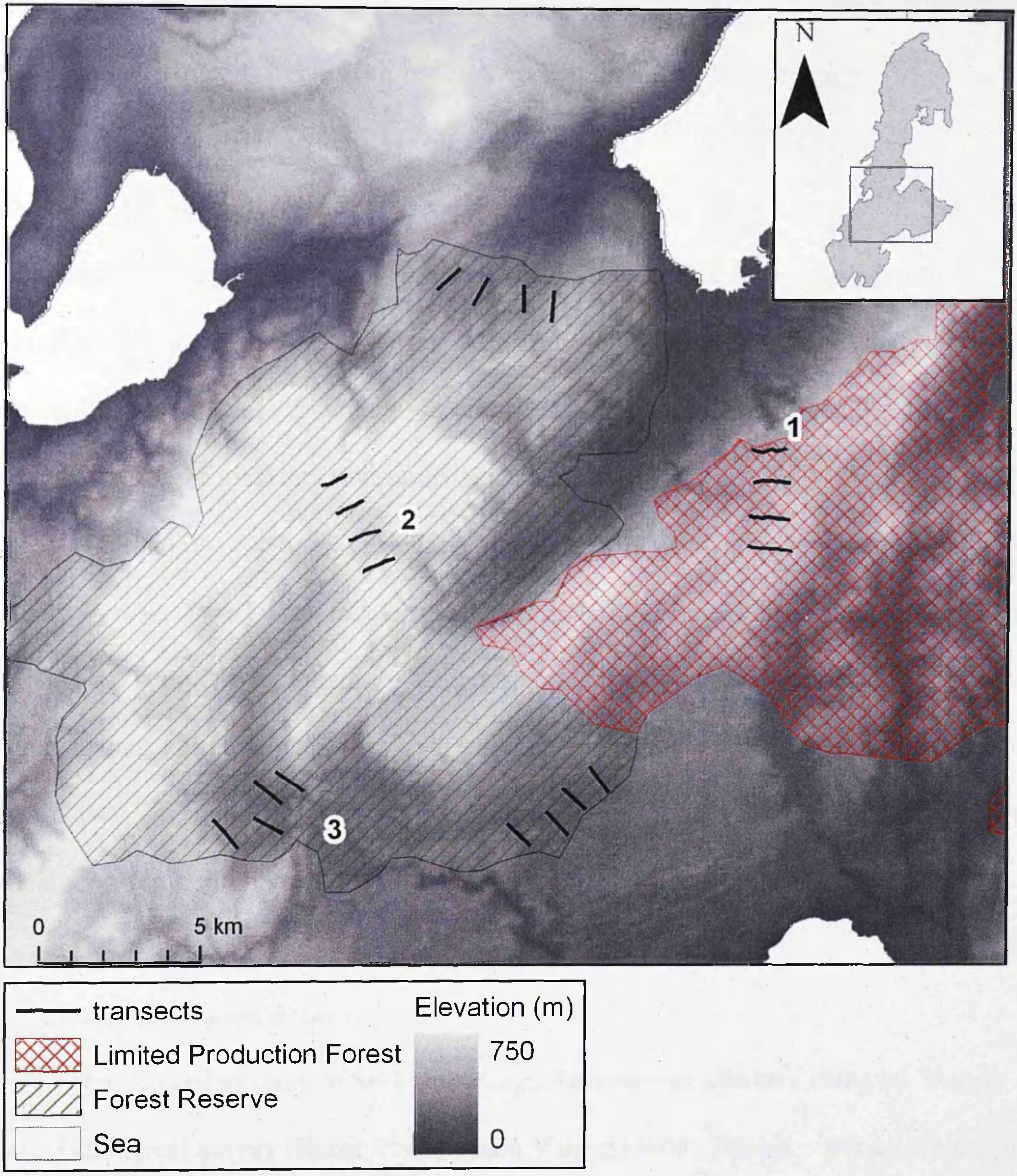


Figure 6.1 - The Lambusango Forest reserve and locations of study transects. Inset shows study area's location within Buton Island. Transects located within areas of primary forest, regenerating secondary forest and disturbed secondary forest are notated 1, 2 and 3 respectively.

6.3.3 - Bird Surveys

Avifaunal populations were sampled at each sample point using 50m fixed-radius circular plot point counts (Bibby *et al.* 2002). Point count methodologies were indentical to those described in Chapter 4. Details can be found in section 4.3.4 of this chapter.

6.3.4 - Vegetation analysis

A 20m radius vegetation survey was conducted at each of the 140 sample points, with ten habitat variables being assessed at each. Although a 50m radius vegetation survey may have provided better comparisons with bird point-count and remote sensing samples, this was not possible due to logistical and time constraints.

The sum total of large trees, mean large tree dbh, canopy cover and rattan and undergrowth density were measured using methods identical to those described in section 4.3.3 of Chapter 4. The total number of epiphytes of the genus *Asplenium* was also counted at each site, as a high abundance of these plants has been associated with undisturbed forest habitats (Schulze *et al.* 2004). The number of monocot plants of the genus *Pandanus* (Screw-pines), palm trees, fallen trees, ferns and lianas with a diameter >10cm were also counted in each plot.

6.3.5 - Remotely sensed data

Remotely sensed imagery of the Lambusango Reserve was obtained using the United States Geological Survey Global Visualisation Viewer (2009). Imagery was acquired from Landsat 5 Thematic Mapper (TM), (Path 112/ Row 64) dating from October 2006. This was the cloud-free image closest in time to the field data acquisition. The image was imported into ERDAS Imagine v9.3 and geometrically and radiometrically corrected. A Normalised Difference Vegetation Index (NDVI) image formed from a composite of bands three and four (red and near infra-red) was calculated, and a Principal Component Analysis (PCA) was used to condense information across all seven bands into a small number of uncorrelatated principal component images. The original seven TM bands, the NDVI image and the first three PC images were imported as a layer into ArcGIS v9.2., for subsequent analyses.

6.3.6 - Scaling and data aggregation

Associations between the bird communities, vegetation variables and remote sensing variables were determined using a range of analyses on three spatial scales: points (c.0.2ha per sample site), transects (c.10ha), and areas (c.400ha). (*n.b.* forest type classifications could only be analysed appropriately on an area scale). Bird census data was aggregated at transect scale by pooling all contacts recorded along its seven constitute points, and at an area scale by pooling all contacts recorded across its four constitute transects. Likewise, vegetation variables were aggregated by taking mean values of each variable at constitute points/ transects for transect/area spatial scales, respectively. In ArcGIS remotely sensed data at point scale were extracted by placing a 50m buffer around each sampling point location and calculating mean pixel values within each c0.2ha area. Transect values were calculated by placing a 50m buffer around the entire transect line, providing a strip with an area of c.10 ha from which mean pixel values were extracted. Area values were calculated by constructing a polygon encompassing all four transects and placing a 50m buffer around this, giving an area of c.400 ha from which mean pixel values were extracted.

Bird communities were also subdivided into three subcategories for analysis: endemics (species endemic to the Sulawesi sub-region), frugivores and insectivores after Coates and Bishop (1997).

6.3.7 - Statistical analysis

A one-way analysis of similarity test (ANOSIM) using Bray-Curtis distance estimates (Clarke and Gorley 2006) was conducted using PRIMER version 6 on an area scale to determine if bird community structure differed significantly between the three identified forest type classes (primary forest, regenerating secondary forest and disturbed secondary forest). The two heterogeneous forest areas were excluded from ANOSIM analysis as these could not be assigned a definitive 'class', although data from these sites was used in all other analysis. A sample percentage discrimination test (SIMPER) was run using PRIMER to determine the species most important in determining community similarity and dissimilarity across sites (Clarke and Gorley 2006). All species which cumulatively constituted ≥66% of total similarity/dissimilarity were considered in this analysis. Species richness estimates for each forest habitat class were compared based on visual comparisons of sample-based rarefaction curves plotting numbers of individuals recorded against number of species, produced using the software package EstimateS (Colwell 2006). A further series of non-parametric richness estimators were calculated in EstimateS; the mean value of these was taken to estimate total species richness, as the effectiveness of different estimators is expected to vary with different data sets (Herzog *et al.* 2002). This was included to corroborate the results of the accumulation curve, as information in larger samples may be lost when 'rarefied' to the size of the smallest sample (Lee *et al.* 2007, Sodhi *et al.* 2005).

Comparisons between bird community structure and combined vegetation properties and TM bands 1-7 at each scale were determined by constructing similarity matrices using PC-ORD version 5.0 (McCune and Grace 2002) and comparing congruence using a series of Mantel tests. Significance of these tests was determined by a Monte-Carlo procedure utilising 999 permutations. A Biota and Environment matching (BIOENV best) algorithm (Clarke and Gorley 2006) was also utilised to assess which individual vegetation structure and remote sensing variable (including NDVI and PC's) provide the strongest correlation with avifaunal community composition.

Relationships between species richness of bird communities and vegetation and remote sensing variables were examined using a series of step-wise general linear models with SPSS version 15.0 (Zar 1999). This analysis was only carried out on a transect scale due to insufficient degrees of freedom on an area scale and lack of homogeneity of variance and autocorrelation issues on a points scale, although research has shown that 'pooling' point scale data into transects can give the best correlations between bird communities and environmental factors (Jansson 2002). All correlations significant to a 95% confidence interval were recorded.

6.4 - RESULTS

Point-count surveys recorded a total of 2422 individual birds from 49 species. <1% of contacts were unidentified and these were excluded from analysis. Most contacts (92%) were detected by sound, with 8% being detected visually.

6.4.1 - Area scale analysis

One-way ANOSIM analysis demonstrates there was a significant variation in bird community structure between the three identified forest classes (primary, regenerating secondary forest and disturbed secondary) (Global R = 0.431, $p < 0.05$). Analysis of community dissimilarity suggests that different compositions of forest specialist species and generalist species occur between sites (Table 6.2).

Table 6.2 - Sample percentage discrimination (SIMPER) test displaying species contributing most to average community ***dissimilarity*** *in primary, regenerating secondary and disturbed secondary forest sites in the Lambusango forest reserve, Buton Island, South-East Sulawesi. Species that together constitute >66% of dissimilarity are shown. Endemic species are indicated with *. Species occurring predominantly in non-edge forest habitats are indicated †. Feeding guilds are indicated by superscript letters after Coates and Bishop (1997).* ^{N} *indicates nectarivores,* ^{F} *indicates frugivores,* ^{I} *indicates insectivores,* ^{o} *indicates omnivores. +/- indicates difference in abundance between first and second named forest types. First bracketed figures show abundance difference. Second bracketed figures show percentage value contribution of species to community dissimilarity.*

	Primary forest ↔ regenerating secondary forest	Primary forest ↔ disturbed secondary forest	Regenerating secondary forest ↔ disturbed secondary forest
Average dissimilarity (%)	42.95	53.59	48.57
	_Prioniturus platurus_*† $^{F+}$ (18.5/5.25) (14.63%)	_Prioniturus platurus_*† $^{F+}$ (18.5/1.25) (16.74%)	_Nectarina aspasia_ $^{N+}$ (15.5/6.25) (8.87%)
	Dicrurus hottentotus $^{I-}$ (7/12.75) (8.19%)	_Scissirostrum dubius_* $^{F-}$ (0.25/6.5) (6.6%)	_Coracina bicolour_* †$^{I+}$ (10.25/4.73) (8.61%)
	_Coracina bicolour_* ^{I}†$^{-}$ (6.5/10.25) (6.52)	_Nectarina aspasia_ $^{N+(12/6.25)}$ (5.77%)	_Scissirostrum dubium_* $^{F-}$ (0.00/6.5) (6.38%)
	Ducula aenea† $^{F-(3/7.5)}$ (5.28%)	_Trichastoma celebense_* $^{I-}$ (9/13.5) (5.75%)	_Dicrurus hottentotus_ $^{I+}$ (12.75/0) (5.28%)
	Oriolus chinensis $^{F-}$ (6/5.75) (5.10%)	_Oriolus chinensis_ $^{F+(5.75/5)}$ (5.03%)	_Trichastoma celebense_* $^{I-}$ (7.5/13.5) (4.47%)
	_Trichastoma celebense_* I – (9/10) (4.84%)	_Coracina bicolour_* † $^{I+}$ (6.5/4.73) (4.73%)	_Aplonis panayensis_ $^{F+}$ (3.75/0) (4.17%)
	Aplonis panayensis $^{F-}$ (0/3.75) (4.84%)	_Hypothymis azurea_ $^{I-(6/8.5)}$ (4.59%)	_Prioniturus platurus_*† $^{F+}$ (5.25/1.25) (4.07%)
	Penelopides exarhatus *† $^{F-}$ (1.75/4.5) (4.37%)	_Zosterops consobrinorum_* $^{F-}$ (4.75/0.75) (4.32%)	_Hypothymis azurea_ $^{I+}$ (6/7.75) (3.89%)
	Nectarina aspasia $^{N-}$ (12/15.3) (4.09%)	_Rhyticeros cassidix_*† $^{F+(4/0)}$ (4.17%)	_Penelopides exarhatus_ * †$^{F+}$ (4.5/2.75) (3.81%)
	_Rhyticeros cassidix_*† $^{F+}$ (4/3.25) (3.9%)	_Culicicapa helianthea_* $^{I-}$ (3.5/5) (3.77%)	_Culicicapa helianthea_* $^{I-}$ (3.5/5) (3.76%)
	Hypothymis azurea $^{I-}$ (6/7.75) (6.15%)	_Mulleripicus fulvus_*† $^{I+(4/1)}$ (3.12%)	_Ducula aenea_† $^{F+(7.5/4)}$ (3.73%)
	_Corvus typicus_* $^{o-}$ (0.75/3.25) (2.96%)		_Zosterops consobrinorum_* F – (2.75/4.75) (3.67%)
			_Rhyticeros cassidix_*† $^{F+}$ (/3.25/0) (3.3%)
Cumulative dissimiliarity (%)	67.53	69.05	67.8

Comparisons between disturbed secondary forest and primary and regenerating secondary forest show that five species occur at higher densities in disturbed forest sites. These were comprised of four endemic species: *Trichastoma celebense* (Sulawesi Babbler), *Scissirostrum dubius* (Finch-billed Mynah), *Zosterops consobrinorum* (Sulawesi White-eye) and *Culicicapa helianthea* (Citrine Flycatcher), and one wide ranging species: *Hypothymis azurea* (Black-naped Monarch). Coates and Bishop (1997) describe each of these species as occurring in a wide range of forest and/or non-forest habitats. Conversely, a majority of species found in greater abundance in primary or regenerating secondary forest are described by Coates and Bishop (1997) as being restricted largely to old growth or tall secondary forest. These species mostly comprised of large-bodied endemic species with specific feeding niches, including frugivores such as *Prioniturus platurus* (Golden-mantled Racquet-tail Parrot), and both of Sulawesi's Hornbill species: *Rhyticeros cassidix* (Knobbed Hornbill) and *Penelopides exarhatus* (Sulawesi Dwarf Hornbill), and insectivores such as *Mulleripicus fulvus* (Ashy Woodpecker) and *Coracina bicolor* (Pied Cuckoo-shrike). One of these species, *C. bicolour*, is listed as Near-Threatened by the IUCN (2009). Comparisons between primary and regenerating secondary forest display similar species compositions, although most species occur in greater abundance in regenerating secondary forest. The exceptions to this were two large frugivores: *R. cassidix* and *P. platurus,* which occur at higher densities in primary forest.

Table 6.3 – Sample percentage discrimination (SIMPER) test displaying top five species contributing most to average community ***similarity*** *in primary, regenerating secondary and disturbed secondary forest sites in the Lambusango forest reserve, Buton Island, South-East Sulawesi. Endemic species are indicated with an asterix. Feeding guilds are indicated by superscript letters after Coates and Bishop (1997).* ^{N} *indicates nectarivores,* ^{F} *indicates frugivores,* ^{I} *indicates insectivores. Percentage values in brackets indicate contribution of species to community similarity.*

		Primary forest	Regenerating secondary forest	Disturbed secondary forest
Average similarity (%)		57.07	63.76	53
	1	*Nectarina aspasia* $^{N\,(20.62\%)}$	*Nectarina aspasia* $^{N\,(18.04)}$	*Trichastoma celebense** $^{I\,(24.38\%)}$
	2	*Trichastoma celebense** $^{I\,(18.46\%)}$	*Dicrurus hottentotus* $^{I\,(11.96)}$	*Dicrurus hottentotus* $^{I\,(12.82\%)}$
	3	*Hypothymis azurea* $^{I\,(10.15\%)}$	*Trichastoma celebense** $^{I\,(10.27)}$	*Hypothymis azurea* $^{I\,(11.76\%)}$
	4	*Coracina bicolour** $^{I\,(8.35\%)}$	*Coracina bicolour** $^{I\,(9.4\%)}$	*Nectarina aspasia* $^{N\,(10.81\%)}$
	5	*Dicrurus hottentotus* $^{I\,(6.95\%)}$	*Ducula aenea* $^{F\,(8.13\%)}$	*Oriolus chinensis* $^{F\,(5.6\%)}$
Cumulative similarity (%)		64.54	57.8	65.38

SIMPER analysis suggest that three species make an important contribution to community similarity between forest classes (Table 6.3): *T. celebense*, contributing a mean similarity of 17.7% across sites, *Nectarina aspasia* (Black Sunbird) contributing 16.3% mean similarity, and *D. hottentotus,* contributing 10.58% mean similarity (Table 6.3). Other important contributing species were *H. azurea* in primary (10.15% of similarity) and disturbed secondary (11.76%) forest, *C. bicolour* in primary (8.35%) and regenerating secondary forest (9.4%), *Ducula aenea* (Green Imperial Pigeon) in regenerating secondary forest (8.13%) and *Oriolus chinensis* (Black-naped Oriole) in disturbed secondary forest (5.6%).

Table 6.4 - Non-parametric species estimators for primary forest, regenerating secondary forest and disturbed secondary forest within the Lambusango forest reserve, Buton Island, South-East Sulawesi. n represents sample size. ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, Bootstrap, MMRuns and MMMeans are non-parametric species estimators (Colwell and Coddington, 1994).

Parameters	Primary forest	Regenerating secondary forest	Disturbed secondary forest
n	28	28	28
Species observed	29	35	35
Individuals observed	417	472	359
ACE	31.83	37.21	37.68
ICE	33.61	39.05	42.88
Chao1	34	35.37	37
Chao2	32.68	37.45	40.05
Jack1	34.89	40.89	43.83
Jack2	37.83	41.94	46.83
Bootstrap	31.74	38.04	39.3
MMRuns	31.25	37.02	38.09
MMMeans	30.99	37.33	38.35
Average species estimate	**33.2**	**38.256**	**40.45**

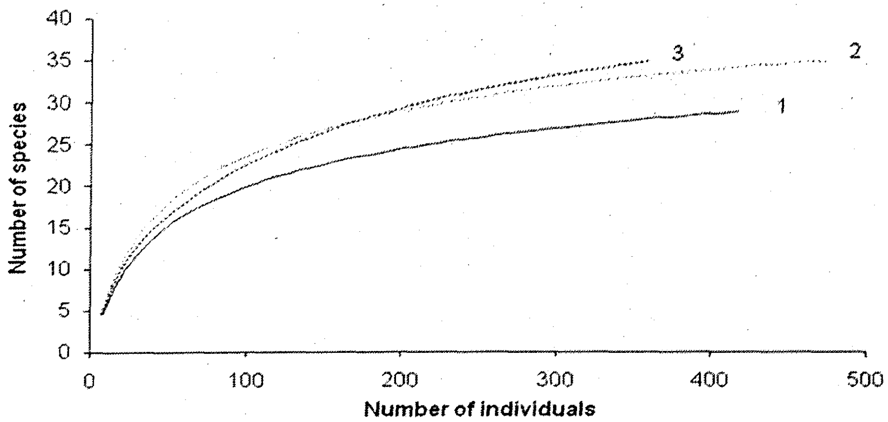


Figure 6.2 - Sample-based rarefaction curves displaying number of individuals against number of species recorded in primary forest (notated as 1), regenerating secondary forest (notated at 2) and disturbed secondary forest (notated as 3) sample sites within the Lambusango forest reserve, Buton Island, South-East Sulawesi.

Species richness estimators for each forest class reveal an inverse relationship between species richness and forest disturbance (Figure 6.2 and Table 6.4). Disturbed secondary forest had the highest overall species richness estimate (40.45), followed by regenerating secondary forest (38.26) and primary forest (33.2).

Mantel tests comparing overall community similarity between bird communities and combined vegetation variables at this scale demonstrated significant congruence with total bird communities (R = 0.533, $p < 0.05$) and frugivores (R = 0.631, $p < 0.05$) (Table 6.5). No significant congruence occurred between bird community and sub-community compositions and remote sensing variables on this scale.

BIOENV best estimates examining correlations of individual vegetation variables with bird community composition identified canopy density as the best predictor for composition of total bird communities (Rho = 0.745, $p < 0.05$), and all avian subgroups (endemic communities Rho = 0.982, $p < 0.05$, frugivores Rho = 0.853, $p < 0.05$, insectivores Rho = 0.985, $p < 0.01$) at this scale. No individual remote sensing bands were reported as significant in predicting bird community composition.

6.4.2 - Transect scale

Mantel tests comparing bird community similarity and combined vegetation and remote sensing variables demonstrated fairly high congruence at the transect scale. Correlations between combined vegetation variables and community composition were significant ($p = < 0.05$) for all avian groupings except frugivores. Significant correlations were also reported for comparisons of combined remote sensing variables and community composition of endemic species (R = 0.248, $p = < 0.05$) and frugivores (R = 0.242, $p < 0.05$) (Table 6.5).

BIOENV best estimates predicted no significant relationships occurring between bird community structure and combined vegetation and remote sensing variables at this scale.

*Table 6.5 - Mantel test r-values comparing a) similarity of bird communities and habitat structure variables, and b) similarity of bird communities and remote sensing variables (bands 1-7), in the Lambusango Forest Reserve, Buton Island, South-East Sulawesi. Bold figures indicate statistically significant correlations. * indicates significance at a 95% confidence interval.*

a)

	Points scale	Transect scale	Area scale
Total species richness	0.060	***0.287**	***0.533**
Endemic richness	0.059	***0.309**	0.490
Frugivore richness	0.003	0.170	***0.631**
Insectivore richness	0.095	***0.324**	0.317

b)

	Points scale	Transect scale	Area scale
Total species richness	0.047	***0.242**	0.657
Endemic richness	0.008	0.153	0.689
Frugivore richness	0.054	***0.248**	0.710
Insectivore richness	0.015	0.115	0.502

Significant (p <0.05) step-wise general linear model correlations (Table 6.6) indicate variables most effective in predicting richness in bird communities, and demonstrate how avian sub-groups respond differently from communities as a whole to environmental and remote sensing variables. Results indicated total avifauna richness to be positively correlated with mean tree size (F = 6.075) and negatively correlated with undergrowth density (F = 7.460). Frugivore richness was correlated positively with tree size (F = 7.899), frequency of large trees (F = 10.641), liana abundance (F = 10.584), canopy density (F = 11.038), frequency of *Asplenium* epiphytes (F = 12.53) and frequency of palms (F = 15.794). Richness of frugivores was also negatively correlated with *pandanus* abundance (F = 14.217).

No vegetation variables demonstrated positive correlations with endemic or insectivorous bird richness. Similar remote sensing bands displayed significant correlations with different avian groupings. TM band three (red) and the NDVI displayed significant negative correlations for all bird groupings except insectivores, while TM band four (near infra-red) displayed positive correlations for these groups.

*Table 6.6 - Significant step-wise general linear model correlations between species richness of bird communities and sub-groups and vegetation and remote sensing variables on transect-scale data aggregations in the Lambusango Forest Reserve, Buton Island, South-East Sulawesi. * indicates significance to a 95% confidence interval. ** indicates significance to a 99% confidence interval. (–) indicates a negative relationship.*

Avifauna variables	**Vegetation comparisons**		**Remote sensing comparisons**	
	Variable	F	Variable	F
Total bird richness	Mean tree size	6.075*	Band 3	(-)7.951*
	Undergrowth	(-)7.460*	Band 4	8.094*
			NDVI	(-)8.069*
Endemic richness	NONE		Band 3	(-)5.652*
			Band 4	5.561*
			NDVI	(-)5.642*
Frugivore richness	Mean tree size	7.899*	Band 3	(-)11.5**
	Vines	10.584*	Band 4	12.14**
	Number of trees	10.641*	NDVI	(-)12.061**
	Canopy	11.038*		
	Asplenium	12.53**		
	Pandanus	(-)14.217**		
	Palms	15.794**		
Insectivore richness	NONE		NONE	

6.4.3 - Point scale

Mantel tests displayed in Table 6.5 demonstrate that no significant congruence occurred between bird communities and vegetation or remote sensing variables at this scale, and BIOENV best analysis predicts no single vegetation variable or remote sensing band to be positively correlated with community composition.

6.5 - DISCUSSION

Results of ANOSIM and SIMPER analysis demonstrate that broad forest type classes are associated with significantly different bird community compositions. Community dissimilarity analysis shows that many species adapted to a range of habitats can be found in higher abundance in disturbed secondary forest, while primary and regenerating secondary forest support higher abundance of several large-bodied species, such as both Sulawesian hornbills and the Near-Threatened *C. bicolor*. In the case of hornbills this could relate to these species requiring large spatial areas of high quality forest habitat supporting a diverse range of fruiting plant species, which has been shown to be highest in undisturbed forest ecosystems (Gray *et al.* 2009, Sodhi *et al.* 2004b). It could also relate to the hypothesized lower ecological tolerance of large-bodied species generally, due to their possessing low population densities, large habitat patch requirements and a susceptibility to hunting pressures (Boyer 2008, Sodhi *et al.* 2004b, Gaston and Blackburn 1995). However, although abundance of these species is lower in disturbed secondary forest, most continue to persist at low densities within this forest class, as noted in Martin and Blackburn (2009). This contributes to the high overall species richness displayed for this forest class (Table 6.4 and Figure 6.2).

Indications that the greatest abundance of the Lambusango Forest's largest frugivores occurs in primary forest is in concordance with other studies in the Wallacean hotspot. Research by Cahill (2003), Anggraini *et al.* (2000) and Marsden and Jones (1997) demonstrates that abundance of large frugivorous birds such as hornbills (including *R. cassidix*) and parrots is closely linked to forest structure, particularly the frequency of large trees which act as roosts and perennial foraging resources. In our Lambusango study sites, the greatest frequency and size of large trees occured in primary forest (Table 6.1), which provides further indications of the dependence of these species on high quality forest habitats.

It should be noted, however, that while populations of certain large frugivores are centred on areas of high quality forest, the density of other endemic species (ie. *T. celebense, Z. consobrinorum C. helianthea* and the monotypic *S. dubius*) is greatest in disturbed forest classes. Composition of endemic species differs between these forest classes, but richness of endemics is similar, which should be taken into account when evaluating the conservation value of secondary forest habitats (Martin and Blackburn 2009).

The three species contributing most to similarity across all forest classes, *T. celebense, N. aspasia* and *D. hottentotus*, are not unexpected; these were the three most commonly detected species in all forest classes and for point-count surveys as a whole, constituting 10.36%, 10.48% and 9% of all contacts recorded respectively. All three are generalist species adapted to a wide range of forest habitats (Coates and Bishop 1997). This is also true for other species contributing heavily to species similarity, i.e. *H. azurea* and *O. chinensis.*

The negative correlations between species richness and forest quality, as expressed by forest type class, could result from differences in habitat heterogeneity. Martin and Blackburn (2009) suggest that while primary forest may be able to support high species richness at any given point, as a fairly homogenous ecosystem the same assemblage of species might occur throughout the extent of this forest type. Regenerating and disturbed secondary forests may, however, represent a more heterogeneous canopy structure, possessing a mix of habitat conditions capable of supporting an overlap of forest specialist and generalist species that facilitates a higher overall species richness. This relates to Connell's (1978) intermediate disturbance hypothesis.

Mantel tests suggest congruence between bird community composition and vegetation and remote sensing variables are highly dependent on the spatial scale of data aggregation used. The comprehensive lack of community similarity occurring at local point- scale data aggregations is in concordance with results reported by Shankar-Raman and Sukumar (2005), who found low associations between bird communities and vegetation profiles based on data gained from 50m radius plots. This may result from the birds detected during point counts utilising habitat of greater heterogeneity and spatial extent than those described by the 20m vegetation survey or 50m remote sensing radius. All species detected are likely to possess territorial ranges extending far beyond such radii, exploiting habitat niches and micro-habitats not represented in these small-scale samples; hence why community similarity may be low. Transect-scale aggregations of vegetation and remote sensing data may better reflect the true variance of habitat that bird communities are utilising; thus analysis at this scale displays strong community similarity. The decline in levels of congruence between groupings at an area scale may result from these data aggregations assessing variables on a scale beyond most species habitat ranges. The spatial extent of area-scale analysis (c. 400ha) may be extensive enough to represent landscape-scale γ diversity rather than local α diversity, hence representing a variance of habitats and microhabitats beyond those utilised by bird communities described by point counts. This could be particularly relevant for remote sensing variables where a spatial area much greater than that represented by the transect surveys is represented, resulting in low community similarity at this scale. Positive congruence of frugivore communities and habitat variables on an area scale could perhaps result from most of these species having comparably large spatial ranges. As year-round fruiting sources in tropical rainforests are a spatially and temporally scarce resource, frugivores generally require large foraging areas compared to other feeding guilds (Gray *et al.* 2009, Sodhi *et al.* 2004b). As frugivores are also represented by more species than any other feeding guild in the Lambusango Forest (51.06% of species detected during point counts) this could also contribute to bird communities in their entirety possessing significant congruence with vegetation variables.

BIOENV best analysis predicting canopy density as the most important vegetation variable influencing composition of bird communities on an area scale is in concordance with the findings of several other studies. Hansen *et al.* (1995, 1994) has demonstrated that canopy structure in temperate ecosystems is not only associated with community composition of organisms occurring in higher ecosystem stratigraphy, but is also closely linked to habitat niche diversity and species dispersal processes for biotic communities as a whole. Canopy structure is strongly associated with vertical habitat complexity, which in turn facilitates niche creation which influences community structure. Canopy density may also have a more directly important relevance to community structure of birds in the Lambusango Forest as a high proportion of bird species there (53.19%) are associated mainly with canopy-level habitat strata (based on Coates and Bishop 1997).

General linear model analysis indicates that several vegetation and remote sensing variables have strong associations with bird species richness. Tree size possessing positive associations with species richness of all bird groupings could relate to larger trees being indicative of higher vertical niche stratification which could support more species (Whitmore 1998). A dense understory may be a proxy indication of a broken forest canopy, which in turn may signify a low frequency of large canopy-level trees (Bell *et al.* 2004). This may suggest low vertical niche stratification, hence the negative correlation with species richness, especially considering the high proportion of the Lambusango Forest's avifauna associated with canopy-level habitat niches as previously described. Results indicate frugivore richness to be associated with a wide range of habitat structure variables. Gray *et al.* (2009) describes how diversity of frugivores is strongly linked to diversity of fruiting tree species, which in turn have been negatively correlated with forest disturbance. The majority of variables displaying positive associations with bird richness (mean size and frequency of large trees, canopy density, liana and *asplenium* epiphytes) have been associated with high quality forest types (i.e. Schulze *et al.* 2004, Bell *et al.* 2004, Hansen *et al.* 1994). This is an opposite finding to those reported by large-scale habitat classifications, which suggest that increasingly disturbed forest types support greater overall species richness. This could again result from different scales of aggregations; wide niche diversity in high quality forest types may support a high species richness locally, as reflected on transect scale aggregations, although habitat homogeneity could mean that richness on larger area-scale aggregation is not as more heterogeneous habitats in disturbed forest, as previously discussed.

The negative relationships of TM band three and the composite NDVI and positive relationship of band four with bird species richness across most avifaunal groupings might again be a function of habitat heterogeneity in different transects. Transects in areas of high-quality forest with consistent heavy canopy cover would generate a high NDVI score based on high leaf density, and these areas of pristine, homogenous forest habitats have been shown in Figure 6.2 to support a relatively low species richness compared to other forest types on larger spatial scales. A lower NDVI may reflect greater heterogeneity of forest structure with a lower overall leaf density, which in turn has been shown to support higher species richness. This may seem to contradict the positive correlations of species richness with mean tree size and other variables associated with high quality, spatially homogenous forest types, although as remote sensing data aggregations are based on larger spatial estimates than vegetation variables, they may give better estimates of this habitat variability on a transect scale. Sodhi *et al.* (2004b) describes how insectivore richness in tropical forests is often linked to very specific foraging microhabitats, which may occur at a scale too small for the broad-scale vegetation and remote sensing variables to pick up on, which may explain why no significant correlations occur within this feeding guild.

6.6 - CONCLUSION

This study has demonstrated that broad forest type classifications, *in-situ* vegetation measurements and remote sensing imagery can provide useful inferential data on the habitat associations of bird communities in the Lambusango forest reserve, and that spatial scale has an important influence on these associations. Results suggest broad forest type classification can be used to a certain extent for predicting general characteristics of bird communities. These patterns indicate that more disturbed forest types can represent areas of high overall species richness. However results also indicate the importance of primary and old secondary forest for the conservation of high population density of several important large-bodied endemic species, including at least one Near-Threatened species, and the local conservation flagship species *R. cassidix*, the faunal symbol of South Sulawesi province. The utility of broad forest type classifications in predicting the composition of avifaunal assemblages should be used with caution, however, as the great variation of environmental variables that can occur locally in tropical rainforest ecosystems means that categorical habitat classes cannot always be applied to regions of forest, as was the case in two study areas in this paper.

Results have also demonstrated that intermediate (c.10 hectares) transect-scale data aggregations can be effective in comparing congruence between bird communities and vegetation variables, and in suggesting which variables are most influential in determining species richness in different avifaunal subgroups. This study has shown how remotely sensed NDVI can be particularly effective in this respect, with values being negatively correlated with richness in most avifaunal groupings at this scale.

Very local point-scale data aggregations were demonstrated to be ineffective in describing habitat associations of avifaunal communities, and it is suggested that these aggregations should not be used for informing conservation policy.

The findings of this study therefore suggest the most effective vegetation structure and remote sensing variables for examining habitat associations of a Wallacean avifauna, and the most appropriate spatial scales to analyse these variables. These findings could be extrapolated and applied more broadly in several ways. NVDI imagery could be used to map habitat type and associated species richness estimates over large spatial scales; a technique that has been successfully applied elsewhere (Cannon et al. 2007). The results also imply that by mapping broad habitat categories such as tracts of primary or old growth secondary forest it is possible to estimate avian richness and community structure across extensive forested landscapes. These proxy indicators can then be used to identify priority areas for field biologists to concentrate survey effort towards.

It should be noted, however, that while strong associations were found between proxy habitat variables and most avifaunal sub-groups, certain groupings, particularly insectivores, were not well-represented by our choice of surrogate variables. It may be necessary therefore for further studies to include a wider range of habitat variables, such as availability of dead wood (Cleary et al. 2007), leaf litter depth (Shankar-Raman & Sukumar 2002), or other feeding substrates as biodiversity indicators of this feeding guild.

It should also be noted that while our findings show several useful associations between proxy environmental variables and bird communities, the direct applications of our findings may be limited to forest ecosystems on other small islands with a high representation of endemic and frugivorous species, such as those found across much of Wallacea, Papua and the Islands of the South-West Pacific (Stattersfield et al. 1998, Coates and Bishop 1997, White and Bruce 1986). Composition of bird communities on continental landscapes often differ greatly from those of our study site (Stattersfield et al. 1998), and it may therefore be inaccurate to apply our findings directly here without further research. However, this study has demonstrated that useful information on the richness and community structure of a taxonomical group can be obtained by analysis of proxy habitat variables when appropriate scales of data aggregation are used, and this approach to identifying priority conservation areas is worthy of further research in other ecosystems.

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CHAPTER 7 - DIFFERENTIAL VULNERABILITIES OF WALLACEAN AND MESOAMERICAN CLOUD FOREST RANGE-RESTRICTED AVIFAUNA

A DISCUSSION

Strangler fig in the Lambusango Forest

7.1 – SUMMARY

Endemic birds have been hypothesised to be inherently more vulnerable to habitat disturbance than wide-ranging species, although little research has examined how vulnerability of endemic species varies on a global scale and across ecosystem types. This study aims to explore this by examining how richness of endemic bird communities varies in different forest types in Cusuco National Park, North-West Honduras, and the Lambusango Forest Reserve, South-East Sulawesi. Endemic species in Lambusango were initially hypothesised to prove more susceptible to habitat disturbance than those in Cusuco due to possessing a higher ratio of endemic species, greater evolutionary distinctiveness and more species with characteristics associated with a high risk of habitat extirpation. Results demonstrate, however, that endemics in Cusuco were less tolerant of moderate habitat modification than those in Lambusango. Species richness of Mesoamerican endemics per study site declined significantly between core zone forest (6.34 ± 0.81) and more degraded forest in the boundary zone (3.86 ± 0.69). Richness of Wallacean endemics was similar in primary forest (4.89 ± 1.68) and disturbed secondary forest (4.52 ± 1.62). Non-parametric species estimators and sample-based rarefaction curves comparing Wallacean endemics and highland forest endemics display similar results. We propose a series of hypotheses that may explain the differential vulnerabilities in Wallacean island and Mesoamerican cloud forest avifauna, with particular focus on the apparent resilience of Wallacean birds. These include differential richness in bird and vegetation communities, different evolutionary histories, and the influence of figs, climatic regimes and patterns of human settlement. Further research projects to test the relative importance of these hypotheses are proposed.

7.2 - INTRODUCTION

A key element of the research presented in this thesis has been to assess the response of range-restricted avifaunal species to habitat disturbance in the two biological 'hotspots' within which our study areas were located. This constituted a major theme in the research papers presented in Chapters 4, 5 and 6. It has often been theorised that range-restricted bird species are more vulnerable to habitat disturbance than wide-ranging species due to their being confined to small spatial areas and tending to possess small populations, hence they are more sparsely distributed across their limited habitat (Sutherland 2000, Pimm and Raven 1999). This relates to the 'cookie cutter' theory described by Pimm *et al.* (1995), which conceptualises that a swathe of habitat destruction on a spatially-restricted fragmented or island ecosystem will destroy a greater proportion of total existing habitat than a similar-sized swathe on a larger, continental landscape, where extensive intact habitat areas will remain and opportunities for habitat regeneration are greater. Range-restricted birds have also been theorised to possess narrower ecological tolerances than other species, often being adapted to highly specialised, local habitats created by the same biogeographical factors which facilitate evolutionary isolation and endemism (Jankowski and Rabenold 2007, Trevino *et al.* 2007, Mckinney 1997, Renjifo 1997, Macarthur and Wilson 1967). However, there has been no quantitative research we are aware of which examines how vulnerability of endemic bird communities varies on a global scale and across ecosystem types. We aim to explore this by synthesizing data from previous chapters to examine how responses of endemic birds to habitat disturbance vary between Cuscuo National Park and the Lambusango Forest.

The discussed theories of endemic vulnerability would suggest that the diverse assemblages of endemic and habitat-restricted birds found in the Lambusango Forest and Cusuco National Park would both be sensitive to habitat modification. Biogeographical theory and historical records of bird extinctions may also suggest endemic species in the Wallacean archipelago to be more vulnerable to disturbance than equivalent species in Mesoamerican cloud forest. Wallacean avifaunal communities have a considerably greater proportion of endemic species than communities in Mesoamerica; 40% compared to 19% (Brooks *et al.* 2002, Coates and Bishop 1997, Kinnaird 1995). Wallacean endemics are also more evolutionarily distinct; the Sulawesi Endemic Bird Area (EBA) contains 14 unique genera of birds, compared to just two in both the EBA's overlapping in Cusuco National Park (Northern Central American Highlands and Central American Caribbean Slope), neither of which are represented in the Park's avifauna. It could perhaps therefore be hypothesized that Wallacean island avifaunal communities would possess a higher ratio of endemic species with greater specialization due to longer evolutionary isolation, and therefore may prove more vulnerable to habitat modification than endemic bird communities in Mesoamerica. The theorized vulnerability of island ecosystems with high rates of endemism is indicated quantitatively by estimates that endemic birds on oceanic islands are up to 40 times as likely to be threatened with extinction as continental species (Trevino *et al.* 2007). Indeed, of the 101 bird species listed as having become extinct since 1600 CE, 88 species (>87%) were island endemics, with habitat destruction being an important causality in many of these extinctions (Clements 2007, Milberg and Tyrberg 1993, Johnson and Stattersfield 1990, Olsen and James 1982). There is some evidence that as many as 2000 further unrecorded prehistoric extinctions may have also occurred among island birds (Steadman 1995). Blackburn *et al.* (2004) and Fuller (2000) describe how the greatest concentrations of these island extinctions have occurred in archipelagos where bird communities have experienced extensive periods of evolutionary isolation and possess high rates of endemism to a genus level, such as the Mascarene and Hawaiian island groups. This isolationary distinctiveness is also characteristic in Wallacean avifauna.

It could be counter-argued that the cloud forests of Mesoamerica represent 'island' habitats themselves, being comprised of small, highly fragmented ecosystems surrounded by a matrix of very different lowland habitats, thus representing 'continental islands' or habitat patch 'archipelagos' (Martinez-Morales 2005). However, a matrix of non-forest may not present as formidable a barrier to many bird species as ocean, especially as the majority of bird species endemic to the Mesoamerican hotspot appear to utilize a fairly wide range of habitat types. Of the 43 regional endemic species recorded in Cusuco National Park, only seven (16%) are described by Howell and Webb (2005) as being found exclusively in cloud forest ecosystems. A further eleven species (26%) occur in a wide range of highland forest habitats >800m, while the remaining 25 species (58%) occur in a wide range of forest habitats or are generally associated with non-cloud forest lowland ecosystems; therefore the theory of cloud forest as an 'island' habitat is not directly applicable for most endemic species.

Several studies have also demonstrated that, as well as endemics, certain sub-categories and guilds of birds experience greater vulnerability to habitat modification than others. Large-bodied birds are considered to be particularly susceptible to local extirpation from habitat disturbance as these species typically occur at naturally low densities, require large patches of forest habitat, tend to occupy higher trophic levels and possess lower reproductive rates than smaller-bodied species, all of which have been shown to increase vulnerability to local extinction (Boyer 2008, Sodhi *et al.* 2004, Gaston and Blackburn 1995). Certain avian feeding guilds have also been hypothesized to be more susceptible to habitat modification than others. Diversity of forest frugivores is strongly linked to the richness of fruiting plant species, which are most diverse in undisturbed forest ecosystems, and birds of this feeding guild often require large foraging areas due to the spatial and temporal scarcity of year-round fruit resources; thus degradation and fragmentation of forest ecosystems impacts strongly upon these species (Gray *et al.* 2009, Sodhi *et al.* 2004). Insectivores have likewise been considered to be strongly affected by habitat modification and fragmentation due to their dependence on specific foraging microhabitats and possessing limited dispersal capabilities (Sodhi *et al.* 2004). Observational experience during fieldwork and visual comparisons of species lists from both study sites suggests that the avifauna of the Lambusango Forest possesses higher proportions of these 'high risk' categories than the avifauna of Cusuco National Park, although this requires quantitative verification.

This study shall therefore examine two hypotheses. The first will determine whether different ratios of endemic birds in 'high risk' categories occur between the two study sites, with a null hypothesis that no difference exists between sites. The second will compare responses of endemic bird assemblages to disturbance, using a null hypothesis that no difference occurs between sites.

7.3 - METHODS

7.3.1 - Comparisons of 'high risk' characteristics

Ratios of 'high risk' species in endemic bird assemblages were examined by comparing body size and feeding guild affinities of all endemic birds recorded during survey work in the Lambusango Forest and Cusuco National park. Differences in body size were examined by comparing body length (cm) of all endemic species with an unpaired t-test (Zar 1999). We also compared proportions of large birds with a body length of > 30cm using a χ^2 test (Zar 1999). We recognize that measurements of body mass rather than body length would have been more appropriate for this analysis, but biometric data describing the body mass of many Wallacean species could not be found in the literature.

Differences in feeding guild compositions were examined by calculating the ratio of frugivores and insectivores compared to endemic bird assemblages as a whole.

These analyses were applied to comparisons of both Wallacea/Mesoamerican hotspot endemics, and also between Wallacean endemics in the Lambusango and 'highland endemics' restricted to upland forest habitats >1000m (Howell and Webb 2005), thus discounting endemic species found at lower altitude sites of the buffer zone associated with non-cloud forest ecosystems, as discussed in Chapter 5.

7.3.2 - Study sites, vegetation surveys and bird surveys

All fieldwork data used for analysis in this chapter is based upon material previously reported in Chapter 4: 'Impacts of tropical forest disturbance upon avifauna on a small island with high endemism: implications for conservation' and Chapter 5: The effectiveness of a Mesoamerican 'paper park' in conserving cloud forest avifauna'. Details of study sites and data collection methods can be found here.

7.3.3 - Bird census data aggregation and statistical analysis

Vegetation variables measured in both study sites were collated and combined into a single table for comparative purposes. The mean number of hotspot-endemic species detected per sample site, as reported in previous chapters, were combined and presented here for comparison. Non-parametric species estimators comparing richness of Wallacean endemics and highland forest endemics were also calculated, using methods described in previous chapters.

Sample-based rarefaction curves comparing number of individual birds against endemic species detected in the Lambusango and highland forest endemics in Cusuco were also constructed and presented together for comparative purposes.

7.4 - RESULTS

Results indicate that the endemic avifauna of Lambusango possess higher proportions of each of the evaluated 'high-risk' categories compared to the avifauna of Cusuco National Park. The mean body length of endemic bird species in the Lambusango Forest (32.91cm) is significantly higher than that of both Mesoamerican endemics (Unpaired T-test $F = 6.315$, $p < 0.05$) and highland forest endemics ($F = 4.817$, $p < 0.05$) in Cusuco (Table 7). There is also a significantly higher proportion of endemic birds with a body length of >30cm in the Lambusango forest compared to Mesoamerican ($\chi^2 = 5.126$, $p < 0.05$) and highland forest ($\chi^2 = 7.021$, $p < 0.05$) endemics in Cusuco. Endemic avifaunal assemblages in the Lambusango Forest also possess a greater proportion of both frugivores (48% of species assemblage compared to 38.9/44.4%) and insectivores (36.4% compared to 19.4/14.8%) birds than endemic and highland forest restricted avifauna assemblages in Cusuco.

Table 7.1 - Comparison of characteristics of endemic bird assemblages in the Lambusango forest reserve, Buton Island, South-East Sulawesi and endemic and highland-restricted species in Cusuco National Park, Honduras. N represents sample size. Categories compared are mean body length (cm) the percentage of endemic species with a body length of >30cm, and the proportion of frugivore, insectivore and other feeding guilds in each avifauna community. Bracketed numbers indicate total number of species represented in percentage values. Measurements and feeding guild information based on Coates and Bishop (1997) and Howell and Webb (2005).

	N	Mean body length (cm)	% N body length >30cm	% Frugivores	% Insectivores	% Other
Lambusango endemic species	33	32.91	51.52 (17)	48.5 (16)	36.4 (12)	15.15 (5)
Cusuco endemic species	36	21.06	16.7 (6)	38.9 (13)	19.4 (7)	41.7 (15)
Cusuco highland-restricted species	27	20.63	14.8 (4)	44.4 (12)	14.8 (4)	40.7 (11)

Vegetation survey results displayed in Table 7.2 indicate that point count survey sites encompassed a similar variety of forest types in both the Lambusango Forest and Cusuco National Park. The primary forest sites surveyed in the Lambusango Forest correspond fairly well with the deep and boundary core sites surveyed in Cusuco as 'high quality' habitats, with the highest frequency and mean size of large trees and sparsest understorey. Disturbed secondary forest in the Lambusango Forest corresponds approximately with forest structure in Cusuco National Park's buffer zone, with a marked reduction in the frequency and size of large trees and denser understory, both being representative of substantially modified secondary forest habitat. It is therefore reasonable to use these habitat categories for comparing effects of disturbance on endemic bird communities.

Table 7.2 - Vegetation variables in a) primary forest, regenerating secondary forest and disturbed secondary forest in the Lambusango Forest Reserve, South East Sulawesi, and b) deep core, boundary core and buffer zone sites in Cusuco National Park, Honduras. ± indicates variance to 1 standard deviation.

a)

	Mean canopy cover (%)	Mean frequency of large trees (>50cm dbh diameter)	Mean dbh of large trees (cm)	Undergrowth density (%)
Primary forest	83.92 ± 5.08	4.8 ± 1.89	83.9 ± 35.2	17.17 ±5.1
Regenerating secondary forest	81.36 ± 5.2	2.1 ± 0.9	68.77 ± 18.32	2.4.4 ± 0.7
Disturbed secondary forest	74.56 ± 6.92	2.3 ± 1.1	61.763 ± 15.2	7.8 ± 1.6

b)

	Mean Canopy cover (%)	Mean frequency of large trees (>50cm dbh diameter)	Mean dbh of large trees (cm)	Undergrowth density (%)
Deep core	89.5 ± 5.85	14.4 ± 7.69	108.56 ± 22.62	1.4 ± 0.64
Boundary core	90.4 ± 6.34	17.61 ± 7.06	105 ± 28.7	1.72 ± 0.41
Buffer zone	88.59 ± 8.95	7.85 ± 4.4	83 ± 18.01	1.6 ± 0.59

Point count surveys in the Lambusango forest indicated that endemic bird species in general were relatively resilient to moderate habitat modification; the number of endemic species detected per sample site was statistically similar in primary forest (4.89 ± 0.98) and disturbed secondary forest (4.52 ± 0.98) (Kruskal-Wallis $H = 2.112, p = 0.348$) (Figure 7.1), and it was only in wholly cleared agricultural land that endemic species dropped markedly, as discussed in Chapter 4. This was not true of all species; results in Chapters 4 and 6 demonstrate that populations of several large-bodied frugivores and insectivores were concentrated in primary and regenerating secondary forest sites, with low densities occurring in disturbed secondary forest. However, community dissimilarity analysis in Chapter 6 demonstrated that several endemic species associated with a wide range of forest/non-forest occur at greatest density within disturbed forest habitats. These included frugivores (Grosbeak Starling, Sulawesi White eye) and insectivores (Sulawesi Babbler, Citrine Flycatcher). Although the compostion of endemic bird assemblages differed between forest classes, richness of endemic species as a whole were found to be similar across all forest categories.

Endemic avifauna communities in Cusuco, however, appear to be more vulnerable to habitat modification, with the number of endemic birds detected per sample dropping significantly (Kruskal-Wallis H = 14.04, $p < 0.05$) between the boundary of core zone forest (6.34 endemic species per sample site ± 0.81) and the buffer zone (3.86 endemic species per sample site ± 0.69) (Figure 7.1).

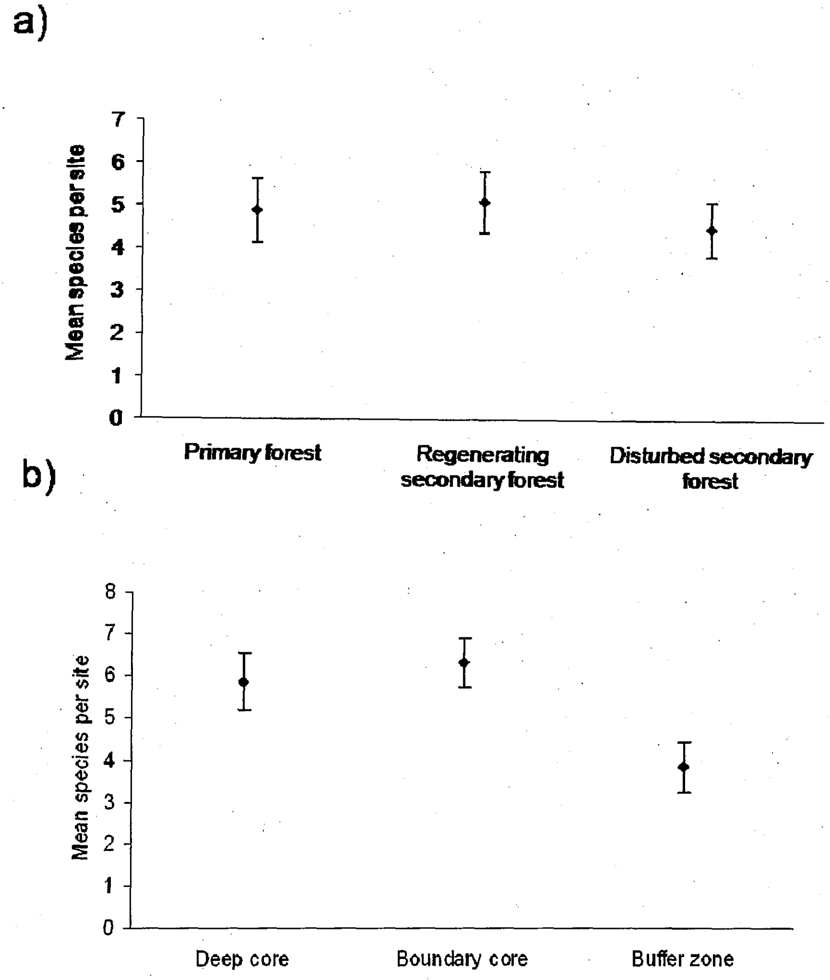

Figure 7.1 - a) Mean species endemic to the Wallacea hotspot detected per site in primary forest, regenerating forest, disturbed secondary forest and cleared farmland in the Lambusango Forest, South-East Sulawesi, (Kruskal-Wallis $H = 2.112$, $p = 0.348$*). b) Mean species endemic to the Mesoamerican hotspot detected per site in deep core, boundary core and buffer zone sites within Cusuco National Park, Honduras (Kruskal –Wallis* $H = 14.04$, $p < 0.05$*). Error bars represent 95% confidence intervals.*

This first series of results therefore suggest that some difference exists between endemic birds' response to habitat disturbance in the Lambusango Forest and Cusuco. Non-parametric estimators in Table 7.3 and species rarefaction curves reproduced in Figure 7.2 suggest this difference to be even greater when comparisons are made between highland endemics in Cusuco and all endemics in Lambusango. Species estimators for the Lambusango study sites demonstrate similar results to those shown in Figure 7.1, with species estimates in disturbed secondary forest (21.59) being only slightly less than those in primary forest (24.91). Estimators for Cusuco National Park, however, demonstrate a marked drop in predicted richness estimates between boundary core sites (26.22) and the sites at upper elevation in the buffer zone (11.69) – a decline of >50%. Species accumulation curves in Figure 7.2 display similar patterns, with forest categories in the Lambusango Reserve producing very similar trajectories while the buffer zone curve in Cusuco levels out at a much lower number of species than the deep or boundary core.

Table 7.3 - Non-parametric species estimators for ***a)*** *primary forest, regenerating secondary forest, disturbed secondary forest and cleared agricultural land within the Lambusango forest reserve, Buton Island, South-East Sulawesi and* ***b)*** *deep core, boundary core and buffer zone sites within Cusuco National Park, Honduras. n represents sample size. Sp obs and Ind obs represent total number of species and individuals observed, respectively. ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, Bootstrap, MMRuns and MMMeans are non-parametric species estimators (Colwell and Coddington 1994).*

a)

Parameters	Primary	Regenerating secondary	Disturbed secondary
N	28	28	28
Sp obs	22	22	20
Ind obs	287	243	214
ACE	24.07	24.63	20.27
ICE	24.45	23.97	20.91
Chao1	25	22.75	21.62
Chao2	23.47	23.96	20.91
Jack1	25.92	25.92	21.96
Jack2	26.94	27.89	20.1
Bootstrap	24.01	23.78	21.44
MMRuns	25.1	24.55	23.49
MMMeans	25.23	24.47	23.63
Average species estimate	**24.91**	**24.66**	**21.59**

b)

Parameters	Buffer >1000	Boundary Core	Deep core
N	28	39	59
Sp obs	11	23	23
Ind obs	106	539	880
ACE	11	29.17	24.27
ICE	11	29.02	24.25
Chao1	11	24.66	23.16
Chao2	11	24.65	23.16
Jack1	11	27.95	24.98
Jack2	11	27.99	24.05
Bootstrap	11.47	25.51	24.55
MMRuns	14.08	23.09	23.07
MMMeans	13.73	23.99	23.12
Average species estimate	**11.69**	**26.22**	**23.85**

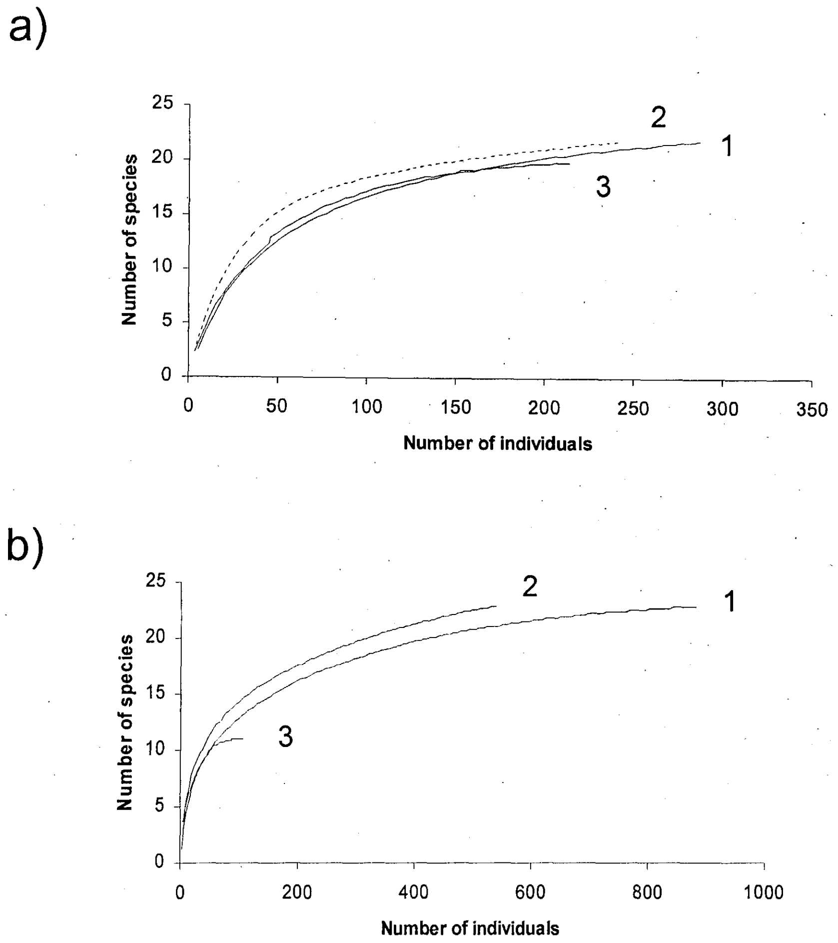

*Figure 7.2 - Sample-based rarefaction curves displaying number of individual birds detected against **a)** number of endemic species detected in primary forest (notated as 1), regenerating secondary forest (notated at 2), and disturbed secondary forest (notated as 3) within the Lambusango forest reserve, South-East Sulawesi, and **b)** number of highland forest species detected in deep core forest (notated as 1), boundary core forest (notated as 2) and buffer zone forest (notated as 3) in Cusuco National Park, Honduras.*

7.5 - DISCUSSION

Comparisons of body size and feeding guild composition demonstrate that the endemic avifauna of the Lambusango Forest has greater proportions of all evaluated 'high risk' categories compared to endemic avifauna in Cusuco. Therefore, the null hypothesis that no difference in the proportion of high risk groups exists between study sites can be rejected and an alternative hypothesis that the Lambusango possesses significantly higher ratios of these groups accepted. This is in concordance with the hypothesized elevated risk associated with endemic island birds discussed in the introduction. However, results also show that, despite possessing theoretically greater vulnerability to disturbance, endemic birds in the Lambusango forest were in actuality significantly less impacted by moderate habitat disturbance than Mesoamerican and highland forest endemics in Cusuco.

The response of endemic bird species to habitat disturbance in Cusuco National Park appears to be concurrent with deterministic theories concerning the vulnerability of range-restricted species (Trevino *et al.* 2007, Sutherland 2000, Pimm and Raven 1999). Species richness of endemic and cloud-forest restricted species declines markedly between high quality core zone forest sites and more degraded buffer zone sites. The sensitivity of endemics to habitat modification has been reported widely across the Neotropics (Barlow *et al.* 2007, Gardner *et al.* 2007, Canaday 1996), tropical Africa (Burgess *et al.* 2002, Fjeldsa 1999, Lawton *et al.* 1998) and continental South-East Asia (Peh *et al.* 2008, 2005).

Endemic bird communities in the Lambusango Forest, however, do not display the same response to disturbance. Similar species richness of endemic birds were reported in degraded secondary forest and primary forest, with persistence of endemics only dropping markedly in heavily modified cleared farmland sites. Indeed, results from dissimilarity analysis displayed in Chapter 6 indicate that several Wallacean endemics were found at higher densities in disturbed forest environments. The resilience to moderate environmental disturbance of Sulawesian endemic bird assemblages as a whole has also been reported in other locations in Central Sulawesi (Sodhi *et al.* 2005, Thiollay and Rahman 2002) as well as for species in other taxonomical groups within Wallacea; notably herpetofauna (Gillespie *et al.* 2005).

There are also circumstantial indications that Wallacean bird communities may be resilient to ecological pressures and extinction causalities other than the habitat disturbance measured in this study. A leading cause of bird extinctions on island archipelagos has been the introduction of foreign predators by humans. A review of bird extinctions on three other Indo-Pacific archipelagos with high ratios of avian endemism shows that in 11 out of 16 extinctions on New Zealand (69%), 8 out of 19 extinctions on the Hawaiian Islands (42%) and 10 out of 25 extinctions on the Mascarene Islands (40%) introduced mammalian predators are regarded as a major factor in their extinction, including species where causes of extinction are unknown (Birdlife International 2009, IUCN 2009, Fuller 2000). Theoretically, endemic bird species within Wallacea should be similarly vulnerable to this threat. The archipelago has very few native mammalian predators; Sulawesi has a single native carnivore, the endemic palm civet (*Macrogalidia muschenbroekii*) which is poorly known and is believed to have always been rare throughout its range (Lee *et al.* 2003, Whitten *et al.* 2002) and many smaller Wallacean islands have no native mammalian predators at all (Flannery 1995). However, since the onset of human settlement of the region two species of predatory civet have been introduced to Sulawesi; the Malayan Civet (*Viverra tangalunga*), now the island's top mammalian predator, and the Asian Palm civet (*Paradoxurus hermaphroditus*) (Jennings *et al.* 2005). Large feral populations of cats, dogs, pigs and rats (*Rattus norvegicus* and *Rattus rattus*) have also been introduced (Birdlife International 2009, Pangau-Adam 2003). While these introduced species have been shown to be significant nest predators and are at least partly responsible for declining populations in some endemic species (Birdlife International 2009, Pangau-Adam, 2003), they do not seem to have created a wave of extinctions as seen in other island ecosystems; not a single resident Wallacean bird species is listed as extinct by the IUCN (2009). One species, the Cerulean Flycatcher (*Eutrichomyias rowleyi*) was for several years considered as possibly extinct (Whitten *et al.* 1987) but has since been rediscovered by ornithologists (Riley and Wardill 2001).

The lack of regional extinctions or extirpations seems inconcurrent with the findings of Blackburn et al. (2004) who predicted avifauna on more geologically isolated archipelagos, such as Wallacea, to be particularly susceptible to extinctions from introduced predators. This could perhaps be partly due to a lack of understanding of Sulawesian avifaunal communities; Wallacea remains one of the most poorly understood ornithological regions on Earth, having been explored by ornithologists later than many other biogeographical regions, and some islands have not been surveyed for over 100 years (Trainor 2007, Coates and Bishop 1997). It is therefore possible that several species may have become extinct before their discovery, or since their initial description, as hypothesised by Whitten *et al.* (1987). However, the disparities in the number of recorded extinctions is still marked even considering unrecorded extinctions; at least 24 are known on the Mascarene Islands, for example, compared to none recorded across the whole of Wallacea (IUCN 2009).

Results from this study therefore suggest that the null hypothesis that no significant difference exists in the response of endemic bird communities to disturbance in the Lambusango Forest and Cusuco National Park can be rejected, and an alternative hypothesis, that endemic bird species in the Lambusango are more resilient to moderate environmental disturbance, accepted. The reasons for this difference pose an interesting research question, given the theorised higher vulnerability of endemic avifauna in the Lambusango as described earlier in this chapter. There are a number of potential ecological and biogeographical factors which could contribute to creating these apparent differences in ecological vulnerabilities, which the remainder of this chapter will explore.

7.5.1 - Differential species richness of bird communities

One possible control contributing towards differential endemic avifaunal response to disturbance could result from substantial differences in total avian richness between the study sites. Only 51 species were detected during our survey effort in the Lambusango Forest, of which 33 (64.7%) were Wallacean endemics (Martin 2008). The checklist of bird species in Cusuco National Park described in Chapter 2, however, totals 209 species with just 43 (20.57 %) being endemic to the Mesoamerican hotspot and 27 (12.9%) being restricted to highland forest types (Howell and Webb 2005). This means Cusuco has a lower overall ratio of endemic: non-endemic species, and over four times as many bird species in a spatial area less than half the size of the Lambusango (23,440 hectares vs 65,000 hectares). The relatively depauperate species richness of bird communities in the Lambusango is characteristic across all Wallacean islands (Coates and Bishop 1997, White and Bruce 1986), especially when compared to avian richness on islands immediately to the east and west of the region (Table 7.4). Relatively low species diversity may result in lower niche competition, and therefore endemics here may need to be less specialised and possess higher ecological tolerance, thus could be less vulnerable to habitat modification. Low niche competition may be further influenced by the low number of species in most avian families within the Lambusango. Table 7.4 shows how 65% of bird families with at least one endemic species in the Lambusango have ≤3 species represented, and only 3 families are represented by >4 species.

Low species richness in families represented by endemics is also characteristic of the avifauna of Sulawesi as a whole. Table 7.4 shows that families represented by endemic species in the Lambusango Forest have consistently far fewer species represented across the island compared with comparable biogeographical regions bordering Wallacea. The Australasian families generally have far higher species diversity in New Guinea, and Oriental families typically have a higher species diversity across the Makassar Straits in Borneo; the singular exception is the family Coraciidae, which has a low diversity across the region. As niche competition is often greatest within species of the same family which share similar habitat and dietary requirements (Graves and Gottelli 1993), the low number of species in each family may result in low inter-species competition and allow endemics to be less specialised.

Table 7.4 - Comparison of richness of avifaunal families represented by at least one endemic species in the Lambusango Forest Reserve, Buton Island, South-East Sulawesi with richness of these families to the West of Wallacea in Borneo and to the East in New Guinea. Families listed as having centre of diversity as Australasian have greatest number of species occurring East of Lydekkers' line. Families listed as having centre of diversity as Asian have greatest number of species occurring West of Wallace's line (Coates and Bishop 1997). Cosmopolitan families are evenly distributed across the Oriental and Australasian Zoogeographical zones. Species list for Sulawesi based on Coates and Bishop (1997). Species list for Borneo and New Guinea based on Clements (2007).

Family	Centre of diversity	Endemics in Lambusango	Species in Lambusango	Species in Sulawesi	Species in Borneo	Species in New Guinea
Accipitridae	Cosmopolitan	3	4	18	31	33
Columbidae	Australasia	3	8	24	20	56
Psittacidae	Australasia	5	6	10	5	51
Cuculidae	Cosmopolitan	2	5	15	22	20
Centropidae	Cosmopolitan	1	1	2	3	5
Tytonidae	Australasia	1	1	4	1	7
Strigidae	Cosmopolitan	1	1	3	12	9
Coraciidae	Asia	1	1	2	1	1
Bucerotidae	Asia	2	2	2	8	1
Picidae	Asia	1	1	2	18	0
Campephagidae	Australasia	3	3	10	11	18
Corvidae	Cosmopolitan	1	2	2	8	4
Timallidae	Asia	1	1	2	35	0
Petroicidae	Australasia	1	1	1	0	23
Sturnidae	Asia	3	4	11	7	11
Dicaeidae	Asia	2	2	3	12	6
Zosteropidae	Cosmopolitan	1	2	7	7	11

7.5.2 - High vegetation diversity

While the richness of most faunal groups in Wallacea is low, diversity of plants, which have not been inhibited from colonization by the regions biogeographical barriers (Whitten 2002), is remarkably high, and it is possible this may also facilitate resilience of endemic avifauna to moderate anthropogenic disturbance in the Lambusango. While most South-East Asian rainforest ecosystems are characteristically dominated by a single family of tree species, namely Dipterocarps (Corlett and Primack 2005), forests on Sulawesi are highly diverse, with no plant families being predominant (Whitten *et al.* 2002, O' Donovan 2001). No comprehensive quantitative survey of plant diversity on Sulawesi has yet been conducted, although Kessler *et al.* (2005) described how a single hectare plot of sub-montane primary rainforest in Central Sulawesi possessed 148 tree species (DBH >10cm) comprised of 82 genera and 42 families. This represents a diversity considerably greater, particularly at a family level, than research at comparable sample sites have demonstrated to exist in other areas of insular South-East Asia. Hamann *et al.* (1999), for example, described only 92 tree species (also defined as DBH >10cm) from an identical sized plot of sub-montane rainforest in the Philippines.

This high floristic diversity may have created ecosystems with a wide variety of trophic niches and microhabitats, to which endemic avifauna may by necessity have adapted to. As they could already be adapted to a diverse floristic structure they might be more resilient to changing habitats caused by anthropogenic modification. A species-rich plant assemblage is, however, by no means unique to Wallacean rainforests. Central American cloud forests also possess rich and diverse floral assemblages; Nadkarni *et al.* (1995), for example, counted 114 tree species from 83 genera and 47 families in a 1.5 hectare plot of forest in Costa Rica's Monteverde reserve. However, the hypothesis that high floral diversity may contribute to the apparent resilience of Wallacean endemic bird to moderate habitat disturbance may be worthy of further consideration.

7.5.3 - Low specialisation and ecological distinctiveness of endemic species

Many sources have emphasised how the endemic species of Sulawesi are among the most taxonomically distinct globally; the result of a complex geological history and long periods of tectonic isolation (Stattersfield *et al.* 1998, Coates and Bishop 1997, White and Bruce 1986). Thus, theoretically, many species on the island have followed distinct, highly specialised evolutionary pathways and become highly adapted to the forest ecosystems in which they are found. This general pattern may apply to endemic organisms across Sulawesi as a whole, but may not be the case in the Lambusango reserve. White and Bruce (1986) describe Buton's avifauna as 'impoverished Sulawesian' and describe how many of the region's most evolutionary distinct endemic birds are concentrated in the mountainous interior of the mainland. Examination of the endemic species present in the Lambusango Forest appears to support this view. Table 7.5 demonstrates that 16 (59.3%) of the 27 Sulawesi endemic species detected in the Lambusango were probable or possible close evolutionary relatives of non-endemic species, being considered potentially con-specific, an allospecies or part of a super-species complex with non-endemic species. The Table also shows that 10 of these species (37.4% of all endemics) were considered closely related to a wide-ranging, generalist species found in a wide variety of habitat types. It could perhaps be possible, therefore, that a substantial proportion of the Lambusango reserve's endemic avifauna are not as evolutionary distinct as many species found on the mainland, and could possibly be more recent divergents from wide-ranging generalists found in a large range of habitat types. Thus they might not be highly specialised to Wallacean forest ecosystems but instead be relatively tolerant to a range of habitat types. This theory would not, however, explain the habitat response patterns of endemics described by Sodhi *et al.* (2005) and Thiollay and Rahman (2002), who conducted research in mountainous regions of mainland Sulawesi where more distinct evolutionary lines are found (White and Bruce 1986), or the response patterns of Herpetofauna in the Lambusango described by Gillespie *et al.* (2005); but again this theory may be a factor worthy of consideration.

Table 7.5 - Taxonomical relationships of endemics found in the Lambusango. Taxonomical status based on Gamauf et al. (2005), Sibley and Monroe (1990) and White and Bruce (1986). Endemic genus status relates to endemism within the Wallacean hotspot.

Endemic species	Endemic genus?	Relationships?	Related species	Status
Spilornis rufipectus	No	Allospecies	*S. Cheelah*	Widespread generalist. Found from South Asia to China and Greater Sundas
Accipiter trinotatus	No	No close relationships		
Spitzaetus lanceolatus	No	Superspecies	*S. philippensis, S. pinkskeri, S. cirrhatus*	two widespread generalists found across South, South-East and East Asia. Two endemic to Philippines
Turacoena manadensis	Yes	No close relationships		
Ducula forsteni	No	Allospecies; possibly conspecific	*D. mindorensis*	Endemic to the central Philippines
Ducula luctuosa	No	Allospecies; possibly conspecific	*D. bicolour*	Widespread on island ecosystems from South Asia to Philippines and New Guinea
Trichoglossus ornatus	No	Allospecies	*T. haematodus*	Widespread across Indonesia, Melaneasia and Australasia
Prioniturus platurus	No (Near)	No close relationships		
Loriculus stigmatus	No	Super-species	Five *Loriculus* species	All endemic to Wallacea or New Guinea
Cuculus crassirostris	No	No close relationships		
Phaenicophaetus calyorhynchus	No	Allospecies	*P. curvirostris*	Widespread from South Asia to Greater Sundas
Centropus bengalensis	No	Probable allospecies	*C. sinensis*	Widespread across South, South-East and East Asia
Coracias temminckii	No	No close relationships		
Penelopides exhartus	No (Near)	Super-species	Five *Penelopides* species	All others endemic to the Philippines
Rhyticeros cassidix	No	Super-species	*R. corrugatus, R. leucocephalus*	One widespread across Sundaland, one endemic to Southern Philippines
Mulleripicus fulvus	No	No close relationships		
Coracina bicolour	No	No close relationships		

Coracina leucopygia	No	Allospecies	*C. papuensis*	Occurs in Eastern Wallacea through New Guinea, Melaneasia and Northern Australia
Coracina morio	No	Possible superspecies	Three *Coracina* species	All others endemic to Wallacea and Phillipines
Corvus typicus	No	No close relationships		
Trichastoma celebense	No	Possible allospecies	*T. abbotti*	Widespread across South and South-East Asia
Basilornis celebensis	No (Near)	No close relationships		
Streptocitta albicollis	Yes	No close relationships		
Scissirostrum dubium	Yes	No close relationships		
Dicaeum aureolimbatum	No	Allospecies	*D.nigrilore*	Endemic to the Southern Philippines
Dicaeum celebicum	No	Allospecies; possibly conspecific	*D. hirundinaceum*	Widespread in Australia, New Guinea and Melaneasia
Zosterops celebense	No	Allospecies; sympatric	*Z. chloris*	Endemic to Indonesia

7.5.4 - Presence of strangler figs as a food resource in degraded forest habitats

A further factor to consider with regard to differences in disturbance vulnerabilities between Mesoamerican cloud forest and Wallacean endemics concerns the difference in the trophic composition of bird communities between the two hotspots and the persistence of strangler figs in disturbed forest patches on Sulawesi. Figs (Moracae) are a pan-tropical plant family, and species of the true-fig genus (*Ficus* sp.) are considered to be among the most important food resources for frugivorous birds in both South-East Asia and the Neotropics. They are considered particularly important when other food sources are low, due to producing large quantities of fruit in aseasonal patterns throughout the year (Shanahan *et al.* 2001, Nason *et al.* 1997, Lambert and Marshall 1991). 'Strangler' figs are a subgroup of the *Ficus* genus which are hemiepiphytic, germinating as epiphytes in the canopy but later sending roots to the ground, which then grow upwards to envelop the host tree. This usually results in the death of the host tree, either through girdling or light competition, after which the strangler's roots fuse to form a trunk-like 'cylinder' (Putz and Holbrook 1989). Strangler figs have been noted as particularly important food resource, producing substantially larger fruit crops than non-strangler fig species (Primack and Corlett 2005); a study by Tello (2003) describes how a single Neotropical strangler fig can be utilised as a food resource by more than 40 vertebrate species.

Fig species as a whole have been shown to be heavily utilised by frugivorous birds on Sulawesi. Walker (2007) describes how figs form by far the largest proportion of resident frugivorous bird species diet, despite being less common than non-fig fruiting trees. His study in Northern Sulawesi found figs formed 59% of the total diet of pigeon species (*Columbidae*) and 52% of passerine species, while Kinnaird (1998) found figs constituted >70% of the breeding season diet of the endemic hornbill *Rhyticeros cassidix.* Indeed, the density and biomass of fig trees have been shown to be a key controlling factor in determining abundance of large Wallacean frugivores (Kinnaird *et al.* 1996). Figs are therefore considered a 'keystone' resource for frugivores across much of the tropics, but are perhaps particularly important in Wallacea. This is firstly because Wallacean figs are particularly productive. Kinnaird and O'Brien (2005) report Sulawesian fig species as producing over five times as much fruit mass as equivalent species in Western Indonesia. Figs are also of particular importance here as frugivores make up a high percentage of endemic bird assemblages (48.5% of all endemic bird species) (Coates and Bishop 1997). Strangler figs are a notable feature throughout the Lambusango forest, occurring at low densities at all study sites, including areas of degraded secondary forest which otherwise had few large, fruiting tree species (Personal observation 2008). This could perhaps be because the twisted wood of stranglers is less valuable as a timber resource compared to other hardwood sources, and as such may have be left by loggers who have harvested other large trees in these degraded habitats. These stranglers may therefore be a highly important resource for endemic frugivorous birds in disturbed landscapes where other food sources are scarce. As frugivorous birds form such a large proportion of endemic avifaunal species in the Lambusango, this could contribute to the persistence of nearly equal numbers of endemic species in primary and disturbed secondary forest, as displayed in Figure 7.1a. Results reported earlier in the thesis suggest that the presence of strangler figs in disturbed forest does not contribute to the persistence of certain larger frugivores, such as hornbills and *Prioniturus* parrots, given that these occur at very low densities in disturbed forest sites; however other research has reported high abundances of these species in disturbed habitats, suggesting that persistence of feeding resources may be an important factor (Sodhi *et al.* 2005, Cahill 2003). Other non-frugivorous endemic species may also benefit from the presence of strangler figs, as these may provide roostings sites in landscapes where other large trees are scarce.

Strangler figs are also common in Cusuco National Park, but are generally confined to the park's core zone, those in the buffer having been largely felled (personal observation 2007). As frugivores also constitute a high proportion of Mesoamerican endemic bird assemblages in Cusuco (38.9%) (Howell and Webb 2005), and data analysis has shown that endemic bird richness is significantly less in buffer zone sites where strangler figs are scarce, this could perhaps support arguments for strangler figs being a highly important resource for endemic bird communities elsewhere.

7.5.5 - Climate and natural disturbance patterns

A further, biogeographical, reason concerning different responses of avifaunal communities to disturbance could relate to different climatic regimes. The forests of Buton experience a tropical monsoon climate with a pronounced November – April wet season when the bulk of the region's 1500 – 2000mm of rain falls, and a June – September dry season where <50mm of rain can fall (Whitten *et al.* 2002). The vegetation of the region reflects this seasonality; Collins *et al.* (2001) defines the natural vegetation of Buton as lowland monsoon forest, with many species being semi-deciduous, losing their leaves during the dry season. Forest fires also occur fairly frequently during the dry season (O'Donovan 2001). This means the forest ecosystems of Buton experience a wide degree of variation in habitat structure and natural disturbance on an annual basis; thus endemic birds here may be more adapted to changing habitats than range-restricted species in many other tropical forest ecosystems. These species may therefore be less influenced by anthropogenic disturbance unless to a degree far greater than vegetation structure's natural variation, such as in the farmland sites.

High seasonality is not uncommon in tropical ecosystems; Cusuco also has two distinct wet and dry seasons. The cloud forest here experiences an October – December 'invierno' wet season, when 45% of the region's 2500 – 3000mm precipitation falls, and a February – May 'verano' dry season (Fundación Ecologista 1994). Temperature ranges within this seasonality are also greater than in Sulawesi, ranging from a mean average of 12.9° in December to 20.2° in April, while the Lambusango remains at a fairly consistent temperature (mean 25°) throughout the year (Whitten *et al.* 2002). However, despite a seasonal climate, Cusuco's forests are non-seasonal. Cloud forest is characteristically humid year-round, with perennial precipitation and additional moisture being provided by ever-present enveloping cloud banks, thus almost all plant species are evergreen and vegetation characteristics remain fairly consistent (Bubb *et al.* 2004). Perennially humid conditions also limit the frequency of forest fires; thus this form of natural disturbance is limited in these ecosystems.

These differences in year-round vegetation structure variability and frequency of natural disturbance from forest fires may partially explain apparent differences in disturbance sensitivities of endemic bird species in the Lambusango Forest and Cusuco National Park. However, the cloud forests of Honduras do experience an intermittent source of natural disturbance that is absent from Sulawesi in the form of tropical cyclones. The whole Mesoamerican hotspot lies in the Northern Hemisphere hurricane belt, and is subject to storm systems formed in both the North-East Pacific and North Atlantic hurricane basins, with an annual hurricane season running from April - November (McIlveen 1998). On average, one hurricane or tropical storm hits the region each year (Urquiza- Haas *et al.* 2007). Hurricanes in this region frequently create very heavy natural disturbance in the region's forests (Yih *et al.* 1991); Cusuco itself has many areas still regenerating from damage caused by Hurricane Mitch in 1998 (Lenkh 2005, Field 2004, personal observation 2007). This natural disturbance has been shown to have impacted upon the population dynamics and species composition of bird communities in the region (Whigham and Lynch 1998). The Wallacean hotspot, however, is not subject to cyclone disturbance, being located close to the equator where high pressure belts and weak coriolis force inhibit the genesis and intrusion of cyclones and tropical storms (McIlveen 1998). Differences in the frequency of cyclones and tropical storms between the two sites are shown in Figure 7.3. This demonstrates that although the cloud forests of Mesoamerica do not experience the predictable seasonal variation in habitat structure caused by a monsoon climate or frequent fire disturbance, they do experience more unpredictable disturbance, occasionally of a very high magnitude in the case of 1-in-100 year storms such as Hurricane Mitch, to which the forests of Wallacea are not usually subject. This should be taken into account when considering how natural disturbance may influence the resilience of endemic birds to anthropogenic disturbance. It should also be acknowledged that, while not subject to hurricanes, Wallacean islands are also subject to a number of unpredictable, low frequency/high magnitude environmental phenomena which do cause significant natural disturbance, albeit not always on the same scale as high-force hurricanes, such as extreme drought/flooding and increased fire-risk caused by El Nino/ Southern Oscillation events (Leemhuis and Gerold 2006, Uhl 1998).

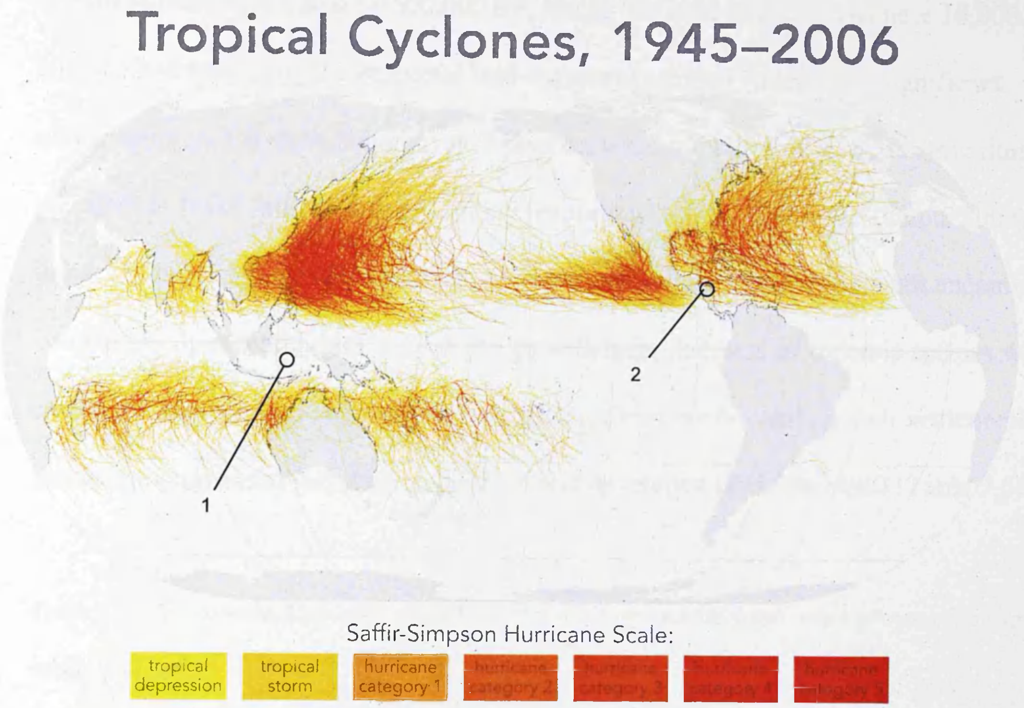

Figure 7.3 - Distribution of tropical cyclone tracks 1945 – 2006 in relation to study site locations. Notation 1 indicates location of Lambusango Forest Reserve, Indonesia. Notation 2 indicates location of Cusuco National Park, Honduras. Based on National Oceanographic and Atmospheric Administration (2008).

7.5.6 – **History of human settlement**

A final factor which may contribute to the apparent differential responses of endemic avifauna in the two study sites may relate to timing of human settlement. The global spatial distribution of endemic bird species are overwhelmingly concentrated into the two broad ecosystem types examined in this thesis; oceanic islands and montane forest. A review of Stattersfield's (1998) 218 endemic bird areas show that 74% (160 sites) consist solely of these habitat types, which together encompass the entire ranges of >80% of all range-restricted bird species. There appears to be a strong overlap between these areas of high endemism and areas where human colonization was comparatively late, as the biogeographical factors which promote speciation and endemism have also acted as barriers to the spread of human immigration. Roberts (1998) describes how hominids had successful colonised much of Eurasia by 500,000 BP, and by the start of the Holocene ± 10,000 BP humans had spread to all continental land-masses other than Antarctica. Significant modification of the environment would have occurred in colonised areas as agricultural practises diffused following the Neolithic revolution 10,000 – 7,000 BP (Gupta 2004). The impact of human disturbance was not, however, felt in many centres of avian endemism until comparatively recently. Most island groups with large numbers of endemic species were not colonised until the mid-Holocene or later, oceanic barriers preventing their settlement until sufficiently advanced maritime technology was developed (Roberts 1998) (Table 7.6).

Table 7.6 – Approximate dates of human colonisation of oceanic archipelagos with high rates of avifaunal endemism.

Island group	**Date of colonisation (BP)**	**Source**
Lesser Sundas	100,000	Whitten *et al.* 2002
New Guinea	>50,000	O' Connell & Allen 2003
Sulawesi	> 30,000	Whitten *et al.* 2002
Lesser Antilles	5,000	Keegan & Diamond 1987
Madagascar	2000	Burney *et al.* 1997
Hawaii	1400	Keegan & Diamond 1987
New Zealand	800	McGlone 1989
Mascarenes	400	Keegan & Diamond 1987

The majority of montane forests were also first subject to heavy anthropogenic modification relatively recently. While records of ancient agriculture in lower-montane slopes do exist in some regions, such as South-East Asia and New Guinea (Denham *et al.* 2003), most areas of mountainous forest, particularly at mid-high elevations, were much less impacted by early agriculture compared to lowland areas due to unfavourable topography, accessibility and climate. This is the case across much of the Tropical Andes, the greatest centre of avian endemism in the world (Myers *et al.* 2000), and also in Mesoamerica. While complex agrarian societies have existed in this biodiversity hotspot since at least 5000 BP, most of these pre-historical and historical cultures have been centred in lowland forest or the Central Mexican Plateau (Bray and Klepis 2005, Goman and Byrne 1998, Metcalfe 1995). Most of the region's cloud forest, such as that found in Cusuco, was left relatively undisturbed until as recently as the mid-20th century, when mechanised forestry and modern infrastructure made these regions accessible (Bray and Klepis 2005). This pattern of recent initial disturbance is true of many cloud forest ecosystems globally (Bubb *et al.* 2004).

Many centres of avifaunal endemism therefore correspond with ecosystems which have been isolated from anthropogenic disturbance until comparatively recently, leading to resident endemic birds inhabiting habitats with relative long-term stability and, in the case of oceanic islands, low competition environments with little predation or hunting pressure. The recent appearance of humans and associated habitat modification after long periods of ecological isolation may therefore have had a disproportionately heavy impact on these species adapted to previously stable forest ecosystems which have been little changed since the early Holocene (Bush *et al.* 2004). On oceanic islands this would have been further exacerbated by the sudden introduction of feral and domesticated livestock and mammalian predators associated with human settlement on previously predator-free island (Blackburn *et al.* 2004, Milberg and Tyrberg 1993). This may represent a smaller-scale model of Martin's (1984) 'Blitzkrieg' hypothesis relating to the sudden extinction of Pleistocene megafauna following waves of immigrating humans. Recent colonisation by humans in centres of endemism may therefore be a further contributing factor concerning why most current research reports endemic birds as being highly vulnerable to habitat modification.

The Wallacean region, however, along with the neighbouring New Guinea Island group, represents one of the few areas where a high concentration of endemic bird species coincides with a long history of human settlement. The biogeographical barriers isolating the archipelago's flora and fauna have not been nearly as formidable for inhibiting human migration, who were able to cross the encompassing deep ocean trenches with comparative ease. Hominids have been present in insular South-East Asia for at least 1.6 million years (Semah *et al.* 2000), while evidence suggests modern humans have been present on Sulawesi since at least 30,000 BP (Whitten *et al.* 2002) (Table 7.6). Evidence of swidden-system farming on Sulawesi dates back at least to 4000 BP on Sulawesi, and indications of agriculture and widespread deforestation goes back as far as 6,500 BP on nearby New Guinea (Denham *et al.* 2003, Whitten *et al.* 2002). Continual shifting cultivation and anthropogenic disturbance of forest ecosystems for most of the Holocene may be long-term enough for species to have adapted to this as an almost integral ecological process. While the scale of habitat loss today is of a different magnitude to that of pre-20th century cultivation patterns, it may have allowed species to become adapted to edge and secondary forest habitats, hence this could contribute to why research in Wallacea shows endemic species to be tolerant of moderate habitat disturbance. This could perhaps be linked to Brook and Bowman's (2002) wider hypothesis concerning survival of megafauna in areas with long-term human presence, such as in Africa, due to co-evolution and slow adaptation to anthropogenic activity. It might also provide a partial explanation as to the previously discussed lack of recorded bird extinctions resultant from introduced predators on Wallacea. The long-term human settlement of the region makes it very likely that most invasive species are prehistoric introductions: there is evidence that introduction of the Malayan Civet, for example, dates back to the late Pleistocene (Whitten 2002). This may have facilitated a wave of unrecorded bird extinctions shortly after colonization began, as hypothesised by Whitten (1987). Early introductions may have eliminated species most susceptible to predation, of which no record remains, and remaining endemics may have possessed characteristics making them less susceptible to extinction, and have had millennia to adapt further to the challenges presented by invasive mammals. This could perhaps partially explain the lack of recent Wallacean extinctions, and the absence of flightless birds and low diversity of ground-nesters in the region (Coates and Bishop 1997).

7.6 - FURTHER RESEARCH

Each of these hypotheses represents potential factors which could influence the apparent differential vulnerability of Wallacean and Mesoamerican cloud forest endemic avifauna. However, the concepts explored are at this stage purely theoretical; further empirical research is required to test the relative importance and weighting of each of these hypotheses. Potential research projects to assess the importance of each hypothesis could be as follows:

Differential species richness of bird communities: Assessing the extent to which the low species richness of the Lambusango Forest's avifaunal community facilitates reduced niche competition and low specialisation of endemic species would require an extensive, long-term behavioural study examining the foraging and roosting behaviour of endemic bird species in both biological hotspots. Detailed studies describing the behaviour of several of the larger, more charismatic species found in these areas have been published, for example Knobbed Hornbills and Resplendent Quetzals (Kinnaird and O'Brien 2008, Lourdes-Avila *et al.* 1996) but a detailed understanding of the ecology of most endemic species in the study areas is lacking.

High vegetation diversity: Studying how far the influence of the Lambusango's high floral diversity affects the provision of endemic species with a wide range of ecological niches would require an intensive botanical survey of plant species present in each study site. This survey would be taken in combination with the behavioural studies described previously in order to provide an understanding of how bird species utilise different floral species as resources.

Low specialisation and ecological distinctiveness of endemic species: Assessing the importance of this potential factor would require two research projects, both focussing on avifaunal communities in the Lambusango Forest. The first would be to obtain a more detailed understanding of evolutionary relationships between Sulawesi endemics and suggested closely related generalists based upon modern molecular phylogenetic comparisons. Most current descriptions of the evolutionary relationships of Sulawesi endemics are based upon outdated physical taxonomy comparisons (White and Bruce 1986, Sibley and Monroe 1990), and while taxonomic descriptions based on molecular analysis have been completed for a very few species (ie: Gamauf *et al.* 2005), these data are lacking for the vast majority of Wallacean endemics. The second study would be an extension of the behavioural studies already described; it would be valuable to determine if those species considered allospecies or conspecific with wide-ranging generalists utilise a wide range of habitat types and floristic resources as hypothesised, or if they are highly specialised to discrete ecological niches.

Presence of strangler figs as a food resource in degraded forest habitats: Assessing the relative importance of strangler figs for Wallacean and Mesoamerican endemic species in degraded habitats could be assessed by quantifying the abundance of these plants within disturbed forest habitats through an extensive botanical survey. Assessment of the value of strangler figs as a feeding resource could then be examined through observational studies; species encountered feeding at a series of fruiting figs could be recorded utilising methods similar to those employed by Walker (2007) in Sulawesi and Guevara and Laborde (1993) in the Neotropics. As much avian activity at strangler figs would occur at a high canopy level (strangler figs in both study sites can grow to >30m), it might be necessary to conduct observational studies from emergent forest giants above canopy level. This could be achieved with assistance from Canopy Access Ltd, a company working with Operation Wallacea at both study sites, which specialises in facilitating scientific research within the canopy of tropical forest ecosystems.

Climate and natural disturbance patterns: Determining the influence that seasonal and extreme climate change events and natural disturbance patterns have on facilitating low specialisation in endemic avifauna would require several extensive, long-term research projects. Studies would need to examine behavioural changes in endemic species in response to seasonality, and the impact forest fires and other natural disturbances have upon endemic bird species. The frequency of these events would also have to be quantified more specifically.

History of human settlement: This represents a difficult hypothesis to evaluate empirically, although the ideas discussed could perhaps be strengthened by examining archaeological or palaeoenvironmental records to provide more detailed information on human settlement history and environmental disturbance on Buton Island or the Merendón Cordillera. This could firstly establish a firmer appreciation of when human settlement and agriculture began in the more immediate vicinities of our study sites, and secondly develop an understanding of how this impacted upon local vegetation. The lack of peat deposits and lakes in the North-west Honduran mountains may pose a problem for obtaining palaeoenvironmental data for the Cloud forests of this region, although the extensive peat swamps of Rawu Aopa National Park, in close proximity to Buton Island, might be a useful source of palynological records concerning past forest disturbance patterns around the Lambusango (Coates and Bishop 1997).

It might also be valuable to compare behaviour and competitive adaptations of avifauna (nesting strategies, wariness and approachability, competence of flight etc.) with birds on Wallacea with other island groups with many endemic species to ascertain adaption to introduced predators.

7.7 - CONCLUSION

This chapter has explored several possible ecological and biogeographical controls which could account for the apparent differences in vulnerabilities to disturbance displayed by endemic bird species across the study sites utilised in this thesis. It has also identified potential research projects which could quantify the importance and relative weightings of these factors empirically. It should be acknowledged that these hypotheses only represent a range of considerations which could account for the different responses of endemic bird communities and there may be other controls not considered in this chapter, such as the ecological history of the study sites, the different spatial habitat area and relative isolation of each study site, and disturbance effects that cannot be assessed by vegetation surveys, such as human traffic, hunting pressures etc. It should also be acknowledged that the hypotheses outlined are based on the results of just two three-month studies in two field sites, and these findings should be used with caution when extrapolating these concepts on a wider scale.

However it would seem feasible that lower niche competition, more recent evolutionary divergence, cyclical patterns of habitat structure change, presence of strangler figs and long-term human settlement may all contribute to the apparently higher resilience to moderate disturbance of endemic bird assemblages in the Lambusango Forest than that of endemic species in Cusuco, which seem to conform more to the expected paradigms of vulnerabilities in range restricted birds. These hypotheses represent worthwhile avenues for future research into the relationships between endemic birds and habitat disturbance in these important biological hotspots.

7.8 - REFERENCES

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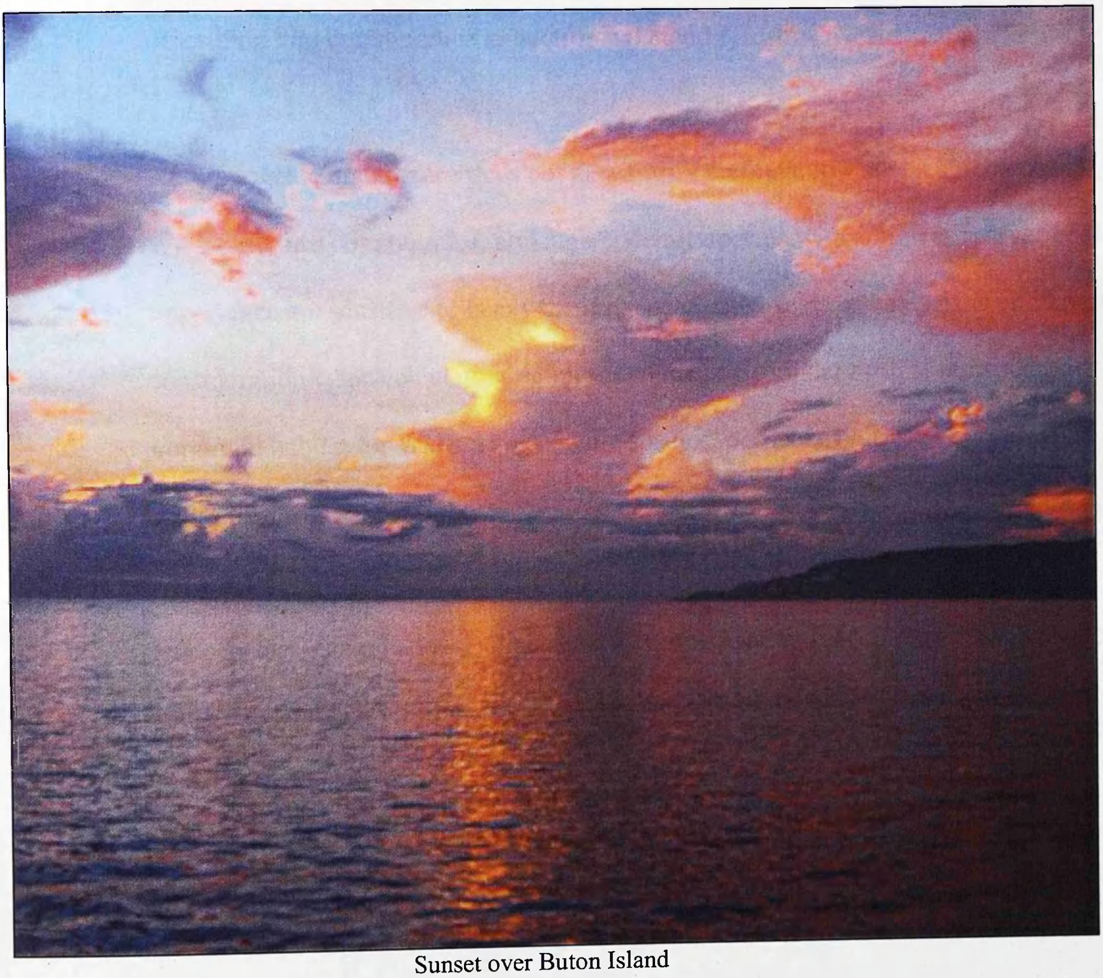
CHAPTER 9 - CONCLUSION



Sunset over Buton Island

8.1 – Research summary

The key findings of the research presented in this thesis can be summarised as follows:

- Point counts can be considered more effective than mist-nets as a methodology for describing bird communities in neotropical cloud forest.

- Anthropogenic disturbance does not necessarily facilitate low species richness in Wallacean bird communities, although endemic species with a high conservational importance are sensitive to heavy disturbance. Spatial scale of analysis is an important consideration when calculating richness estimates. Secondary forest represents an important habitat for Wallacean endemic species, particularly in later successional stages of forest regeneration.

- High species richness does not necessarily correspond to high conservation value of species assemblages in forest ecosystems. Range-restricted Mesoamerican cloud forest avifauna are highly sensitive to even moderate environmental disturbance, although under-resourced 'paper parks' can still provide important protection for these species.

- The composition of Wallacean bird communities shows strong associations with broad-scale habitat classifications and several vegetation and remote sensing variables, particularly canopy density and NDVI index measurements. These classifications and variables can be used to predict priority conservation areas for the preservation of endemic avifauna. Spatial scale is an important factor to consider when examining associations between bird communities and local habitat structure.

- Differences in vulnerabilities to habitat modifications between Wallacean and Mesoamerican endemic bird assemblages may be due to a range of biogeographical and ecological factors, although this requires further research.

These key findings are summarised in Figure 8.1, which also shows how research outcomes relate to the original objectives defined in Figure 1.9, and how each research outcome relates to the structure of thesis as a whole.

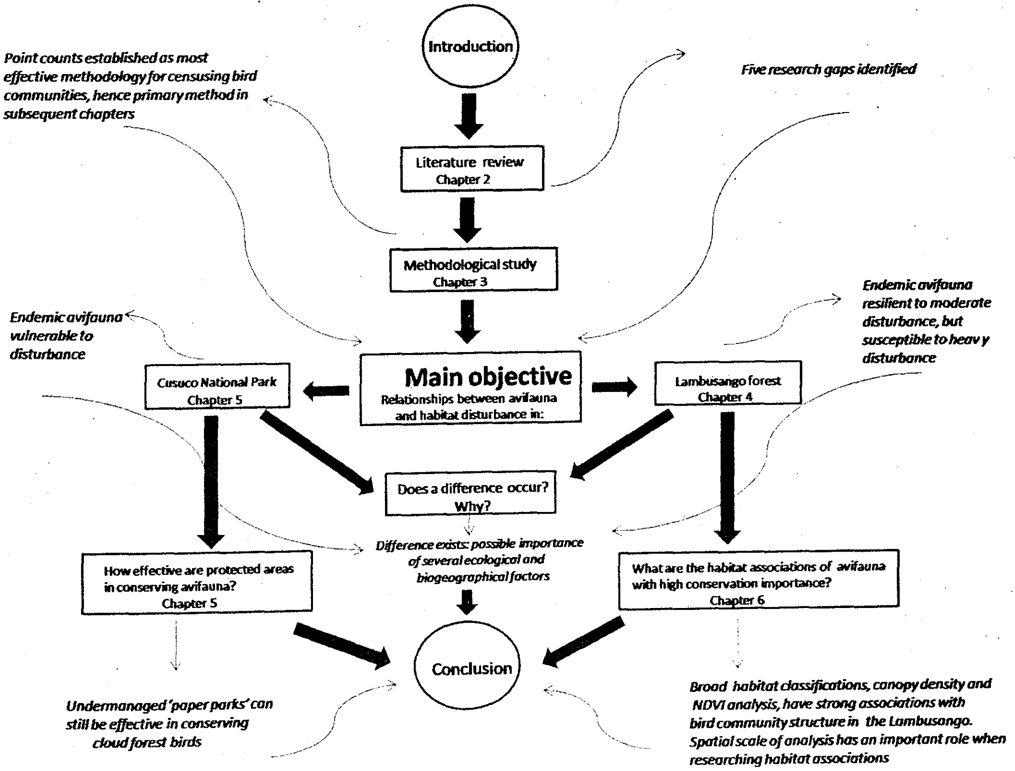


Figure 8.1 – Conceptual diagram summarising main research findings in relation to original objectives and how the results of each research objective relate to the structure of the thesis.

The linkages between the broad range of study objectives shown in Figure 8.1 demonstrate the importance of employing multiple perspectives when approaching environmental problems in order to develop deeper understandings of these issues. The different avenues of inquiry examined in this research (methodological, ecological, conservational, spatial and biogeographical) have combined to provide a greater understanding of the interactions, consequences and causalities of avifaunal response to habitat disturbance than any of these research frameworks could have achieved alone. This demonstrates the value of multi-disciplinary holistic geographical inquiry into issues of human-environment interactions.

The thesis has also produced additional research providing descriptive accounts of the avifauna of the Lambusango forest and morphometric data for Mesoamerican cloud forest birds which is unpublished elsewhere.

8.2 – **Further research**

While the findings presented in this thesis has successfully addressed a series of important research areas, further work could be conducted to either strengthen this research or investigate new avenues of study our results have identified.

The fieldwork component of this thesis was carried out in conjunction with Operation Wallacea. Their assistance was invaluable during data collection, providing the author with all logistical requirements, skilled field assistants and the diplomatic links and permits required to conduct research in the chosen study sites. While the issues involved in collaborating with an organisation such as Operation Wallacea were overwhelmingly beneficial, there were several factors which imposed limitations on research. Foremost among these were the temporal and spatial restrictions placed on fieldwork, in that data collection was only possible during the Operation Wallacea 'season' which ran for just eight weeks each summer, and this collection was limited to the study areas in which Operation Wallacea was working. While the bird surveys conducted in the course of this thesis represent an intensive survey effort considerably greater than that displayed in many similar published studies, it would have been preferable to have been able to spend longer periods in Indonesia and Honduras, allowing for more data collection and possibly facilitating fieldwork spanning breeding and non-breeding seasons, providing a more comprehensive overview of bird communities. It would also have been useful to return to each site over several more seasons to repeat the bird surveys used in analysis in order to procure a greater sample size and to corroborate the findings presented in this thesis.

Research in a wider range of study sites than was possible when collaborating with Operation Wallacea may also have improved the strength of our findings. A notable example of constraints in fieldwork sites occurred while collecting the data used in Chapter 5. When trying to ascertain the effectiveness of Cusuco National Park in preserving endemic avifauna, we had to work entirely within the boundaries of that protected area. The study could perhaps have been improved if we had been able to undertake bird surveys in another nearby cloud forest habitat that had no legal protection, thus allowing a direct comparison of sites which working with Operation Wallacea did not permit. This would have been an ideal scenario, although would have been difficult to achieve even without the discussed study site constraints, as all land in Honduras above 1800m, where most cloud forest ecosystems occur, is automatically protected under the 1987 Cloud Forest Act and the 1993 General Environmental Law.

Working within the constraints of the survey framework set up by Operation Wallacea also placed restrictions on availability of study sites at a local level, particularly in the Lambusango Reserve. Our fieldwork here constituted part of a long-term survey of bird communities which has been running since 1995, and we were required to use the same point-count sample sites as those in previous years to ensure that datasets were comparable. These sites were spaced only 150m apart, however, which is slightly less than the convention apparent in the literature, where points are usually spaced ≥200m to ensure independence of sample sites. A spacing of sample sites at this distance would have been preferable, but was not possible under the circumstances.

It might also be possible to strengthen and expand some of the minor research presented in the thesis. There is potential, for example, to upscale the brief overview of the Lambusango avifauna presented in Appendix 1 into a fuller account of the birds of South-East Sulawesi. Plans for producing an appropriate article for publication in the journal *Forktail* have already been discussed with David Kelly at Trinity College, Dublin.

There is also opportunity to examine new avenues of research, as well as strengthen the studies already presented in this thesis. It might be valuable to expand some of the analysis chapters to including both study areas rather than a single hotspot site. For example, it may be worthwhile to compare the effectiveness of point count and mist net surveys in the Lambusango, and to examine the congruence of habitat variables, remote sensing responses and bird communities in Cusuco National Park. These studies were not included in this thesis largely due to time-restrictions, but also because expanding these studies into the second hotspot appeared unnecessary or problematic. Mist-netting surveys in the Lambusango, for example, where population abundance of avifauna is low and the majority of species are associated with mid-storey habitat strata or above, proved very poor. We captured only five individual birds during the entire 2008 eight-week field season, so the results of a methodological comparison study here would appear evident. Habitat associations of avifaunal communities in Cusuco National Park would have also proved difficult to study, as vegetation variables measured here were much more restricted and the difficulties in obtaining cloud-free satellite imagery corresponding with the timing of field work in the park would have limited the effectiveness of remote sensing comparisons. This could be a valuable future study, though, if vegetation surveys were up-scaled and high quality imagery were obtained.

Further research could also investigate some patterns briefly considered in this thesis, but not examined in detail due to the importance of these patterns not being recognised until field work was complete. A key example of this would be to examine the relative weighting and importance of the ecological and biogeographical factors that may contribute to the apparent differential vulnerabilities of Wallacean and Mesoamerican cloud forest avifauna discussed in Chapter 7. However, each of the described opportunities for further research represents large-scale research proposals branching into disciplines not utilised in this thesis (in-depth behavioural studies, broad botanical surveys, comparative molecular analyses etc), and so attempting to build on these ideas would require extensive investments of time and substantial research grants considerably beyond the remit provided for this thesis.

There may also be opportunities to expand the themes described in this thesis to encompass a further biodiversity hotspot in the third major tropical region: Maputaland-Pondoland-Albany in Southern Africa. Study sites have been identified in the Northern extremity of this region, spanning the South Africa/Mozambique border, which cover a wide range of forest and non-forest habitats in protected and non-protected areas. An initial pilot study consisting of 25 point-count sites has already been analysed by the author, describing response patterns of avifaunal communities to disturbance very similar to those in Cusuco National Park. Up-scaling this to involve full-scale survey work could produce a valuable extra dimension to the themes discussed in this thesis.

While further work remains to be done, the research outcomes of this thesis have made a significant contribution to the understanding of relationships between avifauna and anthropogenic disturbance in two poorly studied hotspot ecosystems, providing discourses on the surveying, disturbance response, habitat associations, conservation and biogeographies of these unique bird communities.

Appendix 1 - The avifauna of the Lambusango Reserve and vicinity

Juvenile Spot-tailed Goshawk (*Accipiter trinotatus*) mist-netted in the Lambusango Forest

SPECIES SUMMARY

This list provides a brief overview of 139 bird species from 50 families which have been recorded in the Lambusango Forest Reserve and its vicinity between 1999-2009. Most of the survey effort involved in the production of this species list focussed on the Lambusango and Kakenaue forest reserves, and adjacent farmland and urban areas in Kikalu, Labundo-bundo and Lawele. Opportunistic sightings from across Southern and Central Buton have also been included to give a more extensive account of the region's avifauna. This includes open and cultivated land between Labundo-bundo and Bau-bau, beaches, mangroves, and ocean sightings in the straits between Buton and Muna.

A checklist summarising the reserve's avifauna is also included (Table A.1.1).

Fregatidae (Frigatebirds)

Great Frigatebird *Fregata minor*

Widespread across Indo-Pacific. Uncommon to rare around Buton. Seen occasionally on Kendari-Bau-bau ferry journey.

Lesser Frigatebird *Fregata ariel*

Widespread across Indo-Pacific. Commonly seen on Kendari-Bau-bau ferry journey in large flocks >10 birds.

Phalacrocoracidae (Cormorants)

Little Pied Cormorant *Phalacrocorax melanoleucos*

Occurs across Indonesia and Australasia. Rare. Occasionally observed singly or in pairs in paddy fields. Larger groups of 20+ birds have also been sighted at regular roosting sites just outside Bau-bau.

Ardeidae (Herons)

Purple Heron *Ardea purpurea*

Widespread across Eurasia. Fairly common – Individuals frequently observed in paddy fields around reserve's periphery.

White-faced Heron *Ardea novaehollandiae*

Occurs across Wallacea east to New Guinea and Australia. Uncommon. Occasionally observed in paddy fields around reserve's periphery.

Great Egret *Egretta alba*

Cosmopolitan species. Very common. Individuals frequently observed in paddy fields around reserve's periphery.

Intermediate Egret *Egretta intermedia*

Widespread across Africa and Eurasia. Very common. Individuals frequently observed in paddy fields around reserve's periphery.

Little Egret *Egretta garzetta*

Widespread across Africa and Eurasia. Very common. Individuals frequently observed in paddy fields around reserve's periphery.

Cattle Egret *Bubulcus ibis*

Cosmopolitan species. Uncommon to Rare in paddy fields around reserve's periphery

Javan Pond-Heron *Ardeola speciosa*

Occurs across much of South-East Asia. Uncommon. Seen occasionally in paddies and waterways around Buton.

Little Heron *Butorides striatus*

Cosmopolitan species. Commonly observed in paddy fields, mangroves and beaches near mangrove edge.

Pacific Reef-Egret *Egretta sacra*

Occurs across East and South-East Asia to Australasia. Uncommon. Occasionally encountered on the Buton coast.

Cinnamon Bittern *Ixobrychus cinnamomeus*

Occurs across South, East and South-East Asia. Fairly commonly observed in paddy fields.

Black Bittern *Ixobrychus flavicollis*

Occurs across South and South-East Asia to Australasia. Uncommon. Occasionally observed in paddy fields.

Ciconiidae (Storks)

Woolly-necked Stork *Ciconia episcopus*

Widespread across Asia and Africa. Locally quite common. Often observed on sand beaches and in mangroves. Usually seen singly or in pairs. Seen quite frequently soaring over roads near the coast.

Accipitridae (Eagles and Hawks)

Osprey *Pandion haliaetus*

Cosmopolitan species. Fairly common. Observed frequently along the coast. Kakenauwe beach is a good observation point.

Jerdon's Baza *Aviceda jerdoni*

Occurs across South and South-East Asia. Apparently rare. Known from a few scattered sightings in cultivated land on reserve's periphery and in Labundo-bundo village.

Barred Honey-buzzard *Pernis celebensis*

Occurs across the Sulawesi sub-region and the Philippines. Fairly common. Individuals frequently observed around Labundo-bundo, Waubau and edge forest on reserve's periphery. Rarely observed in forest interior.

Brahminy Kite *Haliastur indus*

Occurs across South and South-East Asia and Australasia. Commonly observed singly and in pairs around farm land, paddies and coastal areas, particularly along roads. Occasionally observed in forest interior.

White-bellied Sea Eagle *Haliaeetus leucogaster*

Occurs across South and South-East Asia and Australasia. Fairly common. Individuals observed fairly regularly around coast.

Grey-headed Fish Eagle *Ichthyophaga ichthyaetus*

Distributed across South and South-East Asia. Rare. Individuals occasionally sighted along river systems, and from Wabau.

Sulawesi Serpent Eagle *Spilornis rufipectus*

Endemic to Sulawesi sub-region. Common. Individuals and pairs observed very frequently. Inhabits forest, forest edge, and frequently seen over farmland and mangroves.

Spotted Harrier *Circus assimilis*

Occurs across Wallacea to Australia. Locally fairly common. Seen quite regularly in hills of South-Central Buton around Hill House.

Sulawesi Goshawk *Accipiter griseiceps*

Endemic to Sulawesi sub-region. Apparently rare –two individuals observed in vicinity of Labundo-bundo in 2009.

Spot-tailed Goshawk *Accipiter trinotatus*

Endemic to Sulawesi sub-region. Common accipiter frequently detected singly or in pairs within forest interior, forest edge and occasionally cultivated areas, although infrequently sighted. 'Laughing' call easily recognizable.

Black Eagle *Ictinaetus malayensis*

Occurs across South and South-East Asia. Moderately common. Usually seen singly. Most frequently seen from roads around reserve's periphery.

Rufous-bellied Eagle *Hieraaetus kienerii*

Distributed across South and South-East Asia. Apparently rare – two individuals observed near Labundo-bundo village in 2009.

Sulawesi Hawk-Eagle *Spitzaetus lanceolatus*

Endemic to Sulawesi sub-region. Moderately common. Individuals and pairs observed fairly frequently around reserve's periphery. Rarely recorded in forest interior.

Falconidae (Falcons)

Spotted Kestrel *Falco moluccensis*

Endemic to Indonesia. Locally fairly common. Seen quite regularly in hills of South-Central Buton around Hill House.

Oriental Hobby *Falco severus*

Occurs across South and South-East Asia to New Guinea. Uncommon. Known from occasional sightings in open areas around reserve's periphery. A breeding pair were located in a tree near Labundo-bundo in 2003.

Dendrocygnidae: (Whistling-ducks)

Wandering Whistling-duck *Dendrocygna arcuata*

Occurs across South-East Asia and Australasia. Observed fairly frequently at beaches, paddy fields and mangroves. Usually in pairs or small flocks of 3-10 birds.

Anatidae (Waterfowl)

Sunda Teal *Anas gibberifrons*

Indonesian endemic. Uncommon. Small flocks occasionally recorded in paddy fields and waterways.

Megapodiidae (Megapodes)

Philippine Megapode *Megapodius cummingii*

Occurs in the Philippines, Borneo and Sulawesi. Uncommon. Recorded occasionally in forest habitats. Usually identified by call.

Phasianidae (Pheasants)

Blue-breasted Quail *Coturnix chinensis*

Occurs across South and South-East Asia to Australasia. Rare. Known from an individual mist-netted in Kaikalu in 2003.

Red Junglefowl *Gallus gallus*

Occurs across South and South-East Asia. Fairly common in forest interior. Less common but also still frequent in forest edge. Occasionally observed in cultivated areas in close proximity to forest edge. May interbreed with domestic chickens. Usually detected singly or in pairs. Heard far more regularly than seen, although still flushed quite regularly.

Turnicidae

At least one species of Buttonquail is known to inhabit deep forest, forest edge and cultivated areas in close proximity to forest, although sightings of these birds have been fleeting. Species present is believed to be Barred Buttonquail (*Turnix susicitator*), although further observations are required to confirm this.

Rallidae (Rails)

Buff-banded Rail *Gallirallus philippensis*

Occurs across much of Wallacea, the Philippines, and New Guinea. Fairly common. Individuals regularly observed along river systems, irrigation and cultivated areas and forest edge.

Barred Rail *Gallirallus torquatus*

Occurs across much of Wallacea, the Philippines and New Guinea. Uncommon. Individuals seen occasionally in similar habitats to *G. philippensis*, although with less regularity.

Isabelline Bush-hen *Amaurornis isabellinus*

Endemic to Sulawesi. Fairly common. Individuals recorded regularly in cultivated land, particularly paddies and irrigation systems, as well as edge forest.

White-breasted Waterhen *Amaurornis phoenicurus*

Occurs across South and South-East Asia. Less common than Isabelline Bush-hen, but individuals still observed regularly in cultivated land, particularly paddies and irrigation systems. Also observed occasionally along river systems in forest interior.

Common Moorhen *Gallinula chloropus*

Cosmopolitan species. Individuals and pairs commonly observed in paddy fields and river systems in cultivated areas.

Scolopacidae (Waders)

Whimbrel *Numenius phaeopus*

Cosmopolitan species. Commonly observed singly, in pairs and small flocks on beaches and mangrove edge.

Common Sandpiper *Actitis hypoleucos*

Widespread across Eurasia, Africa and Australasia. Common. Frequently observed in flocks of 5 – 10 birds on rocky coasts, sandy beaches and mangrove edge.

Red-necked Phalarope *Phalaropus lobatus*

Cosmopolitan species. Locally common. Large flocks occasionally seen in channel between Buton and Muna.

Sternidae (Terns)

Bridled Tern *Sterna anaethetus*

Cosmopolitan species. Observed frequently on Kendari-Baubau ferry journey. Storm-blown individuals have also been found inland.

Lesser Crested Tern *Sterna bengalensis*

Occurs coastal throughout Africa, South and South-East Asia and Australasia. Regularly observed on Kendari-Baubau ferry journey

Columbidae (Pigeons)

Spotted Dove *Streptopelia chinensis*

Widespread across South and South-East Asia. Abundant in farmland, paddies and urban areas. Very rare in interior forest but has been encountered here. Usually in flocks of 5-10 birds.

Brown Cuckoo-dove *Macropygia amboinensis*

Occurs across Wallacea and Australasia. Fairly common bird of forest and forest edge. Also seen regularly in cultivated areas near forest edge. Usually occurs singly or in pairs.

Sulawesi Black Pigeon *Turacoena manadensis*

Endemic to Sulawesi sub-region. Fairly common pigeon found in most forest habitats, forest edge and occasionally cultivation. Usually encountered singly.

Stephan's Dove *Chalcophaps stephani*

Occurs across Wallacea and in New Guinea. Uncommon to rare. Has been recorded in Anoa camp at same location in 2005 and 2008. Also recorded several times in forest edge around reserve's periphery. Observed singly or in pairs.

Sulawesi Ground-Dove *Gallicolumba tristigmata*

Endemic to Sulawesi sub-region. Rare. A shy and inconspicuous species that is difficult to observe. Known from a single individual captured in Lapago in 2009. This individual showed noticeably different plumage from other descriptions, having extensive green coloration on the neck which is absent in all other sub-species described in Coates and Bishop (1997). Further captures and DNA extraction of this species in the Lambusango would be of interest.

Pink-necked Green Pigeon *Treron vernans*

Occurs across South-East Asia. Although common across much of range, this pigeon appears to be very local in the Lambusango area. Known to occur regularly at Togomotano lake, but has not been observed elsewhere.

Grey-cheeked Green Pigeon *Treron griseicauda*

Indonesian endemic. Fairly common in cultivated areas near forest edge and forest edge. Much less common in forest interior, but has been recorded from all node camps. Encountered singly, in pairs or flocks of up to 20 birds.

Black-naped Fruit-Dove *Ptilinopus melanospila*

Found across Indonesia and Southern Philippines. Buton's only fruit-dove species. Common in interior forest, forest edge and cultivated land in close proximity to forest. Usually encountered singly, in pairs or small flocks of up to 10 birds.

White-bellied Imperial Pigeon *Ducula forsteni*

Sulawesi endemic. Found almost exclusively in interior forest. Most abundant in areas of relatively undisturbed forest, particularly Bala and Anoa. Much less common in peripheral areas of the reserve ie- Wahalaka, Lasolo and Lapago Rare in Kakenawe and forest edge, although has been encountered here. Usually encountered in small flocks of 3-6 birds, although much larger groups of up to 30 birds have been encountered around fruiting figs. Occasionally observed in mixed flocks with other Imperial Pigeon species. Almost always occurs at canopy level, so difficult to observe, although diagnostic call is unmistakable. The churt ridges on transect 3 in Bala are a good place to observe this species.

Green Imperial Pigeon *Ducula aenea*

Occurs across South and South-East Asia. Very common- most abundant forest pigeon. Observed very frequently in undisturbed forest, secondary forest, forest edge and cultivated land near forest edge. Usually occurs in flocks of up to 20 individuals. Often seen in mixed-species flocks with other pigeon species.

Pied Imperial Pigeon *Ducula bicolor*

Occurs on small island ecosystems across South-East Asia. Locally common in coastal areas around reserve's periphery. Found singly, in pairs or small flocks on rocky islets and mangroves, as well as cultivated land near these habitats. Has been recorded up to 1km inland from coast. Has been observed in mixed-species flocks with other imperial pigeons, including the similar Silver-tipped Imperial Pigeon.

Silver-tipped Imperial Pigeon *Ducula luctosa*

Sulawesi endemic. Fairly common in most forest habitats, forest edge and cultivated land close to forest. Observed singly, in pairs or in small flocks of up to 10 birds. Often seen in mixed-species flocks with other Imperial pigeons (including the similar Pied Imperial Pigeon) and occasionally with parrot species, including Yellow-Crested Cockatoo on at least one occasion.

Psittacidae (Parrots)

Ornate Lorikeet *Trichoglossus ornatus*

Sulawesi endemic. Lambusango's only Lory species. Infrequently observed and apparently rare. Most sightings have occurred in forest interior, which is in contrast to Coates and Bishop's (1997) description of this species as occurring primarily in edge habitats, plantations and mangroves. Seen in small flocks of up to 10 birds.

Yellow-crested Cockatoo *Cacatua sulphurea*

Indonesian endemic. Critically endangered species – threatened with extinction due to trapping for pet trade, habitat destruction and population fragmentation. Rare. A single pair have been observed each year between 2006-2009 flying between a stand of trees near coastal mangrove and the forest edge near Labundo-bundo. Unknown if these birds are truly wild, or are escaped cage birds.

Golden-mantled Racquet-tail *Prioniturus platurus*

Sulawesi endemic. The most common parrot species in Lambusango. Very common in forest interior at Bala and Anoa camps. Less common in secondary forest habitats in Wahalaka and forest edge, although still observed frequently in these habitats. Usually occurs in flocks of up to 20 birds. Larger flocks of 30+ birds have been encountered at Bala camp.

Blue-backed Parrot *Tanygnathus sumatranus*

Occurs in Wallacea and the Southern Philippines. The region's largest parrot (excluding Cockatoo). Fairly common in most forest habitats, forest edge and cultivation close to forest edge. Usually encountered in pairs or small flocks, although towards end of dry season can form larger flocks of 30+ birds when this species can be a crop pest on cashew plantations.

Large Sulawesi Hanging Parrot *Loriculus stigmatus*

Sulawesi endemic. Fairly common in forest edge and adjacent cultivation. Less common in forest interior but still encountered frequently. Usually occurs singly or in pairs.

Small Sulawesi Hanging Parrot *Loriculus exilis*

Sulawesi endemic. Less common than L. stigmatus. More frequently observed in forest edge and adjacent cultivation than forest interior, where it is uncommon. Usually encountered singly or in pairs.

Cuculidae (Cuckoos)

Sulawesi Hawk-Cuckoo *Cuculus crassirostris*

Sulawesi endemic. Common.. Frequently recorded in forest and forest edge, but very rarely observed. Almost always detected by diagnostic 2-3 note call, which is repeated at regular intervals throughout the night, early morning and occasionally later in the day.

Oriental Cuckoo *Cuculus saturatus*

Occurs across Asia and Australasia. Migratory. Known only from a single individual observed in the hand in Lawele in 2009.

Plaintive Cuckoo *Cacomantis merulinus*

Widely distributed across Asia. Described as fairly common by Catterall (1998), although recorded infrequently during surveys in Lambusango. Most records have been from cultivated land, with a few observations in peripheral node camps, particularly Lasolo.

Rusty-breasted Cuckoo *Cacomantis sepulcralis*

Occurs across South-East Asia. Uncommon to rare. Most frequently recorded in cultivated land, with a few observations in peripheral node camps, particularly Lasolo.

Gould's Bronze Cuckoo *Chrysococcx russatus*

Occurs across insular South-East Asia and Australasia. Rare. Known from a single sighting near Labundo-bundo in 2009.

Drongo-Cuckoo *Surniculus lugubris*

Occurs across South and South-East Asia. Found throughout the Lambusango forest, but can be quite local. Common in Lasolo, Wahalaka and Lapago camps, less common in Bala and Anoa camps, although still detected quite frequently. Also quite common in edge habitats. Usually encountered singly, sometimes in pairs. Easily identified by diagnostic call.

Black-billed Koel *Eudynamys melanorhyncha*

Sulawesi endemic. Apparently quite rare. Observed most frequently in Lasolo camp, where flocks of up to six birds have been recorded. Individuals have also been encountered at least once in Bala, Anoa and Kakenauwe.

Yellow-billed Malkoha *Phaenicophaeus calyorhynchus*

Sulawesi endemic. Fairly common throughout reserve interior, forest edge and cultivated land near forest edge. Frequently found in association with foraging troops of Buton Macaques, hence local name of Burung Andoke (Monkey Bird). Usually occurs singly, in pairs, and small groups of up to five birds. Has occasionally been seen in larger groups of 15+ birds.

Centropodidae (Coucals)

Lesser Coucal *Centropus bengalensis*

Widespread across South and South-East Asia. Fairly common in open farmland. Uncommon in forest edge and never recorded in forest. Usually encountered singly or in pairs.

Bay Coucal *Centropus celebensis*

Sulawesi endemic. Common in forest and edge habitats, although can be quite difficult to see. Rare in cultivated land. Almost no habitat overlap with *C. bengalensis*. Vocalisation is one of the most characteristic sounds of the dawn chorus in the Lambusango. Usually occurs in small groups of 3-4 birds.

Tytonidae (Grass Owls)

Sulawesi Masked Owl *Tyto rosenbergii*

Sulawesi endemic. Rare and infrequently detected. Occasional records from edge habitats around Labundo-bundo, Kakenauwe and Kikalu. Presence confirmed by mist-net capture in 2008.

Strigidae (Typical Owls)

Sulawesi Scops-owl *Otus manadensis*

Sulawesi endemic. Region's most frequently encountered owl. Common, but can be quite local in the forest camps. Very common around Wahalaka and Wahalamba, although much rarer around Bala camp. Also recorded frequently in edge forest and cultivation near forest edge.

Ochre-bellied Hawk-owl *Ninox ochracea*

Endemic to Sulawesi. Rare. Occasionally heard forest adjacent to Kaikalu between 1999 and 2003. No visual records of this species exist in the study area.

Caprimulgidae (Nightjars)

Great-eared Nightjar *Eurostopodus macrotis*

Widespread across South and South-East Asia. Presumably quite common in suitable habitat, but has been poorly surveyed. Known from individuals captured in agricultural land in 2003 and 2009.

Sulawesi Nightjar *Caprimulgus celebensis*

Endemic to Sulawesi. Recorded infrequently, although probably under-recorded due to insufficient surveying of nocturnal birds. Call of this species heard several times in agricultural land between 1999 – 2003, and presence confirmed by examination of a bird captured by locals in 2003.

Apodidae (Swifts)

Uniform Swiftlet *Collocallia vanikorensis*

Occurs across Indonesia, Papua New Guinea and Melanesia. Less common than Glossy Swiftlet, but observed fairly frequently in open habitats. Sometimes occurs in mixed flocks with Glossy Swiftlets.

Moluccan Swiftlet *Collocallia infuscatus*

Endemic to Wallacea. Occasionally seen flocking with other swiftlets in the Labundo-bundo area

Glossy Swiftlet *Collocallia esculenta*

Widespread across South-East Asia. Abundant in open areas. Frequently seen above forest clearings and river systems in reserves interior. Usually occurs in large flocks of 30+ birds. Often forms mixed flocks with Uniform Swiftlets and Tree-Swifts.

Hemiprocnidae (Tree-swifts)

Grey-rumped Tree-swift *Hemiprocne longipennis*

Widespread across South-East Asia. Very common in open areas around reserve's periphery. Frequently seen above forest clearings and river systems in reserve's interior. Occurs in flocks of up to 30+ birds. Often forms mixed flocks with swiftlets.

Halcyonidae (Wood Kingfishers)

Green-backed Kingfisher *Actenoides monachus*

Sulawesi endemic. Rare. Known only from a single mist-net capture in Anoa camp in 2005.

Great-billed Kingfisher *Halcyon melanorhyncha*

Sulawesi endemic. Locally quite common along coasts, mangroves and river systems near coastal areas. Usually observed singly.

Ruddy Kingfisher *Halcyon coromanda*

Widespread across South, East and South-East Asia. Uncommon. Usually observed singly flying up and down river systems in forest or cultivated areas. Also occasionally seen in farmland on stumps, trees etc. Call occasionally heard after dusk or before dawn near rivers.

Collared Kingfisher *Halcyon chloris*

Widespread across Asia and Australasia. Most abundant Kingfisher. Very common in cultivated areas and forest edge. Seen regularly singly, in pairs or small groups on wires, stumps, fences etc. Less common in forest areas but still recorded regularly.

Sacred Kingfisher *Halcyon sancta*

Migratory. Breeds in Australia, winters in Wallacea, New Guinea and Melanesia. Less common than Collared Kingfisher in Southern winter, but frequently seen in suitable habitat near coast (beaches, mangroves, river systems, paddies etc). Usually seen singly and in pairs. Sometimes seen in association with Collared Kingfishers. Never observed in the forest.

Alcedinidae (Small Kingfishers)

Sulawesi Dwarf Kingfisher *Ceyx fallax*

Sulawesi endemic. Uncommon. Most frequently observed solitarily in forested river systems at night roosting on overhanging branches. Utilizes same roosting spots each night- regular roosts known in Lapago. Has been observed on river systems in most node camps.

Common Kingfisher *Alcedo atthis*

Widespread across Eurasia. Fairly common along river systems in coastal areas, cultivated land and forest ecosystems. Usually observed singly.

Blue-eared Kingfisher *Alcedo meninting*

Occurs across South and South-East Asia. Identified by Catterall (1998) as being present across Buton island, but in lower densities than Common Kingfisher. Individuals have been mist-netted by Operation Wallacea on Kabaena and mainland Sulawesi, but no records currently exist from the Lambusango. This species is probably present in the study area, although individuals need to be sighted or captured to confirm its presence.

Meropidae (Bee-eaters)

Rainbow Bee-eater *Merops ornatus*

Migratory. Breeds in Australia and winters in Wallacea, New Guinea and Melanesia. Fairly common in clear and lightly wooded areas around reserve's periphery, although distribution can be quite local. Usually observed in small flocks of 5-6 birds. Never observed in forest interior.

Coraciidae (Rollers)

Purple-winged Roller *Coracias temminckii*

Endemic to Sulawesi sub-region. Fairly common in forest edge around reserve's periphery. Much less common in forest interior. More common in peripheral camps i.e Lasolo, than camps in the centre of the reserve ie Anoa. Usually observed singly.

Bucerotidae (Hornbills)

Sulawesi Dwarf Hornbill *Penelopides exarhatus*

Endemic to Sulawesi sub-region. Fairly common in undisturbed forest, although markedly less abundant in secondary forest i.e.; Wahalaka. Usually observed in small flocks of 3-6 birds, although larger flocks of 10+ have been observed around fruiting fig trees.

Knobbed Hornbill *Rhyticeros cassidix*

Endemic to Sulawesi sub-region. Quite common in most forest types throughout the reserve and forest edge. Can be locally very common in some areas of forest such as around Bala, particularly near fruiting figs. Usually seen in pairs, although larger groups of 12+ birds can be found in proximity to fruiting trees.

Picidae (Woodpeckers)

Sulawesi Pygmy Woodpecker *Dendrocopos temminckii*

Endemic to Sulawesi sub-region. Quite rare. Occasionally observed singly or in pairs around forest edge or mangroves near Kakenauwe beach. This bird has so far not been observed in the forest interior, despite its description by Coates and Bishop (1997) as a forest species. May be under-recorded.

Ashy Woodpecker *Mulleripicus fulvus*

Endemic to Sulawesi sub-region. Quite common in the reserve's interior and edge forest. Usually observed singly or in pairs on trunks or dead wood on the ground. Loud drumming is diagnostic of this species.

Pittidae (Pittas)

Blue-breasted Pitta *Pitta erythrogaster*

Distributed across Insular South-East Asia and Northern Australasia. Uncommon and shy. Rarely observed but occasionally heard in forest, edge habitats and cultivation close to forest edge.

Hirundinidae (Swallows)

Barn Swallow *Hirundo rustica*

Cosmopolitan species. A common migrant observed frequently in open cultivated land, especially paddies, and along river systems.

Pacific Swallow *Hirundo tahitica*

Distributed across Southern Asia and Australasia. Common resident species observed frequently in open cultivated land, especially paddies, and along river systems.

Campephagidae (Cuckoo-shrikes)

Pied Cuckoo-Shrike *Coracina bicolor*

Endemic to Sulawesi sub-region. Listed as Near-Threatened by the IUCN – one of two red-listed species found in the study area (along with Yellow-crested Cockatoo). Common throughout reserve's interior and forest edge, and in places locally abundant. Rarely observed in cultivated land. The Lambusango Forest appears to possess a healthy population of this species.

White-rumped Cuckoo-shrike *Coracina leucopygia*

Endemic to Sulawesi sub-region. Considerably less common than Pied Cuckoo-Shrike. Observed more frequently in forest edge and disturbed forest habitats than more pristine forest ecosystems. Usually observed in small groups of 3-4 birds.

Sulawesi Cicadabird *Coracina morio*

Endemic to Sulawesi sub-region. Common, although seldom seen. Usually identified by diagnostic call. Found in most forest habitats and occasionally in cultivated land near forest edge.

Sulawesi Triller *Lalage leucopygialis*

Endemic to Sulawesi sub-region. Rare. Observed once in old agricultural land near Wabau.

White-shouldered Triller *Lalage suerii*

Indonesian Endemic. Rare. Observed once outside cave system near Wakanka.

Dicruridae (Drongos)

Hair-crested Drongo *Dicrurus hottentottus*

Distributed across South and South-East Asia. Very common. Encountered regularly in most forest and non-forest habitats. Usually observed singly or in pairs, although sometimes in flocks of up to four birds. Displays a wide range of vocalizations. Often associates with troops of foraging macaques. Frequently exhibits mobbing behaviour towards raptors.

Oriolidae (Orioles)

Black-naped Oriole *Oriolus chinensis*

Distributed across South and South-East Asia. Very common, although usually occurs at canopy level and can be difficult to see. Recorded very frequently in all forest habitats, forest edge and cultivated land near forest. Usually observed singly or in pairs.

Corvidae (Crows)

Slender-billed Crow *Corvus enca*

Resident across Malaysia and insular South-East Asia. Common in farmland, paddies and forest edge. Uncommon to rare in forest interior. Usually observed singly, in pairs or small flocks of up to five birds.

Piping Crow *Corvus typicus*

Endemic to Sulawesi sub-region. Fairly common in forest edge. Less common in forest interior although can be locally common in areas i.e Anoa camp. Usually observed in pairs or small groups. Exhibits a wide range of vocalizations.

Timaliidae (Babblers)

Sulawesi Babbler *Trichastoma celebense*

Endemic to Sulawesi sub-region. Very common. Abundant in forest, forest edge and cultivated land near forest edge. Usually encountered singly or in pairs. Can be difficult to observe and usually identified by its diagnostic call. Most vocal between 05:45 – 07:00.

Turdidae (Thrushes)

Red-backed Thrush *Zoothera erythronota*

Endemic to Sulawesi sub-region. A cryptic and rarely observed understory forest species. Known from several sightings of lone individuals in node camps. Presumably under-recorded.

Pied Bushchat *Saxicola caprata*

Occurs across South and South-East Asia to New Guinea. Fairly common. Found in open, scrubby areas of Buton. Observed fairly regularly around Hill House.

Pardalotidae (Australian Warblers)

Flyeater *Gerygone sulphurea*

Widespread across South-East Asia. Common in cultivated areas and towns. Usually encountered singly or in pairs. Never encountered in interior forest. Can be hard to observe – usually identified by diagnostic song.

Cisticolidae (African Warblers)

Zitting Cisticola *Cisticola juncidis*

Widespread across Old World. Uncommon in open cultivated areas. Usually observed singly. Does not occur in forest interior.

Golden-headed Cisticola *Cisticola exilis*

Widespread across Asia and Australasia. Uncommon in open cultivated areas and sometimes urban areas. Usually observed singly. Does not occur in forest interior.

Muscicapidae (Old World Flycatchers)

Rufous-throated Flycatcher *Ficedula rufigula*

Endemic to Sulawesi sub-region. A shy, cryptic species. Rarely seen or heard during point-count surveys but individuals captured quite regular in mist-nets. Not presumed to be rare but rather severely under-recorded by primary survey methods. Records exist from most forest node camps. One sighting was also made at forest edge near Labundo-bundo.

Monarchidae (Monarch Flycatchers)

Black-naped Monarch *Hypothymis azurea*

Occurs across South and South-East Asia. Very common. Recorded very frequently in all forest types, forest edge and cultivated land near forest. Can be difficult to see and usually identified by call. Usually encountered singly or in pairs.

Petroicidae (Australasian Robins)

Citrine Flycatcher *Culicicapa helianthea*

Occurs in Sulawesi sub-region and Southern Philippines. Very common in forest and edge habitats. Can be difficult to see during the day and is usually identified by song. Individuals can often be found roosting on narrow branches over rivers at night. Known roosting sites at Lapago and Lasolo.

Artamidae (Wood-swallows)

White-breasted Wood-swallow *Artamus leucorynchus*

Occurs across insular South-East Asia and Australasia. Very common and often abundant in open areas around reserve's periphery (farms, paddies, towns etc) and also frequently observed along river banks and in clearings within forest interior. Usually seen singly, in pairs or in small flocks.

Ivory-breasted Woodswallow *Artamus monachus*

Endemic to Sulawesi sub-region. Much less common than *A. leucorynchus*, although still observed fairly frequently in similar habitats, particularly forest clearings.

Sturnidae (Starlings)

Asian Glossy Starling *Aplonis panayensis*

Widespread across South and South-East Asia. Very common in large flocks in urban areas and cultivation. Occasionally observed in forest reserve near periphery. Flock sizes of 100+ individuals have been observed. Have been observed in mixed flocks with other starling species, particularly Grosbeak Starling..

Sulawesi Crested Myna *Basilornis celebensis*

Endemic to Sulawesi sub-region. Quite uncommon, although found in a variety of forest and edge habitats. Usually encountered in pairs or small flocks, but occasionally in larger flocks. A flock of 25+ individuals was observed on one occasion near a fruiting fig tree.

White-necked Myna *Streptocitta albicollis*

Endemic to Sulawesi sub-region. Common in forest edge in small groups of 2-5 birds. Less common but still frequently recorded throughout the reserve's interior. Often observed perching conspicuously on exposed bare branches in forest clearings.

Grosbeak Starling *Scissirostrum dubium*

Endemic to Sulawesi sub-region. Primarily an edge forest species, where is observed fairly frequently in large flocks of 20 – 60 birds. Much less common in reserve's interior, although nest-sites have been identified in Wahalamba and Wahalaka camps. Roosts in conspicuous, exposed dead trees excavated with many individual nesting holes.

Meliphagidae (Honey-Eaters)

Scarlet Honeyeater *Myzomela sanguinolenta*

Occurs across Wallacea and in Eastern Australia. Fairly uncommon in cultivated land and forest edge. Never observed in forest interior. Usually encountered singly.

Nectariniidae (Sunbirds)

Brown-throated Sunbird *Anthreptes malacensis*

Occurs across South-East Asia. Fairly common in urban areas, cultivation and forest edge. Rarely observed in forest interior. Usually observed singly or in pairs.

Black Sunbird *Nectarina aspasia*

Occurs across Wallacea and in New Guinea. Very common across all habitats in the region. Most common sunbird encountered in reserve's interior. Usually occurs singly or in pairs, although males are sometimes observed in small groups of up to five birds.

Olive-backed Sunbird *Nectarina jugularis*

Occurs across South-East Asia. Very common in urban areas, cultivation and forest edge. Much less common in forest interior, but still recorded fairly frequently here. Usually encountered singly or in pairs.

Crimson Sunbird *Aethopyga siparaja*

Occurs across South and South-East Asia. Fairly common in urban areas, cultivation and forest edge. Uncommon in reserve's interior. Usually encountered singly. Sometimes in pairs.

Dicaeidae (Flowerpeckers)

Yellow-sided Flowerpecker *Dicaeum aureolimbatum*

Endemic to Sulawesi sub-region. Quite common in forest edge and cultivated land in close proximity to forest. Observed in forest interior much less frequently. Usually observed in pairs.

Grey-sided Flowerpecker *Dicaeum celebicum*

Endemic to Sulawesi sub-region. Quite common in forest edge and cultivated land in close proximity to forest. Less common in forest interior, although observed more regularly there than *D. aureolimbatum*. Usually encountered in pairs. Mixed flocks with *D. aureolimbatum* and White-eyes have been observed.

Zosteropidae (White-eyes)

Lemon-bellied White-eye *Zosterops chloris*

Occurs irregularly across Indonesia and New Guinea. Fairly common in urban areas and cultivation around reserve's periphery. Less common in forest edge and uncommon reserve's interior.

Sulawesi White-eye *Zosterops consobrinorum*

Endemic to South-East Sulawesi. Common in forest interior and edge forest. Reasonably common in cultivation around reserve's periphery. Usually encountered in small groups of 4-6 individuals, although larger flocks of 10+ birds sometimes observed. Sometimes occurs in mixed flocks with flowerpeckers, sunbirds and *Z. chloris*.

Passeridae (Sparrows)

Tree Sparrow *Passer montanus*

Occurs across Eurasia. Abundant in urban areas and paddies. Common in other cultivation. Almost entirely absent from forest habitats. Usually observed in small-medium sized flocks.

Estrildinidae (Estrildine Finches)

Black-faced Muniah *Lonchura molucca*

Endemic to Indonesia. Near-Wallacean endemic. Fairly common in cultivated land, particularly paddies. Does not occur in forest habitats. Usually observed in small-medium sized flocks. Sometimes occurs in mixed flocks with other Muniahs.

Scaly-breasted Muniah *Lonchura punctulata*

Occurs across South and South-East Asia. Fairly common in cultivated land, particularly paddies Does not occur in forest habitats. Usually observed in small-medium sized flocks. Sometimes occurs in mixed flocks with other Muniahs.

Chestnut Muniah *Lonchura malacca*

Occurs across South and South-East Asia. Occurs in same habitats as *L. molucca* and *L. punctulata*, although appears to be somewhat less common. Forms mixed flocks with both these species.

Pale-headed Muniah *Lonchura pallida*

Endemic to Wallacea. An apparently rare species. Very occasionally observed in paddy fields and other cultivated land.

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*Table A.1.1 – Checklist of bird species recorded in the Lambusango Reserve and vicinity between 1999 – 2009. Species notated * are Wallacean endemics. Species noted ‡ are endemic to Indonesia. Species notated † are listed as threatened by the IUCN (2009). Abundance estimates are notated as follows: A – abundant, C – common, Fc – fairly common, Lc – locally common, U – uncommon, R – rare. Species notated <M> are seasonal migrants to the study area. Species marked X in the final column have been recorded within the protected area of the Lambusango Forest Reserve. All families and species named after Coates and Bishop (1997).*

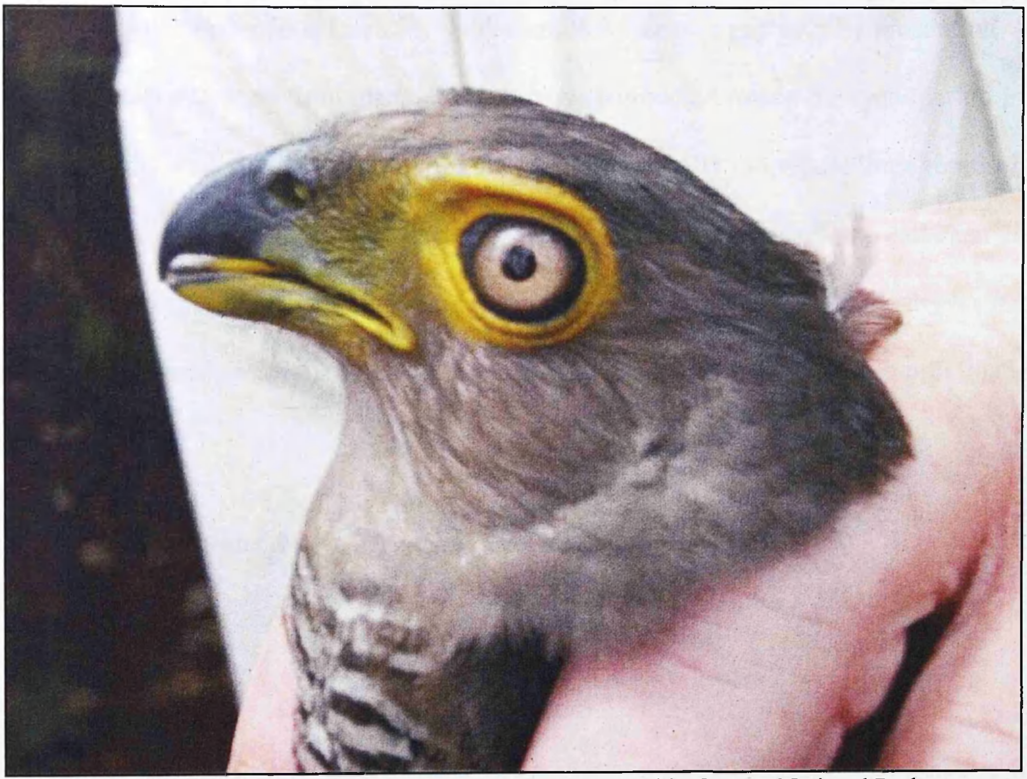
Family	Common name	Scientific name	Abundance	Occurs in reserve?
Fregatidae	Great Frigatebird	*Fregata minor*	U/R	
	Lesser Frigatebird	*Fregata ariel*	C	
Phalacrocoracidae	Little Pied Cormorant	*Phalacrocorax melanoleucos*	U	
Ardeidae	Purple Heron	*Ardea purpurea*	Fc	
	White-faced Heron	*Ardea novaehollandiae*	U <M?>	
	Great Egret	*Egretta alba*	A	
	Intermediate Egret	*Egretta intermedia*	A	
	Little Egret	*Egretta garzetta*	A	
	Little Heron	*Butorides striatus*	C	
	Pacific Reef-Egret	*Egretta sacra*	U	
	Cinnamon Bittern	*Ixobrychus cinnamomeus*	Fc	
	Black Bittern	*Ixobrychus flavicollis*	U	
Ciconiidae	Woolly-necked Stork	*Ciconia episcopus*	Fc	
Accipitridae	Osprey	*Pandion haliaetus*	Fc	
	Jerdon's Baza	*Aviceda jerdoni*	R	
	*Barred Honey-Buzzard	*Pernis celebensis*	Fc	X
	Brahminy Kite	*Haliastur indus*	C	X
	White-bellied Sea Eagle	*Haliaeetus leucogaster*	Fc	
	Grey-headed Fish Eagle	*Ichthyophaga ichthyaetus*	R	
	*Sulawesi Serpent Eagle	*Spilornis rufipectus*	C	X
	Spotted Harrier	*Circus assimilis*	Lc	
	*Sulawesi Goshawk	*Accipiter griseiceps*	R	
	*Spot-tailed Goshawk	*Accipiter trinotatus*	C	X
	Black Eagle	*Ictinaetus malayensis*	Fc	X
	Rufous-bellied Eagle	*Hieraaetus kienerii*	R	
	*Sulawesi Hawk Eagle	*Spitzaetus lanceolatus*	Fc	X
Falconidae	‡ Spotted Kestrel	*Falco moluccensis*	Lc	
	Oriental Hobby	*Falco severus*	U	
Dendrocygnidae	Wandering Whistling Duck	*Dendrocygna arcuata*	Fc	
Anatidae	‡ Sunda Teal	*Anas gibberifrons*	U	
Megapodiidae	Philippine Scrubfowl	*Megapodius cummingii*	U	X
Phasianidae	Blue-breasted Quail	*Coturnix chinensis*	R	
	Red Junglefowl	*Gallus gallus*	Fc	X

Turnicidae	Barred Buttonquail?	*Turnix suscitator*	?	X
Rallidae	Buff-banded Rail	*Gallirallus philippensis*	Fc	
	Barred Rail	*Gallirallus torquatus*	U	
	*Isabelline Waterhen	*Amaurornis isabellinus*	Fc	
	White-breasted Waterhen	*Amaurornis phoenicurus*	Fc	X
	Common Moorhen	*Gallinula chloropus*	C	
Scolopacidae	Whimbrel	*Numenius phaeopus*	C <M>	
	Common Sandpiper	*Actitis hypoleucos*	C <M>	
	Red-necked Phalarope	*Phalaropus lobatus*	Lc <M>	
Sternidae	Bridled Tern	*Sterna anaethetus*	Fc	
	Lesser Crested Tern	*Sterna bengalensis*	Fc	
Columbidae	Spotted Dove	*Streptopelia chinensis*	A	X
	Brown Cuckoo-dove	*Macropygia amboinensis*	Fc	X
	*Sulawesi Black Pigeon	*Turacoena manadensis*	Fc	X
	Stephan's Dove	*Chalcophaps stephani*	R	X
	*Sulawesi Ground Dove	*Gallicolumba tristigmata*	R	X
	Pink-necked Green Pigeon	*Treron vernans*	R	
	‡Grey-cheeked Green Pigeon	*Treron griseicauda*	Fc	X
	Black-naped Fruit-Dove	*Ptilinopus melanospila*	C	X
	*White-bellied Imperial Pigeon	*Ducula forsteni*	Fc	X
	Green Imperial Pigeon	*Ducula aenea*	A	X
	Pied Imperial Pigeon	*Ducula bicolor*	Lc	
	*Silver-tipped Imperial Pigeon	*Ducula luctuosa*	Fc	X
Psittacidae	*Ornate Lorikeet	*Trichoglossus ornatus*	R	X
	†‡Yellow-crested Cockatoo	*Cacatua sulphurea*	R	X
	*Golden-mantled Racquet-tail	*Prioniturus platurus*	C	X
	Blue-backed Parrot	*Tanygnathus sumatranus*	Fc	X
	*Large Sulawesi Hanging Parrot	*Loriculus stigmatus*	Fc	X
	*Sulawesi Small Hanging Parrot	*Loriculus exilis*	U	X
Cuculidae	*Sulawesi Hawk-Cuckoo	*Cuculus crassirostris*	C	X
	Oriental Cuckoo	*Cuculus saturatus*	R <M>	
	Plaintive Cuckoo	*Cacomantis merulinus*	U	X
	Rusty-breasted Cuckoo	*Cacomantis sepulcralis*	U	X
	Gould's Bronze Cuckoo	*Chrysococcx russatus*	R	
	Drongo Cuckoo	*Surniculus lugubris*	C	X
	*Black-billed Koel	*Eudynamys melanorhyncha*	R	X
	*Yellow-billed Malkoha	*Phaenicophaeus calyorhynchus*	Fc	X
Centropodidae	*Bay Coucal	*Centropus celebensis*	C	X
	Lesser Coucal	*Centropus bengalensis*	Fc	
Tytonidae	*Sulawesi Masked Owl	*Tyto rosenbergi*	R	X
Strigidae	*Sulawesi Scops-owl	*Otus manadensis*	C	X
	Ochre-bellied Hawk-owl	*Ninox ochracea*	R	X
Caprimulgidae	Great-eared Nightjar	*Eurostopodus macrotis*	Lc?	

	*Sulawesi Nightjar	*Caprimulgus celebensis*	R?	
Apodidae	Glossy Swiftlet	*Collocalia esculenta*	A	X
	*Moluccan Swiftlet	*Collocallia infuscatus*	U	
	Uniform Swiftlet	*Collocallia vanikorensis*	Fc	X
Hemiprocnidae	Grey-rumped Tree-swift	*Hemiprocne longipennis*	A	X
Halcyonidae	Green-backed Kingfisher	*Actenoides monachus*	R	X
	*Great-billed Kingfisher	*Halcyon melanorhyncha*	Lc	
	Ruddy Kingfisher	*Halcyon coromanda*	U	X
	Collared Kingfisher	*Halcyon chloris*	A	X
	Sacred Kingfisher	*Halcyon sancta*	C <M>	
Alcedinidae	*Sulawesi Dwarf Kingfisher	*Ceyx fallax*	U	X
	Common Kingfisher	*Alcedo atthis*	Fc	X
	Blue-eared Kingfisher	*Alcedo meninting*	?	?
Meropidae	Rainbow Bee-eater	*Merops ornatus*	Lc <M>	
Coraciidae	*Purple-winged Roller	*Coracias temminckii*	Fc	X
Bucerotidae	*Sulawesi Dwarf Hornbill	*Penelopides exarhatus*	Fc	X
	*Knobbed Hornbill	*Rhyticeros cassidix*	C	X
Picidae	*Sulawesi Pygmy Woodpecker	*Dendrocopos temminckii*	R	
	*Ashy Woodpecker	*Mulleripicus fulvus*	Fc	X
Pittidae	Blue-breasted Pitta	*Pitta erythrogaster*	U	X
Hirundinidae	Barn Swallow	*Hirundo rustica*	C <M>	X
	Pacific Swallow	*Hirundo tahitica*	C <M>	X
Campephagidae	*†Pied Cuckoo-shrike	*Coracina bicolor*	C	X
	*White-rumped Cuckoo-shrike	*Coracina leucopygia*	U/Fc	X
	*Sulawesi Cicadabird	*Coracina morio*	C	X
	*Sulawesi Triller	*Lalage leucopygialis*	R	
	‡White-shouldered Triller	*Lalage suerii*	R	
Dicruridae	Hair-crested Drongo	*Dicurus hottentottus*	A	X
Oriolidae	Black-naped Oriole	*Oriolus chinensis*	A	X
Corvidae	Slender-billed Crow	*Corvus enca*	C	X
	*Piping Crow	*Corvus typicus*	Fc	X
Timaliidae	*Sulawesi Babbler	*Trichastoma celebense*	A	X
Turdidae	*Red-backed Thrush	*Zoothera erythronota*	R	X
	Pied Bushchat	*Saxicola caprata*	Fc	
Pardalotidae	Flyeater	*Gerygone sulphurea*	C	
Cisticolidae	Zitting Cisticola	*Cisticola juncidis*	U	

	Golden-headed Cisticola	*Cisticola exilis*	U	
Muscicapidae	*Rufous-throated Flycatcher	*Ficedula rufigula*	R/U	X
Monarchidae	Black-naped Monarch	*Hypothymis azurea*	A	X
Petroicidae	Citrine Flycatcher	*Culicicapa helianthea*	A	X
Artamidae	White-breasted Wood-swallow	*Artamus leucorynchus*	A	X
	*Ivory-breasted Wood-swallow	*Artamus monarchus*	U	X
Sturnidae	Asian Glossy Starling	*Aplonis panayensis*	A	X
	*Sulawesi Crested Myna	*Basilornis celebensis*	U	X
	*White-necked Myna	*Streptocitta albicollis*	Fc	X
	*Grosbeak Starling	*Scissirostrum dubium*	Lc	X
Meliphagidae	Scarlet Honeyeater	*Myzomela sanguinolenta*	U	
Nectariniidae	Brown-throated Sunbird	*Anthreptes malacensis*	Fc	X
	Black Sunbird	*Nectarina aspasia*	A	X
	Olive-backed Sunbird	*Nectarina jugularis*	A	X
	Crimson Sunbird	*Aethopyga siparaja*	Fc	X
Dicaeidae	*Yellow-sided Flowerpecker	*Dicaeum aureolimbatum*	Fc	X
	*Grey-sided Flowerpecker	*Dicaeum celebicum*	Fc	X
Zosteropidae	Lemon-bellied White-eye	*Zosterops chloris*	Fc	X
	*Sulawesi White-eye	*Zosterops consobrinorum*	C	X
Passeridae	Tree Sparrow	*Passer montanus*	A	
Estrildinidae	‡Black-faced Muniah	*Lonchura molucca*	C	
	Scaly-breasted Muniah	*Lonchura punctulata*	C	
	Chestnut Muniah	*Lonchura malacca*	Fc	
	*Pale-headed Muniah	*Lonchura pallida*	R	

APPENDIX 2 -Morphometric data for Mesoamerican cloud forest bird species



Barred Forest-falcon (*Micrastur ruficollis*) mist-netted in Cusuco National Park

Summary

Avifaunal assemblages in Neotropical cloud forest remain poorly understood, particularly in comparison with bird communities in lowland tropical forest. There is a shortage of data describing even basic morphometric measurements for many cloud forest birds, particularly range-restricted, endemic species. We addresses this research gap here by presenting biometric data collected from mist netting surveys conducted over a five year period in Cusuco National Park, North West Honduras. A total of 1501 individual birds representing 121 species and 27 avian families were captured over five research seasons between 2004-2008, with wing length and weight being recorded and reported here. This provides important base-line information for many cloud forest bird species, data for which was previously lacking.

Keywords – ***Cloud forest, Mesoamerica, Morphometrics***

Introduction

The tropical montane cloud forests of Mesoamerica are a rare, distinctive ecosystem with well-defined biogeographical characteristics, being subject to cooler temperatures, steeper topography, distinct precipitation patterns and a different vegetation structure than forest ecosystems at lower altitudes (Powell and Palminteri 2001, Reyes, 1994, Hamilton 1993). This physical geography has facilitated the evolution of a very distinctive avifaunal community which displays significantly different trophic and taxonomical compositions to those found in other forest ecosystems, and which includes many range-restricted and endemic species (Holwell and Webb, 2005, Stattersfield *et al.*1998., Renjifo *et al.* 1997).

While Mesoamerican cloud forests are of high ornithological importance, a full description of their avifaunal communities is lacking as most avian research in the region has been conducted in more spatially extensive and generally more accessible lowland forest sites. Of the little ornithological research which has been conducted in montane cloud forest, the majority has focussed on countries with a tradition of scientific research, such as Costa Rica. This has led to cloud forest bird communities in the northern part of the Mesoamerican hotspot being particularly poorly researched, with even basic data such as simple morphometric measurements remaining unpublished for many species.

This short communication seeks to address this research gap. It displays wing length and weight measurements for a wide range of bird species from a cloud forest park in Honduras, many of which we believe to be previously unpublished.

Methodology

Research was conducted in the Parque Nacional Cusuco, Departmento Cortez, North-West Honduras (15° 29.8'-15° 32.1'N / 88° 13.0- 88° 26.3' W); a 23,440 hectare area of tropical montane cloud forest. Elevation ranges from 500m-2242m above sea level, with climate being relatively cool (Mean temperature 18.65°) and with high annual precipitation (Mean annual rainfall 2788mm) (Lenkh, 2005) (Fundación Ecologista 1994). Sampling was completed in eight week blocks between June-August over a four year period between 2004-2008.

Bird sampling were conducted at seven locations scattered throughout the National Park at altitudes between 700m - 2200m, with three sites being located in core zone primary forest, two sites in the disturbed forest ecosystems of the buffer zone and two sites on the transitional zone between the buffer and core. This wide spatial scale of sampling ensured that samples caught were representative of bird species occupying most ecological and altitudinal niches in the National Park.

Each year, sampling was conducted by two teams of two observers each employing 2.6m X 12m, 36-mm mesh mist nets. The nets were opened at dawn each morning (05:30), checked for captures every 20 minutes, and closed three hours later. Two different sites were netted for two consecutive mornings for 25 days, giving a total of 50 sample sites with one repetition per site for each year. The cumulative sampling effort of this amounted to ±1900 netting hours. Netting was not carried out in the rain or in excessively windy conditions.

All birds captured were first identified to a species level and where possible sexed utilising descriptions in Holwell and Webb (2005) or Pyle *et al.* (1987). Captures were also classified into age categories (adult/ juvenile) by visual observation of moult. All captures were then measured for wing length and birds captured in 2006-2008 were also weighed. Wing length was measured using maximum cord with a wing ruler to 1mm. Weight was measured using a scale to 1g. Only the morphometric data for adult birds were analysed in this study.

Results

A total of 1501 adult birds representing 121 species from 27 avian families were captured and measured during the sampling. 434 birds were captured during the 2004 sampling period, with 166, 233 and 497 birds being sampled in 2005/2006/2007 respectively and the remaining 171 birds being captured during the 2008 sampling period. Table A2.1 displays a summary of the number of individuals of each species caught and sex ratios of capture for each species, as well as biometric measurements for wing length and weight. Bracketed numbers in the weight column indicate the total number of birds measured where this differs from the total number of samples.

Table A2.1 – Wing length and weight measurements for cloud forest species. Bracketed numbers in weight column indicate number of measurements taken, which may differ from total N number. Measurements for male, female and total birds displayed where applicable. ± represents ± 1 standard deviation. Family groupings based on Wells (1998).

Family	Common name	Scientific name		N	Wing (mm)	Weight (g)
Accipitridae	**White Breasted Hawk**	*Accipiter chionogaster*		**1**	**173 ± 0**	**N/A**
			♂	1	173 ± 0	N/A
Falconidae	**Barred Forest Falcon**	***Micrastur ruficollis***		**2**	**167 ± 9.9**	**(1) 182 ± 0**
			♀	1	174 ± 0	183 ± 0
Columbidae	**White-winged Dove**	***Zenaida asiatica***		**1**	**160 ± 0**	**185 ± 0**
	Grey-chested Dove	***Leptotila cassini***		**3**	**138 ± 2.65**	**163.67 ± 16.65**
	White-faced Quail Dove	***Geotrygon albifacies***		**3**	**157.33 ± 2.52**	**(2) 273.5 ± 7.78**
			♂	1	157 ± 0	268 ± 0
	Ruddy Quail Dove	***Geotrygon montana***		**1**	**145 ± 0**	**215 ± 0**
Cuculidae	**Groove-billed Ani**	***Crotophaga sulcirostris***		**3**	**131.67 ± 3.79**	**N/A**
			♀	1	136 ± 0	N/A
Trochilidae	**Long-tailed Hermit**	***Phaethornis superciliosus***		**35**	**66 ± 3.36**	**(32) 6.54 ± 0.62**
			♂	6	66.17 ± 2.32	6.43 ± 0.52
			♀	5	65.4 ± 1.67	6.64 ± 0.96
	Little Hermit	***Pygmornis longuemareus***		**8**	**39.71 ± 2.21**	**3.24 ± 0.42**
			♂	1	41 ± 0	4.1 ± 0
			♀	1	46 ± 0	3.8 ± 0
	Violet Sabrewing	***Campylopterus hemileucurus***		**99**	**81..88 ± 4.04**	**(76) 10.46 ± 1.44**
			♂	35	83.97 ± 4.35	(27) 11.74 ± 1.4
			♀	60	78.76 ± 4.8	(46) 9.68 ± 0.78
	Green Violet-ear	***Colibri thalassinus***		**48**	**64 ± 2.95**	**(29) 4.93 ± 0.61**
			♂	8	63.22 ± 2.54	4.83 ± 0.41

			♀	2	63 ± 2.53	4.7 ± 0.32
	Emerald-chinned Hummingbird	***Abeillia abeillei***		**13**	**49.85 ± 2.61**	**(11) 3.25 ± 0.36**
			♂	5	51 ± 2.55	(4) 3.35 ± 0.37
			♀	6	48.5 ± 2.38	(4) 3.1 ± 0.48
	Black-crested Coquette	***Lophornis helenae***		**2**	**42 ± 2.83**	**2.9 ± 0**
			♀	2	42 ± 2.83	2.9 ± 0
	Crowned Woodnymph	***Thalurania colombica***		**11**	**53.55 ± 4.84**	**(10) 3.98 ± 0.87**
			♂	2	64 ± 1.41	4.75 ± 0.35
			♀	7	51.43 ± 4.08	3.61 ± 0.76
	***Salvin's Emerald**	***Chlorostilbon salvini***		**1**	**53 ± 0**	**4 ± 0**
			♂	1	53 ± 0	4 ± 0
	White-eared Hummingbird	***Hylocharis leucotis***		**9**	**51.11 ± 4.76**	**3.69 ± 0.64**
			♂	3	53.33 ± 1.53	3.77 ± 0.61
			♀	6	50 ± 5.55	3.65 ± 0.71
	Blue-throated Sapphire	***Hylocharis eliciae***		**3**	**52.67 ± 1.15**	**4.6 ± 0.35**
			♂	3	52.67 ± 1.15	4.6 ± 0.35
	White-bellied Emerald	***Agyrtria candida***		**39**	**52.54 ± 2.58**	**(29) 4.34 ± 0.72**
			♀	5	53.8 ± 4.82	3.98 ± 0.46
	Azure-crowned Hummingbird	***Agyrtria cyanocephala***		**80**	**61.22 ± 4.28**	**(27) 5.43 ± 0.83**
			♂	5	58.6 ± 3.21	(4) 5.9 ± 0.84
			♀	3	54.5 ± 0.71	(2) 4.25 ± 0.35
	Berylline Hummingbird	***Saucerottia beryllina***		**2**	**55.5 ± 0.71**	**5.2 ± 0.42**
			♂	1	56 ± 0	5.5 ± 0
			♀	1	55 ± 0	4.9 ± 0
	Cinnamon Hummingbird	***Amazilia rutila***		**1**	**55.8 ± 0**	**2 ± 0**
			♀	1	55.8 ± 0	2 ± 0
	Rufous-tailed Hummingbird	***Amazilia tzacatl***		**11**	**58.55 ± 4.57**	**(5) 5.14 ± 0.63**
			♂	4	61 ± 5.23	(3) 5.3 ± 0.26
			♀	4	58.25 ± 1.89	(1) 5.8 ± 0
	Stripe-tailed Hummingbird	***Eupherusa eximia***		**20**	**59.88 ± 4.52**	**(17) 4.24 ± 0.69**
			♂	12	60.75 ± 4.47	(11) 4.28 ± 0.65
			♀	4	56.25 ± 4.27	4.03 ± 0.64
	Amethyst-throated Hummingbird	***Lampornis amethystinus***		**1**	**70 ± 0**	**7 ± 0**
			♀	1	70 ± 0	7 ± 0
	Green-throated Mountain-gem	***Lampornis viridipallens***		**164**	**65.72 ± 4.48**	**(112) 5.97 ± 1.01**
			♂	68	69.25 ± 3.51	(48) 6.41 ± 0.67
			♀	85	62.86 ± 3.07	(60) 5.57 ± 1.09
	Magnificent Hummingbird	***Eugenes fulgens***		**24**	**75.38 ± 4.22**	**(18) 8.21 ± 1.61**
			♂	11	75.82 ± 5.65	(8) 8.88 ± 2.2
			♀	11	74.82 ± 2.89	(10) 7.92 ± 0.84
	Long-billed Starthroat	***Heliomaster longirostris***		**1**	**61 ± 0**	**N/A**
	Sparkling-tailed Woodstar	***Philodice dupontii***		**1**	**35 ± 0**	**N/A**
			♀	1	35 ± 0	N/A
	Wine-throated Hummingbird	***Atthis ellioti***		**5**	**37.8 ± 3.19**	**(4) 2.75 ± 0.29**
			♂	1	36.75 ± 0	3 ± 0
			♀	4	38.67 ± 4.16	(3) 2.67 ± 0.29
Trogonidae	**Resplendent Quetzal**	***Pharomachrus mocinno***		**1**	**211 ± 0**	**N/A**
			♀	1	211 ± 0	N/A
Momotidae	**Tody Motmot**	***Hylomanes momotula***		**1**	**71 ± 0**	**30 ± 0**
	Blue-crowned Motmot	***Momotus momota***		**6**	**137.33 ± 5.39**	**(1) 120 ± 0**
			♂	2	131.5 ± 0.71	120 ± 0
			♀	1	144 ± 0	N/A
Alcedinidae	**Green Kingfisher**	***Chloroceryle americana***		**2**	**85 ± 1.4**	**N/A**
			♂	1	84 ± 0	N/A
			♀	1	86 ± 0	N/A
Galbulidae	**Rufous- tailed Jacamar**	***Galbula ruficauda***		**1**	**86 ± 0**	**N/A**
			♀	1	**86 ± 0**	N/A

Picidae	**Smoky-brown Woodpecker**	***Veniliornis fumigatus***		**1**	**83 ± 0**	**32 ± 0**
			♀	1	83 ± 0	32 ± 0
	Golden-fronted Woodpecker	***Centurus aurifrons***		**7**	**128 ± 6.48**	**(1) 66 ± 0**
			♂	3	129 ± 5.57	N/A
			♀	2	126.5 ± 13.44	N/A
	Golden-olive Woodpecker	***Piculus rubiginosus***		**2**	**128 ± 0**	**N/A**
			♂	1	**128 ± 0**	N/A
			♀	1	**128 ± 0**	N/A
Dendrocolaptidae	**Tawny-winged Woodcreeper**	*Dendrocincla anabatina*		**1**	**93 ± 0**	**N/A**
	Ruddy Woodcreeper	***Dendrocincla homochroa***		**1**	**104 ± 0**	**45.5 ± 0**
			♀	1	104 ± 0	45.5 ± 0
	Olivaceous Woodcreeper	***Sittasomus griseicapillus***		**6**	**75.8 ± 6.37**	**(5) 12.98 ± 0.98**
			♂	1	87 ± 0	14 ± 0
			♀	2	71.5 ± 3.54	12.05 ± 0.07
	Wedge-billed Woodcreeper	***Glyphorynchus spirurus***		**2**	**74 ± 0**	**16.2 ± 1.7**
	Ivory-billed Woodcreeper	***Xiphorhynchus flavigaster***		**1**	**118 ± 0**	**N/A**
			♂	1	118 ± 0	N/A
	Spotted Woodcreeper	***Xiphorhynchus erythropygius***		**7**	**112 ± 4.4**	**(3) 43.6 ± 2.09**
			♂	2	113 ± 8.49	(1) 42.2 ± 0
			♀	2	110.5 ± 2.12	N/A
	Spot-crowned Woodcreeper	***Lepidocolaptes affinis***		**3**	**103 ± 3.61**	**(1) 28 ± 0**
			♀	1	106 ± 0	N/A
Furnariidae	**Spectacled Foliage-gleaner**	***Anabacerthia variegaticeps***		**14**	**86 ± 3.3**	**(7) 24.36 ± 0.68**
			♂	1	89 ± 0	N/A
	Buff-throated Foliage-gleaner	***Automolus ochrolaemus***		**3**	**89.33 ± 3.06**	**42.42 ± 4.2**
			♀	1	86 ± 0	37.8 ± 0
	Ruddy Foliage-gleaner	***Anabacerthia rubiginosus***		**9**	**91.78 ± 2.82**	**(4) 47.63 ± 2.43**
			♀	1	**92 ± 0**	**47 ± 0**
	Tawny-throated Leaftosser	***Sclerurus mexicanus***		**8**	**84.5 ± 3.12**	**(7) 30.58 ± 4.13**
			♂	1	86 ± 0	29.5 ± 0
	Plain Xenops	***Xenops minutus***		**1**	**60 ± 0**	**12 ± 0**
Thamnophilidae	**Barred Antshrike**	***Thamnophilus doliatus***		**2**	73 ± 0	N/A
			♂	1	73 ± 0	N/A
			♀	1	73 ± 0	N/A
	Slaty Antwren	***Myrmotherula schisticolor***		**1**	**52 ± 0**	**8 ± 0**
			♀	1	52 ± 0	8 ± 0
Tyrannidae	**Ochre-bellied Flycatcher**	***Mionectes oleagineus***		**60**	**63.85 ± 3.02**	**(48) 13.16 ± 1.41**
			♂	9	64.33 ± 2.06	(8) 13.5 ± 0.59
			♀	10	62.3 ± 3.23	(8) 13.26 ± 1.27
	Sepia-capped Flycatcher	***Leptopogon amaurocephalus***		**1**	**66 ± 0**	**12.5 ± 0**
			♀	1	66 ± 0	12.5 ± 0
	Eye-ringed Flatbill	***Rhynchocyclus brevirostris***		**8**	**76.19 ± 8.25**	**(6) 20.48 ± 6.27**
			♀	1	85 ± 0	25.5 ± 0
	Tufted Flycatcher	***Mitrephanes phaeocercus***		**1**	**67 ± 0**	**10.3 ± 0**
	Yellowish Flycatcher	***Empidonax flavescens***		**37**	**65.52 ± 2.85**	**(22) 11.65 ± 1.51**
			♂	1	61 ± 0	11.5 ± 0
			♀	8	63.75 ± 1.75	(7) 11.2 ± 1.19
	Rufous Mourner	***Rhytipterna holerythra***		**1**	**97 ± 0**	**44.4 ± 0**
	Bright-rumped Attila	***Attila spadiceus***		**1**	**83 ± 0**	**43 ± 0**
	Dusky-capped Flycatcher	***Myiarchus tuberculifer***		**5**	**77.4 ± 3.44**	**(1) 20 ± 0**
			♂	1	74 ± 0	20 ± 0
	Brown-crested Flycatcher	***Myiarchus tyrannulus***		**1**	**81 ± 0**	**N/A**
	Great Kiskadee	***Pitangus sulphuratus***		**2**	**117 ± 4.24**	**(1) 60 ± 0**
			♂	1	114 ± 0	60 ± 0
			♀	1	120 ± 0	N/A
	Social Flycatcher	***Myiozetetes similis***		**1**	**94 ± 0**	**N/A**

			♀	1	94 ± 0	N/A
Pipridae	**White-collared Manakin**	***Manacus candei***		**8**	**57 ± 3.21**	**(7) 19.37 ± 1.88**
			♂	5	56.4 ± 3.65	(4) 19.88 ± 0.85
			♀	3	56.5 ± 0.71	18.7 ± 2.88
	Red-capped Manakin	***Pipra mentalis***		**15**	**61 ± 2.07**	**16.39 ± 1.22**
			♂	4	61.75 ± 1.5	16.02 ± 0.62
			♀	9	60.89 ± 2.26	16.2 ± 1.22
Cinclidae	**American Dipper**	***Cinclus mexicanus***		**1**	**86 ± 0**	**53 ± 0**
			♂	1	86 ± 0	53 ± 0
Troglodytidae	**Spot-breasted Wren**	***Thryothorus maculipectus***		**16**	**57.63 ± 3.82**	**(5) 17.74 ± 2.02**
			♂	1	59 ± 0	19 ± 0
			♀	5	57 ± 3.24	(4) 16.77 ± 2.14
	Plain Wren	***Thryothorus modestus***		**12**	**57 ± 2.22**	**(9) 17.43 ± 1.52**
			♂	2	58.5 ± 0.71	18.45 ± 0.78
			♀	3	56.75 ± 2.36	17.43 ± 2.11
	Southern House Wren	***Troglodytes aedon***		**17**	**50.24 ± 2.84**	**(7) 11.99 ± 1.37**
			♂	2	50 ± 0	11.6 ± 0.28
			♀	1	46 ± 0	N/A
	White-breasted Wood-Wren	***Henicorhina leucosticta***		**11**	**54.64 ± 2.66**	**(9) 16.51 ± 1.17**
			♂	3	54.33 ± 2.52	16.93 ± 1.1
			♀	1	49 ± 0	16 ± 0
	Grey-breasted Wood-Wren	***Henicorhina leucophrys***		**23**	**55.87 ± 3.06**	**(14) 14.73 ± 0.88**
			♂	2	56.5 ± 0.71	14.85 ± 0.5
			♀	1	55 ± 0	15 ± 0
	Nightingale Wren	***Microcerculus philomela***		**4**	**57 ± 2.71**	**(3) 7.47 ± 1.36**
			♂	3	55.67 ± 0.58	7.47 ± 1.36
Turdidae	**Slate-colored Solitaire**	***Myadestes unicolor***		**46**	**96.93 ± 2.54**	**(33) 35.45 ± 3.4**
			♂	18	97.94 ± 2.41	(15) 36.27 ± 2.44
			♀	10	96.9 ± 2.64	(5) 36.46 ± 2.04
	Ruddy-capped Nightingale-Thrush	***Catharus frantzii***		**4**	**86.5 ± 3.32**	**(1) 26.5 ± 0**
	Black-headed Nightingale-Thrush	***Catharus mexicanus***		**45**	**89.11 ± 2.87**	**(32) 32.15 ± 1.97**
			♂	16	90.81 ± 2.9	(13) 31.47 ± 1.42
			♀	14	88.07 ± 2.27	(9) 32.99 ± 2.14
	Clay-colored Thrush	***Turdus grayi***		**55**	**124.84 ± 4.88**	**(32) 77.02 ± 7.41**
			♂	14	125.43 ± 4.13	(11) 79.45 ± 7.48
			♀	14	124.64 ± 6.45	(6) 76.5 ± 4.72
	Black Thrush	***Turdus infuscatus***		**6**	**124.17 ± 4.88**	**(4) 70.75 ± 3.4**
			♂	2	127 ± 7.07	(1) 75 ± 0
			♀	2	122.5 ± 3.54	(1) 72 ± 0
	White-throated Thrush	***Turdus assimilis***		**8**	**122.63 ± 4.41**	**(4) 71.83 ± 7.42**
			♂	2	121 ± 2.83	67.75 ± 3.81
			♀	2	119 ± 3.34	80 ± 0
Sylviidae	**Long-billed Gnatwren**	***Ramphocaenus melanurus***		**3**	**48.33 ± 1.53**	**10.83 ± 1.26**
			♂	1	50 ± 0	12 ± 0
			♀	2	47.5 ± 0.71	10.25 ± 1.06
Corvidae	**Green Jay**	***Cyanocorax yncas***		**2**	**158.5 ± 4.95**	**N/A**
	Azure-hooded Jay	***Cyanolyca cucullata***		**2**	**141 ± 2.83**	**(1) 100 ± 0**
Emberizinae	**Variable Seedeater**	***Sporophila corvina***		**2**	**63.5 ± 13.44**	**13.5 ± 6.37**
			♂	1	73 ± 0	18 ± 0
			♀	1	54 ± 0	9 ± 0
	White-collared Seedeater	***Sporophila torqueola***		**6**	**50.5 ± 1.38**	**(4) 9.45 ± 0.71**
			♂	3	51.33 ± 0.58	(1) 9 ± 0
			♀	1	48 ± 0	10.5 ± 0
	Thick-billed Seedfinch	***Oryzoborus funereus***		**3**	**56 ± 4**	**12.15 ± 1.91**
			♂	1	60 ± 0	
			♀	2	54 ± 2.83	12.15 ± 1.91
	Blue-black Grassquit	***Volatina jacarina***		**7**	**48.14 ± 1.68**	**N/A**

			♂	5	48.6 ± 1.67	N/A
			♀	2	47 ± 1.41	N/A
	Yellow-faced Grassquit	***Tiaris olivacea***		**15**	**51.57 ± 5.62**	**(1) 9.7 ± 0**
			♂	8	52.81 ± 4.58	N/A
			♀	6	48.83 ± 1.83	(1) 9.7 ± 0
	Orange-billed Sparrow	***Arremon aurantiirostris***		**7**	**80.43 ± 5.16**	**(5) 34.12 ± 2.39**
			♂	4	81.25 ± 5.91	33.85 ± 2.68
			♀	1	76 ± 0	35.2 ± 0
	Prevost's Ground-Sparrow	***Melozone biarcuatum***		**7**	**71.86 ± 4.91**	**(5) 31.4 ± 1.85**
			♂	2	71.5 ± 10.61	32.25 ± 0.35
			♀	2	70 ± 1.41	31.75 ± 2.47
	Rusty Sparrow	***Aiomophila rufescens***		**4**	**71.5 ± 4.65**	**N/A**
			♂	1	76 ± 0	N/A
	Yellow-throated Brush-Finch	***Atlapetes gutteralis***		**5**	**73.8 ± 3.11**	**(2) 33.25 ± 2.47**
			♂	2	73 ± 4.24	(1) 31.5 ± 0
			♀	1	75 ± 0	N/A
	Chestnut-capped Brush-Finch	***Atlapetes brunneinucha***		**41**	**84.41 ± 4.56**	**(31) 42.17 ± 2.56**
			♂	10	86.9 ± 2.64	(7) 42.76 ± 2.21
			♀	5	83.2 ± 2.49	41.76 ± 2.82
Cardinalinae	**Black-headed Saltator**	***Saltator atriceps***		**7**	**123.9. ± 3.76**	**(5) 94 ± 12.02**
			♂	1	130 ± 0	90 ± 0
			♀	2	121 ± 4.24	(1) 115 ± 0
	Buff-throated Saltator	***Saltator maximus***		**11**	**101 ± 4.58**	**(4) 50 ± 4.97**
			♂	2	98 ± 7.07	52 ± 2.83
			♀	4	102.75 ± 2.22	(2) 48 ± 7.07
	Blue-black Grosbeak	***Cyanocompsa cyanoides***		**6**	**76.17 ± 7.68**	**(4) 30.78 ± 2.41**
			♂	2	80.5 ± 2.12	(1) 31 ± 0
			♀	2	76 ± 4.24	31.55 ± 3.61
	Blue Grosbeak	***Passerina caerulea***		**2**	**79.5 ± 0.71**	**29.55 ± 0.07**
			♂	1	79 ± 0	29.6 ± 0
			♀	1	80 ± 0	29.5 ± 0
Thraupinae	**Common Bush-Tanager**	***Chlorospingus ophthalmicus***		**141**	**69.82 ± 2.89**	**(101) 16.91 ± 1.33**
			♂	54	70.72 ± 2.91	(39) 17.26 ± 1.37
			♀	26	68.43 ± 2.59	(25) 16.8 ± 1.3
	Red-crowned Ant-Tanager	***Habia rubica***		**3**	**97 ± 6.08**	**(1) 37.2 ± 0**
			♂	1	104 ± 0	N/A
	Red-throated Ant-Tanager	***Habia fuscicauda***		**2**	**89.5 ± 4.95**	**33 ± 0**
			♀	2	89.5 ± 4.95	(1) 33 ± 0
	Flame-colored Tanager	***Piranga bidentata***		**7**	**95.71 ± 2.21**	**(3) 34.57 ± 0.51**
			♂	1	100 ± 0	34 ± 0
			♀	4	95 ± 1.41	(3) 35.23 ± 0.68
	Hepatic Tanager	***Piranga flava***		**2**	**94 ± 2.83**	**36.65 ± 1.63**
	Blue-crowned Chlorophonia	***Clorophonia occipitalis***		**2**	**79 ± 2.83**	**N/A**
			♂	1	81 ± 0	N/A
	Yellow-throated Euphonia	***Euphonia hirundinacea***		**3**	**61.67 ± 1.15**	**(2) 13.9 ± 0.14**
			♂	2	61 ± 0	13.9 ± 0.14
	Olive-backed Euphonia	***Euphonia gouldi***		**2**	**54.5 ± 0.71**	**13.6 ± 0.14**
			♂	2	54.5 ± 0.71	13.6 ± 0.14
	Cinnamon-bellied Flowerpiercer	***Diglossa baritula***		**11**	**55.32 ± 1.1**	**(6) 8.98 ± 0.52**
			♂	6	55.67 ± 1.21	(3) 8.83 ± 0.73
			♀	2	55 ± 0	9.05 ± 0.35
Coerebinae	**Bananaquit**	***Coereba flaveola***		**3**	**54.33 ± 2.08**	**9.13 ± 1.63**
			♂	1	56 ± 0	11 ± 0
Parulinae	**Black-and-white Warbler**	***Mniotilta varia***		**9**	**69.44 ± 1.94**	**(5) 9.64 ± 0.33**
			♂	1	71 ± 0	N/A
			♀	6	69.67 ± 1.75	(4) 9.7 ± 0.35
	Golden-cheeked Warbler	***Dendroica chrysoparia***		**3**	**64.33 ± 1.53**	**9.43 ± 0.6**

			♂	1	64 ± 0	8.8 ± 0
	Blackburnian Warbler	***Dendroica fusca***		**1**	**68 ± 0**	**N/A**
			♀	1	68 ± 0	N/A
	Kentucky Warbler	***Oporornis formosus***		**1**	**67 ± 0**	**12.7 ± 0**
			♂	1	67 ± 0	12.7 ± 0
	Northern Waterthrush	***Seiurus noveboracensis***		**1**	**80 ± 0**	**19.4 ± 0**
	Louisiana Waterthrush	***Seiurus motacilla***		**15**	**80.7 ± 2.87**	**(10) 18.33 ± 1.43**
	American Redstart	***Setophaga ruticilla***		**1**	**60 ± 0**	**6.2 ± 0**
			♂	1	60 ± 0	6.2 ± 0
	Slate-throated Redstart	***Myioborus miniatus***		**64**	**62.12 ± 2.57**	**(40) 8.96 ± 0.76**
			♂	29	62.02 ± 2.79	(19) 8.84 ± 0.85
			♀	14	61.79 ± 1.67	(8) 8.98 ± 0.69
	Golden-crowned Warbler	***Basileuterus culicivorus***		**12**	**57.83 ± 3.19**	**(7) 9.74 ± 0.69**
			♂	3	56 ± 5.29	9.87 ± 0.76
	Chestnut-capped Warbler	***Basileuterus rufifrons***		**13**	**53.85 ± 1.46**	**(1) 10.5 ± 0**
			♀	2	55 ± 2.83	(1) 10.5 ± 0
Vireonidae	**Brown-capped Vireo**	***Vireo leucophrys***		**2**	**69.5 ± 2.12**	**12.2 ± 1.13**
			♂	1	71 ± 0	11.4 ± 0
			♀	1	68 ± 0	13 ± 0
	Tawny-crowned Greenlet	***Hylophilus ochraceiceps***		**1**	**55 ± 0**	**11 ± 0**
			♂	1	55 ± 0	11 ± 0
Icteridae	**Melodious Blackbird**	*Dives dives*		**1**	**152 ± 0**	**N/A**
	Great-tailed Grackle	*Quizcalus mexicanus*		**1**	**154 ± 0**	**N/A**
			♀	1	154 ± 0	N/A
	Yellow-backed Oriole	*Icterus chryater*		**2**	**91.5 ± 4.95**	**N/A**
			♀	2	91.5 ± 4.95	N/A
	Yellow-billed Cacique	*Amblycercus holosericeus*		**1**	**104 ± 0**	**N/A**

*Taxonomy of Salvin's Emerald (*Chlorostilbon salvini*) remains unclear. Some sources list as potential distinct species (Holwell and Webb 2005), although most consider conspecific with Fork-tailed Emerald (*Chlorostilbon mellisugus*) or Canivet's Emerald (*Chlorostilbon canivetii*) (American Union of Ornithologists 1998).

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APPENDIX 3 - PHOTOGRAPHIC EXAMPLES OF STUDY SITES AND HABITAT TYPES IN THE LAMBUSANGO FOREST AND CUSUCO NATIONAL PARK

Examples from the Lambusango forest

Plate A3.1 – A stand of large hardwood trees in primary forest with the limited production forest

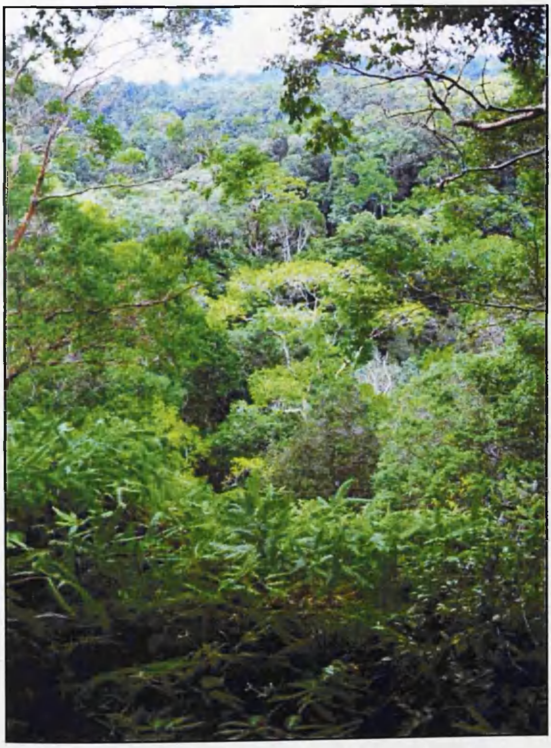


Plate A3.2 – A viewpoint over the high forest canopy of the primary forest

Plate A3.3 – Smaller trees in regenerating secondary forest in the centre of the strict reserve

Plate A3.4 – One of the large strangler figs commonly found in secondary forest habitats in the Lambusango forest.

Plate A3.5 – Disturbed secondary forest around the Lambusango's periphery (Photo used with permission of Andrew Snyder)

Plate A3.6 – Cleared farmland surrounding the Lambusango's borders.

Examples from Cusuco National Park

Plate A3.7 – Bosque enano elfin forest found on exposed mountaintops in the highest elevations of the core zone

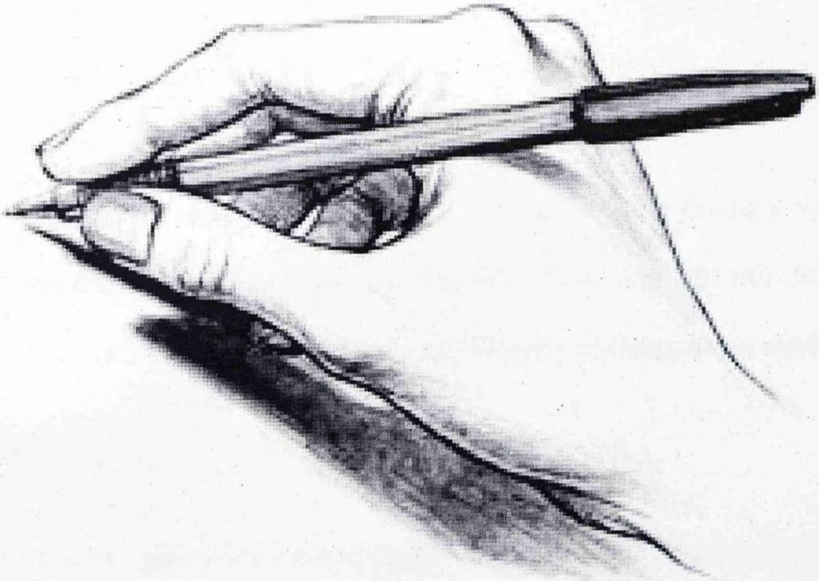
Plate A3.8 – A stand of large hardwood trees in the interior core (Photo used with permission of Andrew Snyder).

Plate A3.9 – Large trees supporting many epiphytes and bromeliads in the periphery of the Park's core zone.

Plate A3.10 – Degraded habitats in the buffer zone, fairly close to the buffer-core boundary (Photo used with permission of Andrew Snyder).

Plate A3.11 – *Pine forest (Pinus oocarpa) at lower elevations in the Park's buffer zone*

APPENDIX 4 - PROGRESS OF PAPERS SUBMITTED FOR PEER- REVIEW



Status of articles submitted for publication in peer-reviews journals at time of thesis submission (16/10/09)

Chapters three, four and five of this thesis have been submitted for publication in International peer-reviewed journals. Authorship of all submitted publications is shared between myself and my supervisor, Alan Blackburn. I am the first author of all published and submitted material, having personally collected all data for and written up each publication. Alan is the second author of each, his contribution largely limited to a supervisory role.

The status of each research paper is as follows:

Chapter 3 – 'An assessment of the effectiveness of two methods in describing a Neotropical cloud forest bird community'. Submitted to *Ornithologia Neotropical* 30/11/08. Manuscript returned with request for revisions 13/08/09. Revisions made and manuscript resubmitted 30/09/09.

Chapter 4 – 'Chapter 4 - Impacts of tropical forest disturbance upon avifauna on a small island with high endemism: implications for conservation'. Submitted to Conservation and Society 18/06/09. Manuscript accepted for publication 06/01/10.

Chapter 5 – 'The effectiveness of a Mesoamerican 'Paper park' in conserving cloud forest avifauna'. Submitted to Biodiversity and Conservation 03/12/08. Manuscript returned with request for revisions 18/01/09. Revisions made and manuscript resubmitted 24/05/09. Manuscript accepted 18/06/09. Published as:

Martin, T.E. & Blackburn, G.A. (2009). The effectiveness of a Mesoamerican 'Paper park' in conserving cloud forest avifauna. *Biodiversity and Conservation*, 18, 3841-3859.

Additionally, Appendix 1 'The avifauna of the Lambusango Reserve and vicinity' has been published on-line on the Opwall website. It can be accessed at http://www.opwall.com/Library/Indonesia/Indonesia%20Terrestrial/Birds/The%20avifauna%20of%20the%20Lambusango%20Reserve.pdf

The data presented in this report is currently being compiled by the author into a potential peer-review paper, in conjunction with David Kelly at Trinity College, Dublin. We aim to submit a manuscript to the journal 'Forktail' by 06/10.