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Tropical production landscapes and conservation: a study investigating the biodiversity value of a native timber plantation landscape in Papua New Guinea

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To my magical daughter Amelia

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I will start with a little story. For many years I have listened to and supported a community radio station (3RRR) in Melbourne. Years back I won their first prize after donating what was at the time, my last $66.00 (until my next pay-day). The prize was a $4000 gift voucher to a travel agent. In one of those "the universe is trying to tell me something" moments, I quit my job as a molecular biologist and went and took up a volunteer position as a field biologist in the central highlands of Papua New Guinea (PNG). Why? Because I'd seen pictures of people working with the Tenkile and thought "that looks like a lot more fun than working in a lab". I was right.

A few years later, after a number of set-backs (something I would have to get used to) I embarked on my own PhD project on New Britain Island, Papua New Guinea. In retrospect, I can't believe I pulled it off – there were so many variables that had to fall into place. Tom 'diwai' Vigus inspired me to work at Open Bay, in what he termed 'the safest' logging camp in PNG (thank-you Tom). But there was one hurdle: convincing the Japanese company directors to permit me access to their operation for a two-year period. So, my fantastic husband Simon and I raised some funds and took on a reconnaissance mission to charm the directors into granting me access. We had heard that the local company head in Rabaul was underwhelmed by the food options available, and so we hatched a plan to convince him via his stomach. For 2 weeks, Simon was up every morning at 5am making his famous pikelets for breakfast, and we even managed an attempt at spaghetti bolognese (by request) *sans* tomatoes, beef and Italian herbs (don't try this at home). But it was when Simon fixed the ailing generator that my fate was sealed and access was granted. The rest as they say, is history!

Simon, I cannot thank you enough for joining me on my adventure, for sticking with me through this long process while we experienced the birth of our beautiful daughter and the loss of your wonderful mother. It has been hard, and challenging and stressful and isolating and you have been an incredible support. Words cannot express, but there is no doubt that I would not have been able to finish this work without you.

Fieldwork in PNG is not an easy task. I took my little brother up with me on a pilot mission to figure out the best methods for measuring stand-level attributes and to have an idea of how to design the surveys. Tim, it was an enormous shock to your system I know, but I hope (and I believe) that you will have life-long memories of a spectacular country. Thank you for coming

along and for making me realise that I would need to be very picky when hiring volunteers for the ensuing field work!

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Being in the field was tough but rewarding. But the long slog of grappling with the thesis was far more grueling: trying to write papers and analyse data while having a baby, working part-time and full-time to make ends meet and having to pick up where I left off. I was not prepared

for the roller coaster of emotions, for crises of confidence and anxiety. My ‘rock’ during this stage of the project has been Dale Nimmo from Deakin University. This thesis would not have come off so spectacularly had I not had the great sense to meet Dale and squeeze out as much useful analysis, editing and general academic and life skills from him as I could without backlash. Dale you are a superstar and I owe so much to you. Through Dale I met Simon Watson and Greg Holland who have been equally wonderful at teaching me what it takes to publish. Thank you all for picking up my spirits and giving me confidence when you could see it was wavering, for critiquing my work aggressively but reassuring me at the same time. I know you are all doing that balancing act of the early-career scientist and ‘Dad’ to very young children and so I am even more grateful for the time you have given.

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ABSTRACT

The majority of old-growth tropical forests and the vast biodiversity they support exist outside of protected areas, either embedded within production landscapes or adjacent to them. As a consequence, conserving the world's tropical biodiversity depends largely on the effective management of production landscapes (landscapes containing one or multiple production land-uses). Effective conservation management necessitates a balance between production goals (e.g. crop or timber yields) and biodiversity conservation. 'Land-sharing' strategies attempt to achieve this balance in production landscapes by encouraging lower-intensity production land-uses and where possible, the retention of pre-conversion vegetation cover. This presents a promising way forward for conservation in production areas but is hampered by inadequate information on the capacity of production landscapes to support native biodiversity in most tropical ecosystems.

In this thesis I investigated the biodiversity conservation value of a multi-use production landscape comprised of native timber (*Eucalyptus deglupta*) plantations interspersed with (historically logged) secondary forests and unlogged forest remnants. The study was based in the lowlands of New Britain Island, Papua New Guinea and represents one of the only studies of the impact of production landscapes on Melanesian biota. To assess the state of biological diversity within this production landscape I had three principal objectives: (1) understand which forest species can and cannot persist in production land-uses and how these patterns are mediated by species' biological attributes; (2) evaluate the effect of land-use type on vegetation and stand-level structural attributes; and (3) examine which properties of the native plantation landscape most influence the occurrence patterns of lowland forest birds. Surveys were conducted at 156 survey sites over a two-year period (2007–2008). Sites were stratified among the five main management elements that comprised the plantation landscape and represented a gradient in land-use (from least-to-most disturbed): unlogged forest, secondary remnant forest, secondary riparian buffer strips, mature plantations and young plantations. At each survey site I recorded data on the occurrence of forest bird and tree species and measured the incidence of vegetation types and the stand structural attributes. Based on the knowledge gained from this research, I formulated conservation management strategies that can effectively balance the maintenance of forest biodiversity in the landscape with timber yield targets.

Investigation into the patterns of forest species occurrence among landscape elements (the main land-use types) revealed that at least 70% of tree species and 90% of bird species were capable of existing outside of unlogged remnant forest, within the matrix of mature plantations and forestry-affected secondary forest. These levels are high compared to the tropical literature on timber plantations and suggest both a resilient species pool along with management practices that may encourage biodiversity retention. However, species richness at sites within mature plantations was lower than within unlogged and secondary forest and their species assemblages were compositionally dissimilar to those of unlogged forest, demonstrating a successive loss of more vulnerable species (e.g. late-successional trees, and frugivorous and forest-specialist birds). In addition, young plantations (2–6 years old) supported very few forest species and these species were in low abundance. These trends highlight the importance of considering the temporal as well as spatial aspects of production types when assessing conservation value.

Evaluation of land-use effects on vegetation and habitat structure provided insight into both the post-disturbance recovery trajectory of the island’s flora and the ramifications of this for their provision of potentially important habitat resources. In general, structural attributes recovered more rapidly than tree and plant species composition in the modified landscape elements. The secondary remnant forest, which was protected by a conservation reserve, demonstrated a very high regenerative capacity. By contrast, the unprotected secondary riparian element, which was subject to ongoing human disturbance and was of more linear shape and fragmented distribution, displayed simplified canopy structure and contained less late-successional vegetation. A similar but more extensive reduction in many old-growth habitat properties was observed for mature plantations, and young plantations suffered acute losses (and absences) for all habitat properties measured.

Building on these findings, I examined the influence of both habitat properties and landscape spatial context on the species richness of forest birds. I found that habitat attributes (e.g. canopy cover and tree species richness) had a greater influence than spatial context (the proportion of unlogged and high-quality secondary forest within a 2km radius) on the richness of bird species among survey sites. In addition, for a sub-set of more vulnerable species (forest-specialists) I found palm cover to also be an important predictor of richness. These results further demonstrate the value of unlogged and secondary forest in terms of their quality as habitat for sustaining avifaunal populations, underscoring the need to formally protect these forests to achieve long-term biodiversity conservation benefits. These results also revealed the properties of mature plantations that facilitated visitation by forest birds and conversely drew attention to management practices that could negatively affect this relationship.

The outcomes of this thesis indicate that land-sharing strategies incorporating production types such as native timber plantations, which permit high canopy cover and tree species richness, can be effective at balancing yield production with biodiversity conservation. Native species are used in <15% of tropical plantation forests globally and given their potential to deliver conservation outcomes, research should be directed at countering barriers to their use over exotic species. However, this study also concluded that such conservation outcomes are dependent on the sympathetic management of plantations, as well as land-use planning directed at facilitating the spatial and temporal continuity of old-growth forest features in the landscape. In addition, without the formal protection and careful management of unlogged and secondary forest reserves, the likelihood of long-term conservation of many forest-dependent species will diminish. Basing conservation management of production landscapes on scientific research is a vital but often unachievable undertaking in the tropics, particularly over the long-term. It is likely that the adoption of recommended management actions can be supported by more targeted research and importantly, through greater collaboration between research institutions, sustainable management organisations, land managers and local communities. Science can go a long way to assist with decision-making but ultimately decisions rest with the values of society.

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General Introduction

Native plantation logs on the roadside: an example of sustainable forestry?

GENERAL INTRODUCTION

Multi-use production landscapes are becoming increasingly important for the conservation of tropical biodiversity. Today, around half of the world's remaining tropical rainforests are made up of secondary regrowth or degraded old-growth forests (Gardner et al. 2009). The majority of remaining old-growth (unmodified, late-successional) forest and the vast biodiversity it supports (Sodhi et al. 2010; Dirzo & Raven 2003) occurs outside of protected areas, either embedded within and around production landscapes, or as remnant tracts with an uncertain development future (Sutherland et al. 2009). 'Land-sharing' conservation strategies, which aim to balance biodiversity conservation with production in multi-use landscapes (Perfecto & Vandermeer 2010) are proposed as a potentially promising way forward for conservation in lowland tropical forests (Fischer et al. 2008; Melo et al. 2013). However, assessing the capacity for multi-use production landscapes to achieve conservation outcomes will be complex because of the variety of land-uses, management scenarios, spatial compositions and biogeographic contexts in which they occur (Gardner et al. 2009; Tscharntke et al. 2012; Chazdon, Harvey, et al. 2009a). Currently, research has provided comparatively little information on the ability of these landscapes to support organisms across many tropical ecosystems (Sekercioglu & Sodhi 2007; Chazdon, Harvey, et al. 2009a).

In this thesis I assess the biodiversity conservation value of a multi-use native timber (*Eucalyptus deglupta*) plantation landscape in Papua New Guinea and in doing so, I endeavour to address knowledge gaps in current conservation research. Firstly, primary forest research still dominates the ecology and conservation literature, despite the identification of production landscapes as a global conservation priority and their proportionally greater cover of the world's terrestrial area (Sutherland et al. 2009; L. J. Martin et al. 2012). Secondly, conservation research of tropical native timber plantations is poorly represented in the literature (Stephens & Wagner 2007) and yet the capacity of native plantations to support remnant forest biota is posited to be higher than for exotic plantations (Bremer & Farley 2010; Brockerhoff et al. 2008). Providing evidence of the conservation potential of different plantation types is vital, given that plantations are predicted to represent over 20% of total forest area by the end of this century (Brockerhoff et al. 2013). Thirdly, Papua New Guinea itself is part of Oceania, home to some of the most highly endemic floral and faunal communities in the world (Woinarski 2010 and references therein). However, many of Oceania's nations face unprecedented loss and modification of forests (Woinarski 2010). Still, the region is one of the most understudied globally and the consequences of modern anthropogenic change on Oceania's unique biodiversity remains largely unknown (L. J. Martin et al. 2012; Kingsford et al. 2009). By addressing these knowledge gaps, I hope to contribute valuable ecological knowledge to this research area and engender a greater understanding of some of the limitations and values of land-sharing conservation strategies.

1-1 The state of tropical forests worldwide

Recent analysis estimates that currently, around 64,000 km^2 of tropical forest is deforested or degraded every year, primarily through conversion to smallholder agriculture, wood collection for fuel and commercial logging (Wright 2010). Many commercially logged countries (especially those of Southeast Asia and the Pacific) have either been overharvested or are at risk of overharvesting in the near future (Shearman et al. 2012). Hence, logging activities are necessarily intensifying in regions where accessible forests are comparatively intact, such as central Africa, pockets of South America, and Oceania (including Papua New Guinea, Wright 2010; Shearman et al. 2012; Blaser et al. 2011). The encroachment by logging activities is compounded by rising human populations and global demand for rainforest products, food crops and biofuels. Demand for these products drives the extensive conversion of both old-growth (forests of late-succession that have been long-undisturbed by large-scale human modification or natural disturbance; Clark 1996) and recovering secondary forest to novel, multi-use production landscapes (Wright 2010; Shearman et al. 2012). The remaining old-growth forests—particularly those of value to industry ↓are further imperilled by a lack of effective, formalised protection, which is a consequence of their distribution being mostly in poor countries with unstable governance and little centralised advocacy for landowners’ rights and biodiversity conservation (Wright et al. 2007; Barrett et al. 2011). The loss and degradation of tropical forests has broad ramifications as they contain over half of the world’s terrestrial plant and animal species (Peres et al. 2010; Gardner et al. 2010), including 79% of the world’s threatened bird species (Sodhi, Sekercioglu, Barlow & Robinson 2011b) and because they play a key role in maintaining global carbon and hydrological cycles (Bradshaw et al. 2007; Houghton 2012).

Today, secondary regrowth and degraded (modified) old-growth forests are estimated to make up around half of all remaining tropical forest (Chazdon, Peres, et al. 2009b). This change in forest composition is considered by some to mark the era of the novel tropical forest: regenerated forests comprised of novel species assemblages in response to advanced human alteration (Lugo 2009). However, being human-driven, these forest changes are dynamic and unevenly distributed across the tropics, reflecting their relationship to prevailing global and local socio-economic conditions (DeFries et al. 2010). For example, lowland forests in particular experience extensive conversion to novel, multi-use production landscapes (e.g. oil palm, timber plantations, agriculture), as they are the most accessible and valuable areas in terms of resource production (Miettinen et al. 2012; Blaser et al. 2011). In contrast, significant forest recovery is occurring in previously exploited areas where modern farming practices are deemed unprofitable, such as those with steep slopes and montane habitats (Aide et al. 2012; Wright 2010). More recently, recognition of the importance of tropical forests for carbon sequestration and critical ecosystem services (e.g. soil stabilization, nutrient cycling, watershed maintenance) has resulted in small increases in protected forest reserves, sustainably managed permanent forests, and the need for incorporation of sustainable goals in production landscapes (Gardner et al. 2009; Blaser et al. 2011; Dennis et al. 2008). This has been aided by a surge in market-based mechanisms that reward land-managers who manage their landscapes sustainably (e.g. Reduced Emissions from Degradation and Deforestation Plus (REDD+, Harvey et al. 2010), forest certification (Blaser et al. 2011), and Payments for Ecosystem Services, (PES, Tacconi et al. 2011)). To date these activities are far-overshadowed by the continued exploitation of forested areas, particularly in the lowlands, but recent estimates have recorded an almost doubling, over just five years (2005–2010), of the total production and protected forest estate falling under sustainable management (Blaser et al. 2011, although some of this may be attributable to improved reporting).

1-1-1 Changing conservation strategies: seeing the value of production landscapes

To fully understand the current state of biological diversity in the tropics, and to make decisions for its future management, conservation biologists have begun to alter their research focus. The traditional preservationist approach is still considered important (Gibson et al. 2012), but is certainly not effective nor representative enough to sustain the vast diversity of tropical organisms (Dirzo & Raven 2003). Throughout the tropical lowlands in particular, the majority of species exist in production landscapes: mosaics comprised of human-modified land-uses (the production matrix) interspersed with remnant old-growth and fallow secondary forests (Kennedy et al. 2010). While there is still an urgent need to protect old-growth forests from further encroachment, effective conservation of lowland species necessitates management of these production landscapes to achieve a balance between resource production and biodiversity conservation (Gardner et al. 2009). There are competing philosophies regarding the best way to attain this balance. ‘Land-sparing’ describes the partitioning of landscapes into distinct areas dedicated to high-intensity, high-yielding land-use (usually agriculture) and to biodiversity conservation (usually ‘sparing’ remnants of pre-conversion vegetation, Perfecto & Vandermeer 2010). Conversely, ‘land-sharing’ is typified by a more heterogeneous landscape incorporating multiple land-uses of lower intensity, and encourages the retention of remnants of pre-conversion vegetation wherever possible (usually smaller than their 'sparing' counterparts, Fischer et al. 2008). In reality, the choice of conservation strategy for a given landscape is often dictated by environmental factors (e.g. topography) economic circumstances, and land-ownership (Fischer et al. 2008). However, in this thesis, I refer to the strategy of balancing conservation and production outcomes as 'land-sharing' because it exemplifies the predominant situation in the tropics (Melo et al. 2013) including the multi-use landscape I studied.

1-2 How can multi-use, production landscapes conserve biodiversity?

For land-sharing conservation strategies to work, ecologists and conservation managers face key challenges: (1) to identify species that can and cannot survive in production landscape elements and establish why some species are more sensitive to land-use change than others; (2) to determine the relative habitat quality provided to species by different land-uses; (3) to determine the influence of spatial context on the occurrence of native species within multi-use heterogeneous landscapes. These fundamental challenges have been the focus of numerous studies over the past two decades. While they are far from being resolved, particularly for tropical ecosystems (Lindenmayer 2010) patterns of species occurrence in these landscapes may be broadly underpinned by the following ecological theories.

The ability of a species to colonise and exploit novel land-use types and to tolerate changing spatial availability of key resources is thought to be largely mediated by their physiological and behavioural traits (Tscharntke et al. 2012). Generally, forest species with more forest-specialised traits will have difficulty adapting and persisting in modified habitats because the modified habitats no longer meet the species' resource, microclimate and microhabitat requirements. Additionally, traits governing fecundity and life-cycle stages can influence species recovery when declines are caused by habitat loss or stochastic events (Purvis et al. 2000; Van Allen et al. 2012; Beissinger 2000). Meta-analyses and large-scale studies have described new community assemblages in modified landscapes which are disproportionately comprised of generalists, at the expense of forest specialists (Barnagaud et al. 2011; Devictor et al. 2008; T. M. Blackburn et al. 2009; Mandle & Ticktin 2013). However, determining universal 'generalist' or 'specialist' traits for taxa has proven difficult, possibly because of the influences of biogeography and evolutionary history in different regions. Biogeography and history of anthropogenic disturbance shape a given species pool (Carstensen et al. 2013) and may influence the composition of traits in biotic communities and potentially also their overall resilience to disturbance (Gray et al. 2007). Understanding how traits confer either vulnerability or advantage in a given context, and which traits can be readily adapted in the face of disturbance, would provide crucial information for conservation targeting (Lavergne et al. 2012).

Traits do not act in isolation. The environmental filter imposed by production land-use types may interact with traits to determine which species can exist in the matrix, outside old-growth remnants (Mayfield et al. 2010; Lebrija-Trejos et al. 2010). The capacity of production land-uses to provide habitat for native species (in terms of resource, microclimate and microhabitat requirements) is of direct interest to conservation-managers. For a given production type, habitat quality will be influenced by the intensity, duration, and scale of disturbance necessary for resource production and harvest. For example, more intense land-uses (e.g. agricultural crops, cattle pastures) involve clearfelling and complete conversion of forest habitat, resulting in the simplification of vegetation structure and loss of plant species diversity (Letcher & Chazdon 2009; Zurita & Bellocq 2012; Catterall et al. 2012). By contrast, less intense land-uses, which permit the retention of a degree of structural complexity and pre-disturbance vegetation cover (e.g. selectively logged forests, agroforests), may be capable of supporting a greater richness of forest biota (Gibson et al. 2012; Thiollay 1995).

In addition to the effects of disturbance associated with the establishment of a particular land-use, disturbance intensity may also change over time, altering the provision of resources available. For example, some land-uses, such as agricultural crops and pasturelands, require intense management throughout their production leaving little possibility for colonisation by native species besides ubiquitous pioneers (Danielsen et al. 2009; Zurita & Bellocq 2012). In contrast, land-uses demanding less frequent management for yield production may be more dynamic in their provision of resources. This may be particularly the case for production types which encourage tree growth (e.g. selectively-logged forests, agroforests, timber plantations), whereby habitat attributes such as basal area, canopy cover and nutrient turnover can change as they age (Brockerhoff et al. 2008; Letcher & Chazdon 2009). Therefore, an understanding of how the biodiversity value of different landscape elements changes through time and disturbance intensity must be incorporated into the development of land-sharing conservation strategies (Watson et al. 2014) (Ewers et al. 2013).

Spatial context is also likely to influence the occurrence patterns of species in tropical, multi-use landscapes (Fischer & Lindenmayer 2007). Spatial context includes the composition of landscape elements (e.g. production, secondary, remnant land-covers) and their proportional coverage over the landscape (i.e. the scale of each land-cover). These factors may affect the dispersal ability of some species as well as their capability to exploit resources and extend their populations throughout the landscape (Didham et al. 2012). Theory predicts that landscapes with a high proportion of remnant forest cover— compared to production cover—can provide important refuge for populations of more disturbance-vulnerable species as well as supplement populations of species capable of using the matrix (Chazdon, Harvey, et al. 2009a; DeClerck et al. 2010). A hospitable matrix may similarly compensate for habitat loss and fragmentation by minimising dispersal barriers and extending structural and dietary resources beyond remnants (Kennedy et al. 2010; Ewers & Didham 2006). Therefore, understanding the relative contribution that the composition of landscape elements make to the persistence of species throughout the landscape is vital in informing landscape-wide spatial management decisions (Gardner et al. 2009), for example, what is the best way to achieve sufficient spatial and temporal continuity of habitat for forest species? (Chazdon, Harvey, et al. 2009a; Lindenmayer, Franklin, et al. 2012a). However, relatively few studies of multi-use landscapes have investigated the effects of all landscape elements (encompassing the gradient of disturbance existing within a landscape) on species patterns of occurrence (Chazdon:2009wh, but see, E. Nichols et al. 2007).

1-3 Knowledge gaps in tropical multi-use production landscapes

Research into tropical, human-modified landscapes is gaining momentum but the literature still reflects a disproportionately high publication of studies in protected forests (L. J. Martin et al. 2012). Historically, these forests have attracted the greater share of research funding because they represent areas of highest biodiversity and conservation value (Ahrends et al. 2011). Practically, gaining permission for on-going conservation research on industry- or privately-owned land is also much more arduous than for unproductive or state-owned, protected land (L. J. Martin et al. 2012). As a consequence, to date the majority of studies investigating human-affected land-covers have taken place in fallow secondary forest: previously forested areas recovering from degradation (harvesting of timber and non-timber forest products) or deforestation (abandoned or restored areas recovering from clearfelling and land-conversion) (Putz & Redford 2009). In addition, access to production landscapes across the tropics may be restricted by the remoteness of some areas (e.g. oceanic islands), by political instability, and by lack of government or donor support (Amano & Sutherland 2013).

As a consequence, tropical research tends to be aggregated around hubs where access and funding are secure (Ahrends et al. 2011). These hubs occur predominantly in primary and secondary forest monitoring sites in the continental Neotropics (tropical areas of North, Central and South America): La Selva, Costa Rica; Los Tuxtlas, Mexico; Barro Colorado Island, Panama; and Manaus and Jari in the Brazilian Amazon (L. J. Martin et al. 2012; Gardner et al. 2010). While studies of these ecosystems have contributed to our understanding of primary forest dynamics, habitat fragmentation, edge effects, forest restoration and matrix ecology, they are not representative of the variety of production landscapes that exist throughout the tropics in terms of land-use types, spatial contexts or their biogeographic species pools. For example, the rate of forest replacement by oil palm and timber plantations in southeast Asia is proportionally far greater than any other tropical region (Miettinen et al. 2012), and yet comparatively few studies have investigated the impacts of these two land-uses on biodiversity (Stephens & Wagner 2007; Danielsen et al. 2009).

This aggregation of research also means that much of the theory underlying conservation management decisions pan-tropically is necessarily extrapolated from a subset of un-representative studies. Clearly, standard 'rules' apply across the board for biodiversity conservation, such as the need to retain old-growth forest remnants. However, in land-sharing conservation scenarios, management decisions are complicated by the need to trade-off management options in order to balance the dual outcomes of resource yield and biodiversity conservation. Without clear, contextual evidence to inform management, there is a danger in either over- or under-stating the required conservation management actions. In the case of under-statement the result could lead to population or biodiversity declines, whereas over-statement will likely present unobtainable options with respect to yield targets, and may lead to a rejection of conservation management altogether. To comprehensively assess biological diversity patterns in tropical production landscapes, the relative influence of contextual factors needs to be more fully explored. From a research perspective there still remains a need to investigate the responses of taxa to human modification in poorly studied tropical regions, to evaluate the support provided to biota by all major types of land-use and under different management scenarios. Moreover, a landscape-wide approach that incorporates the influence of component landscape elements on the persistence and dispersal of taxa is required to comprehensively assess the biodiversity value of a given human-modified landscape and to inform land-sharing conservation management strategies (Chazdon, Harvey, et al. 2009a; Stephens & Wagner 2007).

1-4 The context of the study

1-4-1 Assessment of a multi-use native timber (*Eucalyptus deglupta*) plantation landscape on New Britain Island, Papua New Guinea

In this thesis I assess the biodiversity conservation value of a native *Eucalyptus deglupta* plantation landscape on New Britain Island, a province of Papua New Guinea (PNG). Specifically, I quantify and explain the processes affecting the occurrence patterns of forest vegetation and bird species among the landscape's main elements: a mixture of forestry-production landscape elements (plantations and selectively-logged forest) and intervening, old-growth remnant forest, representing land-uses of different timing and degree of modification. In assessing biodiversity value, it is important, but not always practical, to include a range of faunal taxa alongside vegetation to appropriately inform conservation management decisions (Lawton et al. 1998). As this was a PhD study, field data collection was constrained by limited funding and time and working in a tropical, developing country added considerable logistical challenges. Therefore, birds were chosen as the single faunal indicator because they occur at a suitable scale for landscape research, they play an important role in shaping forest plant community dynamics (Neilan et al. 2006), and they are the most well-studied, conspicuous and diverse vertebrates of New Britain's forests (Mayr & Diamond 2001). These attributes meant that comprehensive data collection was feasible, patterns of bird occurrence could provide useful information about landscape ecology, and conclusions could be drawn from and referenced to a large body literature.

Papua New Guinea is located in the Pacific Ocean north of Australia and east of the Moluccas, and as such it lies within the Oceanic and Asia-Pacific regions. The nation is comprised of the eastern half of the island of New Guinea and a series of archipelagos, the largest of which is the Bismarck Archipelago. Papua New Guinea is one of the few tropical countries with extensive rainforest cover, comprising 61% of its land area (Shearman et al. 2008). These forests have very high levels of endemism, which has led to PNG's classification as one of the world's three most significant tropical wilderness areas (Myers et al. 2000), and its inclusion in a high-priority Endemic Bird Area (Stattersfield et al. 2005). Unfortunately, less than 2% of the country's forests are formally protected and logging rates have increased in PNG over the past two decades because of dwindling forest stocks in southeast Asia (Shearman et al. 2010; Woinarski 2010; Wright 2010). The consequences for PNG's unique avifauna have rarely been formally assessed, and PNG remains the nation with the highest number of data deficient bird species in the tropics (Sodhi, Sekercioglu, Barlow & Robinson 2011b; Butchart & Bird 2010).

New Britain Island, the largest island of the Bismarck Archipelago, has one of the highest rates of logging and land conversion in the world (Woinarski 2010). Between 1972–2002, 47% of New Britain's lowland rainforests were deforested or degraded (Shearman & Bryan 2011), driven by population growth (increase in subsistence agriculture), logging, and conversion of logged-forest to oil palm (*Elaeis guineensis*) plantations (Shearman et al. 2009). Oil palm plantations are extensive on New Britain, with 17% of the lowland forest of West New Britain Province (WNB) now converted to this land-cover, representing >80% of the country's oil palm industry (Nelson et al. 2010). The few studies investigating the biodiversity value of oil palm concur that these plantations provide very little habitat for most forest taxa, even when ‘wildlife-friendly’ management is attempted (Danielsen et al. 2009; Fitzherbert et al. 2008). There are plans to further expand this high-revenue crop into East New Britain and the PNG mainland, with applications submitted for over one million hectares of ‘special agricultural and business leases’ on tropical rainforest (Nelson et al. 2010). These leases are predicted to cause significant encroachment into PNG’s remaining old-growth lowland forest, enhancing forest loss and fragmentation with adverse consequences for the persistence of many unique species (Shearman & Bryan 2011). On New Britain, the combination of these pressures has led to the listing of 21 of its bird species/subspecies as threatened or near-threatened (Buchanan et al. 2008).

1-4-1-1 Native timber plantations – a potential solution?

Tropical timber plantations are increasing worldwide (Carnus, Parrotta, et al. 2006b), and have been embraced as an alternative timber source in regions where natural stocks are depleted yet demand is increasing in areas such as southeast Asia and Brazil (Paquette & Messier 2010; Carnus, Parrotta, et al. 2006b; Brockerhoff et al. 2013). Under these circumstances plantations may reduce logging encroachment into old-growth remnant forests in the short-term, although it is contentious whether this would be maintained in the long-term (Shearman et al. 2012). Recent global forestry reports have noted a trend emerging among plantation proprietors towards more sustainable forestry management to enhance productivity and be eligible for fiscal rewards through schemes such as certification and future REDD+ funds (Blaser et al. 2011; Davis et al. 2012; Dennis et al. 2008). However, studies investigating the impacts of timber plantations on biodiversity have only taken place in a handful of locations across the tropics, which have formed the basis of knowledge from which global guidelines have been extrapolated (Nájera & Simonetti 2010; Stephens & Wagner 2007). There is, therefore, a critical need for further research into the potential ecological benefits and limitations of timber plantation landscapes for local biota in order to provide management guidelines with clear, evidence-based biodiversity conservation priorities (Wairiu 2004).

The potential ecological value of timber plantations largely lies in the continuity of tree cover they provide, especially on abandoned or degraded land (Lamb, 2010; Paquette & Messier 2010). For example, plantation cover can reduce soil erosion and water evaporation, contribute to soil nutrient turnover, and influence understorey microclimatic conditions to facilitate successional progression of native rainforest vegetation (in concert with suitable stand-level management, Putz 2011; Günter et al. 2011; Carnus, Parrotta, et al. 2006b). Thus, timber plantations may offer suitable habitat for a greater diversity of native biota compared to alternative land-uses such as low annual crops, which provide fewer structural resources (Zurita & Bellocq 2012; Peh et al. 2005; Brockerhoff et al. 2008). Beyond their role as habitat, plantations may also play a role in landscape connectivity for vagile species resistant to crossing more open spaces (Carnus, Parrotta, et al. 2006b; Lamb et al. 1997, although this would depend on sympathetic spatial management). The consequences of such connectivity would be particularly important for seed-dispersers (e.g. birds) because of their role in distributing rainforest plant species (C. Moran et al. 2009).

The extent to which plantations can realise these ecological functions will be influenced by the environmental context and the objectives of land managers (Pawson et al. 2013; Paquette & Messier 2010). Specifically, the choice of plantation timber species is emerging as an important factor for biodiversity conservation. Theory predicts that native timber plantations should support a greater biodiversity of native species than exotic plantations because of their shared evolutionary history with local biota, with some studies offering support for this hypothesis (Haggar et al. 1997; Farwig et al. 2008; Volpato et al. 2010). In addition, incorporating the use of native species may avoid the potentially damaging effects of exotic plantation trees invading neighbouring remnant forest (e.g. Acacia species in southeast Asia, Osunkoya et al. 2005). As a result, research into the viability of native trees for use in plantations has increased (e.g., Montagnini & Piotto 2011; J. D. Nichols & Vanclay 2012), in line with the changing perspective of the role of production landscapes for biodiversity conservation (as summarised in, Davis et al. 2012). However, the impacts of native plantations on tropical lowland biodiversity remain understudied (Stephens & Wagner 2007).

1-5 Aims of the study

The purpose of this thesis is to assess the biodiversity conservation of forest species in a 40 year-old native *Eucalyptus deglupta* timber plantation landscape, given current management practices, and to use this information to inform management guidelines to enhance future conservation of species with little impact on timber yield. There are three reasons for doing this. Firstly, timber plantations are expanding in southeast Asia and Oceania (Paquette & Messier 2010; Blaser et al. 2011) and yet relatively few studies have investigated their impact on local biota (Stephens & Wagner 2007; Nájera & Simonetti 2010). For example, in PNG I could find only one published study on a timber plantation (*Tectonia grandis*), which was conducted over just three weeks more than 30 years ago (Bell 1979). Secondly, New Britain's provincial government and industry agents have mounted a sustained campaign to replace these *E. deglupta* plantations with oil palm despite opposition from local landowners and the timber company. In a bid to make the plantations more economically and politically competitive with oil palm, the company sought to gain certification status. Therefore, baseline information on the patterns of biological diversity existing within the landscape was required to determine their conservation value and to inform conservation management. Thirdly, national Forestry Stewardship Council (FSC) certification guidelines for PNG are still in the draft stage and to date there is no empirical evidence informing management priorities specifically for native timber plantations.

Thus, the aims of this study were:

(1) To assess the biodiversity conservation value of a native plantation timber production landscape;
(2) To provide evidence-based management recommendations for biodiversity conservation for this production landscape, and for timber plantation landscapes more generally.

In order to achieve these aims, my study had three objectives (outlined in Figure 1.1):

Objective 1: to identify species of forest trees and forest-using birds that can and cannot persist in production land-uses and how occurrence patterns are mediated by species' traits (Chapters 3 & 4). The *E. deglupta* plantation landscape was comprised of five main management types (landscape elements): young plantations, mature plantations, secondary riparian buffers, secondary remnant forest, and unlogged forest (detailed in Chapter 2, sections 2-1-1 and 2-1-2). Identifying which species can and cannot survive in production land-uses provides crucial information for conservation targeting. Understanding what may be driving species' differential survival can assist in informing the extent and type of conservation action required (e.g. setting monitoring targets for adaptive management, design of buffer areas, retention forestry). I analysed the community composition of two indicator taxa: (i) tree (Chapter 3) and bird (Chapter 4) species that occurred in old-growth forests, among the main landscape elements to determine the effect of land-use on species occurrence. I further investigated whether relative occurrence patterns among elements could be explained by species traits (and successional status for tree species). Finally, I discussed what these patterns may reveal about the mechanisms underlying trait-disturbance interactions.

Objective 2: to assess the effect of land-use on vegetation and stand-level structural attributes (habitat properties) (Chapter 5). To assess the capacity of a production landscape to conserve biodiversity it is important to understand the effects of land-use on the condition of vegetation structure and plant species composition (i.e. habitat quality). I first described, quantified and compared attributes of vegetation structure and species richness and composition among the five landscape elements (Chapter 5). I then selected a subset of these attributes that may be important for forest birds in terms of structural/food resources, microclimate and microhabitat requirements. In Chapter 6, these were used as predictor variables of forest bird species richness.

Objective 3: to investigate the relative influence of habitat attributes and spatial context on forest bird species occurrence (Chapter 6). Forest bird species richness at a site will be influenced by the habitat quality of the site as well as a species' ability to access it. Understanding the relative influence on species occurrence patterns of (i) site-level resource provision and (ii) the provision of preferred habitat within the wider landscape provides vital information for the spatial and temporal management of the landscape. I used an information theoretic approach to simultaneously compare the influence of (i) site-level habitat attributes and (ii) the proportion of unlogged and old-growth secondary remnant forest within a 2 km buffer, on the richness of forest-occurring and forest-specialist birds.

Objective 4: to provide suggestions for stand-level and landscape-wide management consistent with balancing conservation and yield outcomes (Chapter 7). Biodiversity conservation in production landscapes involves a trade-off between yield production and provision of habitat for native species. While general principles can be extrapolated from the literature, there are many contextual influences that can either assist or hamper efforts to achieve a level of balance between conservation and production. The results of my data chapters (Chapters 3–6) provide empirical and contextual data that inform my recommendations for stand-level and landscape-wide management aimed at achieving conservation objectives for birds and vegetation with minimal impact on yield (Chapter 7). Furthermore I suggest incentives and frameworks which can assist the application of these guidelines in other tropical forests.

1-6 Thesis structure and outline

I have written this thesis with the intention of publishing all of the data-related chapters. As a consequence, these chapters have been written as self-contained publications, resulting in some necessary overlap between them (e.g. study design, site selection, data collection). Therefore, in addition to a general introductory chapter (Chapter 1) I have included a general methods chapter (Chapter 2) in order to avoid repetition in subsequent chapters that may impede the narrative (Figure 1.1). Similarly, in-keeping with the University's thesis protocol, I have removed the manuscript abstracts from these chapters and replaced them with brief summaries at the start of each chapter, outlining the purpose of the chapter and placing it within the thesis framework. I have also provided summaries of key findings at the end of each chapter to likewise assist readability. My four data chapters (Chapters 3–6) follow the general introduction and methods chapters, and address objectives 1–3 of the thesis. The final general discussion chapter (Chapter 7) summarises and interprets the results of the thesis and addresses objective 4.

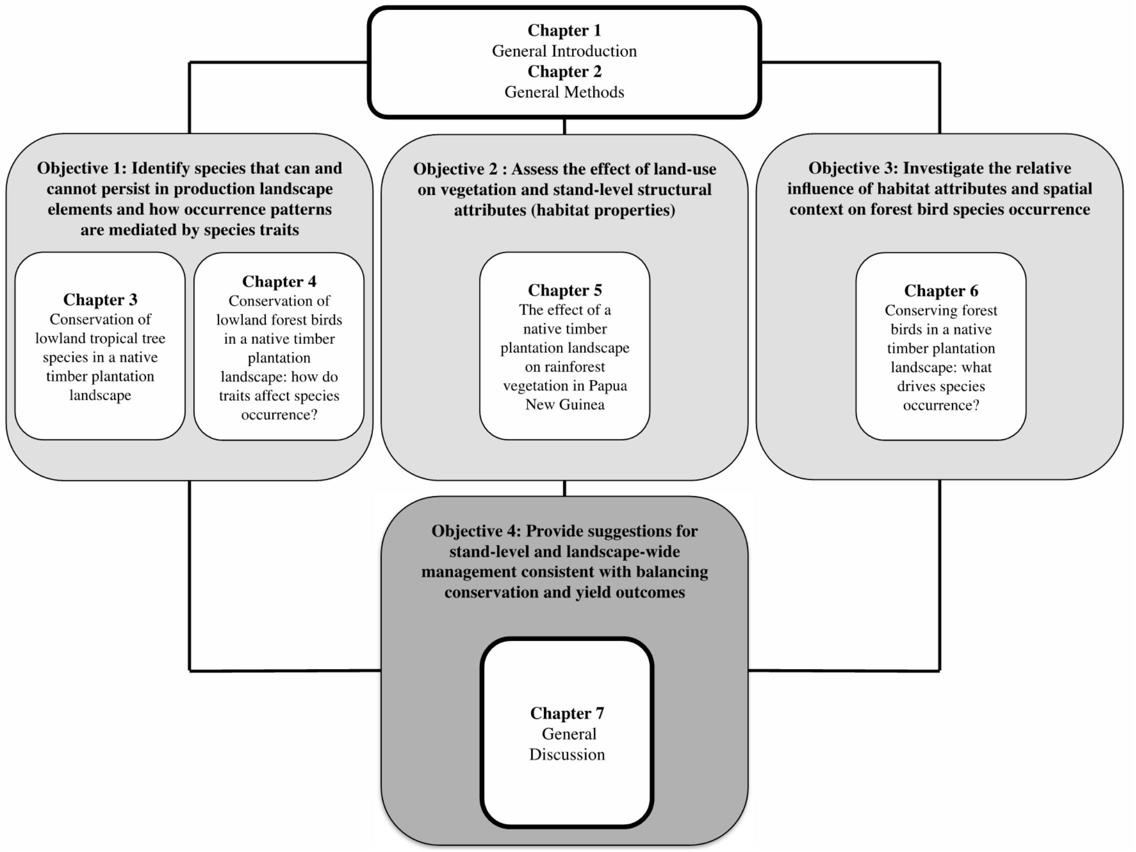

Figure 1.1 The thesis structure.

Chapter 1 – General Introduction. In this chapter I provide a general introduction to the state of tropical forests worldwide and discuss how this has precipitated a change in conservation strategy from its traditional preservationist approach, to one that recognises the importance of including land-sharing strategies. I briefly explain the main ecological theories underpinning assessment of multi-use production landscapes where land-sharing strategies are considered, and highlight areas where further research is needed. Finally, I introduce the study, its ecological and political context and my aims and objectives.

Chapter 2 – General Methods. The purpose of this chapter is to provide site context and methodological information that is common to all data chapters and whose repetition would impede readability of the thesis. Thus, I present detailed information about the study area and survey design. Specifically, I explain my approach of surveying biota in the five main landscape elements comprising the native timber landscape in order to capture the effect of land-use heterogeneity on the occurrence of biota, which is a common feature of multi-use production systems that is rarely surveyed. The landscape elements represent land-uses of different timing and degree of modification (from most to least modified at the time of the study): young plantations, mature plantations, secondary riparian forest, secondary remnant forest and unlogged forest. I also explain some of the limitations of the survey design arising from logistical constraints, and describe the statistical approaches I took to account for them. Finally, I explain the new method of multivariate analysis conducted in Chapters 3 and 4 (multivariate generalised linear models) and justify its application to this study.

Chapter 3 – Conservation of lowland tropical tree species in a native timber plantation landscape. In this Chapter I identify the differences in tree species composition among landscape elements to assess the capacity of native timber plantations and secondary (logged) forest elements to support tree species otherwise restricted to old-growth, remnant forest. I also seek to explain the ecological mechanisms involved in community assembly among landscape elements by determining (1) the relative importance of the successional stage of trees on their occurrence and (2) the effects of tree species' mode of dispersal on their establishment in modified elements. Finally, I suggest management protocols aimed at maintaining populations of trees that are most vulnerable to anthropogenic disturbance.

Publication

Pryde, EC, Watson, SJ, Holland, GJ, Turton, SM, Nimmo DG (*in press*) Conservation of tropical forest tree species in a native timber plantation landscape. *Forest Ecology and Management.*

Chapter 4 – Conservation of lowland forest birds in a native timber plantation landscape: how do traits affect species occurrence? In this Chapter I investigate the relative importance of different land-uses for supporting lowland forest bird species in the *E. deglupta* plantation landscape by comparing the composition of forest-occurring bird species among landscape elements. I then explore the interaction between species traits and disturbance response and assess whether trait inferences hold between different biogeographic regions. Finally, I use my results to discuss the potential of production forestry to be effectively integrated into land-sharing-based conservation strategies in the region, which faces extreme pressure from logging and land conversion.

Publication

Pryde, EC, Nimmo DG, Holland, GJ, Watson, SJ (*in review*) Conservation of lowland forest birds in a native timber plantation landscape: how do traits affect species occurrence? *Biological Conservation.*

Report

Pryde, EC (2009) Does the landscape matrix of native *Eucalyptus deglupta* plantations, logged-over and primary rainforest on the Gazelle Peninsula, Papua New Guinea, provide sustainable habitat for local wildlife? A report to the Australia Pacific Science Foundation, APSF 07/5.
http://apscience.org.au/projects/APSF_07_5/apsf_07_5.html

Chapter 5 – Vegetation in a mixed tropical forest production landscape. Maintaining temporal and spatial continuity of pre-conversion habitat characteristics throughout production landscapes is of great importance for the conservation of both flora and fauna (Lindenmayer, Franklin, et al. 2012a). In this chapter I compare attributes of unlogged forest and human-modified landscape elements for two components of biodiversity: vegetation structure (tree attributes, ground cover), and the composition of adult tree species and rainforest plant life forms. Key goals are (1) to ascertain which vegetation attributes most clearly differentiate unlogged (old-growth) forest from modified landscape elements; (2) to determine the extent of retention of old-growth forest attributes in modified elements. I also assess which of these variables best represent habitat conditions that could influence bird species' occurrence. These variables are then used as candidate environmental predictors for modelling bird species occurrence across the plantation landscape (Chapter 6).

Publication

Pryde, EC (*in prep*) The effect of a native timber plantation landscape on rainforest vegetation in Papua New Guinea. *Journal of Tropical Forest Science.*

Chapter 6 – Conserving forest birds in a plantation landscape: what drives species occurrence? In this chapter I use an information theoretic approach to determine the relative influence of site-level habitat attributes (Chapter 5) and landscape composition on the richness of (1) forest-occurring and (2) forest-specialist birds across the plantation landscape. I then establish the comparative support provided by different landscape elements and speculate how this may be affected by age or management practices. Finally, I discuss the implications of these results for conservation management of this landscape.

Publication

Pryde, EC, Watson, SJ, Nimmo DG, Moloney, JM, Holland, GJ (*in prep*) Conserving forest birds in a native timber plantation landscape: what drives species occurrence? *Biotropica.*

Chapter 7 – General Discussion. In this chapter I synthesise the findings of my four data chapters (Chapters 3–6), integrating the trait-based results with those of environmental predictors. I summarise the outcomes of the thesis and discuss my recommendations for stand-level and landscape-wide management that are required to achieve conservation outcomes for vegetation and birds, while impacting minimally on timber yields. I also attempt to align management recommendations with broad national FSC draft guidelines, to demonstrate the potential assistance such frameworks can provide for management adoption, and to highlight areas where empirical evidence is important to improve current guidelines. I then highlight areas of future research that would improve our understanding of the ecology and conservation management of multi-use production landscapes.

Report

Pryde, EC (2014) Recommendations for sustainable management of the Open Bay Timber *Eucalyptus deglupta* plantation landscape: A Report to Open Bay Timber Company.

CHAPTER 2

General Methods

Our spectacular rainforest 'shower' at an unlogged forest camp-site

GENERAL METHODS

This chapter serves three purposes. Firstly, to enhance readability of the thesis by covering the repeated methods applicable to all data chapters (Chapters 3–6). These include information about the study area, study design and data collection. Secondly, to explain the novel, model-based multivariate analysis method used in Chapters 3 and 4 in more detail. Including this detail in the text of the data chapters would have interrupted their legibility and narrative flow. Thirdly, to explain analytical approaches taken to overcome common issues with ecological data and to identify the potential consequences of limitations arising from the study design.

2-1 Methods

2-1-1 Study area

The study was located within the Open Bay Timber (OBT) operation area on the western coastline of the Gazelle Peninsula, East New Britain, a province of Papua New Guinea (PNG) (Figure 2.1). New Britain Island was formed from volcanic activity and subsequent sedimentation between the Late Eocene and Early Miocene (Madsen & I. D. Lindley 1994). The geology of the Gazelle Peninsula has been shaped by subsequent volcanic events through its central region, and via vast coral uprisings along the coast (D. Lindley 1988). The main vegetation type at Open Bay is tropical wet rainforest. The mean annual rainfall varies from 2000–3500 mm across the region, with a noticeably wetter period between December and March (McAlpine et al. 1983). New Britain Island is rich in faunal endemism because of its evolutionary isolation (Mayr & Diamond 2001), forming part of a high priority Endemic Bird Area (Stattersfield et al. 2005), and along with mainland PNG, is considered one of the world's most significant tropical wilderness areas (Myers et al. 2000).

New Britain has one of the longest recorded histories of anthropogenic colonisation (~35,000 years) and modification of its forests through clearing, harvesting and cultivation of food and medicinal plants (Lentfer, 2010). Recent research estimates that shifting cultivation has occurred on the island since the early–mid Holocene (Lentfer, 2010). No archaeology has been conducted on the Gazelle Peninsula. However, it is likely that these forests have been exposed to thousands of years of similar modification and land-use. Around 400 hundred years ago more intensive slash-and-burn agriculture was employed in PNG, involving clearing of large patches of forest for crop establishment which were left fallow after harvest for periods of varying length (Lentfer 2010; Allen et al. 1995; Hope et al. 1983). Today at Open Bay, four of the six local clan groups (customary land-owners of surrounding forest area) rely on this type of agriculture, with the other groups practicing the more ancient nomadic shifting agriculture, which is less intensive, but which occurs more broadly across the landscape (lowlands to highlands) (Lentfer 2010*;* Allen et al. 1995; *pers obs*). Therefore, it is not possible to consider any of the lowland forest on New Britain to be ‘undisturbed’ by either anthropogenic modification or by large-scale natural disturbances such as regular volcanic events (Lentfer, 2010; Steadman 2006; Boyd et al. 2005; Mueller-Dombois and Fosberg 1998). As such, throughout the thesis I use the term ‘old-growth’ instead of ‘primary’ forest to indicate those forests which have acquired structural and functional characteristics over a long period without large-scale anthropogenic or natural disturbance (sensu Clark, 1996). It is important to recognise that the long history of regular disturbances in these forests (along with forests of most other tropical regions) may have lasting effects on the composition and survival of vegetation and faunal communities in ‘old-growth’ forests (Clark, 2007).

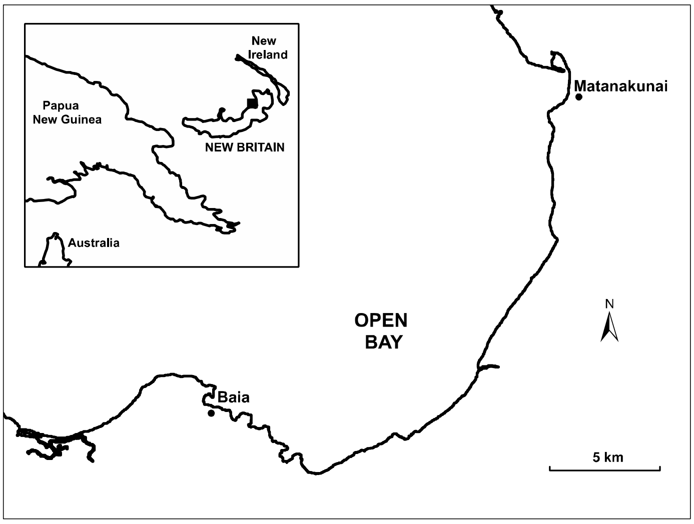

Figure 2.1 The study location on New Britain Island, a province of Papua New Guinea

Open Bay Timber is one of only two plantation enterprise in PNG cultivating locally native tree species. The focal species, *Eucalyptus deglupta,* is native to Indonesia, Timor-Leste, PNG and the Philippines (Ladiges et al. 2003). It is a fast-growing, light-demanding, wind- and water-dispersed species that forms dense, pure stands on river flats and after disturbances such as landslips and volcanic activity (Paijmans 1973). Before logging activity at Open Bay (~1950), *E. deglupta* stands occurred naturally on river flats, and in disturbed patches of lowland forest embedded within late-successional mixed alluvium forest of floristically and structurally complex vegetation (Paijmans 1976).

Eucalyptus deglupta plantations were first established in the 1980s through conversion of selectively-logged secondary forest, between elevations of 10–350 m above mean sea level. Plantation management includes clear-fell harvesting, after which remnant logs are left to decompose and fire often used to clear weeds and vegetative waste prior to seedling planting. *Eucalyptus deglupta* seed stock is sorced locally on the island, with seeds progressively selected from individual plants with highest yield and best form (OBT Management, *pers comm*.). Seedlings are propagated in polythene tube bags at the Open Bay nursery. When more than two pairs of leaves grow above the cotyledons, the seedlings are planted (Srivastava, 1993). Seedlings are planted at an average density between 313 trees/ha (spacing 4 m x 8 m) and 625 trees/ha (spacing 4 m x 4 m). The timber company has taken the unusual step of encouraging local residents to grow food crops among the planted *Eucalyptus* seedlings (e.g. tubers *Dioscorea* spp. and *Ipomoea batatas*, corms such as taro *Colocasia esculenta*, peanuts (*Arachis hypogaea), Musa* spp, *Ananas* spp., and paw-paw (*Asimina* spp.) among others). While typically involving the use of fire, this traditional agricultural practice also produces benefits, such as enhancing soil fertility, reducing the need for chemical inputs, and lessening soil compaction (The Review Team 2005). Manual weed tending occurs from six months-to-three years, and vine cutting from three-to-six years. There is no tree thinning. Plantations are harvested at 15–17 years and *Eucalyptus* timber products (average >80,000 m^3 of sawn logs annually) are exported predominantly to Vietnam for use in construction and furniture (veneer) (The Review Team 2005).

At the time of the study *E. deglupta* plantations covered ~14,900 ha (12,000 ha planted area, and ~2,900 ha of roads, rivers and tributaries, and temporary employee housing). Therefore, while native to New Britain's lowland region, the plantations extend this species beyond the disturbed sites where it naturally colonises. Plantations were organised into management blocks of broadly different ages (young, intermediate, mature) which were separated into evenly aged compartments. Within a given block, compartments could differ by up to four years in age. The plantation landscape included an area of ~36,400 ha of which ~13% was young plantations (2–6 years), ~4% was intermediate-aged plantations (7–12 years), and ~23% mature plantations (13–15 years), interspersed with secondary forest (selectively-logged before 1992) and unlogged forest (~33% and 26% of the plantation landscape respectively, Figure 2.2).

The broader landscape constituting the timber company's production forest was comprised of a further ~18,000 ha of unlogged forest and ~24,000 ha of secondary forest (selectively-logged before 1998). Riparian buffer zones of a minimum width ~50 m either side of water bodies, occur around the two main river systems and their permanent tributaries (the Sai and Toriu Rivers) their permanent tributaries and are embedded within the plantation matrix (we did not have access to high enough resolution data to estimate their coverage in the landscape). Most riparian buffers experienced a degree of selective logging before the 1980s, and accessible edges are still subject to timber extraction and path-cutting by local residents. Within the operation's bounds a logged-over forest remnant of 382 ha was formally designated a watershed conservation area in 1991.

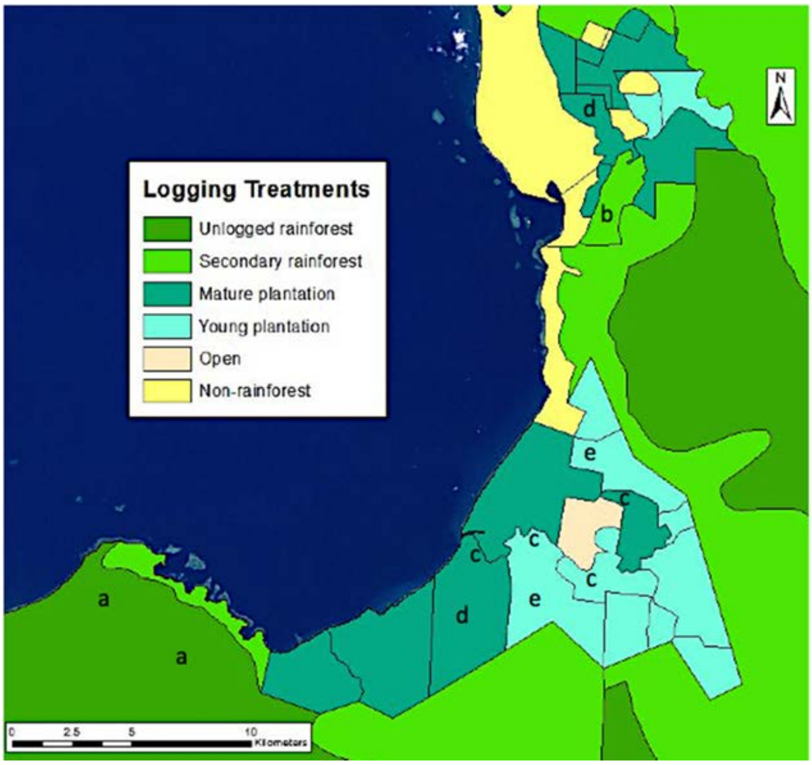

Figure 2.2 The configuration of landscape elements within the multi-use plantation landscape. Broad survey areas are marked with letters corresponding to landscape element type shown in Figure 2.3: (a) unlogged forest; (b) secondary remnant forest; (c) secondary riparian buffer; (d) mature plantations; and (e) young plantations.

2-1-2 Study design

I classified vegetation as one of five elements, reflecting the main management stages and representing land-uses of different timing and degree of modification (from most to least modified at the time of the study): (1) young plantations, 2–6 years after planting; (2) mature plantations, 13–15 years after planting; (3) secondary riparian forest ~20 years since selective logging (plus ongoing ad-hoc timber extraction by local residents); (4) secondary remnant forest (conservation area), 16–25 years since selective logging; and (5) unlogged lowland forest (Figure 2.3).

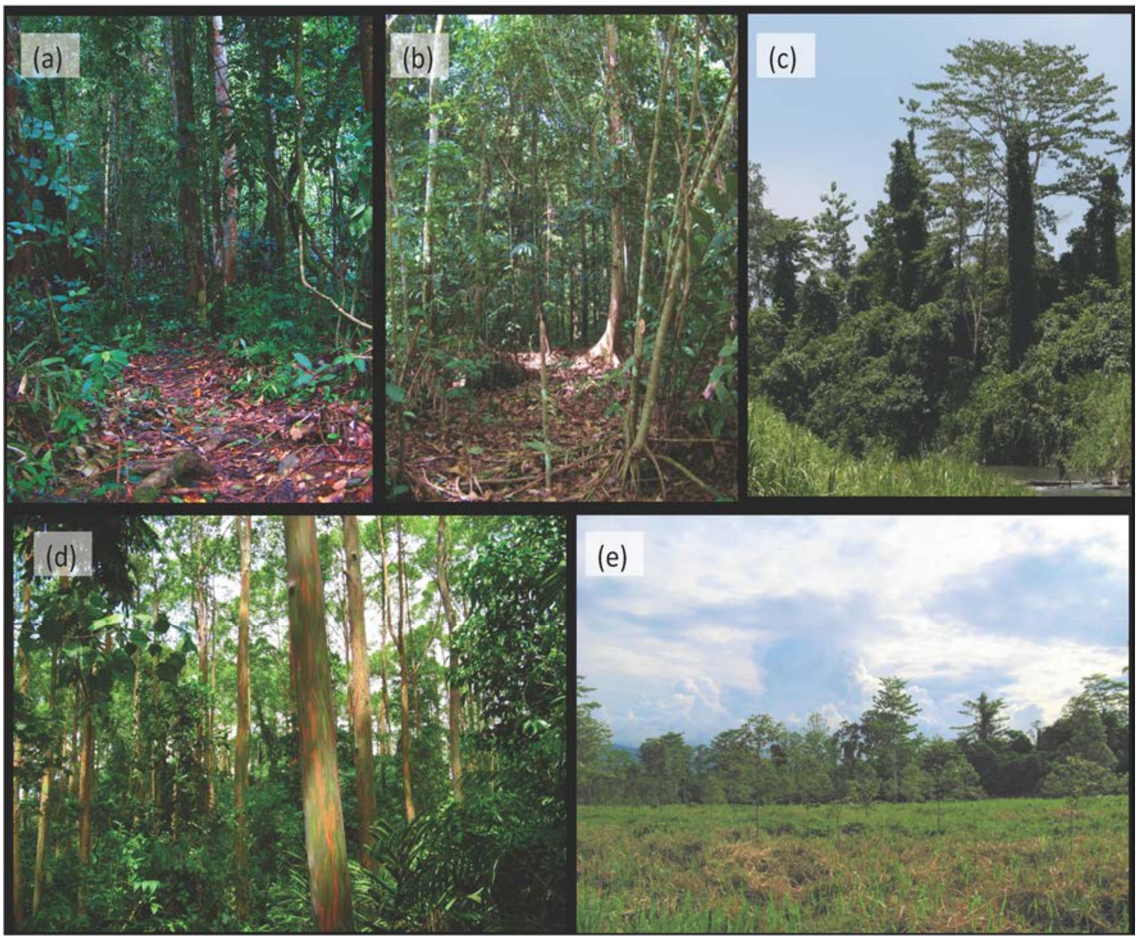

Figure 2.3 The main landscape elements comprising the Open Bay Timber *Eucalyptus deglupta* plantation operation: (a) unlogged forest; (b) secondary remnant forest conservation area; (c) secondary riparian forest buffer; (d) mature plantation, ~14 years old; and (e) young plantation, ~3 years old.

2-1-2-1 Site selection

I used Open Bay Timber Company logging maps to select survey areas that had the highest interior-to-edge ratios of even-aged vegetation to control for contextual noise and edge effects (riparian buffer areas were necessarily linear and thus characterised by edges). Survey areas occurred below 400 m a.s.l. to avoid variation associated with elevation gradients (Paijmans, 1976). Survey areas within a particular forest element were spread across the geographical extent of the element to ensure sampling across the variation in topography and soil type manifest in the region. Plantations, unlogged forest, and the secondary riparian element occurred in discrete patches across a large, accessible region within the landscape (Figure 2.2). This allowed me to sample elements which were interspersed amongst other land use types, thus reducing the potential influence of spatial clustering driving results. However, this was not the case for secondary remnant forest.

Significant logistical constraints existed throughout the study area such as restricted access, extreme topography and geological barriers (e.g. waterfalls), which made random sampling of the landscape impossible. Therefore, I established point transects in each landscape element, locating survey sites perpendicular to transects (Buckland, 2006; Marsden, 2003b). Transects were between 1.2–2.4 km in length (depending on logistical constraints) and were separated by a minimum distance of 1km within each landscape element. The number and length of transects was proportional to element area (young plantations – 3, mature plantations – 6, secondary riparian – 3, secondary remnant – 2, unlogged forest – 5). Along these transects I established a total of 156 survey sites, however not all were used in all analysis (see Table 2.1 for details). For all elements, sites were positioned ≥200 m apart from one another to enhance independence. In northern mature plantations and unlogged forest, I cut 3-m-wide, 1.2 km transects using machetes, positioning survey sites 100 m perpendicular to each transect and 200 m apart. For other landscape elements, transects were located along logging roads. Survey sites were positioned at least 150 m from any roads to reduce potentially confounding edge effects (Ries et al. 2004). The secondary riparian element was embedded within the plantations, and sites were located between the Sai River and the main logging road. The logging road was much closer to the river in some areas compared to others resulting in strips narrower than 150 m. For these sites, I surveyed the midpoint between road and river.

Table 2.1 Numbers of survey sites used in analyses for each Chapter.

Chapter	Data analysed	Number of sites	Reasons for exclusion
3	Trees ≥10 cm DBH	142 Young plantations – 20 Mature Plantations – 50 Secondary remnant – 10 Secondary riparian – 14 Unlogged forest – 48	Four of the young plantation sites contained no trees > 10cm DBH and thus could not be analysed. Ten sites in the mature plantation element were found to be outliers because they either contained experimental stands of mixed-species plots, or because of large, recent tree-fall events.
4	Bird species occurrence	122 Young plantations – 24 Mature Plantations – 43 Secondary remnant – 9 Secondary riparian – 14 Unlogged forest – 32	Ten sites in the mature plantation element were found to be outliers because they either contained experimental stands of mixed-species plots, or because of large, recent tree-fall events. Three of the mature plantation sites were logged between the first and second field season. Four mature plantation sites, one secondary remnant site and ten of the unlogged forest sites were also found to be < 250 m apart by GIS mapping because topography obscured true distance on the ground. This was considered too close for independence of bird surveys. A further six of the unlogged forest sites were compromised in the second survey season because of tree-

Chapter	Data analysed	Number of sites	Reasons for exclusion
			fall events or human modification of sites that occurred in the interim.
5	Vegetation attributes	142 Young plantations – 20 Mature Plantations – 50 Secondary remnant – 10 Secondary riparian – 14 Unlogged forest – 48	The total number of sites is the same as for tree species surveys, however, special life form and/or vertical stratification data was missing for 9 sites (6 of the mature plantation sites through error, and 4 of the young plantation sites which contained no trees).
6	Bird and vegetation data	107 Young plantations – 17 Mature Plantations – 37 Secondary remnant – 9 Secondary riparian – 14 Unlogged forest – 30	Of the 122 bird survey sites, 107 contained all vegetation and GIS data (GIS data points were missing for 2 unlogged forest sites and 3 young plantation sites).

2-1-3 Data collection

I collected both vegetation and bird data throughout the *E. deglupta* plantation landscape. Data were collected over two, five-month periods (from July–November, 2007–2008), in what is considered the ‘drier’ season for the Gazelle Peninsula. It was impossible to collect data outside of these months because of the heavy rainfall which produces sub-optimal conditions for bird surveys, washes away access roads, and creates an unsafe environment in unlogged rainforest camps. Sample plots were jointly used for vegetation and bird surveys, with a single plot per site. Circular plots of 0.79 ha (50 m radius) were used for bird surveys and included nested square subplots of 0.18 ha for vegetation surveys (Figure 2.4). The latter are outlined in detail in Chapter 5 (section 5-2-1).

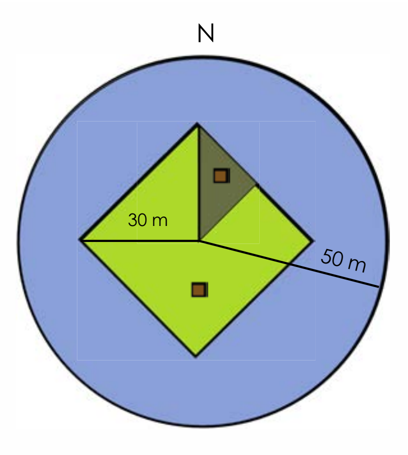

Figure 2.4 Plot design for surveys of vegetation and birds. Blue circle delineates the bird survey plot. Green square represents the ~1800 m^2 vegetation survey plot. Brown squares approximate the location of $1m^2$ ground survey plots. Details of specific vegetation surveys are in Chapters 3, 5 & 6. This configuration complemented bird surveys and was the most efficient and accurate design for the often very dense and uneven forest conditions.

Bird surveys are briefly explained in Chapters 4 and 6 to maintain the flow of the narrative; therefore, a more detailed account is provided here. I restricted surveys to lowland forest species (excluding grassland, coastal, and waterfowl species) because I aimed to observe disturbance impacts on birds that use forest habitat rather than to record responses of non-forest and disturbed-habitat specialists (e.g. grassland birds, Peh et al. 2006). Forest species were defined by their occurrence in lowland forested habitats on New Britain (Coates & Peckover 2001; Mayr & Diamond 2001). Non-breeding and seasonal migrants were excluded because I only surveyed in the dry season, and nocturnal species were excluded because my surveys were not designed to adequately survey them.

At each site I recorded forest birds using circular point-counts recording all birds seen or heard within 50 m of the observer over a 20 min period. I surveyed all sites in both survey years and was accompanied by a single volunteer who acted as scribe. Line transects were considered inappropriate because walking through rainforest disturbed local avifauna and would bias survey outcomes. Mist-netting was avoided because of its limited ability to survey birds above the understorey and because nets can cause social and environmental conflict in these forests (Barlow, Gardner, et al. 2007a). Point counts followed Marsden (2003b) with adjustments to suit logistical limitations and knowledge gaps. Counts lasted 20 minutes because of the density of vegetation and reliance on aural cues (Stouffer et al. 2011). I employed a distance sampling method (Buckland ST et al. 2004), using distance categories (0–10 m, 10–20 m, 20–30 m, 30–50 m) instead of actual distance to individual because despite using a laser range finder (Opti-logic Laser Rangefinder–600 yd), accurate determination of perpendicular distance to each individual (within 5 m) was impossible in forest habitats. I did not record birds flying through the plot or above the canopy. Surveys commenced at sunrise (~ 05.15) and continued until 09.00, after which there was generally a rise in temperature and reduction in bird activity. Surveys were not conducted during rain or on occasions of high wind.

The distance sampling method was used because I had initially intended to estimate absolute bird abundances within habitats. However, there were too few individuals to reliably estimate detectability of each species. Instead, I transformed my data to presence-absence data for analyses: a valid option because relative rates of occupancy within habitats were found to be an appropriate proxy for species abundance (correlations between count data and occupancy data for the most abundant species were $r > 0.8$). I attempted to account for differences in detectability across habitats through long survey time, transformation of counts to presence-absence, the removal of rare birds (< 2 records) and the removal of birds with obvious detection bias across habitats (e.g. raptors) from analysis (Ruiz-Gutiérrez et al. 2010).

2-1-4 Data analysis

All statistical analyses (with the exception of GIS data, section 2-1-4-1) were conducted in the R software package (R Core Team 2013).

2-1-4-1 GIS data preparation and analyses

Sample sites were initially chosen based on existing scanned pdf maps of the plantation blocks within the study area (sourced from Open Bay Timber Ltd) combined with local knowledge and field surveys. However, to allow quantitative spatial analyses of the landscape context of sites, a more complete, georeferenced GIS base map was required. To achieve this, two pdf maps of plantation blocks were first opened in ArcGIS 10.0 (ESRI 2011) and georeferenced to AGD84 Zone 56 using a Landsat ETM satellite image (image-to-image rectification) and second-order polynomial transformation. Secondly, landscape elements (distribution of plantations of differing ages, cleared areas, logged and unlogged forest) were digitized from the now-georeferenced logging block images. Thirdly, the landscape elements map (vector polygons) was edited for completeness, accuracy, and timeliness with reference to the Landsat ETM satellite image (5th June 2003), and extensive field verification.

Spatial Analyses

Spatial analyses were conducted in ArcGIS 10.0 (ESRI 2011). Two types of ecologically relevant landscape measures were derived for each site; distance to unlogged forest, and the proportion of unlogged forest within varying radii of each site. The distance from study sites to unlogged forest was calculated by first selecting the unlogged forests from the treatments layer and then using the 'Near' analysis, which adds a field to the attribute table of the sites layer.

The proportion of unlogged rainforest and other landscape elements within 500 m, 1 km, and 2 km of sites (for use in Chapter 6) was calculated by first creating overlapping circular buffers (non-dissolved boundaries between circles) for each site, and for each radius. This resulted in 178 overlapping buffers in each of three output layers. Each layer was then overlain ('Intersect' tool) with the treatment layer to produce output layers containing polygons with attributes of the particular site buffer (i.e. the area of each landscape element). Finally, the three attribute tables were then exported into Microsoft Excel, where pivot tables were used to summarise the areas (ha) of each treatment that lay within each point buffer, allowing the calculation of proportions as well as absolute areas. A flow-chart outlining these steps is depicted in Figure 2.5.

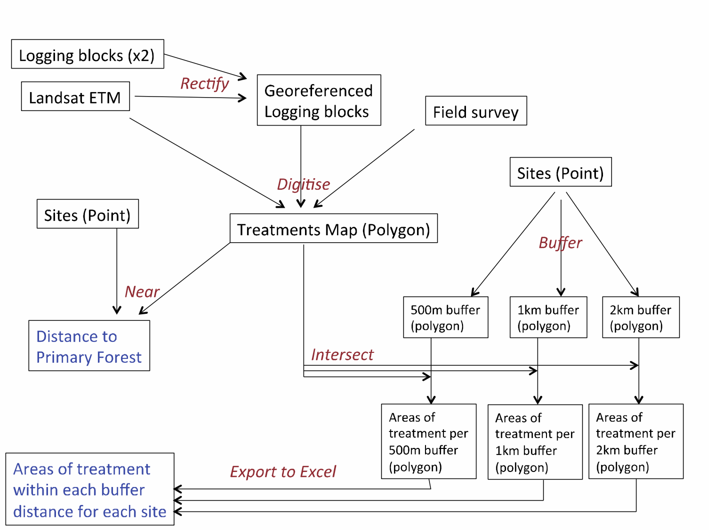

Figure 2.5 The steps taken in GIS mapping and analysis of spatial data. Buffers of 500 m and 1 km were also calculated but were considered unsuitable for analysis. Landscape measure outputs are identified in blue.

2-1-4-2 Multivariate generalised linear models

In Chapters 3 and 4 I analysed tree and bird species community assemblage data using multivariate generalised linear models (GLMs) because of the issues arising from using traditional distance-based metrics. Here I provide a brief explanation of these issues and how the statistical approach overcomes them.

Multivariate abundance data is often collected in ecology in the form of species counts or presence-absence data across sites. To analyse this type of community data, the traditional approach has been to calculate pairwise differences between multivariate abundance values among all study sites. These differences are calculated using distance metrics such as Euclidean distance or Bray-Curtis dissimilarity, and produce a matrix of pairwise distances between sites is created (Clarke & Warwick 1994). To create multi-dimensional scaling (MDS) ordination plots of these distance matrices, fitting algorithms order sites and rank them according to their mean similarity to all other sites, and a two-dimensional 'map' of these ordered relationships is generated. To determine whether there is a treatment effect on the community of interest (e.g. differences between groups), multivariate analogues of analysis of variance (ANOVA), such as PERMANOVA (Anderson & J 2001) or ANOSIM (Clarke 1993) are commonly used. Both methods partition variance of dissimilarities (or their ranks) into within and between-treatment components, and use permutation tests to compare a test statistic to a null distribution (resampling rows of data in an abundance matrix). These tests essentially attempt to separate effects of treatments on 'location' (the mean abundance of key species), and 'dispersion' (the variability in abundances within a treatment) (Warton et al. 2012).

While distance-based ordination methods are very useful for visualizing community assemblages across a study area, they tend not to model the mean-variance relationship appropriately in multivariate abundance data (e.g. Poisson-distributed counts for which variance increases with the mean). When comparing community assemblages between treatments, this can result in the miscalculation of variances within and across treatments (Warton et al. 2012). Given that dispersion effects are considered to be changes between treatments that occur beyond those accounted for by the mean-variance relationship, incorrect specification of this relationship leads to incorrect detection (and magnitude) of dispersion effects. Potential consequences of incorrectly modeling mean-variance relationships in the data are three-fold: (1) dispersion effects on MDS plots can be erroneously large for treatments which have very low mean abundances of taxa; (2) taxa which occur in higher numbers (and thus, higher variance) are preferentially identified as 'differentiating' over rarer taxa between treatments; and (3) multivariate effects which are driven by rare taxa go undetected (there is little power to detect a difference, Warton et al. 2012; Warton & Hudson 2004). Warton (2012) provides a detailed mathematical explanation of how these consequences arise alongside worked examples. Given that rare taxa are often of key conservation concern, correct identification of changes in their abundances due to treatment effects (e.g. changing environmental conditions) is vital.

A novel multivariate analysis method has recently been developed which explicitly models the mean-variance relationships that exist in count and presence-absence data (Wang et al. 2012).

This method fits separate generalised linear models (GLMs) to the multivariate data, using the same set of explanatory variables, in order to test hypotheses about effects. Significance values for ANOVA tests of the effect of treatments on community assemblages are subsequently calculated for these multivariate GLMs by resampling the data using parametric bootstrapping, with the Wald or likelihood ratio employed as the test statistic (Wang et al. 2012). Significance of the effect of treatments on individual species' abundances can also be calculated, and corrected for family-wise error (between species) using Holm's multiple testing procedure (Wang et al. 2012).

2-1-4-3 Pooling bird data

I pooled the bird data across 2007 and 2008. To ensure that this was justifiable, in terms of there being no effect of 'year' on species compositions among landscape elements, I ran multivariate GLMs comparing the composition of the 2 datasets: one with species composition based on data from 2007 and the other from 2008. I built models based on the presence-absence of species at sites, specifying a binomial error distribution. Landscape element was included as a single categorical predictor, and unlogged forest the reference factor. I then compared the two models using analysis of deviance, and found no significant difference in the composition of species between the two years ($p = 0.52$). Therefore, pooling bird presence-absence data over the two collection periods was justified. Multivariate GLM analyses were made using the 'mvabund' package (Wang et al. 2013).

2-1-4-4 Accounting for spatial autocorrelation in the data

By logistical necessity, I surveyed landscape elements using point transects rather than locating sites randomly (Marsden, 2003b). This introduced the possibility of spatial autocorrelation of sites along a given transect. For all univariate generalised linear models I tested for autocorrelation in model residuals using Moran's I tests statistic (P. A. P. Moran 1950), to determine any spatial autocorrelation that remained unexplained by the independent variables. Moran's index of autocorrelation was calculated on an iterative series of nearest neighbours (sites) defined using the R package 'spdep' (Bivand 2014). For models where autocorrelation was present in the residuals (Chapters 3, 5 & 6) I fitted generalised linear mixed models (GLMMs) using the 'lme4' package (Bates et al. 2013), with transect included as a random effect to account for non-independent error structures associated with clustering of study sites (Zuur et al. 2011).

Multivariate data are notoriously difficult to test for autocorrelation (Ramage et al. 2013). For my tree and bird species community data, I accounted for potential autocorrelation by including an interaction term (transects × elements) in my models, as per Wang (2012). For example, for tree species data my model equation was:

$$\log(\mu_{jkl}) = intercept_j + transect_{jk} + element_{jl} + transect \times element_{jkl}$$

where μ_{jkl} is the mean of Y_{jkl} (the number of individuals of a given species at site j along a given transect k, located within landscape element l.

Resulting analyses of deviance found no significant interaction between landscape elements and transects for tree species ($p = 0.06$) nor bird species ($p = 0.18$), meaning that the multiplicative effect found for landscape elements was consistent among transects (Wang et al. 2012).

2-1-4-5 Chronosequence assumptions

Given the time constraints inherent in field-based PhD projects, a chronosequence approach is often necessary to study land-use impacts (Chazdon et al. 2007), as opposed to more rigorous, long-term monitoring (e.g. the Biological Dynamics of Forest Fragments Project in central Amazonia, (Laurance et al. 2002)). Chronosequence studies in forest ecology involve assessing stand changes through time by measuring attributes in stands of different ages within a short time-frame rather than surveying changes within a given stand through time (space-for-time substitutions). In this study, I compared a number of biological attributes among landscape elements with the assumption that differences found were due to 'treatment' effects of a given land-use. However, because this study did not follow changes among landscape elements through many years of monitoring, differences between elements may have been partially caused by effects of location. I attempted to account for variation caused by location effects by sampling many sites within elements, and by attempting to sample across the variation in topography, watercourses and soil types present in the landscape. I also sampled at a uniform distance from the coastline and within the same elevation to reduce effects on composition arising from costal-inland and elevation gradients (Paijmans 1976). However, it is not possible to fully account for the heterogeneous distribution of rainforest plant species richness and composition which would have occurred among landscape elements prior to human disturbance (Ramage et al. 2013; Letcher & Chazdon 2009). Thus, conclusions drawn from the ensuing analyses with respect to changes in species richness and composition among elements are made with acknowledgement of the inherent limitations of this study design.

CHAPTER 3

Conservation of lowland tropical tree species in a native timber plantation landscape[1]

Eddy Kaukia displaying his superior tree measuring skills

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[1] Pryde, E.C., Watson, S.J., Holland, G.J., Turton, S.M., Nimmo D.G. (*in press*) Conservation of tropical forest tree species in a native timber plantation landscape. Forest Ecology and Management.

CHAPTER THREE

In this chapter I investigate the conservation value of native *Eucalyptus deglupta* plantation forests for tree species in the lowlands of New Britain Island, Papua New Guinea. Specifically, I address the first objective of the thesis: to identify forest species that can and cannot persist in production land-uses and how occurrence patterns may be mediated by the biological attributes of species. I compare the tree species composition of unlogged forest to those of different aged native *E. deglupta* plantations and intervening (historically logged) secondary forests. I also evaluate the patterns of occurrence of species of different successional stages and dispersal modes among landscape elements and suggest some underlying processes that may be directing them. Key findings from this study are interpreted in terms of their ramifications for conservation management of this landscape and for similar landscapes in other tropical regions

3-1 Introduction

Deforestation and degradation of tropical forests has precipitated a change in the global composition of rainforest cover, whereby around half of remaining forest cover consists of secondary regrowth and degraded old-growth forests (Chazdon, Peres, et al. 2009b). Tropical lowland forests experience particularly high levels of deforestation because they occur on flat and fertile soil comparative to other tropical forests, making them valuable for agriculture, logging and agroforestry (Wright 2010; Miettinen et al. 2011). The loss and degradation of lowland forests has broad ramifications as they contain over half of the world’s terrestrial plant and animal species (Sodhi et al. 2010; Dirzo & Raven 2003) and play a key role in maintaining global carbon and hydrological cycles (Houghton 2012; Bradshaw et al. 2007). Consequently, sustainable management of these forests has been identified as a conservation priority (Bradshaw et al. 2009; Gibson et al. 2012).

The needs of local human populations and global demand for forest products means that the full protection of tropical lowland forests is unlikely (Coad et al. 2009). For example, despite being recognised as one of the world’s most significant tropical wilderness areas (Myers et al. 2000), the Southeast Asia-Pacific region has one of the world’s highest rates of deforestation and degradation (Shearman et al. 2012). As such, conservation priorities are shifting from using reserve-based systems to ones targeting sustainable management of multi-use landscapes, which attempt to balance biodiversity conservation with production land-uses (Melo et al. 2013). For such approaches to be successful, conservation managers need to understand the capacity of different land-uses to support native biodiversity and the processes which allow persistence of species in heterogeneous production landscapes (Perfecto & Vandermeer 2010).

Native timber plantations may represent a land-use capable of balancing production and conservation in tropical forests. This is because they can potentially support understorey plant and tree species otherwise restricted to remnant forest (Bremer & Farley 2010), which in turn would provide for rainforest-dependent fauna (Brockerhoff et al. 2008). By contrast, most agroforests and tree crops are comparatively limited in this capacity (Wilcove et al. 2012). However, the extent to which native timber plantations can support plant communities similar to natural forests is poorly understood, particularly outside of the Neotropics (Chazdon et al., 2009a; Stephens and Wagner, 2007). Given the expansion of timber plantations in the tropics (Carnus, Parrotta, et al. 2006b) and the push for greater representation of native plantations globally (Davis et al. 2012) it is crucial to gain a better understanding of the contribution that such plantations can make to biodiversity conservation.

Little is known regarding the functional breadth of forest plant species that can be supported in native plantations. For instance, do plantations support species from multiple forest successional stages, or only early successional species? How is this affected by plantation age? The ecological mechanisms underpinning the ability of species to colonise native plantations are also poorly understood. Examining how species' traits affect their ability to become established in plantations may provide valuable understanding of the dynamics of understorey composition. For example, following clearing of tropical forests, recruitment of tree communities is largely dependent on *ex situ* colonisation (Holl 1999; Chazdon et al. 2007) because most of the seed bank and "seedling bank" (pre-existing seeds stored in the soil and small seedlings) is destroyed during land clearing, particularly when fire is used (Mamede & de Araujo 2008). Consequently, dispersal mode is likely to be a fundamental trait influencing assemblages post-clearing (Uhl et al. 1982).

Here, I investigate the role that native plantation forests can play in biodiversity conservation in the lowlands of New Britain Island, Papua New Guinea. I assess: (1) the relative ability of different aged *Eucalyptus deglupta* plantations and intervening secondary forest (historically logged) elements to support tree species of undisturbed forest; (2) the ability of plantations to support a diverse range of successional tree species (e.g. early, mid, and late- successional species); and (3) the effects of dispersal mode on establishment in plantations. Identifying the conservation value of native plantations will provide vital information for management and the design of production landscapes.

3-2 Methods

Study Area, study design and site selection are outlined in sections 2-1-1 and 2-1-2 (Chapter 2).

3-2-1 Data collection

Tree surveys were completed for 142 sites among landscape elements, with a single plot per site (young plantations = 20, mature plantations = 50, secondary riparian = 14, secondary remnant = 10, unlogged forest = 48). At each survey site a 30 m line from the central survey point was marked in each of the cardinal directions resulting in a square vegetation plot of 1800 m^2 (Figure 2.4). All trees ≥10 cm diameter at breast height (DBH) were tallied, and species, size (DBH), mortality status, and phenology (fruit/flower present) were recorded. Plots of 1800 m2 are unlikely to capture all tree species occurring within diverse tropical lowland forest. Consequently, we use these data to compare relative species density and composition between treatments (landscape elements) and discuss broader species richness trends in regard to rarefaction curves.

The successional stage and mode of dispersal for each species was defined using data collected from several sources (Appendix Table A.1). Post-disturbance successional processes occur on a continuum and are influenced by stochastic as well as deterministic factors (e.g. plant species traits, soil conditions) (Guariguata & Ostertag 2001), but for explanatory purposes, successional status is commonly assigned to a species based on its relative ability to develop and compete for resources under differing levels of shade (canopy closure) (Whitmore 1989). Early-successional (heliophilic) species require full sunlight throughout their life cycles, mid-successional species require light in earlier life-stages but tolerate shade once established, and late-successional species (the most species-rich category), are able to tolerate the most amount of shade throughout all life stages (Strauss-Debenedetti & Bazzaz 1996; M. S. Ashton 2011). For this study, I grouped species according to successional classes following the description in van Valkenburg (1994): (1) early-successional species (light-demanding (heliophilic), early maturing species (<5 years) with a relatively short life-span (<80 years) (e.g. *Macaranga species*)); (2) mid-successional species (heliophilic species but with shade tolerant life-cycle stages (e.g. *Octomeles sumatrana*), **and** species that can tolerate shade in earlier developmental stages (e.g. *Canarium indicum*)); and (3) late successional species (species that are relatively slow-growing, and tolerant of shade through all developmental stages (e.g. *Celtis rigescens*)).

Trees often have more than one mode of seed dispersal (Nathan & Muller-Landau 2000), so I classified species according to their primary mode of dispersal: animal dispersed (birds, bats and some arboreal and ground mammals); or non-vertebrate dispersed (NVD) (wind, water or gravity) (Paijmans 1976). Where information regarding dispersal mode was not available at species-level, dispersal mode was inferred from genus-level knowledge (Appendix Table A.1).

3-2-2 Data analysis

All data analysis was performed in the statistical computing program ***R*** (R Core Team 2013). To observe the accumulation of species richness within each landscape element we conducted rarefaction analyses using the function 'specaccum' in R package 'vegan' (Oksanen et al. 2013). Accumulation curves were calculated based on both (i) survey sites (using the 'exact' method) and (ii) individuals sampled (using the 'rarefaction' method).

I modelled species density (sensu Gotelli and Colwell, 2001) for each element using generalised linear mixed models (GLMMs) in the 'lme4' package (Bates et al., 2013). The response variable was the total number of species recorded at each site and was modelled as a Poisson distribution. Each transect was specified as a random effect to account for non-independent error structures associated with potential clustering of study sites (Zuur et al. 2011), and the landscape element sites were located within (i.e. young plantation, mature plantation etc.) was specified as a fixed effect. Landscape elements were considered an important influence on species richness where 95% confidence intervals (CI) for parameter estimates did not overlap zero when compared to the reference element (unlogged forest).

I also used Poisson GLMMs to compare the density of species grouped according to (i) successional stage and (ii) dispersal mode per site. Response variables represented the total number of species belonging to each category that occurred at each site. Each transect was assigned as a random effect, and the landscape element as a fixed effect. Pairwise comparisons between elements (with unlogged forest as reference category, and secondary remnant as reference category) were corrected for family-wise error using a Bonferroni correction to adjust significance levels (Quinn & Keough 2002). All mixed models were tested for overdispersion, and for autocorrelation using Moran's ***I*** statistic (Bivand 2014).

To assess differences in tree species composition across elements, I applied a novel model-fitting method of multivariate generalised linear models (GLMs) to my tree species basal area and count data (Wang et al. 2012). This method directly models the underlying mean-variance relationship in the abundance data rather than using distance based measures of community dissimilarity/similarity (Warton et al. 2012). As such, the approach is useful for assessing treatment effects on community composition because it better detects the influence of treatments on rare species (Warton et al. 2012). This was important for my study because the lowland rainforests are hyper diverse with patchy dominance by any one species (Paijmans 1976; Mueller-Dombois & Fosberg 1998).

Models were fitted using the ‘manyGLM’ function in R package ‘mvabund’ (Wang et al. 2012; Wang et al. 2013). I built models based on the number of individuals of species at sites (counts), specifying a negative binomial error distribution. Landscape element was included as a single categorical predictor. To determine whether landscape elements had a significant effect on tree community assemblage, the data were resampled using parametric bootstrapping, with likelihood ratio employed as the test statistic (Wang et al. 2012). To compare pairwise significance among landscape elements I ran the resampling step twice, first with unlogged forest as the reference factor and second with the secondary remnant forest as the reference factor. The significance of landscape elements on individual species abundances was corrected for family-wise error between species using Holm’s multiple testing procedure (Wang et al. 2012). These significance values were used to identify which species were having a differentiating effect among elements, and abundance plots comparing these species among elements were used to distinguish the element(s) in which they were comparatively most localised (Warton 2008). In this way I was able to determine species characteristic of certain land-covers.

3-3 Results

3-3-1 Tree species richness and composition

In total, 95 tree species with DBH ≥10 cm were recorded across all elements in the plantation landscape. Accumulation of species across sites was similar for unlogged forest and secondary remnant and riparian elements as evidenced by their rarefaction curves and overlapping confidence intervals (Figure 3.1). Accumulation of species in mature plantations was lower than unlogged and secondary forest (although still quite high), and young plantations were depauperate compared to all other elements (Figure 3.1). The slightly steeper accumulation curves of both secondary forest elements compared to the curve of unlogged forest (Figure 3.1a) appears to be mostly caused by an increased stem density in secondary forest elements (Gotelli and Colwell, 2001) as exemplified by the greater similarity in rarefaction curves of these three forest elements (Figure 3.1b). Comparisons between species densities among elements (alpha diversity) supported the overall species richness results, demonstrating that species densities were similarly high in both unlogged (Figure 3.2, $S = 27.60 \pm 0.29$) and secondary elements, but were significantly lower in mature and young plantations (Table 3.1, GLM $p < 0.05$).

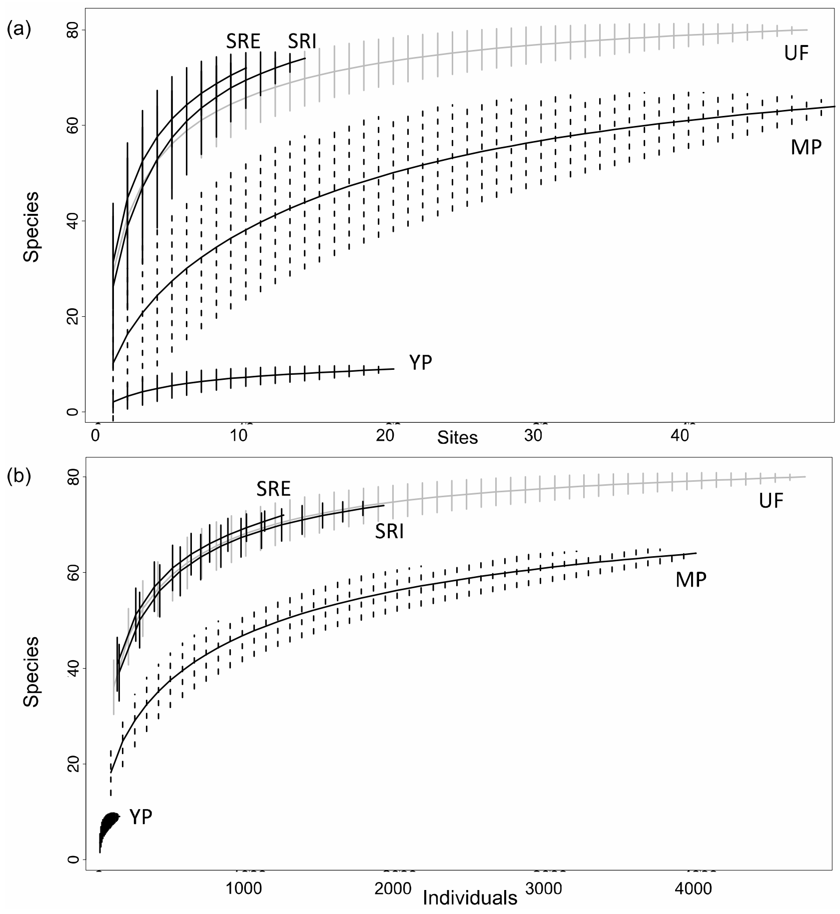

Figure 3.1	Accumulation of species based on (a) sites and (b) individuals (rarefaction) for each landscape element. Landscape elements are: UF – unlogged forest, SRE – secondary remnant, SRI – secondary riparian, MP – mature plantation and YP – young plantation.

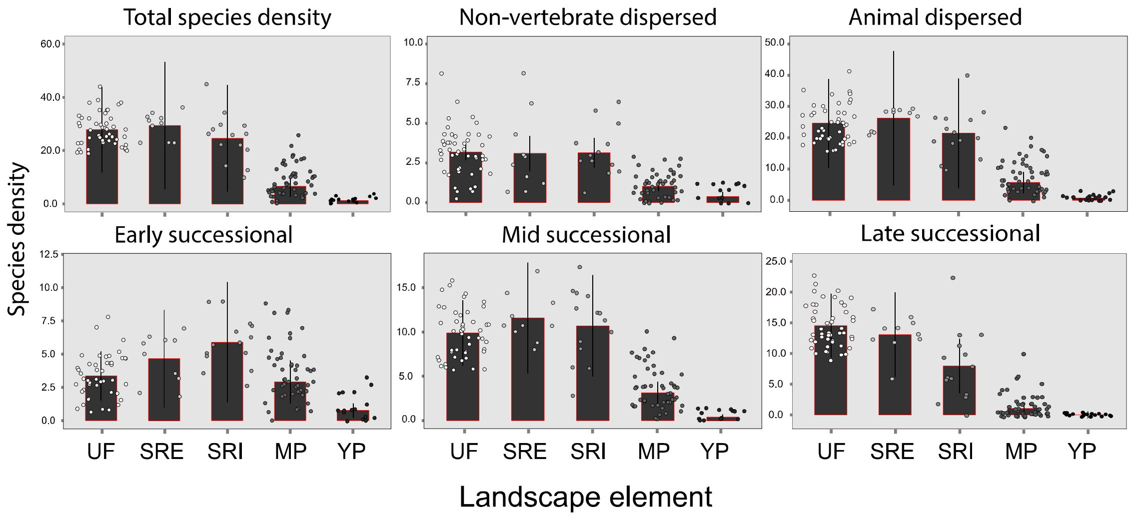

Figure 3.2	Species density of all trees, and species densities grouped according to successional type and dispersal mode. Circles represent the raw data, bars are the predicted mean richness and black lines the 95% confidence intervals. Landscape elements are: UF – unlogged forest, SRE – secondary remnant, SRI – secondary riparian, MP – mature plantation and YP – young plantation.

Table 3.1 Model results of species densities for all tree species, and species densities grouped according to successional type and dispersal mode. Emboldened figures represent values whose 95% confidence intervals do not overlap with zero with unlogged forest as reference group (intercept).

Response variable	**Landscape element**	**Coef**	**SE**	**z value**
All species	Intercept	**3.325**	**0.292**	**11.369**
	Secondary Remnant	0.054	0.508	0.107
	Secondary Riparian	-0.122	0.508	-0.24
	Mature Plantation	**-1.445**	**0.418**	**-3.456**
	Young Plantation	**-3.323**	**0.448**	**-7.208**
Early successional species	Intercept	**1.212**	**0.276**	**4.394**
	Secondary Remnant	0.326	0.487	0.669
	Secondary Riparian	0.562	0.478	1.177
	Mature Plantation	-0.145	0.393	-0.368
	Young Plantation	**-1.489**	**0.444**	**-3.354**
Mid successional species	Intercept	**2.289**	**0.190**	**12.057**
	Secondary Remnant	0.158	0.335	0.471
	Secondary Riparian	0.079	0.333	0.239
	Mature Plantation	**-1.142**	**0.279**	**-4.100**
	Young Plantation	**-3.236**	**0.438**	**-7.380**
Late successional species	Intercept	**1.742**	**0.171**	**16.064**
	Secondary Remnant	-0.099	0.303	-0.327
	Secondary Riparian	-0.548	0.304	-1.802
	Mature Plantation	**-2.024**	**0.261**	**-7.757**
	Young Plantation	**-2.761**	**0.320**	**-8.626**
Animal dispersed species	Intercept	**3.202**	**0.293**	**10.942**
	Secondary Remnant	0.065	0.509	0.128
	Secondary Riparian	-0.136	0.509	-0.267
	Mature Plantation	**-1.463**	**0.419**	**-3.492**
	Young Plantation	**-3.467**	**0.467**	**-7.431**
Non-vertebrate dispersed species	Intercept	**1.159**	**0.081**	**14.339**
	Secondary Remnant	-0.028	0.197	-0.141
	Secondary Riparian	-0.014	0.171	-0.082
	Mature Plantation	**-1.120**	**0.161**	**-6.977**
	Young Plantation	**-2.076**	**0.363**	**-5.723**

Tree species composition differed significantly among landscape elements (multivariate GLM, $p < 0.001$). All modified elements differed in composition from unlogged forest except the secondary remnant for which there was no significant difference (although the p-value was close to significance, $p = 0.052$, Table 3.2). Univariate analyses of species' relative abundance found 38 species were the main drivers of compositional differences among landscape elements (i.e. occurring in different abundance among elements, $p_{adj} < 0.05$, Appendix Table A.2). The majority of these trees were late-successional, animal-dispersed species (Figure 3.3).

3-3-2 Successional stage richness and composition among elements

The unlogged forest was primarily composed of late-successional species (67%), followed by mid-successional (25%), and early-successional (~10%) species across all sites. The composition of the secondary remnant element, while not significantly different to unlogged forest, did contain a higher proportion of early- and mid-successional differentiating species (Figure 3.3). The secondary riparian and secondary remnant elements differed in their composition (multivariate GLM, $p < 0.006$, Table 3.2), even though both elements had a similar richness of tree species belonging to each successional class (Figure 3.2). The secondary riparian element was comprised of a greater proportion of individuals belonging to early- and mid-successional differentiating species, and the secondary remnant had a greater proportion of late-successional individuals (Figure 3.3). Cumulatively across all mature plantation sites 70% of tree species found in the unlogged forest were recorded, however, in mature plantations they were sparsely distributed: 24 were found in significantly lower abundance compared to unlogged forest (Figure 3.3b). Figure 3.3b shows the occurrence of recruited trees in mature plantations, with most individuals representing early-successional and mid-successional heliophilic classes. Young plantations contained very few trees aside from *E. deglupta* (Figure 3.2) leading to either an absence or lower abundance for all species except the invasive exotic, *Mutingia calabura* (cherry), including a complete absence of any late-successional trees.

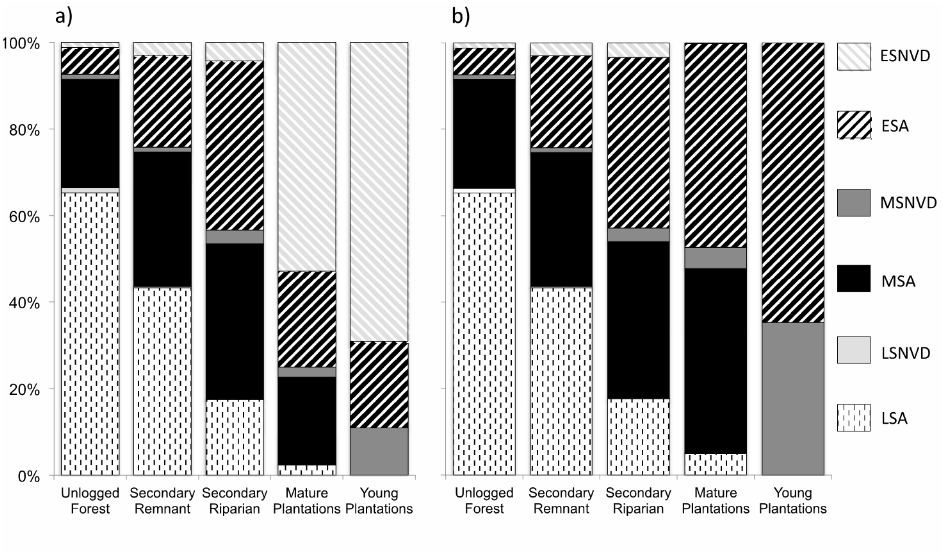

Figure 3.3 Composition of differentiating species (found to occur in significantly different number among elements), grouped by successional class and mode of dispersal; (a) including *Eucalyptus deglupta* (b) without *Eucalyptus deglupta* to show the composition of understorey recruits. LS = Late successional; MS, Mid-successional; ES = Early-successional; NVD = Non-vertebrate-dispersal; A = Animal-dispersal.

3-3-3 Dispersal mode richness and composition among elements

Typical of wet tropical forests where the majority of woody plants are vertebrate-dispersed (Jansen & Zuidema 2001 and refs therein), >93% of the species found in unlogged forest were animal-dispersed. The species densities of dispersal modes was similar for both secondary remnant and riparian elements (Figure 3.2, Table 3.1), although the number of non-vertebrate-dispersed individuals was proportionally greater in the riparian element (Figure 3.3). The species density of animal-dispersed trees was significantly lower on average in mature plantation sites compared to unlogged forest (Figure 3.2, Table 3.1). This was because, although 75% of animal-dispersed trees were recorded across all sites in mature plantations, they occurred in comparatively sparse distribution. Similarly, species densitiy of non-vertebrate-dispersed species was also significantly lower in mature plantations (Table 3.1), however this was caused by an even lower representation of non-vertebrate-dispersed species found in unlogged forest (only 50%), also sparsely distributed. The eight tree species recorded within the young plantations were comprised of animal-dispersed species that were patchily recruited (e.g. *Macaranga* spp., *Endospermum medullosum*) and non-vertebrate-dispersed species (e.g. *O. sumatrana, Alstonia scholaris*) that occurred as large remnant individuals in a few sites (Figures 3.2 & 3.3).

3-4 Discussion

The ability to conserve biodiversity in production landscapes will be critical to biodiversity conservation in the 21st century. Here I have shown that native timber plantations and secondary logged forests support a substantial proportion of forest tree biodiversity. Native plantations supported 70% of forest tree species and the number of tree species in unlogged and secondary forest elements was similar. However, clear differences were evident in the species composition of unlogged forest and most modified elements, and these were related to the attributes of species (namely, species' successional stages and modes of dispersal). While modified landscape elements can be species-rich and play a role in maintaining biodiversity in tropical regions, the retention of secondary and unlogged forests within production landscapes remains critical for conserving populations of old-growth forest tree species.

3-4-1 Species richness and composition of landscape elements

Both secondary forest elements, the secondary remnant forest in particular, demonstrated a high conservation value, as evidenced by the presence of a similar number of tree species in common with unlogged forest. This finding is consistent with the high species richness observed in other selectively-logged tropical forests after relatively short fallow periods (Gibson et al. 2012; Putz et al. 2012; Hall et al. 2003). In some cases, this comparably high richness has been the result of an increased number of early and mid-successional species after selective-logging at the expense of late-successional species, therefore masking compositional differences between forest types (Sheil & Burslem 2003). By contrast, I found no significant difference in composition between the secondary remnant and unlogged forest in this study, although the secondary remnant displayed a trend towards higher abundance of early and mid-successional species.

Compositional similarity between the selectively-logged, secondary remnant element and unlogged forest may be explained by the evolution of these forests in conjunction with regular volcanic disturbances, and one of the longest histories of anthropogenic modification in the world (over 30,000 years) (Lentfer et al. 2010). These regular disturbances may have resulted in the filtering of more disturbance-tolerant plant assemblages—an observation which has been made of forests on neighbouring Melanesian islands (Bayliss-Smith et al. 2003). Therefore, the unlogged forests in this study may resemble secondary forest more closely than studies in other regions experiencing different biogeographic processes and disturbance histories.

Selectively-logged secondary forests can play a vital conservation role as source pools of forest propagules in production landscapes if properly managed (Edwards, Larsen, et al. 2010b). However, the selectively-logged, riparian elements which are subject to ongoing local timber extraction had a lower abundance of late-successional species compared to the secondary remnant, exhibiting a diminished conservation value for these trees which make a substantial contribution to plant biodiversity and ecological function in tropical forests (Orains et al., 1996; Pinotti et al. 2012). Significant decline in the biodiversity value of secondary stands experiencing continuing disturbance has been well documented (Laurance 1997; Chazdon 2003; Gibson et al. 2012) and it is equally likely here that without adequate protection from further modification, the biodiversity value of secondary elements will continue to decline.

Mature plantations demonstrated high cumulative species richness, recruiting 70% of forest species across all sites, although occupation of sites by *E. deglupta* resulted in their sparse distribution (low site-level richness) compared to non-plantation elements. Comparison of tree species richness with other tropical plantation studies is confounded by differences in the age of plantations studied, the life-stage measurement of woody plants (seedling, sapling, tree), and the study site's baseline forest species richness. Nevertheless, the mature *E. deglupta* plantations contained a similar or greater proportion of native rainforest tree species compared to studies in exotic (Parrotta 1995; L. J. Chapman & C. A. Chapman 1996; Lugo 1992b) and native timber plantations (Keenan et al. 1997; Wardell-Johnson et al. 2005). By contrast, young plantations 2–6 years post-clearfell had a substantially reduced richness of recruiting trees, which is not surprising given that only trees ≥10 cm DBH were sampled and few recruits would have grown to that size within the time since plantations were established. This highlights the varying contribution of differently aged plantations to the functional composition of trees in a landscape.

3-4-2 Successional stage is limited by plantation age

Mature plantations were mainly comprised of early- and mid-successional individuals. Most late-successional trees were found in low density, but cumulatively, across mature plantation sites, two-thirds of late-successional species found in unlogged forest were capable of growing to 10 cm DBH in mature plantations. It is possible that even more late-successional species, which were <10cm DBH, were present in mature plantations. Late-successional trees tend to grow slowly (Laurans et al., 2012), resulting in more individuals occurring as difficult to detect saplings and seedlings (<10cm DBH). For example, in some other plantation studies, richness of late-successional trees was found to be higher in juvenile stages compared to adult stages (Farwig et al., 2009; Keenan et al., 1997). The richness of late-successional species is best assessed where juvenile tree species (<10cm DBH) can be identified and recorded. This was not possible in this study and it is therefore likely that we have underestimated richness of these species here. This type of assessment would be especially instructive for those plantations incorporating a restoration role. For the industrial plantations of this study, plantation age is a more influential inhibitor of the density of late-successional trees that can survive beyond juvenile stages.

The ability of *E. deglupta* plantations to support a breadth of successional types may arise from its natural role in these forests as a successional catalyst, where it invades disturbed sites, quickly forms mono-specific stands, suppressing weedy plants and creating abiotic conditions resembling intact rainforest (Paijmans, 1973). Additionally, facilitative germination conditions are likely augmented by the low intensity of stand-level management: thinning was unprofitable and rare, and manual weed tending ceased at three years. In many production plantations, high intensity management has inhibited recruitment of mid- and late-successional species (Kanowski et al., 2005; Keenan et al., 1997).

3-4-3 Dispersal mode drives colonisation in plantations

Of the trees recorded in unlogged forest, mature plantations supported 50% of the non-vertebrate-dispersed species and 75% of animal-dispersed species. This finding likely reflects the lower dispersal capacity of non-vertebrate-dispersed species throughout the landscape (Willson & Crome 1989). Distribution of animal-dispersed trees in this landscape does not appear to be as limited and may be explained by the high permeability of the matrix to local animal vectors (e.g. birds, bats). My contemporaneous studies of forest birds supports this hypothesis: I found just two species restricted to unlogged forest (Chapter 4), and birds, along with bats, are considered the primary tree dispersers in these lowlands (Mayr & Diamond 2001). Permeability is thought to be enhanced in plantation landscapes because of the proportion of the matrix with a continuity of tree cover (Keenan et al. 1997; Brockerhoff et al. 2008).

The recruitment of most animal-dispersed species in the plantations (albeit, in low abundance) suggests that plantations themselves attract visitation by a range of seed-dispersing species. This is most likely in more mature stages when plantations have a higher tree species richness, however, in young plantations I still observed birds exploiting the perching structure and nectar provided by ***E. deglupta,*** a particularly important food resource for the island's parrot species (Marsden & Pilgrim 2003b). Between three-to-six years of age, ***E. deglupta*** can flower and grow to a height of 10 m (Francis 1988). The fast growth rates typical of plantation species has been similarly observed to provide structural resources from very early stages (Parrotta 1995; McClanahan & Wolfe 1993).

3-4-4 Conservation and management implications

The results from this study indicate that the combination of native timber plantations set among older secondary forest elements can support high levels of tree species biodiversity. Native timber plantations are rare in many tropical regions and should be more widely considered for their enhanced capacity to harbor native biodiversity. I found that older plantations held greater benefit for biodiversity, with young plantations demonstrating a poor capacity to recruit all but a homogeneous assemblage of early-successional tree species. Therefore, temporally varying harvesting cycles to ensure the highest possible cover of mature plantations through time (and their presence at all times) would increase the biodiversity conservation value of the landscape. This would involve a trade-off between production and conservation objectives and is discussed in more detail in Chapter 7 (section 7-1-2-2).

Regenerating secondary forest elements were found to be important for populations of rainforest-restricted species, such as slow-growing, late-successional and non-vertebrate-dispersed trees. Therefore, recognition of their high conservation value is vital, and their protection from further encroachment though plantation establishment is recommended. Open Bay's high ratio of unlogged forest to clearfelled area in the broader landscape, and the extensive, old, regenerating secondary forest within the production landscape, have been identified as key contextual characteristics for biodiversity conservation in multi-use landscapes (Gibson et al. 2012; Letcher & Chazdon 2009). Therefore, any future expansion of plantations to meet increasing timber demands should be located on heavily degraded lands (i.e. areas used for industrial agriculture, deforested areas) rather than by encroaching into logged-over forest, as is current practice in New Guinea.

Ultimately, the capacity of plantations to contribute to biodiversity in terms of species population sizes and reproductive success will be modest when compared with that of unlogged and secondary elements because of clearfell practices and competition from plantation trees (Catterall et al. 2005). Thus, ensuring that old-growth rainforest is retained is critical, to provide both refuge for rainforest-restricted species and source pools for species capable of existing in modified elements.

3-5 Chapter summary

I found a high capacity for biodiversity conservation within plantations, with 70% of forest tree species persisting in mature plantations (13–15 years old). However, compositional analyses revealed declines in both late-successional and non-vertebrate-dispersed species in the plantations, demonstrating the difficulty of retaining old-growth forest trees in this land-use. Secondary forest protected by conservation reserves was compositionally indistinct from unlogged forest. However, unprotected and highly fragmented secondary forest (i.e. riparian forest) contained comparatively fewer late successional trees than reserved secondary forest. The results of this chapter demonstrate the potential for tropical native timber plantations to contribute to the retention of biodiversity. Nonetheless, sympathetic management is required to allow the establishment of late-successional species and to ensure the persistence of source populations (i.e. unlogged forest).

CHAPTER 4

Conservation of lowland forest birds in a native timber plantation landscape[2]

***Black-headed paradise kingfisher* (Tanysiptera nigriceps)**

A species endemic to New Britain Island

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[2] Pryde, E.C., Nimmo D.G., Holland, G., Watson, S.J. (*in review)* Conservation of lowland forest birds in a native timber plantation landscape: how do traits affect species occurrence? Biological Conservation.

CHAPTER FOUR

In Chapter 4 I investigate the conservation value of native *Eucalyptus deglupta* plantation forests for bird species of lowland New Britain, PNG. This chapter also addresses (but with avifauna) the first objective of the thesis: to identify forest species that can and cannot persist in production land-uses and how occurrence patterns may be mediated by the biological traits of species. Identification of universally 'susceptible' traits, in terms of bird species' response to disturbance, has proven elusive because studies have been concentrated in a limited number of continental regions, and patterns may not hold in different biogeographic contexts. Here I compare species and trait composition of 41 lowland rainforest birds among the landscape elements comprising the plantation landscape. Traits were selected according to their common association with disturbance responses in birds, according to the literature. Key findings from this analysis are explained in terms of their implications for trait-based ecological studies as well as their significance for conservation management of this and similar tropical production landscapes.

4-1 Introduction

Tropical forests are critical reservoirs of global biodiversity (Myers et al. 2000; Dirzo & Raven 2003; Sodhi, Brook, et al. 2009a). Over one-third of the world's threatened bird species occur in tropical and subtropical lowland forests, making these habitats vital for global avian conservation (IUCN 2014). However, declines of bird species in tropical forests have been widely reported (Sodhi, Sekercioglu, Barlow & Robinson 2011a and refs therein), primarily driven by deforestation and forest degradation (Sodhi, Lee, et al. 2009b; Gibson et al. 2012). Logging has intensified in those tropical regions where forests still remain relatively intact (Shearman et al. 2012), and clearing of primary and secondary forests to make way for agriculture and agroforestry continues across the tropics (Wright 2010; Gardner et al. 2010). In addition, less than 10% of tropical forests are formally protected (Chazdon, Harvey, et al. 2009a) and long-term conservation of their biota depends largely on the activities in neighbouring anthropogenic landscapes (Wittermyer et al. 2008). As a consequence, tropical conservation management based on reserves alone is unlikely to succeed, and conservation strategies are increasingly aiming to manage multi-use landscapes in a manner that balances production and biodiversity conservation, often termed land-sharing (Gardner et al. 2009; Perfecto & Vandermeer 2010).

While land-sharing schemes present a potentially promising way forward for conservation in agricultural systems (Melo et al. 2013; Fischer et al. 2008), there is little information on the capacity of forestry-based production landscapes to support biodiversity (Gardner et al. 2009; Sodhi et al. 2011a, but see Edwards, Gilroy, et al. 2013a). Species' occurrence in historically-forested, production landscapes tends to be greatest where modified elements sustain higher tree cover because dispersal barriers are minimised and structural and dietary resources can extend beyond remnants (Clough et al. 2011; Renjifo 2001). Thus, selectively-logged forest, timber plantations and agroforestry may support more tropical biodiversity compared to agricultural crops (Kennedy et al. 2010; Peh et al. 2005; Brockerhoff et al. 2008). As compared to other forms of agroforestry, native timber plantations may provide additional benefits to biodiversity as they can facilitate recruitment of native flora (Bremer & Farley 2010; Edwards et al. 2011)and may provide enhanced connectivity and habitat area for forest biota within production landscapes.

Understanding why some species can survive in production land-uses while others cannot is a major challenge for ecology and conservation (Chazdon, Harvey, et al. 2009a). Species' traits such as body size, diet, habitat (niche) specialisation, and geographic range have been identified as key determinants of extinction-risk because they mediate species' abilities to adapt to landscape modification (Purvis et al. 2000; Van Allen et al. 2012; Beissinger 2000; Tscharntke et al. 2012). For example, in tropical forests, there is evidence that a range of traits increase the vulnerability of avifauna to landscape modification, including diet specialisation (Newbold et al. 2013; Karp et al. 2011), large body size (Sodhi et al. 2004), dependency on old-growth habitats (Bowman et al. 1990; Peh et al. 2005) and endemism (implying a small global population size and limited dispersal ability, Boyer 2010; Renjifo 2001; Jankowski & Rabenold 2007).

Although some traits have repeatedly been correlated with declines and extirpations of tropical birds, there are also many cases of conflicting results (Sekercioglu & Sodhi 2007; Ewers & Didham 2006). One potentially important reason for the lack of consensus is that most trait-based theory has been developed from research conducted in the continental Neotropics. Consequently, contrasting results may be a product not only of disturbance/habitat modification, but also the biogeographic and historical context of those ecosystems, which is different in other key tropical regions (Gray et al. 2007). A more general understanding of the traits which confer resilience and vulnerability to land-changes may be attained by undertaking studies in regions where the faunal community has developed under different biogeographic processes (Ewers & Didham 2006). For instance, on oceanic islands and archipelagos dispersal ability and niche breadth may be less important because the fauna represent a subset of species which have necessarily needed to be effective dispersers and colonisers (at least historically) and have become established under very different competitive situations to mainland populations (T. E. Martin & G. A. Blackburn 2013).

Here, I examine avian communities in a native timber (*Eucalyptus deglupta*) production landscape, on the oceanic island of New Britain, Papua New Guinea (PNG). I aimed to: (1) examine the occurrence of lowland forest-using birds within land-use elements comprising a native timber plantation landscape (young and mature plantations, forestry-affected secondary forests and unlogged forest); (2) assess what ecological traits are associated with bird species occurring in different landscape elements; and (3) assess the potential of production forestry to contribute to conservation strategies in tropical lowland regions, which face extreme pressure from logging and land conversion.

4-2 Method

Study Area, study design and site selection are outlined in sections 2-1-1 and 2-1-2 (Chapter 2).

4-2-1 Bird data collection

Bird surveys were completed for 122 sites among landscape elements, with a single plot per site (young plantations = 24, mature plantations = 43, secondary riparian = 14, secondary forest = 9, intact forest = 32). I surveyed bird species at each site using circular point-counts, recording all birds seen or heard within 50 m of the observer over a 20 min period. I did not record birds flying through the plot or above the canopy. Surveys commenced at sunrise (~05:15) and continued until 09:00 after which time there was a rise in temperature and reduction in bird activity. Surveys were not conducted during rain or on occasions of high wind.

I restricted analysis to forest-occurring species (excluding grassland, coastal and waterfowl species) because I aimed to observe disturbance impacts on birds that use forest habitat, rather than to record responses of non-forest and disturbed-habitat specialists (e.g. grassland birds) (Koh et al. 2005). Forest species were defined by their regular occurrence in and use of forested habitats on New Britain, although there were varying degrees to which they were restricted to this habitat (Table 1, habitat breadth). Nocturnal and migratory species were excluded because my surveys were not designed to adequately survey them.

4-2-2 Data analysis

4-2-2-1 Effects of landscape elements on species richness and composition

I modelled species richness among elements using Generalised Linear Models (GLMs) with a Poisson error distribution, in the R ‘stats’ package (R Core Team 2013). The response variable was the total number of species recorded at each site, and the single categorical predictor was the landscape element, comprised of five levels (representing each element). Species richness in elements was considered significantly different where 95% CI (confidence intervals) did not overlap other estimates. I conducted multiple comparisons between landscape elements and accounted for family-wise error in significance tests of pairwise comparisons using a Bonferroni correction (Quinn & Keough 2002). Moran’s *I* test statistic was used to test for effects of spatial autocorrelation in model residuals (package ‘spdep’, Bivand 2014).

I determined the effect of landscape elements on bird species composition using multivariate GLMs (Wang et al. 2012). I built models based on the presence-absences of species at sites, specifying a binomial error distribution. Landscape element was included as a single categorical predictor for all species, and unlogged forest the reference factor. Models were built and tested using the ‘manyGLM’ function in package ‘mvabund’ (Wang et al. 2013). To determine whether landscape elements had a significant effect on community assemblage, the data were resampled using parametric bootstrapping, with likelihood ratio employed as the test statistic (Wang et al. 2012). The significance of landscape element on individual species abundance was corrected for family-wise error between species using Holm’s multiple testing procedure (Wang et al. 2012). Significance values were then used to identify species that were responsible for differences among elements, and species abundance plots by landscape element were used to distinguish the element(s) for which they were comparatively most localised (Warton 2008). This allowed me to determine species characteristic of certain land-uses.

4-2-2-2 Effects of traits of species on their prevalence in landscape elements

Based on global literature on the effects of disturbance on tropical bird communities I identified six traits with the potential to affect species’ occupancy of landscape elements: diet, body size, habitat breadth (an index of forest specialisation), primary stratum occupancy layer and species and sub-species geographic range (Table 4.1). Species were included in a trait class based on data from field guides, regional scientific literature, and online databases, along with expert opinion and field observations. For birds with insufficient data, I approximated their trait class from conspecifics (in the case of sub-species) and congeners. Details of the process of trait classification for each species and literature cited can be found in Appendix Table B.1, Appendix B.2 and B.3.

I analysed the effects of landscape elements on the relative occurrence of trait classes using generalised linear models (GLMs). For each trait, I generated a univariate GLM in which the response variable was the proportion of the total number of records of species within each trait class (i.e. across the entire dataset) that occurred at a given site. Landscape element was the single categorical predictor, and unlogged forest was the reference factor. As the data were proportional data, a binomial error distribution and logit link was specified. Autocorrelation analysis (Moran's *I*) revealed autocorrelation in model residuals for carnivores, possibly due to the location of seasonal water bodies. I accounted for this autocorrelation by including 'northing' as a predictor for each site, following Taylor (2012). Model fit was calculated using the percentage of null deviance explained (d^2) (Zuur et al. 2011).

Table 4.1 Species traits and categorisations. Literature cited demonstrate studies where traits have been associated with declines in response to disturbance for the tropics generally and for the SE-Asia/Oceanic bird fauna.

Trait	Measurement	Trait Classes*	Rationale for inclusion of trait	Pan-tropical literature	SE Asian–Oceanic literature
Diet	Primary food consumed by the species	Frugivore Carnivore (vertivores, & insectivores) Omnivore (>2 food sources)	Food resources can vary across landscape elements and drive heterogeneity in species' occurrence.	Canaday, 1997; Gray et al., 2007; Karp et al., 2011; Newbold et al., 2013.	Aratrakorn et al., 2006; Bowman et al., 1990; Kanowski et al., 2004. Sam et al., 2014
Body Size	Body mass and length	Large-bodied (>300 g) Medium (50-250 g) Small (< 50 g)	Body size in birds is associated with fecundity, home range, energy requirements, hunting pressure, and habitat structural requirements.	Laurance and Bierregaard, 1997; Najera and Simonetti, 2011; Pimm et al., 1988; Thiollay, 1999.	Boyer and Jetz, 2010; Cleary et al., 2007.
Habitat Breadth	Index of forest specialisation	Forest (old-growth) Forest edge Secondary closed forest (mature) Secondary open forest (young) Generalist species (all habitats)	Habitat breadth – ability to use multiple land-cover types as well as forest use can be an indicator of specialist requirements of species throughout their life history stages	Devictor et al., 2008; Gage et al., 2004; Kattan et al., 1994; Ruiz-Gutierrez et al., 2010.	Bowman et al., 1990.
Stratum Use	Primary vegetation stratum used by the species	Ground Midstorey Sub-canopy Canopy	Vegetation stratum use is related to species' needs in vertical structure (for foraging, nesting and social activities).	Laurance and Bierregaard, 1997; Ribon et al., 2003; Stouffer et al., 2006; Sodhi, 2004.	Cleary et al., 2007 Ranganathan et al., 2008; Waltert et al., 2004; Peh et al., 2005.

Trait	Measurement	Trait Classes*	Rationale for inclusion of trait	Pan-tropical literature	SE Asian–Oceanic literature
Species Range (historic dispersal ability)	Species geographic range	New Britain & Bismarck Archipelago endemics Northern Melanesian endemics Melanesian range birds Asia-Pacific range birds	Geographic range has been linked to both physical and behavioural ability to leave an area and re-colonise novel habitats (Diamond 1981) and restricted range (e.g. endemism) is considered a criterion for predicting extinction risk in birds according to the IUCN because of localised and globally small population sizes (IUCN, 2012).	Gage et al., 2004; Laurance et al., 2002; Moore et al., 2008; Renjifo, 1999; Van Houtan et al., 2007.	Brooks et al., 2007; Boyer, 2010; Martin and Blackburn, 2013; Posa, 2007; Waltert, 2011.
Sub-species Range (current dispersal ability)	Sub-species geographic range	New Britain endemics Bismarck Archipelago endemics Melanesian range birds			

4-3 Results

I detected 58 of the 68 lowland forest-dwelling bird species known to reside on New Britain (Dutson 2012). Five species were removed from my analysis because they were supra-canopy species (swifts, raptors) and were thus detected differently in closed and open elements. Six species were removed because they had <2 occurrences, and another six were removed because of inconsistent identification throughout the study. This reduced my surveyed forest birds to a subset of 41 species (Table 4.2).

Table 4.2 Species detected at Open Bay. Emboldened species are those included in the analysis.

Species Name	Common Name	Reason if not included
Accipiter novaehollandiae	Variable goshawk	supra-canopy
Accipiter princeps	New Britain Grey-headed Goshawk	supra-canopy
Aceros plicatus	**Blythe's Hornbill**	
Alcedo lepida	**Variable Dwarf-kingfisher**	
Aplonis metallica	**Metallic Starling**	
Aviceda subcristata	**Pacific Baza**	
Casuarius bennetti	Dwarf Cassowary	< 2 records
Centropus violaceous	**Violaceous Coucal**	
Cacatua ophthalmica	**Blue-eyed Cockatoo**	
Cacomantis variolosus	**Brush Cuckoo**	
Caloenas nicobarica	Nicobar pigeon	< 2 records
Centropus ateralbus	**Pied Coucal**	
Chalcophaps stephani	**Stephan's Ground Dove**	
Charmosyna placentis	Red-flanked Lorikeet	inconsistent identification
Charmosyna rubrigularis	Red-chinned Lorikeet	inconsistent identification
Coracina papuensis	**White-bellied Cuckoo-shrike**	
Coracina lineata	Yellow-eyed Cuckoo-shrike	inconsistent identification
Coracina novaehollandiae	Black-faced Cuckoo-shrike	inconsistent identification
Coracina tenuirostris	**Common Cicadabird**	
Corvus orru	**Torresian Crow**	
Ducula rubricera	**Red-knobbed Imperial-pigeon**	
Dicaeum eximium	**Bismarck Flowerpecker**	
Dicrurus bracteatus	**Spangled Drongo**	
Ducula finschii	**Finsch's Imperial-pigeon**	
Ducula melanochroa	Bismarck Imperial-pigeon	< 2 records
Ducula pistrinaria	Island Imperial-Pigeon	< 2 records
Ducula subflavescens	**Bismarck Pied Imperial-pigeon**	
Eclectus roratus	**Eclectus Parrot**	
Eudynamys scolopacea	**Common Koel**	
Falco severus	Oriental Hobby	supra-canopy
Gallicolumba beccarii	Bronze Ground-Dove	< 2 records
Gallicolumba jobiensis	White-breasted Ground-dove	< 2 records
Geoffroyus heteroclitus	**Song parrot**	
Haliastur indus	Brahminy Kite	supra-canopy
Hemiprocne mystacea	Moustached tree-swift	supra-canopy
Lalage leucomela	**Varied Triller**	
Lorius hypoinchrous	**Eastern Black-capped Lory**	

Species Name	Common Name	Reason if not included
Macropygia amboinensis	**Brown Cuckoo-dove**	
Macropygia nigrirostris	Bar-tailed Cuckoo-dove	inconsistent identification
Megapodius eremita	**Melanesian Megapode**	
Micropsitta pusio	Buff-faced Pymy Parrot	inconsistent identification
Mino dumontii	**Yellow-faced Myna**	
Monarcha verticalis	**Bismarck pied Monarch**	
Myiagra alecto	**Shining Flycatcher**	
Myzomela cineracea	**Ashy Myzomela**	
Nectarinia aspasia	**Black Sunbird**	
Pachycephala pectoralis	**Golden Whistler**	
Philemon cockerelli	**New Britain Friarbird**	
Pitta erythrogaster	**Red-bellied pitta**	
Ptilinopus insolitus	**Knob-billed Fruit-dove**	
Ptilinopus rivoli	**White-breasted Fruit-dove**	
Ptilinopus superbus	**Superb Fruit-dove**	
Reinwardtoena browni	**Pied Cuckoo-dove**	
Rhipidura rufiventris	**Northern Faintail**	
Tanysiptera nigriceps	**Black-headed Paradise Kingfisher**	
Todiramphus chloris	**Collared Kingfisher**	
Todiramphus albonotatus	**White-mantled Kingfisher**	
Tricholglossus haematodus	**Rainbow Lorikeet**	

4-3-1 Species richness and composition

Cumulative species richness across all sites in each element did not differ between unlogged forest, secondary remnant and mature plantation elements (Table 4.3). However, sampling effort differed among elements (see section 2.2) preventing direct comparisons. Comparisons between species richness at **individual sites** (alpha diversity) revealed that species richness was highest in secondary habitats (remnant and riparian), followed by unlogged forest, mature plantations, and young plantations (Table 4.3).

In addition to species richness differences at sites, all modified elements differed in species composition compared to unlogged forest (multivariate GLM, $p < 0.006$). Given ≥90% of species found in unlogged forest were also found in all other elements except young plantations (Table 4.3) compositional differences amongst 'mature' elements arose mainly from changes in the frequency of occurrence of species. By contrast, young plantations differed mainly because of the absence of 16 of the unlogged forest species. Individual species abundances were found to be significantly different among landscape elements for 25 species ($p_{adj} < 0.05$ for all models). The habitat association of 6 species conflicted with their categorisation in the literature (Table 4.4).

Table 4.3 Species richness of birds in landscape elements

Landscape element	Cumulative number of species across all sites within a landscape element (n = no. sites)	Site-level species richness (s.e.) ($p < 0.05$)*	Percent of unlogged forest bird species recorded
Unlogged Forest	40 ($n = 32$)	15.06 (0.69)	100 %
Secondary Remnant	40 ($n = 9$)	20.78 (1.52)*	95 %
Secondary Riparian	38 ($n = 14$)	18.21 (1.14)*	90 %
Mature Plantations	40 ($n = 43$)	12.81 (0.55)*	92.5 %
Young Plantations	25 ($n = 24$)	5.25 (0.47)*	60 %

* 95% confidence intervals do not overlap with zero with unlogged forest as reference group.

Table 4.4 Bird species characteristic of habitat types throughout the plantation landscape with increasing levels of disturbance from left to right

Old-growth associated birds		Old secondary associated birds		Secondary associated birds	
Unlogged forest	Unlogged forest and secondary remnant*	Secondary remnant	Secondary remnant and secondary riparian †	Secondary riparian	Mature plantations
Ducula finschii	*Ducula rubricera*	*Aceros plicatus*[F]	*Alcedo lepida*	*Aplonis spp.*	*Tanysiptera nigriceps*^
Ptilinopus insolitus[SEC]	*Mino dumontii*[SEC]	*Cacatua opthalmica*	*Chalcophaps stephani*	*Dicrurus bracteatus*	*Dicaeum eximum*
Ptilinopus rivoli	*Ptilinopus superbus*	*Lorius hypoinchrous*	*Tanysiptera nigriceps*^	*Philemon cockerelli*	*Todhiramphus albonotatus*
Todhiramphus chloris^[SEC]		*Macropygia amboinensis*		*Rhipidura leucophrys*	
		Pachycephala pectoralis[F]		*Todhiramphus chloris*^[SEC]	
		Rhipidura rufiventris			
		Lalage leucomela			
		Megapodius eremita[F]			
		Monarcha verticalis[F]			

[SEC] and [F] denote species that have been categorised in the literature as secondary or forest dependent species

* Birds that occur in unlogged forest and secondary remnant in similar abundance, significantly greater than all other elements

† Birds that occur in secondary riparian and secondary remnant in similar abundance, significantly greater than all other elements

^ Birds that were equally abundant in 2 disparate elements

4-3-2 Trait occurrence across landscape elements

Landscape elements strongly affected the functional composition of bird communities, with the prevalence (mean occurrence) of different trait groups varying between elements (Figure 4.1). All types of species were less prevalent in young plantations. Notably, frugivorous birds and forest specialists were significantly more likely to occur in unlogged forest and secondary remnant elements than in the more disturbed plantations and riparian secondary forest (Figure 4.1). Large and medium sized species, along with canopy and sub-canopy using birds, were more commonly encountered in unlogged and secondary forests than plantations (Figure 4.1). By contrast, ground-dwelling birds, and restricted range endemic bird species and sub-species were prevalent across multiple land-covers, except young plantations.

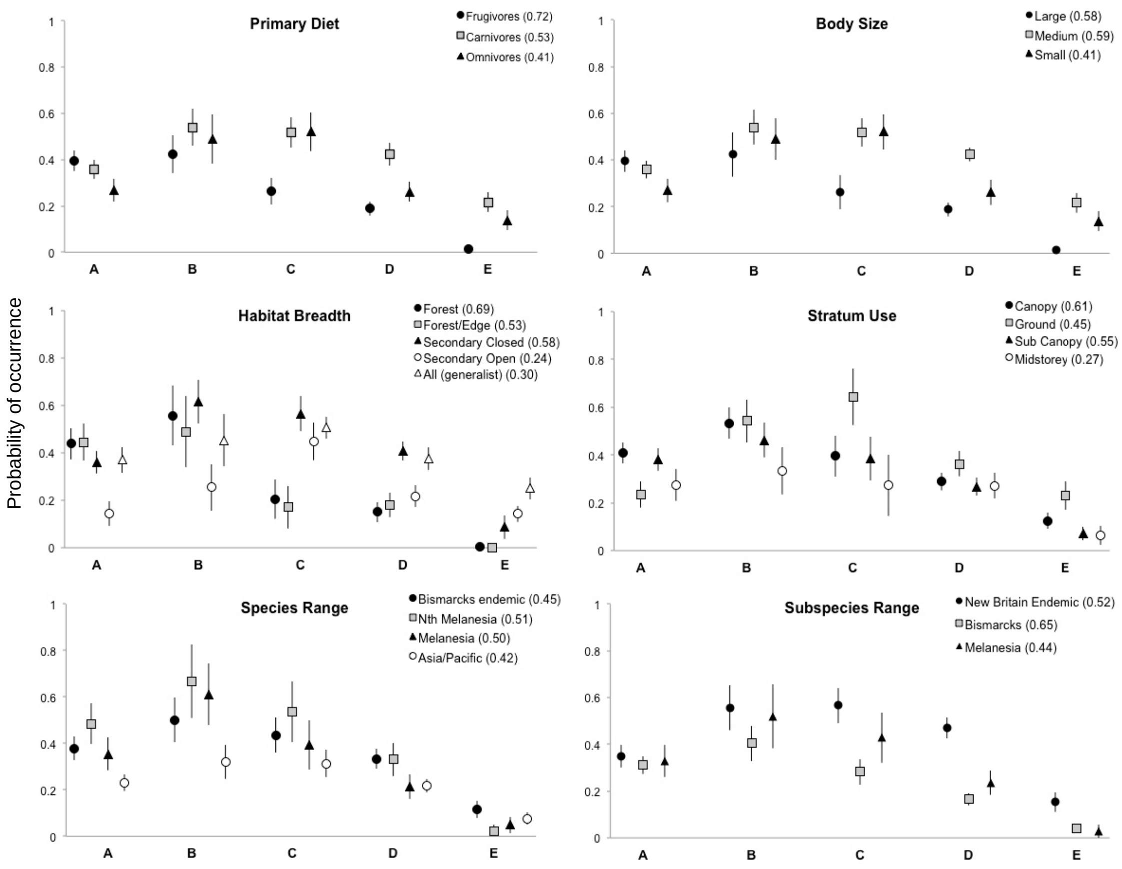

Figure 4.1 Bird trait type analyses showing probability of occurrence (standard error) of birds of each of the six trait classes among landscape elements highlighting changes in functional composition. Model fit for each trait type (d^2) is indicated in brackets. A – unlogged forest, B – secondary remnant, C – secondary riparian, D – mature plantation, E – young plantation. Numerical values and model results are detailed in Appendix Table B.4.

4-4 Discussion

Mature native timber plantations and secondary forest elements supported ≥90% of unlogged forest-occurring birds, indicating that multi-use landscape conservation strategies that incorporate these production elements could contribute towards bird conservation in tropical regions. However, the composition of bird assemblages differed between unlogged forest and modified elements, with fewer specialised species recorded in modified elements. The ecological traits of species affected their vulnerability to landscape change, as modified elements had fewer frugivores, forest-dependent species and, to a lesser degree, species of large/medium body size and canopy/sub-canopy species. This highlights the importance of maintaining unlogged forests in the landscape. In contrast to expectations, a priori-defined specialist endemic and ground-dwelling species displayed equal or greater prevalence in modified elements, with the exception of young plantations.

4-4-1 Bird richness and composition in plantation landscapes

I observed more forest bird species at secondary forest compared to unlogged forest sites. In other studies, similar findings have been attributed to the addition of 'generalist' species that occur in logged, but not unlogged forests (e.g., Johns 1996; Felton, Wood, et al. 2008b). Similarly, I found that secondary forests contained a similar or greater prevalence of wider-ranging secondary-associated species compared to unlogged forest, despite limiting the analysis to species that are predominantly forest occurring. Furthermore, I found secondary forests have a similar or greater occurrence of many species considered old-growth specialists. This suggests that secondary forests contain resources required by old-growth specialists, as has been observed in other studies of recovering, logged tropical forest (see, Chazdon, Peres, et al. 2009b). My concurrent study found no difference in composition of forest tree species between unlogged forest and secondary remnant forest (Chapter 3), further supporting this conclusion.

It is important to note that while the secondary elements did provide key habitat for forest birds, this depended on their frequency and exposure to disturbance, similar to relationships observed in other tropical regions (e.g., Barlow, Mestre, et al. 2007b). For example, narrow secondary riparian forests, which experience ongoing disturbance from non-commercial timber extraction and edge effects, had lower species richness and increased dominance of secondary-associated birds compared to other secondary remnants.

Over 90% of forest bird species were recorded in mature plantations; a high proportion compared to other studies of tropical timber plantations (Marsden et al. 2001; Zurita et al. 2006; Nájera & Simonetti 2010; Farwig et al. 2008; Bell 1979). This finding is likely to be a consequence of both the low-intensity stand-level management of plantations (Marsden et al. 2001) and the focal plantation species (*E. deglupta*) being native to the location (Chey et al. 1998). These factors combined can facilitate the recruitment of a native rainforest understorey (Chapter 3), which along with the plantation species itself, can provide structural and food resources for many forest birds (Nájera & Simonetti 2010). For example, *E. deglupta* is known to be a valuable nectar resource for the island's parrot and cockatoo species (Marsden & Pilgrim 2003b).

However, plantations do not support all species as effectively as unlogged forest does. Mature plantations had a lower incidence of over one-third of old-growth species compared to unlogged forest, and an increased incidence of more 'generalist' species, a common trend in plantation studies (Farwig et al. 2008; Zurita et al. 2006). Moreover, young plantations contained far fewer species than mature plantations, as has been found elsewhere (Sheldon et al. 2010). This highlights the importance of correctly classifying land-covers to understand their conservation potential (i.e. the age of a plantation, not simply its classification as a plantation, is important). Thus, native plantations can provide spatial continuity in the landscape of some, but not all, forest resources and are extremely limited in early stages, where they induce temporal discontinuity.

4-4-2 The role of species' traits

I expected that species with disturbance-susceptible traits would be more common in the unlogged forest and decrease in prevalence with increasing disturbance intensity. While I observed a general trend of species with vulnerable traits characterising less disturbed habitats (e.g. frugivores (Newbold et al. 2013), forest specialists (Gage et al. 2004)), there were also exceptions. If a given trait (e.g. diet) is deterministic across a disturbance gradient, then its most vulnerable class according to the literature (e.g. frugivores and/or carnivores) should explain the most variation in the occurrence model (highest d^2). This pattern held for some traits (e.g. diet, habitat breadth and body size), but not for others (e.g. species range restriction, stratum use).

Frugivores and forest specialists occurred most frequently in unlogged forest, including two species (*Reinwardtoena brownii* and *Ptilinopus rivoli*) that were only found in unlogged forests. The dependence of frugivores on unlogged forest likely relates to the higher diversity of fruiting plants (though not necessarily abundance) in unlogged forests (Gibson et al. 2012; Marsden & Symes 2008). In addition, over half of these species are commonly-hunted throughout PNG and in the study region (Steadman 2006; *pers. obs.*), and would be less exposed to this threat in the more dense, isolated unlogged forests. All frugivores in this study were either medium or large-bodied and are known to range widely to track fruiting resources in tropical forests (Sam et al.

2014; K. M. Holbrook et al. 2002). Therefore, it is possible that the mobility of frugivorous birds facilitated their emigration to preferred habitat, causing their observed deficit in modified elements (Neuschulz et al. 2012).

Medium and large-bodied birds (aside from frugivorous species) and canopy and sub-canopy birds occurred with equal frequency amongst unlogged and secondary forest elements but were less common in plantations. This suggests a general tolerance of these often-found ‘specialised’ traits (Sodhi et al. 2004; Kennedy et al. 2010) for low level disturbance that does not extend to the more simplified stands of monoculture plantations (Nájera & Simonetti 2010).

Endemic birds occurred with equal or greater frequency in modified elements compared to unlogged forest (with the exception of the young plantations). This contrasts with continental plantation studies that have found endemic birds to be more vulnerable to disturbance owing to small population size, limited dispersal capacity and niche specialisation (e.g., Jankowski & Rabenold 2007; Holbech 2009; Renjifo 2001). These conflicting results may arise from the biogeographic context of island systems. There is an emerging consistency among island studies demonstrating a lack of association between range restriction and vulnerability to disturbance (Cleary et al. 2007; T. E. Martin & G. A. Blackburn 2013; Kennedy et al. 2010). Biotic communities of oceanic islands have commonly arisen from repeated colonisation events and subsequent speciation through isolation. Consequently, island species—at least historically—have generally possessed superior colonising traits such as high vagility and niche breadth (ecological tolerance) (T. E. Martin & G. A. Blackburn 2013; Mayr & Diamond 2001).

Moreover, New Britain’s lowland forest species represent a depauperate bird community compared to source pools of New Guinea and Australasia (Steadman 2006). Such species-poor communities are thought to experience less niche partitioning of resources because of reduced competition, leading to reduced specialisation (Clegg 2010; Diamond 1970). On islands east of Wallace’s line, lower avifaunal richness and a broader realised niche are accredited with the increased resilience observed in traditionally vulnerable trait classes such as understorey insectivores and restricted range species (T. E. Martin & G. A. Blackburn 2013; Abrahamczyk et al. 2008; Waltert et al. 2005).

Thus, the different biogeographic and evolutionary processes shaping oceanic island endemic birds may confer a different complement of traits to continental endemic birds. Further, greater niche-breadth of New Britain’s lowland species pool may also explain the greater disturbance tolerance found for commonly susceptible traits than expected (e.g. ground-dwelling birds) (Sekercioglu & Sodhi 2007). Although the processes suggested here are as yet un-tested, it remains that for New Britain’s lowland endemic birds, restricted geographic range was not a surrogate for habitat-level mobility or niche specialisation in birds. Therefore, these traits should be measured explicitly for island birds when investigating the impact of human activities at the habitat- and landscape-scale.

4-4-3 Conservation Implications

The high richness and regular occurrence of forest birds in all production elements (except young plantations) highlights the capacity of native timber plantations to contribute towards bird conservation, given appropriate management. However, while mature plantations support a subset of forest birds, they are inevitably harvested, returning them to young plantations depauperate of forest birds. Thus, the transient nature of mature plantations means that old-growth forest reserves are vital for the temporal continuity of avifaunal biodiversity in the landscape. My work illustrates that selectively-logged secondary forests can also contribute towards tropical bird conservation, including for those of greatest conservation concern (e.g. frugivores and old-growth forest-associated species). Protection of secondary forests would substantially expand the proportion of the landscape providing refuge for forest birds (Sam et al. 2014). In theory, timber plantation establishment should assist this goal by reducing the need for logging of both unlogged and old-growth secondary forests (Brockerhoff et al. 2008). However, there is no guarantee that this will occur in the long-term without formal protection of these forests (Shearman et al. 2012), or at least mechanisms which can incentivise their protection (Dennis et al. 2008).

Trait-based analyses of faunal responses to land-use change are increasingly common in conservation biology, yet a general understanding of which traits confer vulnerability is confounded by contextual factors such as biogeography, land-use history, and disturbance type and intensity (Ewers & Didham 2006; T. E. Martin & G. A. Blackburn 2013; Owens & Bennett 2000). Here, I found a general conformity of disturbance response for trait types which acted at the habitat- and landscape-scale, such as those traits related to forest resource specialisation (Newbold et al. 2013). Trait analyses thus proved helpful for explaining the relative value of different landscape elements to lowland birds, and for informing land-use planning. For example, identifying the importance of unlogged and mature secondary forests for populations of the 17 frugivore and forest-specialist birds. However, analysis of traits such as restricted geographic range, which may act beyond the habitat-scale, was not informative in this landscape. This highlights the importance of understanding the scale at which disturbance interacts with species traits when designing conservation management strategies.

The composition of the multi-use landscape in this study represents an ideal scenario: a high ratio of unlogged forest to clearfelled area in the broader landscape and extensive, old-growth, secondary forest within the production landscape (Chazdon et al. 2009). Such compositions are rarely found outside of recently developed areas (Gibson et al. 2012). Further habitat loss through encroachment on intact forests and the replacement of native plantations by crops (e.g. oil palm), which is planned for New Britain (Nelson et al. 2010), would likely cause the decline of many forest birds in the landscape (Edwards, Hodgson, et al. 2010a). For endemic island species this could lead to their global endangerment (T. E. Martin & G. A. Blackburn 2013; Boyer 2010). Thus, while multi-use landscapes can potentially achieve a balance between conservation and production, success is highly dependent on the choice of land-use and the proportion of remnant primary and secondary forest in the local and broad-scale landscape. Long-term viability of forest biodiversity necessitates the protection of primary forest, and increasingly in the tropical lowlands, older secondary forests.

4-5 Chapter summary

At least 90% of forest bird species occurred in mature plantations and secondary (regrown logged) forest. However, composition changes indicated successive loss of more vulnerable species (medium and large-bodied frugivores, forest specialists) with increasing intensity of disturbance. In contrast to many continental studies, where endemism confers susceptibility to disturbance, I found endemic, island species widely distributed across all land-uses, possibly reflecting their historical colonising aptitude. The findings of this chapter suggest that native plantations, when judiciously managed in concert with unlogged and secondary forest reserves, may assist with biodiversity conservation alongside commercial timber production. Species' traits help explain their responses to landscape management, however, conservation managers should recognise that the type and intensity of disturbance and biogeography of a region will affect the traits-disturbance interaction.

CHAPTER 5

Vegetation in a mixed tropical forest production landscape [3]

An example of Open Bay's mature plantation forest at 14 years

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[3] Pryde, EC (*in prep*) The effect of a native timber plantation landscape on rainforest vegetation in Papua New Guinea. Journal of Tropical Forest Science.

CHAPTER FIVE

This chapter evaluates the effect of land-use on vegetation and stand-level structural attributes (habitat properties) within the *Eucalyptus deglupta* production landscape (objective 2). Vegetation composition and stand-level structural attributes can be indicative of the relative resource availability offered by different land-uses for forest biota. Here I compare a suite of stand-level structural attributes as well as plant species richness and composition among the unlogged forest, plantation and forestry-affected landscape elements. I identify which vegetation attributes most clearly differentiate unlogged forest from modified landscape elements and how different land-use types affect all attributes measured. In doing so, I contribute valuable information to the tropical literature on the disturbance-response of lowland forest in this Pacific island region. This chapter also provides background analysis for the following data chapter by way of evaluating and selecting a set of candidate variables for use as predictors in modelling bird species occurrence across the landscape (Chapter 6).

5-1 Introduction

Multi-use production landscapes are playing an increasingly important role in biodiversity conservation, particularly in tropical lowlands where human-affected landscapes continue to expand and full protection of old-growth forests in reserves has had limited success (Laurance et al. 2012; Sutherland et al. 2009). Yet, the capacity for biodiversity conservation in many tropical production landscapes remains poorly understood (Chazdon, Harvey, et al. 2009a; Paquette & Messier 2010). In tropical lowland forests, the extent to which multi-use production landscapes can conserve native biota is likely to be influenced by the ability of their component land-covers to provide habitat resources for species (Lindenmayer 2010). For tropical vegetation, habitat quality is largely contingent on the physical and nutrient condition of the soil, provision of structural substrates, and suitable microclimate conditions (e.g. light levels and moisture) (M. S. Ashton et al. 2001; M. S. Ashton 2011). For rainforest fauna, habitat quality is associated with the complexity of vegetation structure and the diversity and composition of plant species and life forms present (Nájera & Simonetti 2010; Barlow, Mestre, et al. 2007b).

Tropical lowland forest areas are used for a range of production purposes including agriculture, timber extraction and tree crops (Gardner et al. 2010; Ranganathan et al. 2008). For a given production type, habitat properties can be influenced by the intensity, duration, frequency and scale of disturbance imposed by resource production and harvest requirements (Chazdon 2003;

Lamb 2010). For example, more intense land-uses (e.g. agricultural crops, cattle pasture) implement clearfelling and conversion of pre-existing habitat, causing the simplification of vegetation structure and a reduction in plant species diversity (Letcher & Chazdon 2009; Zurita & Bellocq 2012; Catterall et al. 2012). By contrast, less intense land-uses may encourage the retention of pre-existing structural complexity and vegetation cover (e.g. selectively logged forests, agroforests), and support a greater diversity of plants (Gibson et al. 2012). Multi-use production landscapes are typically comprised of a range of land-covers, representing a gradient in intensity and timing of disturbance (e.g. unmodified forest remnants → secondary forest → production land-cover(s)). Therefore, to assess the biodiversity conservation potential of a production landscape as a whole, it is vital to examine the relative effects of land-use on the compositional and structural properties of component land-covers.

Plant species reassembly after ‘natural’ disturbances in unmodified rainforests generally involves colonisation and dominance of early successional (heliophilic) species that are overtaken by their shade-tolerant counterparts over time and die off (Chapter 3, section 3-2-1). Thus, successional advancement is typified by increasing species richness and dominance of late-successional species co-existing with long-lived mid-successional species, and a contraction of earlier-successional plants to disturbed patches (e.g. canopy gaps , Bazzaz & Pickett 1980). Anthropogenic disturbance may alter this successional trajectory according to the intensity, frequency and scale of disturbance involved (P. M. Ashton et al. 1997). For instance, studies of tropical secondary forests (regenerating after conversion and/or degradation caused by timber extraction) suggest that in some cases plant species richness can be relatively quickly restored (Letcher & Chazdon 2009; Berry et al. 2010), but that compositional recovery may take much longer (P. A. Martin et al. 2013; Dent et al. 2012). This in-turn may imperil faunal species should compositional changes disproportionately effect plant species that provide important resources (Felton, Wood, et al. 2008b; C. A. Chapman et al. 2010).

Similarly, structural attributes of a given land-use may be influenced by the disturbance regimen. In theory, for land-uses where disturbance events are infrequent (e.g. fallow secondary growth, unmodified forests) the accumulation of plant biomass (or basal area) will likely be greater compared to younger or more frequently disturbed land-use types (Day et al. 2014). For example, the presence of large, old trees is a feature of old-growth forests that contributes greatly to stand basal area (Day et al. 2014), which can be reduced in recently-logged forest where larger trees trees are preferentially removed and/or can be damaged during harvest (West et al. 2014). Structural complexity may also be associated with the accumulation of plant species through time (as succession proceeds), potentially incorporating a greater diversity of growth rates and architecture that may add to overall structural complexity (Pinotti et al. 2012).

A more complex stand structure is deemed important for the retention of populations of rainforest fauna because of the provision of a greater number of niche resources it entails (R. H. MacArthur 1964; Kanowski et al. 2010; Nájera & Simonetti 2010).

The incorporation of numerous vertical strata in more complex stands can also serve to augment canopy closure, which may affect levels of heat and light penetration to the understorey (Kabakoff & Chazdon 1996). Understorey microclimatic conditions influence the composition of ground-storey vegetation (Orians et al. 1996). Disturbance that induces canopy openness can cause regular penetration of sunlight to the understorey, and reduce humidity. These conditions favour the growth of pioneer ground covers such as grasses, heliophilic ferns, and herbaceous vines and scramblers (Guariguata & Ostertag 2001; Ewel & Bigelow 1996). When extensive, these pioneer plants may inhibit recruitment of later-successional plant species (Lamb 1994). By contrast, closed canopies are more likely to assist successional progression by providing favourable conditions for understorey recruitment of shade-tolerant, juvenile trees and lianae (seedlings and shrubs) (Hall et al. 2003; D. A. Clark & D. B. Clark 1992; Putz 1984). Successional processes may also influence properties of leaf litter on the forest floor; disturbed habitats where the ratio of early:late successional plants is higher have demonstrated a reduced nutrient quality and decomposition of leaf litter (Vasconcelos & Laurance 2005; Parsons & Congdon, 2008). Disturbance-induced changes in understorey microclimate and plant species composition have been associated with a reduced richness of ground-dwelling fauna such as understorey insectivorous birds (Sam et al. 2014; Canaday 1997).

The intensity, duration, and frequency of disturbance are also thought to influence the composition of unique rainforest life forms, including the structural parasites (epiphytes, vines, lianae, hemi-epiphytes, climbing palms); large, perennial herbs (of order *Zingiberales* (e.g. gingers) and family *Araceae* (e.g. aroids)); and palms (Webb et al. 1981). Structural parasites depend on the presence of trees as substrate for at least part of their life cycles, and have different shade tolerances and growth rates (Benavides et al. 2013; Fayle et al. 2009). Thus, while generally considered indicative of more mature forest with high stem density, some structural parasites may actually abound in the more favourable light conditions present in mid-successional (secondary) forest (Putz 1984; Letcher & Chazdon 2012). Large perennial herbs are similarly variable in their shade tolerance and microclimate requirements (Rundel et al. 1998), but they are associated with conditions of high humidity and canopy cover that permits some regular sunlight (Kubitzki 1998). Rainforest life-forms provide important structural and food resources for fauna, particularly invertebrates (Kaufmann & Maschwitz 2006; Ellwood et al. 2002), and birds (DeWalt et al. 2003; Cruz-Angon & Greenberg 2005). Therefore, their composition can have an important effect on the biodiversity conservation value of a given land-use type.

Here, I sought to understand the capacity for biodiversity conservation in a native ***Eucalyptus deglupta*** timber plantation landscape on New Britain Island, Papua New Guinea by assessing the effects of modified landscape elements on vegetation properties. Few studies of vegetation responses to disturbance in production landscapes have taken place in Oceania, and there is a poor understanding of secondary forest regeneration in this region compared to the rest of the tropics (Woinarski 2010). Similarly, very few studies have quantified the structural and compositional changes occurring in tropical timber plantations globally, particularly within native timber plantations (Stephens & Wagner 2007).

I compared vegetation attributes of landscape elements reflecting land-uses of different timing and degree of modification (unlogged forest and modified landscape elements (secondary forest and plantations)). Vegetation attributes were representative of two components of biodiversity: vegetation structure (tree attributes, ground cover) and the richness and composition of plant species and types (adult tree species, rainforest life forms). I had two principal goals: (1) to ascertain which vegetation attributes most clearly differentiated unlogged (old-growth) forest from modified landscape elements (i.e. which attributes were most affected among landscape elements); and (2) to determine the extent of old-growth forest attributes conserved in modified elements (i.e. how attributes were affected among landscape elements). A secondary goal (3) was to choose a subset of these attributes as candidate variables for modelling bird species occurrence throughout the plantation landscape (Chapter 6). Understanding the effects of land-use disturbance on vegetation and habitat properties can assist with the design of effective conservation management actions to maintain both native rainforest flora and fauna in production landscapes.

5-2 Methods

Study Area, study design and site selection are outlined in sections 2-1-1 and 2-1-2. For each site I collected data on a series of standard structural attributes (Table 5.1), on tree species richness (Chapter 3) and on the occurrence of special rainforest life forms (Table 5.2). I compared site-level differences in vegetation structural attributes among landscape elements by fitting GLMs and GLMMs where appropriate (Table 5.4, section 5-2-2-1). For ground cover and rainforest life forms, I summarised changes in composition in response to the disturbance gradient using principal components analysis (PCA, sections 5-2-2-2 and 5-2-2-3 respectively). To choose a set of variables for use in modeling bird species occurrence, I compared the results of all analyses and tested for correlations between suitable variables (section 5-2-2-4).

5-2-1 Vegetation data

Vegetation surveys were completed for 142 sites across landscape elements, with a single plot per survey site (young plantations = 20, mature plantations = 50, secondary riparian = 14, secondary remnant = 10, unlogged forest = 48). Two attributes, special life forms and vertical stratification had data missing for some sites of young and mature plantation elements, making the total number of sites for these landscape elements 17 and 44 and respectively (Chapter 2, Table 2.1). The vegetation attributes that were selected for survey and their mode of measure were based on the methods presented in the *Monitoring Revegetation Projects for Biodiversity in Rainforest Landscapes Toolkit* (Kanowski & Catterall 2007 hereinafter the ‘toolkit’), and were adapted to the New Guinean context (Table 5.1 and in text). The toolkit was designed to monitor the success of restoration projects in tropical Australian forests and included stand-level properties that were representative of two components of biodiversity: vegetation structure and the richness and composition of plants (Kanowski et al. 2010). These consisted of site-level measures of: tree attributes (plant richness and structural complexity), canopy cover (structural complexity), ground cover (plant composition and structural complexity) and composition of rainforest life forms (plant composition, Table 5.1). Since a key aim of this thesis is to determine the impact of the plantation landscape on the forest bird community, I also added attributes potentially important for bird usage that were not in the toolkit (R. H. MacArthur 1964; R. MacArthur & J. MacArthur 1961).

Plots used for bird surveys were also used for vegetation surveys with nested square subplots of 0.18 ha being employed (Figure 5.1). Tree attributes (outlined in Table 5.1, ‘Tree richness and structural complexity’) were recorded within the entire 0.18 ha, and included the number, species, and size (DBH) of live trees ≥10 cm DBH, as well as the number of dead standing trees. Vertical foliar cover in seven height categories (2–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, 25–35 m and >35 m), and canopy cover were both estimated at two points in the NE and SW ends of the plot. Vertical foliar cover was visually estimated for each height category with the aid of a laser range finder (Opti-logic Laser Rangefinder-600 yd). Vertical foliar cover estimation was conducted using a modified Braun-Blanquet (MBB) (Braun-Blanquet 1932) ordinal scale (outlined in Table 5.2) and the type of vegetation contributing to cover was recorded (Table 5.1, ‘Point measures’). Percent canopy cover was derived from standard digital camera photographs taken at eye-level (~170 cm) pointing up vertically, as per Kanowski (2007). I visually estimated the percentage cover of ground vegetation (vegetation <1m high, leaf litter, rock, bare soil) in two 1 x 1 m quadrats in the north and south of the plot (Figure 5.1). For vertical foliar cover, canopy cover and ground cover, I used the mean of the two surveys at each site in all analyses.

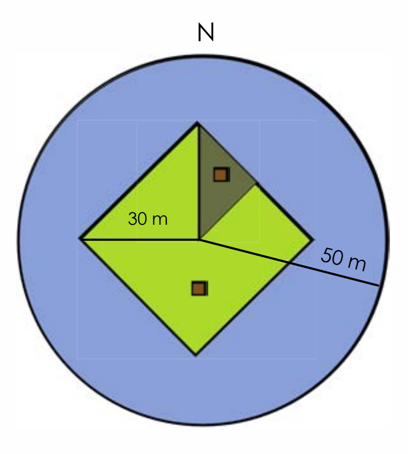

Figure 5.1 Plot design for surveys of vegetation and birds. Blue circle delineates the bird survey plot. Green square represents the ~1800 m^2 vegetation survey plot. The dark green N-NE triangle (~225 m^2) was the location of rainforest life form survey. Brown squares approximate the location of the 1 m x 1 m ground cover quadrats, and canopy and vertical foliar cover estimates.

Table 5.1 Vegetation measurements and their relative scales, taken at each site. Measurements are classified according to the property they represent. The final column explains the method used to derive univariate values for each attribute. Adjusted from Kanowski (Kanowski 2010) Tables 4.2 and 8.2.

Survey area	Habitat Property	Attribute & Measurement(s)	Value & Derivation
Whole plot (1800 m^2)	Tree richness and structural complexity	For each free-standing woody-stemmed plant ≥ 10cm DBH (live trees), we measured:	Species richness Species relative abundance (basal area and counts)
		(a) Species of live trees (genus when species unknown)	
		(b) DBH to the nearest 5cm	Tree size DBH diversity (H') Tree size distribution Site basal area live trees Number of live stems
		(c) For dead trees and stags ≥ 10cm DBH, we measured DBH to the nearest 5cm	Site basal area dead trees Number of dead stems
Point measures		Percent canopy projective foliage cover	Derived from photographs taken on site at each sub-quadrat. Average of 2 x cover estimates calculated from photos as per the toolkit
		For vertical strata (2-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25m, 25-35m and > 35m), MBB* categorisations of foliage cover of: **(a)** stems ≥ 2.5 cm DBH according to DBH class; **(b)** life-forms: vines, climbing palms, hemi-epiphytes, clumping	Vertical foliar diversity (H') Number of height strata (of total n=9) with tree foliage present

Survey area	Habitat Property	Attribute & Measurement(s)	Value & Derivation
		epiphytic ferns, woody vines > 5cm DBH, vine towers	
2 x 1 m^2 quadrat	Ground Cover	Visual estimates of percent of ground covered by: **(a)** Vegetation <1 m high (recorded separately for: grass, ferns, vines and scramblers, shrubs/seedlings (woody stems); **(b)** Leaf litter and fine woody debris (<10 cm diameter); **(c)** Coarse woody debris (>10 cm diameter); **(d)** Rock; **(e)** Bare soil; and **(f)** Moss, and **(g)** Other Ground cover was assessed by looking down at a 1 m x 1 m ground plot, and scoring what can be seen from this vantage point (as if looking at a photo).	Average of 2 x cover estimates for each category Note: 'rocks' and 'other' are not analysed.
Triangular quadrat (225 m^2)	Rainforest life forms	**(a)** Presence /absence of arboreal termite mounds **(b)** Abundance (modified Braun Blanquet (MBB)* categorisations) Life forms: hemi-epiphytes, vines >5 cm diameter, canopy vine towers, sub-canopy vine towers, midstorey vine thickets, ground vine thickets, rattan palms, clumping epiphytic ferns, palm trees, understorey palms, cordylines, other epiphytes, herbs with long wide leaves (Table 5.2).	Life-form richness Life form relative abundance & composition

* MBB = modified Braun-Blanquet categorisations (Table 5.3)

I estimated the relative cover of rainforest life forms using the aforementioned MBB scale within a 225 m^2 sub-quadrat. Life forms were characteristic of rainforest successional stages post-disturbance in the Australasian and New Guinean region (Webb et al. 1976). Many life forms identified in the toolkit were surveyed (Kanowski & Catterall 2007 page 27), but I did not include: cycads and tree ferns because they were absent from the study area; strangler figs and *Pandanus* spp. because they were identified in tree species composition surveys (Chapter 3); and herbs with long, thin leaves because they straddled the descriptions of (i) grasses (counted in ground cover analyses) and (ii) herbs with long, wide leaves, making them difficult to consistently define. Additionally, I included four broad categories to characterise vine structures occurring in different strata (in contrast to just two in the toolkit): understorey vine thicket, midstorey vine thicket, sub-canopy vine tower and canopy vine tower (see Table 5.3 for more detail). All forms of vine masses can potentially provide habitat for fauna, and particularly for birds in upper strata. Conversely, vine thickets can impede growth of other rainforest plant species (Ewel & Bigelow 1996), and vine tangles can contribute to adult tree mortality. Life forms surveyed are listed in Table 5.3 along with detailed descriptions. Appendix Figure C.1 provides some diagrammatic examples of life forms. All Braun-Blanquet measures were converted to midpoint values to make them amenable to GLM analysis (Table 5.2).

Table 5.2 Modified Braun-Blanquet (MBB) cover estimation and corresponding mid-point values used in data analyses.

Braun-Blanquet category	Description	Mid-point value
0	Absent	0
1	< 5% cover and uncommon	0.1
2	< 5% cover and common (numerous individuals)	2.5
3	5 – 25% cover	15
4	25 – 50 % cover	37.5
5	50 – 75% cover	62.5
6	75 – 95% cover	85
7	95 – 100% cover	97.5

Table 5.3 Description of special life forms measured.

Life Form	Description
Hemi-epiphytes	Climbing plants adhering to tree trunks, rooted in ground for part of their life cycle, e.g. climbing pandanus. Much contention surrounds the term ‘hemi-epiphyte’. We surveyed what Zotz (2013) classified as ‘nomadic vines’.
Vines >5 cm diameter	Lianae: climbing woody-stemmed plants dependent on trees for support, and rooted in the ground
Understorey vine thicket	Dense masses of interwoven vine stems in understorey
Midstorey vine thicket	Dense masses of interwoven vine stems in midstorey (may include lianae)
Sub-canopy vine tower	Dense columns of vines growing over and smothering sub-canopy crowns and stems (may include ‘primary’ hemi-epiphytes (N. M. Holbrook & Putz 1996) and lianae)
Canopy vine tower	Dense columns of vines growing over and smothering tree crowns and stems (may include ‘primary’ hemi-epiphytes (N. M. Holbrook & Putz 1996) and lianae)
Rattan palms	These were predominantly *Calamus* species - thicket-forming climbing palms, often spiny.
Palm trees	Palms with stems > 2 m high
Understorey palms	Palms with stems < 2 m high, (also includes juvenile palm trees)

Life Form	Description
Clumping epiphytic ferns	Clumping ferns adhering to plants and trees, e.g. *Asplenium spp.*
Other epiphytes	Growing on trees, e.g. trailing ferns, orchids, not rooted on ground
Cordylines	Shrubs to 5 m high, occasionally branched, with long leaves
Perennial herbs with long, wide leaves	Of order Zingiberales and family Araceae. These were predominantly represented by Zingiberaceae species (gingers). Araceae such as the taros *Colocasia esculenta* and *Cyrtosperma chamissonis* have been cultivated as a food crops in PNG for thousands of years (Denham 2003).

5-2-2 Data analysis

5-2-2-1 Tree species density and structural complexity

To compare the site-level values of tree species density and attributes of structural complexity among landscape elements, I ran a series of generalised linear models (GLMs) in the R ‘stats’ package (R Core Team 2013). Response variables represented the value of a given attribute at each site. For all models the single categorical predictor was the landscape element, comprised of five levels (representing each element). Autocorrelation analyses were conducted using Moran’s *I* test statistic (Chapter 2). Models whose residuals demonstrated autocorrelation were subsequently modelled as generalised linear mixed models (GLMMs), using the ‘lme4’ package (Bates 2010a), with each transect specified as a random effect to account for non-independent error structures associated with clustering of study sites (Zuur et al. 2011). Table 5.4 describes the type of model run, the error distribution and the link function specified for each attribute (response variable). Landscape elements were considered an important influence on a given attribute where 95% CIs for parameter estimates did not overlap zero when compared to the reference element (unlogged forest).

Some structural complexity data required preparation prior to their inclusion as response variables in subsequent models. Tree size diversity was calculated as the Shannon-Weiner index (H’) of the proportion of trees in each of eight DBH classes (10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–90, 90–150 cm), in the R package ‘vegan’ (Oksanen et al. 2013). As such, it represented an index of the size class distribution of trees, with higher values when trees are more evenly distributed among more size classes (Kanowski et al. 2010). Vertical foliar diversity (VFD) was similarly calculated as the Shannon-Weiner index of the proportion of foliar cover in each of seven height classes (2–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25m, 25–

35m and >35 m), with higher values at sites where foliage is more evenly distributed among more strata (Farwig et al. 2008).

Prior to modelling, canopy cover values were logit transformed to conform to linearity assumptions and reduce heteroscedasticity in the residuals, following Warton (2011). The logit transformation was as follows:

$$\ln\left(\frac{y+\varepsilon}{(1-y)+\varepsilon}\right)$$

where ε is a small value added to avoid issues when taking the natural log of percent cover values of 0 or 1. I trialled three values for ε: 0.05 (the smallest non-zero cover value), 0.005 and 0.01 as recommended by Warton (2011). The value of 0.01 was chosen because it best represented the mean cover values from the raw data. There was no difference in significance values for any value of ε.

Basal area data did not conform to the more commonly used exponential family distributions because it combines both count and size data. After checking residuals from a number of different distributions, I found the Tweedie distribution best modelled this data. The Tweedie distribution is a mixed compound Poisson – Gamma distribution that is continuous except for a positive mass at zero (Tweedie 1957). The positive mass at zero is necessary to model species with no biomass at a given site, and the compound Poisson-Gamma can be justified as a sum of Gamma-distributed individual tree biomasses across a Poisson-distributed number of individual trees. The Tweedie distribution is a member of the exponential family with an index parameter (p) between 1–2 in the variance $(var = \phi\mu^p)$, meaning that data can be analysed using a generalised linear model. The index parameter was calculated for each response distribution using maximum likelihood estimation in R package 'tweedie' (Dunn 2012).

I fit a final set of GLM models to analyse the effects of landscape element on the relative vertical foliar richness. Four vertical strata were analysed: (1) understorey (2–5 m), (2) midstorey (5–15 m), (3) sub-canopy (15–25 m) and (4) canopy (25–35 m). For each stratum, I generated a GLM in which the response variable was the proportion of the total number of vegetation types recorded within a stratum (i.e. across all sites) that occurred at a given site. Landscape element was the single categorical predictor, and unlogged forest the reference factor. As the data were proportional data, a binomial error distribution and logit link was specified. For all generalised linear models where I conducted multiple comparisons between landscape elements, I accounted for family-wise error in significance tests of pairwise comparisons using a Bonferroni correction (Quinn & Keough 2002). All non-Gaussian models were tested for overdispersion and I used Moran's *I* test statistic to test for effects of spatial autocorrelation for all model residuals (section 2-1-4-4).

5-2-2-2 Ground cover

I conducted principal component analysis (PCA) to quantify the relative abundance of ground cover vegetation types across sites, in the R 'stats' package, using function 'prcomp' (R Core Team 2013). Variables consisted of the percent cover of each ground cover type (Table 5.1). In using PCA I hoped to summarise the changes in composition of ground cover types in response to the disturbance gradient, and to judge the relative importance of each variable in explaining variation in ground cover among sites (McElhinny 2005). Moss and coarse woody debris were excluded from analysis because they were absent from most sites. Moss occurred sporadically possibly because the study took place below 400 m a.s.l. and moss is thought to be restricted to higher elevations on New Britain (Paijmans 1976). Coarse woody debris was highly variable and rare compared to other ground covers, which may have been a function of its size relative to the 1 m^2 survey plots. This attribute would have been better measured at the whole 0.18 ha plot scale, as counts of ground logs $\geq$10 cm DBH.

5-2-2-3 Rainforest life form composition

Estimating relative abundance of life forms using a modified Braun-Blanquet ordinal scale created difficulties for the implementation of multivariate analyses. My conversion of ordinal measures to midpoints resulted in semi-continuous response data (in that any data point can only take on a limited number of values between 0–100). This method can lead to uncertainty in cover estimates, especially in those classes incorporating a broader range of values (Podani 2006). Additionally, the diversity of structures and sizes of life forms in this study meant that differences in their relative cover may not have been due to differences in abundance, but rather the amount of space they occupied. For example, epiphytic ferns and understorey vine thickets occurred in a similar number of sites, but understorey vine thickets had a mean percent cover three-fold that of epiphytic ferns because they sprawl vertically and horizontally. To compensate for these uncertainties, I analysed both midpoint values and adjusted presence-absence values to draw conclusions about special life form composition. Adjusted presence-absence values were calculated according to the method described by van der Maarel (2007): I analysed the frequency of occurrence of MBB cover values (0–7) for each life form, and those occurring with consistently low cover (MBB = 1–3) were assigned as 'present' (1) for all ordinal values >0; those with consistently high cover (MBB = 3–6) were assigned as present for all ordinal values >2; and those intermediate life forms (MBB = 2–5) were assigned as present for all ordinal values >1.

I used principal component analysis (PCA) to quantify the relative abundance of life forms across sites, to summarise the changes in composition of life forms in response to the disturbance gradient, and to judge the relative importance of each variable in explaining variation in life form occurrence among sites (McElhinny 2005). I ran separate PCAs for each data set such that variables represented (1) the percent cover of life forms, and (2) the adjusted presence-absence of life forms. Small epiphytes (e.g. orchids) were excluded from analyses because their tendency to occur in low density in the canopy meant that many potentially remained undetected in more intact forest elements whose canopy was obscured by foliage of lower strata. Cordylines were also removed from analyses because of their rarity among sites in this landscape.

5-2-2-4 Variable selection for bird species richness models

There were numerous potential covariates for use as predictors of site-level richness of forest-using and forest-specialist birds (definitions in Chapter 6). Tropical bird species richness has been associated with the habitat properties of structural complexity, plant species richness, and incidence of rainforest life forms (Kanowski et al. 2010 and see 5-1 Introduction and 5-4 Discussion). Therefore, I aimed to include variables that represented these properties as predictors in my models. The most suitable predictors for use in generalised linear models are those which are uncorrelated, present at most sites, and that vary across sites in response to site-level disturbance (Burnham & Anderson 2002; Zuur et al. 2013). Thus, my selection process involved assessing these criteria for each variable through interpretation of results from analyses outlined in sections 5-2-2-1 to 5-2-2-3. I conducted spearman correlation tests for all variables using function ‘cor’ in the R ‘stats’ package (R Core Team 2013). Variables with a correlation coefficient $\rho > 0.6$ were considered too closely correlated to be included as covariates and the variable which best fulfilled the aforementioned modelling criteria was preferentially selected.

5-3 Results

5-3-1 Tree composition and structural complexity

5-3-1-1 Tree species density, basal area, and size diversity

Tree species density (richness per given area) results from Chapter 3 are also described here (Table 5.4) because tree species desnity is considered an important stand-level vegetation attribute (Pinotti et al. 2012; Kanowski et al. 2010). Results of tree species desnity analyses are presented in Chapter 3 (section 3-3-1) and repeated here in Table 5.4. In summary, species denisites were similar for unlogged forest and secondary forest elements and significantly poorer for both young and mature plantation elements compared to unlogged forest. However, mature plantations displayed substantially higher species densities than young plantations.

Basal area of both live and dead trees was similar across all landscape elements except the young plantations, where they were much lower (Table 5.4). While basal area did not vary significantly among sites in unlogged forest, secondary forests and mature plantations, there was a trend towards a higher basal area in the secondary forest and plantation elements. Tree size (DBH) diversity—an indicator of horizontal structural diversity and evenness —was highest in mature plantations, followed by unlogged and secondary forest elements, and was lowest in young plantations (Table 5.4).

The tree (stem) size distribution profiles (Figure 5.2) display differences in the distribution of stems across size-classes for each landscape element. Profiles of unlogged and secondary forests appear similar, with an abundance of 10–20cm DBH recruits and a declining representation (and increasingly even distribution) of trees as size-classes increase. However, the secondary remnant forest has a slightly higher proportion of 10–20 cm DBH recruits and lower proportion of 20–40 cm DBH trees compared to unlogged forest, and the secondary riparian element has a lower proportion of 10–20 cm DBH recruits and greater proportion of 20–40 cm trees compared to unlogged and secondary remnant forests. Mature plantations lack large trees (≥70 cm DBH) and are far more even in their distribution of stems among lower size classes than unlogged and secondary forest elements. Finally, young plantations have a similarly high proportion of 10–20 cm recruiting trees as unlogged and secondary elements, and a declining proportion of stems distributed among just four of the six remaining size classes.

Table 5.4 Means (standard errors) for each attribute among landscape elements, calculated using GLMs or GLMMs. Emboldened values indicate elements whose 95% CI for a given attribute did not overlap zero with the unlogged forest as reference category. Tree species richness data is repeated from Chapter 3.

Attribute	Model type & error distribution	Landscape Element				
		Unlogged forest	Secondary remnant	Secondary riparian	Mature plantations	Young plantations
Tree species density† (per 1800m^2)	GLMM, Poisson	29.21 (0.78)	31.30 (1.77)	26.21 (1.37)	**10.22 (0.45)**	**2.10 (0.32)**
Basal Area, live trees (m^2 /1800m^2)	GLM, Tweedie	4.570 (0.353)	6.019 (0.964)	6.347 (0.850)	5.781 (0.421)	**0.312 (0.063)**
Basal Area, dead trees/snags (m^2 /1800m^2)	GLM, Tweedie	0.175 (0.043)	0.145 (0.068)	0.180 (0.064)	0.367* (0.078)	**0.00**
Tree size diversity (per 1800m^2)	GLM, Gaussian	0.792 (0.045)	0.776 (0.100)	0.973 (0.084)	**1.301 (0.044)**	**0.385 (0.070)**
Percent canopy cover	GLM, Gaussian (logit transform)	0.958 (0.005)	0.972 (0.007)	0.956 (0.009)	**0.932 (0.008)**	**0.351 (0.055)**
VFD	GLM, Gaussian (squared transform)	1.570 (0.040)	1.714 (0.088)	**1.306 (0.075)**	1.442 (0.038)	**0.492 (0.058)**

*For this measure, there was missing data for 10 sites

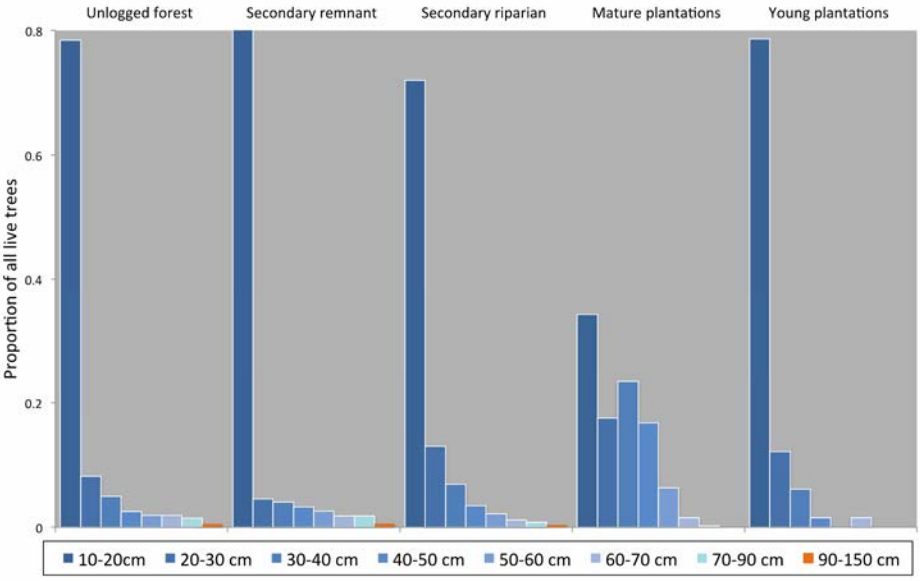

Figure 5.2 Tree size distributions for each landscape element: proportions of all trees for each landscape element found occurring in each DBH size class. Average number of trees per site/total trees per element, for each element are: unlogged forest, 99/4735; secondary remnant, 127/1269; secondary riparian, 138/1928; mature plantations, 84/4194; young plantations, 7/131.

5-3-1-2 Canopy cover, vertical foliar diversity and richness

Percent canopy cover was similarly high in unlogged and secondary forest elements, significantly lower in mature plantations (although still above 90%) and almost three-fold lower in young plantations, where it was also noticeably more variable (standard error 6–7 times greater than other elements) (Table 5.4).

Vertical foliar diversity—an indicator of vertical structural diversity and evenness —was similarly high in unlogged forest, secondary remnant forest, and mature plantation elements (Table 5.4). The secondary riparian element had a significantly lower VFD, and young plantations had a foliar diversity just one-third that of unlogged forest.

Vertical foliar richness, representing the contribution of foliage from different size trees and plant life forms, was significantly lower in young plantations compared to unlogged forest across all strata (Figure 5.3). The secondary riparian element was significantly lower than unlogged forest for canopy VFR, and mature plantations were significantly lower than unlogged forest for sub-canopy VFR.

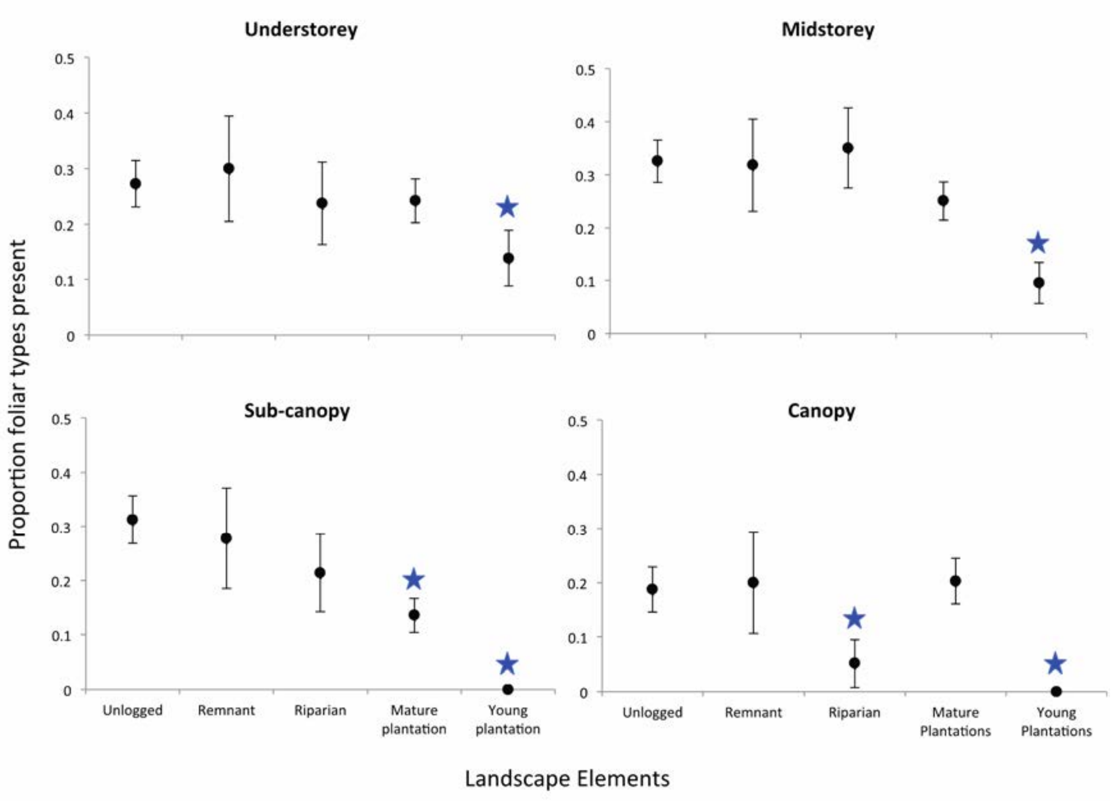

Figure 5.3 Comparisons of mean (standard error) proportion of vegetation types contributing to foliar cover for the four main vertical strata. Blue stars indicate elements whose 95% CI for foliar richness in a given stratum did not overlap zero (unlogged forest as reference category).

5-3-2 Ground cover

The first two PCA components together explained 64.5% of the variation in ground covers (Table 5.5). The first component (PC1) explained 39.3% of the variation in ground covers, and described a gradient of relative site-level abundance of cover types: variables with consistently low site-level cover (e.g. scramblers) took more negative values, and variables with high site-level abundance (e.g. leaf litter) had positive values. The second component (PC2) described the forest disturbance gradient and explained 25% of ground cover variation. Sites at one end were characterised by grasses, ferns and vines and were associated with plantation elements, while at the other end sites were characterised by shrubs/seedlings, and bare soil and were associated with unlogged and secondary forest elements (Figure 5.4). Leaf litter was present in many sites and occurred in similar abundance across all sites when present (Appendix Figure C.2).

Table 5.5 Principal component analysis of ground cover variables recorded in 1 m^2 plots (no rotation). Values represent component scores.

Ground cover variables	PC1 (39.3%) gradient in relative abundance of cover type (least abundant ground cover to most abundant)	PC2 (25%) gradient in ground cover types (undisturbed to disturbed)
Ground vines/ scramblers	–0.478	0.376
Grass	–0.190	0.112
Bare soil	–0.067	–0.313
Shrubs and seedlings	–0.029	–0.342
Ferns	0.261	0.793
Litter	0.813	–0.045

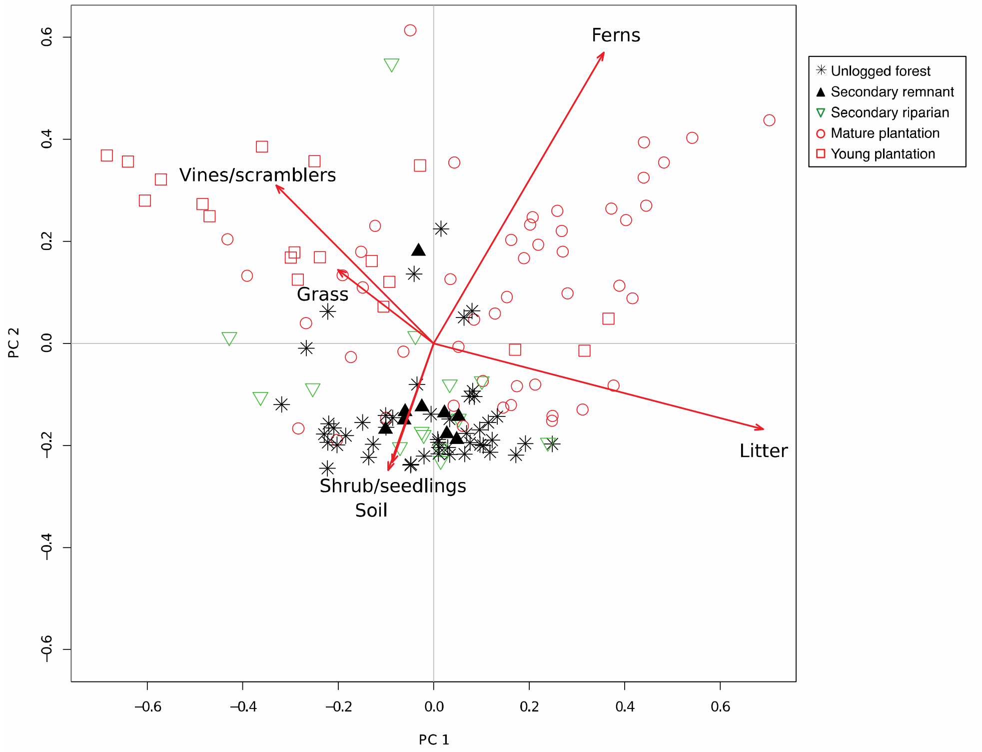

Figure 5.4 PCA biplot of ground covers with sites grouped into landscape elements. Vectors represent the relative importance of each variable in explaining variation among sites, and the correlations between variables (Zuur 2011).

5-3-3 Rainforest life form composition

Of the eleven rainforest life forms analysed, nine were found to vary among elements following disturbance gradient expectations. The two which did not conform were canopy and sub-canopy vine towers, and these were removed from the final PCA. Given the gradient in time since disturbance and intensity of disturbance among landscape elements, I would have expected similar occurrence values among older, less disturbed elements, differentiating them from the values of more recently and intensively disturbed elements. This was not the case (Table 5.6).

Table 5.6 Mean proportion of sites per element with presence of canopy and sub-canopy vine towers

	Landscape elements				
	Unlogged forest	Secondary remnant	Secondary riparian	Mature plantation	Young plantation
Canopy vine towers	0.34	0.21	0.58	0.40	0.00
Sub-canopy vine towers	0.65	0.18	0.92	0.90	0.00

After removal of canopy and sub-canopy vine towers from analysis, two factors were extracted from both PCA analyses of rainforest life forms, representing 51.8% of variance in the midpoint cover data, and 56.2% of variance in the adjusted presence-absence data (Table 6). As more of the variance was explained for presence-absence data, I will only consider the PCA results from that analysis here (Table 5.7 (b)). PC1b described the gradient in richness of life forms co-occurring at sites, ranging from least to most rich. It explained 38% of the variation in life forms' occurrence. Sites of highest richness were characterised by the presence of palm trees and large woody vines in particular, while mid- and understorey-vine masses and ***Zingiberales*** spp. (mostly gingers in these forests) tended to dominate the sites when they occurred. PC2b described the forest disturbance gradient and explained 18.2% of the variation in life forms' occurrence. Sites at one end were characterised by presence of gingers, midstorey vine masses and understorey-vine masses and were associated with plantation and secondary riparian elements (Figure 5.5). At the other end, sites were characterised by highly correlated occurrence of palms, rattan palms, large woody vines, hemi-epiphytes, and epiphytic ferns and were associated with unlogged and secondary remnant forest elements.

Table 5.7 Principal components of rainforest life forms for (a) mid-point cover, and (b) adjusted presence-absence data. PC1b – gradient in the richness of life forms present (from least to most rich); PC2b – gradient in life form types (disturbed to undisturbed).

Life forms	(a) Midpoint cover		(b) Presence-absence	
	PC1a (35.9%)	PC2a (15.9%)	PC1b (38.0%)	PC2b (18.2%)
Clumping epiphytic fern	-0.118	0.014	0.350	-0.003
Calamus	-0.110	0.344	0.368	-0.139
Hemi-epiphytes	-0.370	0.461	0.349	-0.035
Palm tree	-0.189	0.048	0.460	-0.052
Vines >5cm diameter	-0.079	0.158	0.427	-0.033
Understorey Palm	-0.199	0.029	0.407	0.012
Midstorey vine tower	0.144	0.711	0.076	-0.651
Understorey vine thicket	0.193	0.357	-0.097	-0.623
Ginger	0.835	0.079	-0.214	-0.404

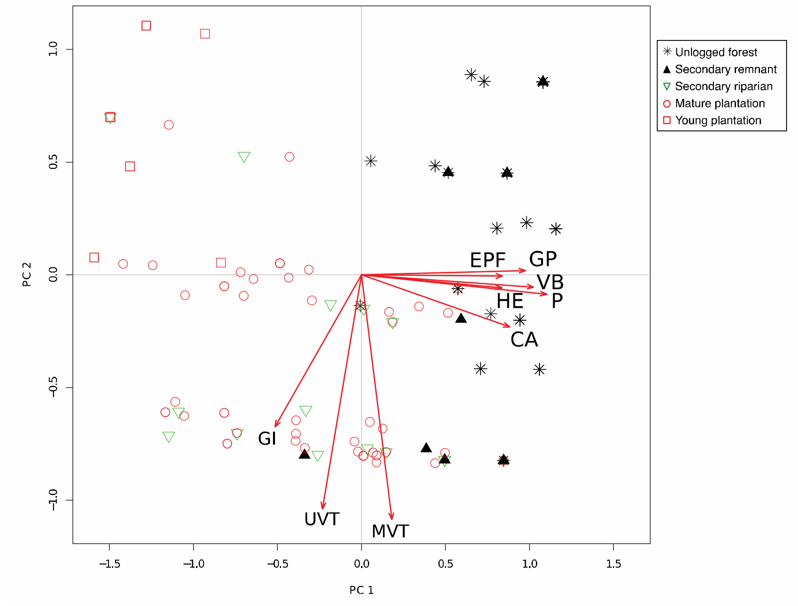

Figure 5.5 PCA biplot of special life forms with sites grouped into landscape elements; HE – hemi epiphyte, VB – lianae (vines > 5cm), UVT – understorey vine thicket, MVT – midstorey vine thicket, CA – *Calamus spp.*, P – Palm, GP – understorey (ground) palm, EPF – epiphytic ferns, GI – *Zingiberales* spp (gingers). Vectors represent the relative importance of each variable in explaining variation among sites, and the correlations between variables.

5-3-4 Variable selection for bird species richness models

I selected variables which were uncorrelated (ρ <0.60), present in most sites, and varied across sites in response to site-level disturbance (Table 5.8). Correlation analyses revealed strong relationships between: (1) VFD and sub-canopy foliar richness, canopy foliar richness and PC1 (ground cover); (2) tree species density and sub-canopy richness, PC2 (ground cover) and PC1b (life forms); and (3) sub-canopy richness and PC1b (life forms) (Table 5.9). Of these correlated variables, tree species density was selected because it reflected the disturbance gradient in of itself and through its correlations with other variables that similarly described the disturbance gradient (sub-canopy richness, PC2 (ground cover) and PC1b (life forms)). Selection of the remaining six variables (Table 5.8) is discussed more fully in section 5-4-4 because it incorporates interpretation from the discussion.

Table 5.8 Summary of predictor variables chosen for models of bird occurrence in Chapter 6.

Habitat property (site-level)	Variables	Description
Tree species richness and structural complexity	Canopy cover	Mean percent cover
	Tree richness	Number of tree species recorded
	Tree size (DBH) diversity (H')	Shannon (H') index of the size class distribution of trees
Ground cover	Shrubs/seedlings†	Mean percent cover, (indicative of less-disturbed elements)
	Ferns	Mean midpoint percent cover (indicative of disturbed elements)
Rainforest life forms	Palm†	Mean midpoint percent cover (indicative of less-disturbed elements)
	Zingiberales spp. (gingers)	Mean midpoint percent cover (indicative of disturbed elements)

Table 5.9 Spearman rank correlation coefficients for all variables. Pairwise relationships where correlation coefficient ρ >0.60 are highlighted in bold font.

	Tree species richness	Basal area, live trees	Tree size diversity	Canopy cover	VFD	Understorey richness	Midstorey richness	Sub-canopy richness	Canopy richness	PC1 (ground cover)	PC2 (ground cover)	PC1b (life forms)	PC2b (life forms)
Tree species richness													
Basal area, live trees	0.449												
Tree size diversity	-0.219	0.518											
Canopy cover	0.599	0.307	-0.031										
VFD	0.545	0.230	0.006	0.472									
Understorey richness	0.246	0.145	0.036	0.337	0.313								
Midstorey richness	0.554	0.195	-0.122	0.490	0.482	0.250							
Sub-canopy richness	**0.621**	0.147	-0.157	0.436	**0.683**	0.271	0.481						
Canopy richness	0.178	0.293	0.238	0.291	**0.605**	0.373	0.191	0.386					
PC1 (ground cover)	-0.009	0.244	0.383	0.026	0.133	0.044	0.012	0.009	0.325				
PC2 (ground cover)	**-0.689**	-0.224	0.168	-0.410	-0.371	-0.234	-0.363	-0.558	-0.097	0.032			
PC1b (life forms)	**0.721**	0.199	-0.138	0.546	**0.628**	0.370	0.503	**0.670**	0.416	0.003	-0.537		
PC2b (life forms)	0.047	-0.247	-0.219	-0.220	-0.125	-0.100	-0.123	0.001	-0.167	-0.249	-0.119	0.086	

5-4 Discussion

In general, changes in species composition reflected the time since disturbance and gradient in disturbance among landscape elements more consistently than did structural attributes. Young and mature plantation elements differed substantially from unlogged and secondary forest elements by their reduced structural complexity (canopy cover, vertical foliar richness, shrubs/seedling cover), lower tree species richness, and reduction in late-successional rainforest life forms (e.g. palms). During the early establishment phase soon after conversion of secondary forest (i.e. young plantations) there was a decrease in all structural attributes and an absence of rainforest plant life forms. However, plantations that had reached harvest age (mature plantations) were capable of recovering some of these attributes to values equal to those of unlogged forest (e.g. basal area of live and dead trees, and vertical foliar diversity) potentially providing habitat for a subset forest fauna. None of the structural attributes considered in the study were able to differentiate secondary remnant forest from unlogged forest elements, and these elements’ tree species richness and plant composition were also similar. This suggests that New Britain’s lowland forests can recover substantially from selective logging within 25 years, and highlights their value for conservation of forest vegetation biodiversity.

5-4-1 Tree richness and structural complexity

5-4-1-1 Tree species richness, basal area, and size diversity

Tree species density (richness per given area) clearly differentiated plantations from non-plantation landscape elements, but not unlogged forest from secondary forest elements (Chapter 3). The capacity of secondary forests (especially those employing low-level extraction methods such as selective logging) to recover species richness after relatively short fallow periods (~20–30 years) has been well documented in the tropics (Cannon et al. 1998; Berry et al. 2010; Baraloto et al. 2012; Putz et al. 2012; Hall et al. 2003). However, richness comparisons tend to mask underlying compositional differences in secondary forests, such as the reduced abundance of late-successional species compared to unlogged forest (Sheil & Burslem 2003). Indeed, a reduction in late-successional trees in the secondary riparian element compared to unlogged forest was found in this study (Chapter 3), although compositional differences between the unlogged and secondary remnant forests were not evident (Chapter 3). Tree species richness and composition are the focus of Chapter 3 of this thesis, and potential reasons for these observations are detailed in section 3-4-1. While species density was significantly lower in plantation elements, mature plantation sites contained a significantly higher density of trees than young plantations (Chapter 3). Therefore, plantation age affects the richness of tree species that can accumulate, which has ramifications for their relative provision of resources for forest fauna.

Basal area of both live and dead trees was a broad indicator of stand age or maturity, with significantly lower values recorded in young plantations compared to all other elements. The similar basal areas found in unlogged, secondary and mature plantations reflect the rapid growth of woody vegetation common in tropical secondary forests (either logged or regenerating after clearing) and timber plantations, in the first 10–30 years post-disturbance (Guariguata & Ostertag 2001; Lugo & Brown 1990; Parrotta 1999; Lugo et al. 1988). For example, in the Neotropics studies have found reduced-impact logged forest can recover 100% of its pre-logging above-ground biomass after as little as 16 years (West et al. 2014), and even secondary forest regenerating after pastureland (when pasture for <10 years) was able to recover biomass within 21–30 years (Costa Rica, Chazdon et al. 1997; Letcher & Chazdon 2009). In addition to this ‘natural’ biomass accumulation, plantations may be further assisted by the rapid growth that characterises selected timber plantation species (usually in the first 10–20 years , Chazdon et al. 2007; Keenan et al. 1999).

However, while basal area was similar among mature plantation and unlogged and secondary forest elements, the composition of stem sizes comprising them differed greatly. In unlogged and secondary forest elements, tree stem distribution profiles revealed that much of the basal area was contributed by a high number of recruiting trees (10–20 cm DBH) and low number of large, old trees > 70 cm DBH. Large, old trees contribute significantly to the basal area of a given stand (Day et al. 2014) and can play an important role in facilitating understorey tree recruitment (Schlawin & Zahawi 2009), as well as providing unique resources for structural floral parasites (Benavides et al. 2013) and arboreal fauna (Lindenmayer, Laurance, et al. 2012b). In contrast, mature plantation basal area was comparatively evenly comprised of stems from four classes (ranging from 10–50 cm DBH) made up of focal *E. deglupta* trees and recruited native trees of 10–25 cm DBH (Chapter 3). Therefore, in modified land-covers promoting growth or retention of trees (e.g. plantations, agroforests) basal area values matching those of old-growth rainforest do not necessarily indicate the same level of structural complexity or the habitat resources they provide (e.g. Day et al. 2014).

Tree size diversity, based on the Shannon-Weiner index, attempts to summarise the stem distribution profile of a given stand by describing both the evenness of distribution of stems among size classes, as well as the diversity of size classes present. Here, tree size diversity was found to be highest in mature plantations, significantly lower in unlogged and secondary forest elements and lower still in young plantations. Thus, while it successfully differentiated plantations from non-plantation landscape elements, its opposite value in young (low) and mature (high) plantations means that this variable did not track the disturbance gradient. Explanation for these values lies again in the stem size distribution profile. For unlogged and secondary forests, stem distribution is skewed towards a high proportion of trees in the 10–20 cm size class, a common finding in more mature forest (e.g. Bowman et al. 1990). This skewness is due to the richness and abundance of propagules supplied by the diversity of trees in these elements, and the slow growth of late-successional trees out of this size class (Condit et al. 1998). Thus, while these forest elements have individuals present across all size-classes, the proportion of stems occurring among size-classes varies greatly. By contrast, the number of trees recruited into the 10–20 cm size class in mature plantations was probably limited by the lower abundance of late-successional propagules, the inhibitory effect of a high ginger cover (Denslow 1996 and section 5-4-3), and competition from fast-growing *E. deglupta* trees, which were sizeable (20–50 cm DBH). Thus, while mature plantations were missing trees for two of the eight size classes, the proportion of stems occupying the remaining six size-classes was relatively similar resulting in their high tree size diversity values compared to unlogged and secondary forest elements.

5-4-1-2 Canopy cover, vertical foliar diversity and richness

Percent canopy cover, like tree species richness, conformed to expectations of the landscape element gradient in time since and intensity of disturbance: it was highest in unlogged and secondary forest elements, significantly lower in mature plantations and almost three-fold lower in young plantations. However, while lower in mature plantations, canopy cover was still above 90%, which is higher than values observed for mature plantations in other tropical studies (Kanowski et al. 2003; Zurita et al. 2006). This may result from the combination of consistent overstorey cover of the emergent *E. deglupta* trees and the foliar cover provided by rainforest trees recruited in the understorey.

The contribution of strata to canopy cover can be elucidated by the analyses of vertical foliar diversity (VFD) and richness (VFR, here modeled as proportion of total possible foliar types occurring at a site). In mature plantations most strata were evenly represented by foliage cover, but the sub-canopy was depauperate in foliar cover contributed by trees of different sizes, vines and epiphytes compared to unlogged forest. Thus, mature plantations were characterised by inconsistent vertical cover, with an even overstorey of thin-leaved emergent crowns, supplemented by understorey–midstorey cover of recruited rainforest trees (<25 cm DBH). In the secondary riparian forest, both VFD and canopy VFR were found to be lower than unlogged forest, which may have been a consequence of their slightly lower density of larger old trees (>60 cm DBH). This relative scarcity of old trees may have been caused by the exposure of trees located on the edges of the riparian strips to wind and anthropogenic disturbance (Ries et al. 2004). In the more narrow riparian sites, there may also have been less space to support these trees and/or increased soil disturbance from seasonal flooding. Nevertheless, the lower vertical foliar diversity and canopy richness found in this element did not result in a lower mean canopy cover compared to unlogged forest, presumably because of the inclusion of foliar richness similar to that of unlogged forest in all other strata.

5-4-2 Ground cover

Principal components analysis of ground cover variables showed that grasses, ferns and vines characteristic of disturbed, open-canopied stands (Guariguata & Ostertag 2001; Denslow 1996) were associated with plantations and some of the secondary riparian sites, as expected. Shrubs/seedlings, and bare soil characteristic of less disturbed forest (Tchouto et al. 2006) were associated with unlogged and secondary forest elements. However, the principal component describing this ground cover disturbance gradient did not explain the majority of the variation between sites, indicating that some trends in ground cover response to disturbance were difficult to determine. This may be a consequence of a number of factors. First, the broad classification of ground covers in this study led to conflation of fern and grass species characteristic of different successional stages. In this study, ferns such as *Pteridium* spp. were classic post-disturbance and canopy-gap pioneers found in abundance in plantations (Henty 1982), however *Lomariopsis* spp. were restricted to unlogged and secondary forest elements. Similarly, weedy grasses like *Saccahrum* and *Imperata* spp. colonised the most disturbed sites, while palm-like grasses of genus *Leptaspis* were found in the least disturbed sites. Differentiation between all fern and grass genera was not possible in the field, so I decided to only include pioneer genera in surveys. This however, led to the exclusion of species that I could not identify to genus-level or successional type, resulting in a loss of potentially useful information.

Second, leaf litter cover was only weakly characteristic of less disturbed forest elements, in contrast to other studies comparing litter abundance between plantations and primary or secondary forests (Gardner et al. 2007). Here, litter consistently occurred in high abundance when present across all sites, making it a poor differentiator of land-cover types. Still, there was a trend for litter to be lower in young plantations, in-keeping with other studies of young (4–5 year old) *Eucalyptus* plantations compared to old-growth and secondary rainforests, and was attributed to their lower above-ground biomass and low tree species richness (Gardner et al. 2007; Lugo 1992a). As tropical plantations age, however, they may accumulate more litter than old-growth forest and some secondary forests because of their comparatively high net primary production and lower levels of decomposition, although the magnitude of these effects depends on the plantation species and microclimate (Gardner et al. 2007; Cuevas & Lugo 1998; Holl et al. 2010). Had I measured more attributes of litter (e.g. litter mass and composition), as was done in the aforementioned studies, differentiation between mature plantation and non-plantation elements may have been revealed. Given the difficulty in summarising the response of all ground covers to disturbance concurrently, a better approach may be to simply describe the effect of land-cover on the two variables most strongly associated with old-growth and disturbed forest, namely shrubs/seedling and ferns, respectively.

5-4-3 Rainforest life form composition

Most of the variation in the occurrence of life forms among sites was explained by differences in the richness of life forms present. Unlogged and secondary remnant forest had the greatest life form richness, comprised of an almost ubiquitous occurrence of more slow-growing plant forms and/or those reliant on tree substrates (palms, rattan palms, large woody vines, hemi-epiphytes, and epiphytic ferns) (Webb et al. 1976). A number of these less disturbed forest sites also contained some of the more disturbance-associated life forms, most likely representing small tree-fall gaps (Denslow 1996). Life forms characteristic of old-growth forest have been observed to occur in secondary forest in other studies, including the more extreme case of secondary forests recovering from clearfell activity (Chazdon 2003; Letcher & Chazdon 2009). However, studies of the composition of life forms at the species-level suggest that it may take many years before they resemble communities of undisturbed forest (Woods & DeWalt 2012; Putz 1984; Letcher & Chazdon 2012; P. H. Martin et al. 2004). An effect of time since disturbance was evident in the secondary riparian element. Secondary riparian sites ranged from a comparatively rich composition of life forms in sites located along wider buffer strips, to a more simple composition with a dominance of gingers (*Zingiberales* spp.) and lower strata vine masses in sites found along narrow buffer strips. This lends weight to the theory that the narrower sites are more prone to disturbance from edge effects, river flooding, and human use and therefore may offer reduced support for native forest biodiversity (Denslow 1996; Ewel & Bigelow 1996).

Young plantation sites had the lowest richness of life forms, with most sites either absent of all rainforest life forms, or with only *Zingiberales* spp. present. Only a few sites contained hemi-epiphytes on young trees, and understorey vine thickets. Young plantations lacked necessary substrates, shade and microclimate conditions required for successful germination of most forest life forms. Similar observations have been made in young plantations of tropical and sub-tropical Australia (Wardell-Johnson et al. 2005). By contrast, the structure and canopy cover available in mature plantations allowed them to support a range of life forms, with some sites dominated by a few life forms and others more closely resembling the composition of unlogged and secondary forest elements. However, almost all sites contained ***Zingiberales*** spp, and contained a high incidence of lower strata vine masses, a consequence of the increased light levels penetrating the ***Eucalyptus*** canopy (Tucker et al. 2004).

The lack of midstorey-to-canopy vine mass differentiation between mature plantations and unlogged and secondary forest elements may be a consequence of their reliance on a high density of adult trees and a sufficiently open canopy (Tchouto et al. 2006; Putz 1984). These conditions are present in mature plantations and unlogged and older secondary forest edges and canopy gaps. Differentiation may have been more successful had the scope of this study extended to identifying the specific life forms contributing to these vine masses. These masses can be composed of a mixture of pioneer-type lianae and herbaceous vines, and late-successional lianae and primary hemi-epiphytes (Zotz 2013). Thus, identification of vine masses dominated by slow-growing lianae and primary hemi-epiphytes would be more indicative of undisturbed sites (Putz 1984; Letcher & Chazdon 2012).

5-4-4 Selection of predictor variables for bird occurrence models

Chapter 6 of this thesis attempts to understand the relative influence of a range of environmental factors on the occurrence of forest bird species. Habitat-level properties such as structural complexity (R. H. MacArthur 1964), tree species richness (Farwig et al. 2008), and incidence of rainforest life forms (e.g. epiphytes, Cruz-Angon & Greenberg 2005; and palms, DeWalt et al. 2003) have been associated with forest bird species richness in production landscapes. Therefore, I selected variables representing these properties as possible predictors of bird species richness. I ensured predictor variables were uncorrelated, present in most sites and also varied across the landscape in accordance with land-use context.

For structural complexity, canopy cover best met these criteria. Tree size diversity may also be considered (although it did not describe the disturbance gradient as expected) because it fulfilled all other criteria and has been observed to correlate with bird species richness in studies comparing secondary regrowth and monoculture plantations (Kanowski et al. 2008; Sekercioglu 2002). Ground cover also represents structural complexity, as well as plant species composition and microhabitat conditions that may effect richness of understorey birds (Stouffer & Stratford 2013). Ground cover was poorly summarised by PCA, so I decided this attribute would be better captured through two variables most strongly associated with old-growth and disturbed forest—cover of shrubs/seedlings and cover of pioneer ferns, respectively. Rainforest life forms separated into two correlated groups, both requiring a level of habitat structure to grow, with one group more reliant on the shaded, moist microclimate of less disturbed forest. Because of the high correlations found, I similarly decided to represent life forms as the two variables most strongly associated with old-growth and disturbed forest—cover of palm trees and cover of gingers respectively. Palms provide an important food resource for forest frugivores (Peres 1994; DeWalt et al. 2003; Genini et al. 2009) and gingers may also provide resources for some nectarivores and insectivores (Sakai et al. 1999; García-Robledo & Kuprewicz 2009).

5-4-5 Conservation Implications

With the exception of young plantations, structural and compositional differences among landscape elements were not as demarcated as expected. The secondary forest and mature plantation elements demonstrated a rapid recovery of some stand structural attributes of old-growth forest and were capable of providing substrates and microclimatic conditions required for growth of some rainforest life forms. This was particularly evident for the secondary remnant forest protected by conservation reserves, which was structurally and compositionally most similar to unlogged forest. In contrast, the continual human disturbance occurring in secondary riparian element (especially where such activity reduced the width of buffer strips, increasing their fragmentation) resulted in a reduced similarity of both its vegetation structure and composition compared to unlogged forest. To avoid further degradation of this landscape element, I recommended that riparian buffer strips be protected from further human encroachment, that degraded sections are restored through enrichment planting, and that roads are relocated further from the river in the narrowest sections.

Conversion of secondary forest to plantations resulted in the drastic reduction of all old-growth structural and compositional attributes, suggesting that they are likely to provide little connectivity or habitat for forest species in early stages. However, habitat provision changed with plantation age, and those that had reached harvest age recovered substantially for all attributes. Nonetheless, the history of disturbance and light penetration of mature plantations also resulted in a simplified ground-storey, and competition from plantation trees inhibited recruitment of a richness and composition of plant species resembling that of both secondary and unlogged forests. Therefore, the *E. deglupta* plantations may provide connectivity and habitat resources for a subset of forest species, but they are not capable of supporting the full complement of old-growth vegetation while still upholding production value. The extent to which this multi-use plantation landscape supports native forest avifauna and the conservation management implications therein will be explored in Chapter 6.

5-5 Chapter summary

The conversion of secondary forest to plantations resulted in the dramatic reduction of all old-growth structural attributes and the absence of late-successional rainforest plant types in the early establishment stage (young plantations). However, by as little as 15 years post-planting (mature plantations) some structural attributes recovered to values found in unlogged forest (e.g. basal area, vertical foliar diversity) and a greater richness of plant species was present compared to young plantations. Therefore, the resources available within plantations for forest biota are largely influenced by plantation age. The composition of late-successional plants differentiated unlogged forest from modified landscape elements more readily than did structural attributes, except for the secondary remnant forest element, which was a 385 ha contiguous remnant protected by conservation reserves. The findings of this chapter further highlight the capacity of tropical forests to recover from anthropogenic disturbance. However, this capacity is reduced in more frequently disturbed land-uses and may never be realised in plantations where production activities involve clearfelling. The importance of a subset of these habitat properties for the occurrence of forest avifauna will be investigated in the following chapter (Chapter 6).

CHAPTER 6

Conserving forest birds in a plantation landscape: what drives species occurrence?[4]

Canopy cover in a mature* Eucalyptus deglupta *stand

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[4] Pryde, EC, Watson, SJ, Nimmo DG, Moloney, JM, Holland, GJ (*in prep*) Conserving forest birds in a native timber plantation landscape: what drives species occurrence? Biotropica.

CHAPTER SIX

In the final data chapter of the thesis I investigate the properties of the native plantation landscape that influence the occurrence patterns of lowland forest birds (objective 3). I use an information theoretic approach to examine the relative influence of habitat attributes (from Chapter 5) and spatial context on the richness of (a) forest-using and (b) forest-specialist birds. Understanding how these habitat and spatial properties influence bird occurrence provides valuable information on what may be required for effective conservation management of these species both landscape-wide and at the stand-level. The ecological inferences based on the findings from this study are discussed and framed in terms of their consequences for biodiversity conservation within this production landscape. Conservation management implications are outlined, and are expanded upon in full in the general discussion (Chapter 7).

6-1 Introduction

Production landscapes continue to expand on a global scale and now dominate many tropical regions (Gardner et al. 2010). This has severe consequences for biodiversity conservation, as natural habitats are cleared and modified to make way for alternative land-uses (Gardner et al. 2010; Gardner et al. 2009). While conservation reserves play a crucial role, their limited number and size necessitates additional conservation measures (Gaston et al. 2008). 'Land-sharing' strategies broadly aim to balance biodiversity conservation with production in landscapes comprised of production land-uses interspersed with remnant habitat (Fischer et al. 2008). Identifying the attributes of production landscapes that influence occurrence of species is fundamental for the successful development of land-sharing conservation strategies (Perfecto & Vandermeer 2010). However, such attributes remain poorly understood (Chazdon, Harvey, et al. 2009a; Paquette & Messier 2010).

Human-affected landscapes present three key threats to local fauna: habitat loss, fragmentation and modification. Therefore, the capacity of a given production landscape to mitigate the effects of these threats depends on: (1) the extent to which remnant (old-growth) forest resources and ecosystem functions can be retained in the matrix (production land-uses); and (2) the coverage of remnant habitat in the landscape, and its location relative to production land-uses (Tscharntke et al. 2012). Areas of tropical lowland forest are used for a range of production purposes including agriculture, timber extraction and tree crops (Gardner et al. 2010; Ranganathan et al. 2008). Different land-uses create a gradient in disturbance. For example, more intense land-uses (e.g. cattle pastures, oil palm/rubber crops) incorporate clearfelling and complete conversion of habitat and result in the simplification of vegetation structure and reduction of plant species diversity (Letcher & Chazdon 2009; Zurita & Bellocq 2012; Catterall et al. 2012). Such land-uses typically experience dramatic losses in faunal biodiversity (e.g. cattle pastures (Saab & D. Petit 1992), agriculture (L. Petit & D. Petit 2003), and tree crops (e.g. oil palm, rubber) (Peh et al. 2005; Koh & Wilcove 2008)). By contrast, land-uses which retain a degree of structural complexity and native vegetation cover (e.g. selectively-logged forests, agroforests) may support a greater richness of forest fauna (Barlow et al. 2006; Thiollay 1995).

In addition to the disturbance associated with a particular land-use, spatial context is also likely to be important (Fischer & Lindenmayer 2007). Theory predicts that production areas in close proximity to remnant forest may support a greater number of species than more isolated areas (Ewers & Didham 2006), with some studies offering support for this hypothesis (Abrahamczyk et al. 2008; Ranganathan et al. 2010). An added complexity is the dynamic nature of production land-covers, whereby provision of resources can change with age (Watson et al. 2014), altering their biodiversity value over time. This effect may be greatest in production types that encourage tree growth (e.g. selectively logged forest, timber plantations, agroforests), where attributes such as tree basal area and canopy cover change through time (Letcher & Chazdon 2009; West et al. 2014). Therefore, to ascertain the processes driving faunal occurrence patterns within a production landscape, an effective approach would be to quantify the relative influences of vegetation resource provision and spatial context, and examine how they change as production land-covers age. Such an understanding is required to weigh the consequences of land-use management on local fauna.

Native timber plantations may represent a production land-use capable of balancing production and conservation in tropical forest regions. This is because in addition to the structural complexity inherent in timber tree growth, they may potentially support native plant and tree species otherwise restricted to remnant forest (Bremer & Farley 2010), which in-turn would provide for rainforest-dependent fauna (Brockerhoff et al. 2008). Here I investigated the capacity of the native timber (*E. deglupta*) plantation landscape to sustain lowland forest bird species on New Britain Island, Papua New Guinea. My results from Chapter 4 indicate that the five main landscape elements are providing differential habitat resources for bird species but that in general, conservation of forest birds within the production landscape is high.

I used an information theoretic approach to assess the relative influence of structural and compositional attributes, and the proportion and proximity of remnant forest, on the richness of forest birds occurring at sites across all elements. I hypothesised that site-level vegetation structural and compositional properties (tree attributes, ground cover and rainforest life form cover), and the proportion of surrounding area made up of intact forest, could influence bird species richness. I aimed to: (1) determine the relative influence of each factor on the richness of (a) forest-using and (b) forest-specialist birds across the landscape; (2) establish the comparative quality of habitat provided to birds by different land-uses and determine how this may be affected by age or management practices; and (3) provide information on the effective management of similar production landscapes.

6-2 Method

6-2-1 Study design and data collection

Study area, study design and site selection are outlined in sections 2-1-1 and 2-1-2. Collection of vegetation and bird data are detailed in sections 2-1-3 (overview), 4-2-1 (birds), and 5-2-1 (vegetation). As mentioned in Chapter 4 (section 4.3), although 58 lowland forest bird species were identified in this study, the removal of five supra-canopy species (swifts, raptors), six rare species, and six hard-to-identify species reduced my forest-occurring birds to a total of 41 species for analysis (Table 4.2).

The total number of survey sites used in analyses differed for bird and vegetation data because of uncontrollable factors (e.g. tree fall events, absence of adult tree cover; for details see Table 2.1). Therefore, for this chapter I only analysed data collected from survey sites that matched for both datasets. This amounted to a total of 107 sites among landscape elements: young plantations = 17, mature plantations = 37, secondary riparian = 14, secondary forest = 9, unlogged forest = 30.

6-2-2 Data analysis

6-2-2-1 Variable selection

Two response variables were chosen. The first represented total forest-using bird species richness, and was comprised of all 41 forest-occurring bird species included in analysis (Chapter 4). The second was the richness of forest-specialist birds (rather than forest-using): a subset of seventeen species identified in community assemblage analyses in Chapter 4 (Table 6.1). These birds were considered likely to respond most strongly to disturbance because of their obligate frugivory and/or their apparent preference for less-disturbed forest.

Table 6.1 Details of forest-specialist bird species identified from analysis in Chapter 4.

Species	Common name	Primary Diet	Habitat Affinity	Nest type
Aceros plicatus	Blythe's hornbill	Frugivore	Forest	Tree hollow
Chalcophaps stephani	Stephan's ground-dove	Frugivore	Secondary	Unknown
Ducula rubricera	Red-knobbed imperial pigeon	Frugivore	Forest	Unknown
Ducula finschii	Finsch's imperial pigeon	Frugivore	Forest edge	Unknown
Eclectus roratus	Eclectus parrot	Frugivore	Generalist	Unknown
Eudynamys scolopacea	Common Koel	Frugivore	Secondary	Unknown
Geoffroyus heteroclitus	Geoffrey's hanging-parrot	Frugivore	Forest	Tree hollow
Lorius hypoinchrous	Eastern black-capped lory	Frugivore	Forest edge	Tree hollow
Macropygia amboinensis	Brown cuckoo-dove	Frugivore	Forest edge	Unknown
Mino dumontii/kreffti	Yellow-faced/Long-tailed myna	Frugivore	Forest edge	Tree hollow, asplenium
Monarcha verticalis	Bismarck pied monarch	Insectivore	Forest	Tree sapling
Pachycephala pectoralis	Golden whistler	Insectivore	Forest	Dense foliage of shrubs/saplings, palms
Ptilinopus insolitus	Knob-billed fruit-dove	Frugivore	Forest	Branches of trees, sub-canopy
Ptilinopus rivoli	White-bibbed fruit-dove	Frugivore	Forest	Tree branch, fork
Ptilinopus superbus	Superb fruit-dove	Frugivore	Forest edge	Tree sapling
Reinwardtoena brownii	Pied cuckoo-dove	Frugivore	Forest	Unknown
Todhiramphus chloris	Collared kingfisher	Insectivore	Forest	Termite nests, hollows in ground/riverbanks

As there were numerous potential covariates for use as predictors of bird occurrence (Table 5.1) I selected predictor variables a priori. Predictors represented my hypothesised drivers of bird responses: tree attributes, ground cover, rainforest life forms, and spatial context (Table 6.2), and included variables that were present in most sites but that varied across the landscape in accordance with land-use context (Chapter 5, Table 5.8). Three variables described tree attributes: canopy cover, tree species richness (density) and tree size (DBH) diversity. Tree size diversity was the Shannon-Weiner index of the proportion of trees in each of eight DBH classes (10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–90, 90–150 cm). As such, it represented an index of the size class distribution of trees, with higher values when trees were more evenly distributed among more size classes (Kanowski et al. 2010) indicating structural properties of importance to forest birds (Sekercioglu 2002; Kanowski et al. 2008). Similarly, high canopy cover and tree species richness indicate complex old-growth rainforest conditions (Kikkawa 1982; Clough et al. 2009).

Ground cover included two variables: percent cover of shrubs and seedlings (juvenile trees and lianae), and pioneer (heliophilic) ferns, which reflect a suite of structural and microhabitat conditions that may affect richness of understorey birds (Stouffer & Stratford 2013). Shrub and seedling growth is promoted by humid, shaded microclimates and moist soil conditions commonly found in more intact forest (Kitajima & Kitajima 1996). By contrast, pioneer plants such as ferns dominate the comparatively open, dry, light-filled understorey of disturbed habitats, impeding germination of late-successional trees (Guariguata & Ostertag 2001; Denslow 1996) and potentially obstructing foraging of forest understorey insectivores (Thiollay 1992; Mason 1996). Rainforest life forms also included two variables: abundance (cover) of palms >2 m and *Zingiberaceae* (ginger) species. Palms are a feature of least disturbed rainforest and may more broadly reflect old-growth microclimate conditions (Webb et al. 1976; Chazdon et al. 1997). They also provide an important food resource for forest frugivores (Peres 1994; DeWalt et al. 2003; Genini et al. 2009). Conversely, gingers thrive where humidity is high yet sunlight is not too sparse (Kubitzki 1998) and can dominate disturbed forest sites (Slik & van Balen 2006). Gingers may also provide food resources for 'generalist' nectarivores and insectivores (Sakai et al. 1999; García-Robledo & Kuprewicz 2009).

A single spatial variable—proportion of surrounding intact rainforest cover—was included to represent the local landscape context of each site (Wintle, Elith, et al. 2005b). This was the proportion of contiguous forest within a 2 km buffer of each site with a mean canopy cover of 95% (unlogged and secondary forests, not including riparian buffer zones). I derived this variable using ArcGIS 10.0 (ESRI 2011), adjusting the total area to include just terrestrial elements for sites whose 2 km buffer overlapped large water bodies.

Table 6.2 Model hypotheses and representative variables. See text for details of model hypotheses and relevant literature.

Model hypothesis	Variables	Abbreviation	Model
1. Tree attributes: tree species richness and structural attributes are associated with the richness of tropical forest birds through provision of resources..	Canopy cover	CC	Species richness ~ CC + TrR + TrDBH
	Tree richness*	TrR	
	Tree size (DBH) diversity (H')	TrDBH	
2. Ground cover: abundance of shrubs/seedlings and ferns reflect a suite of undisturbed and disturbed microclimatic and resource conditions respectively, which may be important for forest birds (particularly understorey species).	Shrubs/seedlings cover†	Shr/sdlg	Species richness ~ Shr/Sdlg + Fern
	Fern cover	Fern	
3. Rainforest life forms: palms are associated with old-growth forest conditions and provide important structural and food resources for forest birds. Gingers are associated with disturbed forest conditions but may provide resources for more 'generalist' birds.	Palm cover†	Palm	Species richness ~ Palm† + Ginger
	Ginger cover	Ginger	
4. Spatial context: the amount of intact (preferred) forest surrounding a site can affect bird species richness by providing source populations of birds and by enhancing landscape connectivity.	Intact rainforest cover	IFC2km	Species richness ~ IFC2km

† log-transformed; * logit transformed

I made scatterplots of predictors against both response variables to determine the nature of their relationship. Tree species richness, cover of shrubs/seedlings, and palms displayed non-linearity with both response variables and were log transformed to fulfill model assumptions of linearity. Canopy cover displayed non-linearity with bird species richness only, and was logit transformed following Warton (2011).

6-2-2-2 Model development and selection

To analyse the determinants of bird species richness I constructed four candidate models representing my four competing hypotheses (tree attributes, ground cover, rainforest life form cover and spatial context). Each model contained all variables associated with the relevant hypothesis (Table 6.2). I also built models that represented all possible combinations of my hypotheses (total models for each response variable = 15). I modelled relationships using generalised linear mixed models (GLMMs), with transect included as a random effect. Bird richness was modelled as a Poisson distribution. To allow direct comparison of regression coefficients, I standardised the predictor variables using the R package “arm” (Gelman et al. 2013), following Gelman (2008). I tested global models of each response variable (with all predictors included) for overdispersion, autocorrelation (using Moran’s *I* statistic) and for collinearity between predictors.

I used an information theoretic approach to compare the relative support for each of my hypotheses (across all combinations of my four models) (Burnham & Anderson 2002). For each response group, model support was determined by calculating AIC_C (AIC corrected for small sample size (Burnham et al. 2011)). Akaike weights (w_i) were used to rank the 15 models based on their relative likelihood of being the most parsimonious: a combination of the fit of the data and number of parameters included (with penalties for increasing complexity) (Burnham & Anderson 2002). In the absence of a standout model (wi ≥0.90, Burnham & Anderson 2002), I calculated model-averaged parameter estimates and standard errors for all predictors to account for model-selection uncertainty (Burnham & Anderson 2002; Richards et al. 2011). These are derived by calculating the weighted average of regression coefficients of each predictor over all subset models, with weights corresponding to the w_i for models that include the predictor of interest (Burnham & Anderson 2002, pp.150-155).

To test the fit of the ‘best’ model for each response variable, I calculated the coefficient of determination using a likelihood-ratio test. This is a pseudo-R^2 statistic and represents the variance explained by the fixed effects of the models, compared to the null model (Nagelkerke 1991). All statistical analyses were conducted in the R software package (R Core Team 2013). GLMMs were constructed using the ‘lme4’ package (Bates 2010b). Model selection, model averaging and model fit were carried out using the 'MuMIn' package (Barton 2013). Autocorrelation analyses were made using the 'spdep' package (Bivand 2014) and multicollinearity variance inflation factors were assessed in the 'car' package (Fox & Weisberg 2013).

6-2-2-3 Analyses of model variables among landscape elements

Although analysed separately in Chapters 3–5, here I present collated analyses of the occurrence of all model response and predictor variables (6-2-2-1) among landscape elements. These analyses are conducted to provide supporting information to assist the interpretation of results (and to summarise relevant previous findings for the reader). The model sets detailed in the previous section (6-2-2-2) analyse relationships across all sites without factoring in land-use type. However, to consider the implications of these relationships for conservation management of the production landscape, it is important to have an understanding of how these variables change among landscape elements.

To that end, I modelled site-level species richness for forest-specialist birds using GLMs with a Poisson error distribution, in the R 'stats' package (R Core Team 2013). The response variable was the total number of species recorded at each site, and the single categorical predictor was the landscape element, comprised of five levels (representing each element). Species richness in elements was considered significantly different where 95% CIs did not overlap zero, with unlogged forest as reference factor. Autocorrelation analyses were made using the 'spdep' package (Bivand 2014), and no autocorrelation was evident in model residuals.

To explore the composition of predictor variables among landscape elements, I used non-metric multidimensional scaling (nMDS) to produce an ordination plot based on the Euclidean dissimilarity matrix of standardised predictor values for each site. I subsequently fit vectors of my predictor variables onto the ordination space to observe the relationship between sites and the distribution of values of each predictor. Ordination plots and vector fitting were performed using the 'metaMDS' and 'envfit' functions in R package 'vegan' (Oksanen et al. 2013).

6-3 Results

6-3-1 Model estimation

For forest-occurring bird species richness the most parsimonious model was that which contained only tree attributes ($w_i = 0.44$), while for forest-specialist birds the most parsimonious model contained both tree attributes and rainforest life forms ($w_i = 0.23$, Appendix Table D.1). This is reflected in the summed Akaike weights for each response group

(Figure 6.1). Tree attributes was clearly the most influential variable category for both forest occurring and forest specialist species (Figure 6.1). Rainforest life forms and spatial context were useful for explaining some variance for forest specialist species. The fit of the most parsimonious models, indicated by the pseudo-R^2 statistic, was quite low for both forest occurring species richness (0.10) and forest specialist birds (0.17). No autocorrelation or overdispersion was found for either response variable, nor was multicollinearity detected between model covariates (vif ≤2.8). As a clear standout model was not identified for either response group (wi ≥0.90, Burnham & Anderson 2002), model-averaging was conducted (Appendix Table D.2).

6-3-2 Tree attributes

Model-averaging indicated that the influence of tree attributes was driven only by tree species richness and canopy cover, not tree size diversity (Figure 6.2). The relationship between tree species richness was positive and linear for both response groups (Figure 6.3b,d). A similar relationship was found between canopy cover and richness of forest-using birds (Figure 6.3a). For forest specialists, however, species richness was found to increase exponentially with canopy cover, with a marked increase in richness evident after canopy cover reached ~70% (Figure 6.3c).

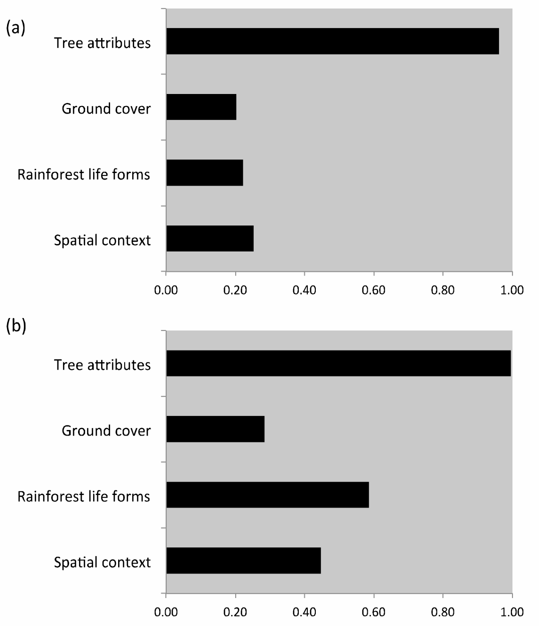

Figure 6.1 The relative magnitude of importance of candidate models derived from summing Akaike weights of all model subsets in which the candidate model occurred ($\sum w_i$); (a) Species richness of forest-using birds; (b) Species richness of forest-specialist birds.

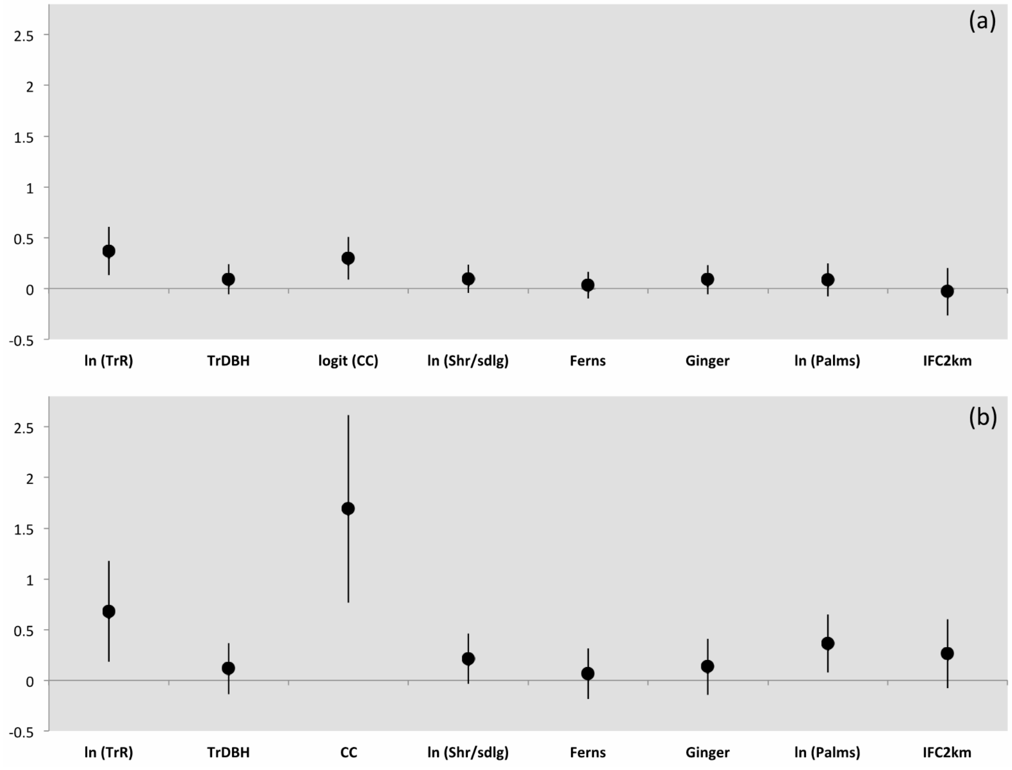

Figure 6.2 Model-averaged parameter coefficients and 95% confidence intervals of predictor variables for (a) species richness of forest-using birds; and (b) species richness of forest-specialist birds. Predictors whose confidence intervals do not overlap zero have an important influence on the response variables. Predictor variable abbreviated labels are given in Table 6.2.

6-3-3 Ground cover

For both response groups, the cover of both shrubs/seedlings and pioneering ferns had 95% confidence intervals for model-averaged parameter estimates that overlapped zero (Figure 6.2). Hence, neither of the ground cover variables considered were found to be an important influence on either response variable group.

6-3-4 Rainforest life forms

Rainforest life forms were not found to be an important influence on the richness of forest-using species, with confidence intervals for model-averaged parameter estimates overlapping zero for both ginger and palms (Figure 6.2a). However, palm cover was found to be an important positive influence on the richness of forest specialist species (Figure 6.2b). Model predictions for this relationship are found in Figure 6.3e and indicate that there is some uncertainty surrounding this relationship, with predicted values having large confidence intervals.

6-3-5 Spatial context

The proportion of contiguous forest within 2 km of a survey site was not found to be a strong influence on the richness of either forest occurring or forest specialist species, with model averaged confidence intervals overlapping zero for both response groups (Figure 6.2).

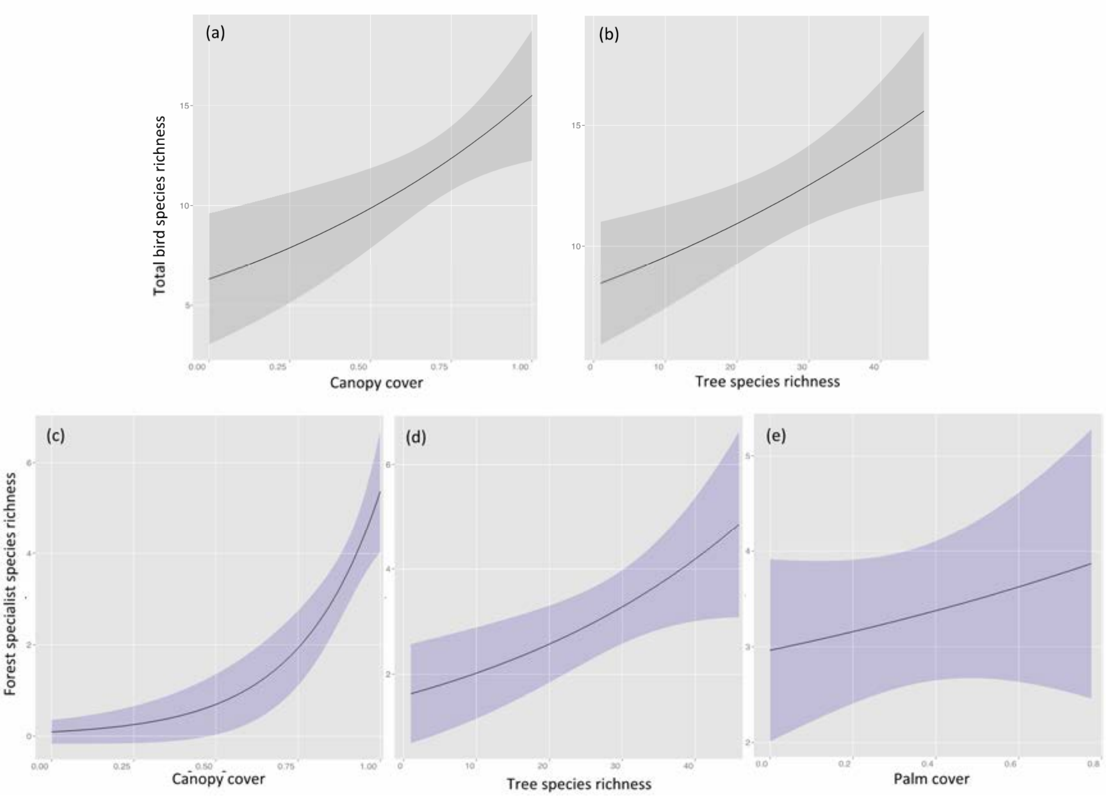

Figure 6.3 Relationships between richness of forest-using species and (a) canopy cover, (b) tree species richness; and between richness of forest-specialist species and (c) canopy cover, (d) tree species richness and (e) palm cover. Unbroken lines represent the predictions from model-averaged models and shading depicts the 95% confidence intervals for the most influential predictors.

6-3-6 Analyses of model variables among landscape elements

Comparisons between species richness among elements for forest-specialist bird species revealed that richness was highest in the secondary remnant and unlogged forest, and lower in the secondary riparian element (GLM $p < 0.01$, with unlogged forest as reference), and mature ($p < 0.01$) and young plantations ($p < 0.001$) (Table 6.3). This differs from values found for forest-occurring birds (Chapter 4 and reproduced here Table 6.3), where species richness was higher in the secondary remnant and riparian elements compared to unlogged forest (GLM, $p < 0.05$), and lower in mature ($p < 0.05$) and young plantations ($p < 0.001$) compared to unlogged forest.

Table 6.3 Means (standard errors) of bird species richness among landscape elements. Emboldened figures represent values whose 95% confidence intervals do not overlap with zero with unlogged forest as reference group (intercept).

	Landscape Element				
Variable	Unlogged forest	Secondary remnant	Secondary riparian	Mature plantation	Young plantation
Richness forest-using species*	15.06 (0.57)	**20.78 (1.26)**	**18.21 (0.95)**	**12.81 (0.45)**	**5.25 (0.39)**
Richness forest-specialist species	7.22 (0.47)	8.33 (0.96)	**4.86 (0.59)**	**3.28 (0.28)**	**0.21 (0.09)**

*Results reproduced here from analysis detailed in Chapter 4

The nMDS ordination demonstrated a similarity in the composition of predictor variables for sites within each landscape element (Figure 6.4). Unlogged and secondary remnant forest sites were most similar in their compositions and were related to the richness of tree species, canopy cover, cover of shrubs/seedlings and palms, and proportion of intact forest within a 2 km buffer. Secondary riparian sites shared a correlation of canopy cover with unlogged and secondary remnant elements but they were distinguished from these elements by their greater correlation with ginger and fern cover. Mature plantations were predominantly correlated with the cover of gingers and ferns. Young plantations were also correlated with fern cover but were mostly defined by low values for all predictors, as evidenced by their negative values for both nMDS axes.

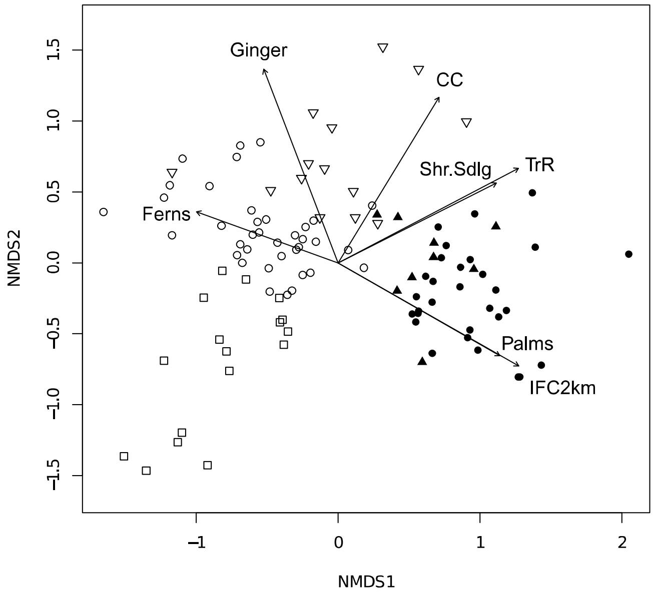

Figure 6.4 nMDS ordination plot of predictor variable composition for each site, stress = 0.13. Vectors of predictor variables display the correlation with sites (direction), and longer vectors indicate a stronger correlation. All predictors were significantly correlated with the ordination ($p < 0.001$). Young plantations – open squares; mature plantations – open circles; secondary riparian – open inverted triangles; secondary remnant – filled triangles; unlogged forest – closed circles. Predictor variable abbreviated labels are given in Table 6.2.

6-4 Discussion

In the *E. deglupta* plantation landscape, richness of both forest-using and forest-specialist bird species was driven by site-level vegetation attributes (primarily canopy cover and tree species richness), rather than spatial context. Mature native timber plantations and regenerating logged forest elements independently supported ≥90% of forest bird species (Chapter 4), indicating that suitable levels of canopy cover and tree species richness were retained within the production matrix. Hence, land-sharing strategies similarly incorporating production land-uses that enable high canopy cover and tree species richness could be effective for conservation of tropical birds while producing required yields. However, I found site-level richness of forest-specialist birds—which were additionally influenced by palm cover—to be lower in plantation and secondary riparian forests indicating a limit to the extension of these three key resources beyond unlogged and secondary forest remnants. This reduction in resources was most pronounced in the young plantations, highlighting the importance of taking the age of land-uses into account when assessing the conservation potential of a production type.

6-4-1 Tree attributes

An increase in canopy cover and tree species richness were key requirements for the attraction of forest bird species to a site, which is unsurprising given their evolution in complex forested habitats (Mayr & Diamond 2001). The positive linear relationship between bird species richness and canopy cover reflects a reliance on tree presence, with a greater breadth of bird species supported by higher cover, indicative of increased tree density. The number of forest-specialist species present substantially increased above a canopy cover threshold of ~70%. This corresponds to the lowest cover value recorded in mature plantations (74%), suggesting that specialist birds prefer continuous canopy cover to the patchy tree cover that characterises young plantations. Reliance on contiguous canopy may be explained by protection from birds of prey and dependence on specialist canopy resources (e.g. nest sites (Lambert & Collar 2002; Cruz-Angon & Greenberg 2005), or foraging habitat (Kennedy et al. 2010)).

I found mature *E. deglupta* plantations to have a higher mean canopy cover (93%, Chapter 5) than that found in studies of other mature plantations (Kanowski et al. 2003; Zurita et al. 2006), which may partly explain why this element supported all but two forest specialists. Canopy cover in mature plantations was high on average because of the contribution of an even overstorey of thin-leaved emergent *E. deglupta* crowns, supplemented by understorey–midstorey cover of recruited rainforest trees <25 cm DBH (Chapter 3). However, total cover values mask a depauperate sub-canopy–canopy layer compared to unlogged and secondary forests (Chapter 5). This may explain why even with high mean canopy cover, both bird groups were found in lower richness in mature plantations compared to unlogged forest. Simplification of vertical structure has been similarly implicated in the lowered richness of forest birds in both crop and timber plantations (Peh et al. 2006; Nájera & Simonetti 2010). Moreover, the emergent canopy of *E. deglupta* plantations was comparatively open, making it more exposed to wind, light and heat than the canopy of unlogged and secondary forests and thus less suitable for canopy-using birds (Kanowski, Catterall & Wardell-Johnson 2005a).

Bird richness was also influenced by increased tree species richness, which concurs with findings from other production forestry studies, such as plantations (Farwig et al. 2008), agroforests (Abrahamczyk et al. 2008) and logged forest (Felton, Wood, et al. 2008b). Like increased canopy cover, higher tree species richness increases structural complexity because of the greater range of architectural forms and stem sizes present (Pinotti et al. 2012). A diversity of tree species also provides a greater variety of food resources for birds. This may be of particular importance for obligate frugivores (which comprise the majority of forest specialists in this study) because of the ephemeral nature of fruiting resources and intense feeding competition (Diamond & Terborgh 1970; Frith et al. 1976; Beissinger 2000). The importance of fruit diversity rather than simply fruit abundance may explain why the more disturbed secondary riparian and mature plantation elements contained a lower richness of forest specialists compared to unlogged forest even though they supported the highest density of trees (but not tree species) in fruit (Appendix D.1, Styring et al. 2011). Nonetheless, while these modified elements did not cater equally well for forest specialists as unlogged forest, their high number of important fruiting pioneers such as *Ficus spp.* (Chapter 3) may be extending food resources in sufficient quantities for the many non-obligate frugivores in this system (Marsden & Symes 2008; Sam et al. 2014).

Given the relationship between structural complexity and bird species richness, it was interesting that tree size diversity—a purported measure of horizontal structural complexity—was not an influential factor. This was probably a result of my choice of diversity index, which incorporated evenness into the measure, an attribute that was highest in mature plantations. Old-growth forests are characterised by a reduction in evenness (Condit et al. 1998), leading us to expect a negative correlation between bird richness and tree size diversity in this landscape. However, because I included young plantations with very low tree size diversity, this relationship was confounded by simultaneously very high and very low bird richness for low-medium tree size diversity values. Therefore, structural complexity was better captured by canopy cover and tree species richness.

6-4-2 Rainforest life forms

For forest-specialist birds the cover of palms was also found to be an important factor. In and of themselves, palms provide key fruiting resources during times of fruit shortage (Peres 1994; DeWalt et al. 2003). Additionally, in this landscape the occurrence of palms was found to be highly correlated with the occurrence of old-growth rainforest life forms: epiphytic ferns, lianas, hemi-epiphytes and climbing palms (Chapter 5), which have similarly been identified as important food and nesting resources for forest-dependent birds (Cruz-Angon & Greenberg 2005; Schnitzer & Bongers 2002; Lambert & Collar 2002). High abundance of palms was strongly associated with unlogged and secondary remnant forests, but abundance was low or absent within the secondary riparian and plantation elements. The inability of palms to extend beyond remnant forest has also been observed in matrix habitat in southeast Asia (Waltert et al. 2005) and the Neotropics (Letcher & Chazdon 2009), suggesting a limitation based on time since disturbance. This idea is supported by a growing number of studies demonstrating that rainforest structural attributes recover well before plant species composition in disturbed forest (Guariguata & Ostertag 2001; DeWalt et al. 2003).

6-4-3 Ground cover

Interestingly, ground covers and the microclimatic conditions they represented, did not significantly influence the richness of either bird response group. This finding contrasts with continental and land-bridge studies reporting declines in understorey birds in response to disturbance-induced habitat changes (Felton, Lindenmayer, et al. 2008a; Thiollay 1997; Peh et al. 2005). The lack of relationship in this study may result from a combination of factors. Firstly, New Britain's lowland understorey birds may have a broader ecological tolerance than their continental and land-bridge counterparts because of reduced inter-specific competition (Clegg 2010) in this comparatively species-poor bird community (Lecroy & Peckover 1983; Steadman 2006). For example, New Britain's understorey insectivore species are not as specialised in their diet as Neotropical counterparts (e.g. ant-followers, Thiollay 1997). A similar ecological tolerance was found in the response of understorey birds to disturbance on oceanic Sulawesi island compared to those of more species-rich Borneo (a former land-bridge island, Abrahamczyk et al. 2008). Secondly, fern cover—which can inhibit insectivore foraging (Sam et al. 2014)—co-occurred in modified elements with gingers, which have been observed to attract a variety of insects in timber plantations (Styring et al. 2011), potentially providing a compensatory food resource.

Disturbance-related declines of understorey birds have also been attributed to changes in nest-site suitability for ground-nesters (Stouffer et al. 2006). At Open Bay, ground-nesting birds were represented by: (1) the megapode (*Megapodius eremita*), which nests seasonally in large colonies at the base of volcanoes (Broome et al. 1984); and (2) kingfishers (*Alcedo lepida, Tanysiptera nigriceps,* and *Todhiramphus* spp.*),* who burrow nest holes into riverbanks or arboreal termitaria (Dutson 2012). Arboreal termitaria were found in high density on the boles of plantation *E. deglupta* trees (Appendix D.2) and I repeatedly observed their use by forest kingfishers. A similar observation was made by Bell (1979) in teak plantations on the north of the island. Therefore, it is unlikely that understorey species were impacted by nest limitation.

6-4-4 Spatial context

The proportion of intact contiguous forest within a 2 km buffer did not influence bird species richness, indicating that site-level attributes were more important for forest birds. Similar findings have been made in studies where much of the production landscape and its surrounds have high tree cover, by way of a low-contrast matrix and a high proportion of regional intact rainforest cover (Kennedy et al. 2010; Peh et al. 2006; Chazdon, Peres, et al. 2009b). In this study, all matrix elements (with the exclusion of young plantations) provided continuous tree cover, which likely facilitated the observed dispersal of all but two forest specialists

(***Reinwardtoena brownii*** and ***Ptilinopus rivoli***) from unlogged forest (Tscharntke et al. 2012). Additionally, all sites occurred within 4 km of contiguous, old-growth primary and secondary (logged) rainforest covering an area larger than the plantation estate, which was capable of supporting populations of forest specialists and of supplementing populations of matrix-using species (Gardner et al. 2010). Thus, the foremost limiting factor for birds in this landscape was suitable habitat rather than access. This effect may have been enhanced by the capacity of most forest specialists to move away from less-suitable sites in search of optimal resources. This has been particularly noted for tropical, medium-large-bodied frugivores (Neuschulz et al. 2012; Sam et al. 2014), which describes the majority of my lowland specialist birds.

6-4-5 Caveats

Models of both bird groups only explained 10–17% of the variation in species richness among sites, signifying that there were other factors involved which were not considered. These may include: (1) structural and environmental variables (Watson et al. 2014; Lira et al. 2012); (2) the impact of the ‘built’ environment surrounding landscape elements (e.g. roads, Laurance et al. 2009); (3) the relative density of humans (Fischer et al. 2013); (4) species-specific responses to the predictors assessed (Smyth et al. 2002); and (5) the effects of inter- and intra-specific competition (Beaudrot et al. 2013; Robertson et al. 2013). Additionally, variation in bird occurrence may be influenced by regional population patterns external to the studied landscape (C. Moran & Catterall 2014). Unfortunately, at an isolated location lacking in previous avian research, I did not have the time or resources to explicitly measure these effects and their relative contribution(s). However, the purpose of these models was to provide explanatory rather than predictive information to guide management. As such, they were effective at identifying the most influential attributes tractable to land-managers.

A key question arising from any study evaluating the conservation potential of production land-covers is whether fauna are capable of breeding within them, thereby effectively mitigating effects of habitat loss and fragmentation (Sekercioglu & Loarie 2007). Unfortunately there is little published information on the nests of many of New Britain’s bird species and it was not possible to formally survey nests in this study. However, I did observe nests of 15 of my 41 surveyed species. Of these, there was evidence that 12 species were capable of nesting in secondary and plantation elements, suggesting that populations of these species can be maintained outside remnant forest (Appendix Table D.3). Moreover, in reading the literature (Appendix B.3) and through my observations I only found seven species requiring tree hollows—a limited resource restricted to mature, old trees (Newton 1994)—and four of these were observed nesting in hollows in secondary remnant and riparian forests.

6-4-6 Conservation implications

The high continuity of canopy cover and richness of rainforest tree species afforded by the native timber plantations and secondary forest elements in this landscape were important for the persistence of forest-occurring birds in the matrix. Therefore, land-sharing strategies that incorporate production types such as plantations, that can provide structure (i.e. tree cover) and recruit native plant species, may prove effective for the conservation of tropical birds while also providing production outcomes. However, stand-level management and choice of plantation species are likely to significantly affect the provision of these resources in different plantation contexts. For example, industrial oil palm (*Elaeis guineensis*) plantations —which are being promoted as a replacement land-use for these *E. deglupta* plantations—may be capable of providing continuity of tree cover, but have proven incapable of recruiting native tree species because of the intensity of tending they demand and their effect on understorey edaphic and microclimate conditions (Sheldon et al. 2010; Azhar et al. 2013). Hence, biodiversity outcomes are more likely in plantations whose focal species can facilitate successional processes of native plants and which involve minimal tending to produce required yields. My study agrees with an emerging body of evidence that timber plantations using species native to an area may fulfill these criteria (Davis et al. 2012; Keenan et al. 1997; Farwig et al. 2009; Lima & Vieira 2013). Native timber plantations account for <15% of tropical timber plantations globally (Montagnini 2001), and they should be more broadly considered for their potential role in conserving biodiversity in the expanding global plantation estate.

Nonetheless, while mature *E. deglupta* plantations demonstrated a high capacity for biodiversity conservation, they would be limited in terms of supporting large, breeding populations of birds because of the dominance of *E. deglupta* trees (precluding greater tree species richness), a lack of late-successional plant species (plantation age at harvest), and the discontinuity of resources created by clearfell harvesting and early plantation stages (Wardell-Johnson et al. 2005). To reduce the impacts of these factors, land-sharing conservation strategies should involve land-use planning that prioritises spatial and temporal continuity of canopy cover, tree species richness and old-growth rainforest plant composition throughout the landscape. For plantations, these attributes were accumulated as they aged therefore, I recommend temporally varying harvesting cycles to ensure the highest possible cover of mature plantations through time (and their presence at all times). A vital counterpart is to ensure the restriction of future developmental encroachment into the unlogged and secondary forest elements, because of their superior habitat quality to that of plantations, and the consequent role they play as refugia for source populations of forest biota (especially more vulnerable specialist species).

Although the proportion of intact rainforest within 2 km did not influence bird species richness at the site-level, it may have greater influence of species patterns at the regional scale, and given future development. For example, were there to be extensive human modification of the currently vast remaining intact forest in this landscape, it is likely that a considerable decline in the richness of birds using modified elements would follow resulting in a greater influence of spatial context, as observed in studies of extensively cleared tropical production landscapes (C. Moran & Catterall 2014; Zurita & Bellocq 2010; Ranganathan et al. 2010). Given the value of the old, regenerating secondary forests to biodiversity conservation, I recommend that they be more formally protected (along with unlogged forest) from any future expansion of plantations to meet increasing timber demands.

6-5 Chapter summary

The richness of both forest-using and forest-specialist birds in this landscape was driven by habitat attributes (e.g. canopy cover and tree species richness) rather than spatial context (the proportion of unlogged or high-quality secondary forest within a 2km radius). Habitat attributes were found to be sufficiently suitable within unlogged forest, secondary forest and mature plantations to support a number of forest-using species. In addition, I found palms were additionally influential for the richness of forest-specialist birds. Palm abundance was associated with unlogged and secondary remnant forest but not secondary riparian or plantation elements. The outcomes of this chapter indicate that land-sharing strategies incorporating production types such as native timber plantations that permit high canopy cover and tree species richness can be effective at balancing yield production with bird conservation. However, the retention of undisturbed old-growth forest remnants are vital for the conservation of forest-specialist species and are likely to become more important as landscapes become more fragmented.

CHAPTER 7

General Discussion

Community meeting with the Kol people

CHAPTER SEVEN

Given the state of tropical forests today, and the likelihood of continued encroachment into primary forest frontiers (especially in the lowlands), it is crucial that we understand the role that multi-use production landscapes play in the persistence or decline of tropical forest species (Chazdon, Harvey, et al. 2009a; Sutherland et al. 2009; Laurance et al. 2012). From an ecological perspective, it is important to understand how and why species persist in multi-use landscapes in order to better predict future species assemblies and the subsequent ramifications for ecosystem integrity. From a conservation management perspective, understanding the ability of different land-uses to support biota and the processes which allow persistence of species in heterogeneous production landscapes is vital to inform effective stand-level management and spatial planning that can deliver conservation outcomes with negligible impact on yield (Melo et al. 2013; Chazdon, Harvey, et al. 2009a). Such understanding is hampered by the complexity of production landscapes, which encompass a variety of land-uses, management scenarios, spatial composition, and biogeographic contexts. There still remains much research to be done in these landscapes in order to characterise the influence of contextual factors, and to consequently produce representative, evidence-based management strategies. Three pressing research requirements include: (1) studies in poorly-represented tropical regions to incorporate variation in biogeography and land-use history; (2) evaluation of the impact of a greater variety of land-uses and different management scenarios on biodiversity; and (3) investigation into the dynamics of species occurrence throughout whole production landscapes, as opposed to assessment of land-use types in isolation.

In this thesis I contribute to the body of research on tropical multi-use production landscapes by addressing some of these knowledge gaps. Specifically, I (1) contribute to the ecological understanding of the biodiversity conservation capacity of tropical native timber plantation landscapes; and (2) provide evidence-based management recommendations for biodiversity conservation for this production landscape and for timber plantation landscapes more generally. I achieved these aims by studying the impact of a native timber (*E. deglupta*) plantation landscape on the occurrence of rainforest vegetation and bird species on New Britain Island, Papua New Guinea (PNG). To assess the conservation value of the production landscape I investigated the patterns and processes involved in native rainforest species occurrence among the landscape's main component land-uses (landscape elements). This landscape approach is rarely taken in multi-use production systems but is necessary to understand the influence of both the matrix and remnant forest elements on the patterns of species occurrence (Chazdon, Harvey, et al. 2009a; Gardner et al. 2009).

In Chapters 3 and 4 I investigated the occurrence of forest tree and bird species among landscape elements and described potential mechanisms for their differential persistence. This provided important information on the current capacity for biodiversity conservation within this production landscape, and also highlighted the role of biogeographic processes and historical land-use in shaping species' responses to disturbance. To assess the relative habitat quality available to local biota within landscape elements, I measured the effects of land-use type on vegetation characteristics in Chapter 5. This adds to the currently sparse literature on the effects of tropical native plantations on rainforest flora (Stephens & Wagner 2007), and of the regenerative capacity of selectively-logged forests in PNG. A selection of these habitat variables were then chosen as predictors of forest bird species richness, along with a spatial predictor which captured the proportion of old-growth primary and secondary forest cover occurring in the heterogeneous landscape. In Chapter 6, these predictors were evaluated for their ability to explain the landscape-wide occurrence patterns of forest birds. This analysis imparted a better understanding of the influence of habitat resources on bird species persistence, providing crucial information for conservation managers.

This research has delivered a comprehensive analysis of the drivers of rainforest species occurrence patterns within a native timber plantation landscape in a rarely studied but biologically important tropical region. The findings of this research provide valuable evidence upon which to base conservation management strategies for this system. In this final chapter, I summarise key findings of the four objectives that underlie the study (Table 7.1). I then provide a synthesis of these findings and their contribution to our knowledge in this field of study, and discuss implications for conservation management of this system and its applicability to other production landscapes. Finally, I identify further areas for research, with a special focus on the application of conservation management in a tropical production context.

Table 7.1 Summary of findings of this thesis in relation to key objectives and their implications for conservation and management. Objective 4 is covered in the final column “Conservation and Management Implications”.

Objectives and Aims	**Key Findings**	**Conservation and Management Implications**
Objective 1a – Identify forest tree species that can and cannot persist in production landscape elements and how occurrence patterns are mediated by the attributes of species		
What is the effect of landscape element on the richness of tree species?	• Tree species richness was highest in unlogged forest, secondary remnant and secondary riparian forest, and lower in mature plantations and young plantations.	• Unlogged and secondary forests are important source pools and refugia for lowland rainforest trees.
	• Cumulatively, across all sites within the secondary remnant element >90% of tree species found in unlogged forest were recorded. This value was >70% in both the mature plantation and secondary riparian elements.	• A combination of stand-level management and biological processes may be interacting to maintain high recruitment in modified landscape elements.
	• Young plantations provided little refuge for forest tree species.	• Spatial and temporal planning will need to address the scale of young plantation areas that exist at any one time.
What is the effect of landscape element on the composition of tree species?	• Tree species composition reflected the gradient in disturbance. Composition was most similar between unlogged and secondary remnant forest, and became less similar as disturbance intensity increased and time-since-disturbance decreased (secondary riparian forest→ mature plantations→ young plantations).	• Unlogged and secondary forests are important source pools and refugia for populations of lowland rainforest trees.
How do attributes of trees affect their response to disturbance types? (a) What is the effect of landscape elements on the richness and composition of successional stages?	• Late-successional species abundance declines in the secondary riparian element and plantation elements compared to unlogged forest. For plantation sites, late-successional species richness is also far lower. Limited recruitment of these species appears most strongly associated with the age of the element (i.e. time since disturbance).	• Late-successional species should be targeted for conservation action. • Ensure maintenance of mature landscape elements spatially and temporally, and reduce disturbance in riparian buffer elements.

Objectives and Aims	Key Findings	Conservation and Management Implications
	• Two-thirds of unlogged forest late-successional species are capable of germinating in the understorey of mature plantations. The remainder may or may not be similarly capable.	• Estimation of biological diversity of plant species in modified tropical forests requires measurement of juvenile stages as well as adult stages. • Increase harvest rotation times where possible (in terms of production yield trade-offs), retain late-successional trees during harvest where viable.
	• Young plantations support no late-successional trees, except occasional remnants.	• Spatial and temporal planning will need to address the scale of young plantation areas that exist at any one time. • Retain late-successional trees during harvest where viable, instead of clearfell.
(b) What is the effect of landscape elements on the richness and composition of NVD and animal-dispersed tree species?	• NVD species are more limited than animal-dispersed species in their ability to colonise plantations, possibly because of a lower dispersal capacity.	• Target NVD species for conservation actions, e.g. incorporate NVD species in enrichment planting activities.
	• Animal-dispersed species are better capable of colonising modified elements, but they are still recruited in far lower density in mature plantations than unlogged forest.	• To ensure this pattern continues in the long-term, need to maintain populations of dispersers (e.g. bird and bat populations) by retaining their key resources in landscape through stand-level and landscape management (Chapter 6).
Objective 1b – Identify forest tree species that can and cannot persist in production landscape elements and how occurrence patterns are mediated by species traits		
What is the effect of landscape element on the richness of forest bird species?	• Species richness of forest birds was higher in secondary remnant and riparian elements compared to unlogged forest, and lower in mature and young plantation.	• Unlogged and secondary forests are important source pools and refugia for lowland rainforest birds.
	• Cumulatively, across all sites within the modified landscape elements >90% of unlogged forest bird species were recorded (except in young plantations).	• Native timber plantation landscape has high conservation value for forest bird species. Many of these species demonstrate a capacity for some tolerance of anthropogenic disturbance and an

Objectives and Aims	Key Findings	Conservation and Management Implications
		ability to exploit resources beyond unlogged forest remnants.
What is the effect of landscape element on the composition of forest bird species?	• Bird species composition reflected the gradient in disturbance. Composition was most similar between unlogged and secondary remnant forest, and became less similar as disturbance intensity increased and time-since-disturbance decreased	• Unlogged and secondary forests are important source pools and refugia for lowland rainforest birds.
	• Young plantations displayed a much lower richness and abundance of birds compared to all other elements	• Spatial and temporal planning will need to address the scale of young plantation areas that exist at any one time.
How do bird species traits influence their response to land-use disturbance?	• Frugivory and forest specialisation were found to be the traits most associated with vulnerability to disturbance.	• Target frugivores and forest specialists for conservation action. • Unlogged and secondary forest reserves will be of greatest importance for long-term persistence of these 17 species.
	• Traits acting at the habitat or landscape-scale (which involved some level of resource specialisation) generally conformed to disturbance response observed in other studies. Although for many, tolerance of low-level disturbance of both secondary elements was generally high (e.g. large body size, canopy and sub-canopy-using birds).	• Many of New Britain’s lowland forest bird species appear capable of tolerating low-intensity disturbance of secondary forests.
	• Endemic and ground-dwelling birds were found to exploit all mature modified elements equally or greater than unlogged forest, in contrast to findings from most continental studies.	• Biogeography and history of disturbance may affect the differential resilience of oceanic island species pools compared to continental species pools. • Traits such as endemism that act beyond the landscape-scale on islands may not be an appropriate indicator of disturbance response that occurs at the landscape or habitat-scale.
Objective 2 –Assess the effect of land-use on habitat properties (vegetation structure and plant species richness and composition)		

Objectives and Aims	**Key Findings**	**Conservation and Management Implications**
Which vegetation attributes most clearly differentiate unlogged (old-growth) forest from modified landscape elements?	• Young plantations were differentiated from unlogged forest by their lower values for all measured attributes. • The gradient in disturbance was more consistently differentiated by the richness and composition of plant species than by structural attributes. • Mature plantations were differentiated from unlogged forest by their lower values for canopy cover, shrubs/seedling cover, vertical foliar richness, tree species richness and late-successional life form composition. And by their higher tree size diversity (evenness among DBH classes). • The secondary riparian element had a reduced **VFD** and lower **canopy VFR**, possibly due to a paucity of **large, old trees (>60 cm DBH**), and demonstrated a decline in late-successional life forms compared to unlogged forest.	• Spatial and temporal planning will need to address the scale of young plantation areas that exist at any one time. • The biodiversity conservation value of secondary riparian element will improve if ongoing human disturbance can be abated. • Unlogged and secondary forests are important source pools and refugia for lowland rainforest plant species and for unique structural resources.
To what extent are old-growth forest attributes retained among landscape elements?	• Mature plantations had recovered basal area of live and dead trees and vertical foliar diversity equivalent to that of unlogged forest.. • Both secondary elements were similar to unlogged forest for all tree and structural attributes (except those mentioned **above (bold)** for the riparian element).	• All elements but the young plantations retain potentially valuable structural resources, representing a large proportion of the landscape. • Unlogged and secondary forests are important source pools and refugia for lowland rainforest plant species and for unique structural resources.
Which vegetation attributes are best candidates for modelling bird species richness?	• Canopy cover, tree species richness, tree size (DBH) diversity, special life form cover (palms and gingers), and ground cover (shrubs/seedlings and ferns).	• Addressed in Objective 3.
Objective 3 – Investigate the relative influence of site-level habitat attributes and spatial composition of landscape elements on forest bird species occurrence		

Objectives and Aims	**Key Findings**	**Conservation and Management Implications**
What is the relative influence of site-level vegetation attributes and spatial context on the richness of: (a) forest-using birds	• (a) The most influential predictors of forest-using bird species richness were: canopy cover and tree species richness.	• Spatial and temporal continuity of canopy cover, tree species richness and palm cover are a priority for the conservation of lowland forest birds (especially forest-specialists) in this production landscape. • These attributes are best maintained outside of active production land-uses: unlogged forest and secondary forest protected by conservation reserves. • Spatial context may play a more important role in future rotations and/or as the broader landscape becomes more fragmented.
(b) forest-specialist birds	• (b) The most influential predictors of forest-specialist bird species richness were: canopy cover, tree species richness, and palm cover. • Habitat attributes were more influential on bird species richness values at a given site than spatial context. • Ground cover predictors did not influence the richness of forest-using or forest-specialist bird species.	
How are key predictor variables distributed among landscape elements?	• Unlogged forest and secondary remnant forest elements had the highest values of the 3 key predictor variables (CC, TrR, Palms) followed by the secondary riparian forest and mature plantations. • These 3 predictor variables were either patchily distributed or completely absent (palms) in young plantations.	

7-1 Synthesis of key findings

7-1-1 What is the value of this native *Eucalyptus deglupta* timber plantation landscape for the conservation of forest vegetation and bird biodiversity?

Native timber plantations may represent a land-use capable of balancing production and conservation in tropical forests because of their delivery of ecosystem services (e.g. soil stabilisation, water retention and nutrient turnover) and facilitation of rainforest vegetation successional processes through provision of site conditions necessary for seed germination (Carnus, Jactel, et al. 2006a; Keenan et al. 1999; Parrotta et al. 1997). In this thesis I investigated the biodiversity conservation value of a native *E. deglupta* plantation landscape on the oceanic island of New Britain, Papua New Guinea. I found that a very high proportion of forest-occurring tree (70%) and bird (>90%) species were capable of existing within the matrix of native timber plantations and forestry-affected secondary landscape elements compared with those of plantation studies from other regions (Chapters 3 & 4). Species persistence among these component landscape elements was influenced by a number of factors: the species' ability to adapt to novel habitats (which is related to their biological traits, Chapters 3 and 4), the support provided by human-affected landscape elements (which is dependent on intensity of disturbance and management, Chapter 5) and the species' ability to disperse freely throughout the landscape (a combination of spatial continuity of resources and species' traits, Chapter 6). Here, I summarise how these factors influenced persistence of species across the landscape, and how this relates to current ecological literature.

The landscape elements represented land-uses of different timing and degree of modification (from most to least modified at the time of the study): unlogged forest → secondary remnant → secondary riparian → mature plantation → young plantation (Chapter 2). For the most part, occupancy of both tree and bird species among these elements reflected this disturbance gradient as expected, with species richness higher at sites in the least modified unlogged and secondary forest elements compared to the plantations. Species compositions were also found to be most similar between unlogged forest and secondary forest elements, and least similar between unlogged forest and plantation elements. For all measures, young plantations resembled unlogged forest the least. However, there were some unexpected findings, such as the higher richness of forest birds in secondary forest elements compared to those in unlogged forest (Chapter 4). Additionally, there was no significant difference between the composition of tree species in secondary remnant forest compared to that of unlogged forest, for which I can find no equivalent in the literature (although, high levels of species conservation in fallow, selectively-logged forest have been well documented (Gibson et al. 2012)). This suggests that

New Britain's selectively-logged lowland secondary forests have a high capacity for regeneration rendering them of great value to biodiversity conservation. This finding, in concert with the elevated levels of both forest tree and bird species in mature plantations compared to other native timber plantation studies (Chapter 3 and 4) indicates that some of this capacity may lie in the tolerance of New Britain's forest species to human modification. Understanding the relationship between species traits and the impact of human modification on the landscape can go some way towards clarifying the limits of this tolerance and the relative influence of management.

7-1-1-1 How and why tree species types persisted in modified habitats

The ability of species to colonise and exploit novel land-use types and to tolerate changing spatial availability of resources is thought to be mediated by their physiological and behavioural traits (Ewers & Didham 2006). The environmental filter imposed by production landscape elements may also determine which species can persist outside old-growth remnants (Mayfield et al. 2010; Tscharntke et al. 2012). For the lowland trees of New Britain Island, late-successional and non-vertebrate-dispersed species were the most vulnerable to the disturbance present in modified elements (Chapter 3). For the majority of late-successional trees, the more influential factor limiting their occurrence in modified elements was time since disturbance (i.e. growing time, Chapter 3), although germination conditions may have been a factor for *some* species (e.g. site specialists, M. S. Ashton 2011). The successful recruitment of many forest species in the plantation understorey was likely to have been facilitated by the conditions provided over time by the *E. deglupta* overstorey—a native successional catalyst—combined with the low intensity of stand-level management three years after planting (Keenan et al. 1997; Wardell-Johnson et al. 2005). The relative influence of both factors warrants further research.

However, it is difficult to gauge the full potential of these plantations to support a diversity of late-successional trees, and to identify potential site specialists. First, because of the occupation of sites by *E. deglupta*, determining true declines in the abundance of tree species because of unsuitable growing conditions per se is impossible. Second, because we only surveyed trees ≥10 cm DBH and late-successional species tend to grow slowly (Laurans et al. 2012), uncounted individuals (<10 cm DBH) possibly occurred as difficult to detect saplings and seedlings (Farwig et al. 2009; Keenan et al. 1997). Third, some unrecorded species may simply not have dispersed to modified sites. Even so, indications from secondary forest elements suggest that given time to grow in the absence of disturbance, a good majority of late-successional species can persist in similar composition after relatively short fallow periods (Chapter 3), which bodes well for the conservation of indigenous trees particularly in older, modified habitats.

By contrast, disturbance intensity played a more prominent role in limiting the occurrence of non-vertebrate-dispersed species across the plantation landscape. The removal of propagules from the plantation areas during establishment activities (e.g. clearfelling and burning), not only reduced their abundance in the landscape, but may also have acted as a barrier to dispersal (Willson & Crome 1989). This may have been further exacerbated by their historical removal from secondary elements because of the generally higher commercial timber value of non-vertebrate-dispersed tree species compared to animal-dispersed trees in these forests (Paijmans 1976). That animal-dispersed trees were not as affected by these processes was likely because their primary dispersers (birds and bats, Mayr & Diamond 2001) were capable of traversing and exploiting resources in most modified elements. I did not survey bats but I did find only two forest bird species restricted to unlogged forest and over 90% of birds occurring in unlogged forest also occurring among modified elements, except in young plantations (Chapter 4).

However, frugivore prevalence declined outside of unlogged and secondary remnant forest (Chapter 4), suggesting a potential limit to the breadth of animal-dispersed trees capable of occurring in more modified habitats (C. Moran et al. 2009). This limit was difficult to quantify for mature modified elements as almost all absent animal-dispersed trees were late-successional and some may not have been true absences (they may have occurred as juveniles). Moreover, omnivorous (and occasionally carnivorous) birds are known to be effective transporters of animal-dispersed tree seeds in tropical forests, potentially compensating for reduced frugivore visits (Marsden & Symes 2008; Bell 1984; Diamond & Terborgh 1970). Still, the depauperate bird assemblage observed in young plantations demonstrated a clear limit to dispersal of tree seeds in this element (Chapter 4). Thus, in early plantation stages, deposition of seeds from birds traversing young plantations to reach neighbouring elements and edge habitats may be of greater importance (Parrotta 1995). As such, the structural complexity and composition of neighbouring elements, and the spatial continuity of resources may greatly influence species reassembly after clearing (Wunderle 1997).

7-1-1-2 How and why bird species persisted in modified elements: the interaction between bird species traits and site-level habitat attributes

In general, the environmental filter imposed on forest birds in human-affected landscape elements is less inhibiting where structural complexity is higher (Nájera & Simonetti 2010; Zurita & Bellocq 2012) and richness of rainforest plant species is greater (Cruz-Angon & Greenberg 2005; Farwig et al. 2008; DeClerck et al. 2010). My findings, that identified canopy cover (structural variable) and tree species richness as the most influential site-level drivers of the richness of forest-using bird species (Chapter 6) are consistent with this axiom. On average, these attributes were highest in unlogged forest and the secondary remnant and riparian elements (Chapter 5), making those landscape elements important refugia for forest-using birds. For the more vulnerable forest-specialist birds (frugivores and forest-dependent birds, Table 6.1) a third attribute—palm cover—positively influenced their probability of occurrence (Chapter 6), most likely because palms are an important fruiting resource (DeWalt et al. 2003) and because they tend to grow slowly, and thus may more broadly reflect microclimate conditions of old-growth forest (Webb et al. 1976; Letcher & Chazdon 2012).

In contrast to unlogged and secondary remnant forest elements (hereafter referred to as intact forest), the secondary riparian element demonstrated a reduced capacity to support these forest-specialists (Chapter 6). This element experienced ongoing human disturbance and may have experienced added exposure to wind and heat disturbance as a result of their high edge-to-interior ratios, a finding common in narrow remnant patches more generally (Ries et al. 2004). Consequently, the riparian element had a reduced richness of old-growth forest life forms (including palms, Chapter 5) and a lower proportion of late-successional individuals compared to intact forest elements (Chapter 3). Thus, secondary riparian sites did not provide the diversity of old-growth resources available in intact forests, which is likely to have contributed to their reduced occupancy of forest-specialists (e.g. frugivores, Sam et al. 2014). Frugivore species occurrence patterns across the landscape suggest that declines in more disturbed elements may be caused by their emigration to preferred habitat (i.e. where tree and plant species richness is highest, Chapter 5), highlighting the importance of protecting primary and fallow secondary forest refugia from disturbance. Additionally, forest-specialists (especially large-bodied frugivores) may have declined in riparian sites because of increased hunting pressure from humans and raptors alike, resulting from their higher visibility along roadsides. Eight of the 17 specialist bird species were either observed to have been preyed upon this way during the study (personal observation), or have been recorded as prey in studies on the PNG mainland (e.g. Ducula and Ptilinopus spp., Sam et al. 2014). Formalised hunting studies would further clarify the threat of hunting to forest birds in this landscape.

The conversion of complex secondary forest to monoculture plantations caused significant changes in vegetation structural and compositional attributes. In the establishment phase (young plantations), structure was dramatically simplified and species composition was dominated by early-successional pioneers (Chapters 3 and 5). On average, the habitat support offered to birds by young plantations was very limited, and the few that were best at exploiting habitat features were a homogeneous group of small, carnivores/omnivores (including nectarivores), who foraged on or near the ground in forest habitats (Figure 4.2, Table 4.S.x). Young plantation sites were patchy in their successful growth of *E. deglupta*, and large, remnant *Octomeles sumatrana* had been retained haphazardly at sites (Chapter 3 and 5). At sites with higher tree species richness (i.e. where remnant trees persisted) and/or those with more consistent *E. deglupta* canopy cover, more forest birds were recorded, suggesting that retention of remnant trees during harvest could provide a valuable connecting resource for forest birds.

As plantation forests matured, there was recovery of some pre-conversion structural complexity and plant species composition. At harvest age (between 13–15 years) average canopy cover was high (93%) and tree species richness was five times that of young plantations (Chapter 5). Forest-using bird richness increased accordingly, with a high richness of forest species compared to other tropical plantation studies (Chapter 4). However, mature plantation assemblages comprised fewer forest specialists, fewer larger-bodied birds, and fewer canopy and sub-canopy-using birds than evident in more intact forest elements (Chapter 4). Like the secondary riparian element, the decline in frugivore occupancy in mature plantations was likely to have been influenced by a reduced diversity of fruiting resources (including palms). However, the plantations had a much lower diversity of fruiting plants than the riparian element (Chapter 3 and 5), which would lead to the expectation of a greater difference in frugivore occurrence between plantations and riparian forest than was observed (Chapter 4). The lack of fruiting-tree diversity in plantations may have been compensated for by their elevated abundance of important early-successional fruiting plants capable of providing a more constant supply of resources (e.g. *Ficus*, *Macaranga* and *Zingiberaceae* spp.) an observation found in other tropical production landscapes (Marsden & Pilgrim 2003a). Thus, the plantations can play an important role in extending key resources beyond forest remnants.

While factors contributing to vertical structural complexity (e.g. ground cover-to-canopy foliar richness, diversity and composition, Chapter 5) were not found to influence site-level richness of forest-using or forest-specialist birds (Chapter 6), they contributed to variables that did (i.e. tree species richness and canopy cover (Chapter 5)). The simplified vertical cover of mature plantations compared to intact forest (especially of the sub-canopy, Chapter 5) is likely associated with their lower incidence of canopy and sub-canopy birds. Simplification of vertical structure has been similarly implicated in the lowered richness of forest birds in both crop and timber plantations (Nájera & Simonetti 2010; Peh et al. 2006). Moreover, the thin-leaved, emergent canopy of *Eucalyptus* plantations compared to the complex, broad-leaved canopies of rainforests provides limited protection for larger-bodied canopy and sub-canopy species from wind, light and heat (Kanowski, Catterall & Wardell-Johnson 2005a) and predation (Sam et al. 2014).

7-1-1-3 The influence of spatial landscape effects on bird species occurrence

The composition of landscape elements and their proportional coverage in a production landscape can affect the dispersal of birds and hence their occurrence patterns among elements. In particular, the proportion and location of preferred (remnant) habitat in a production landscape can influence the richness of species in human-affected landscape elements (Koh 2008; Ranganathan et al. 2010; Styring et al. 2011; Andren 1994; Kanowski, Catterall, Proctor, et al. 2005b; Clough et al. 2009). In the native *E. deglupta* plantation landscape, the proportion of intact contiguous forest within 2 km radius did not significantly influence richness of forest-using or forest-specialist birds at survey sites (Chapter 6). Instead, habitat attributes were found to be driving the patterns of forest species occurrence across the landscape. Similar findings have been made in landscapes where continuity of tree cover is high because of the dispersal facilitation provided by a low-contrast production matrix and a high proportion of regional intact rainforest cover (Farwig et al. 2008; Kennedy et al. 2010; Peh et al. 2006; Reitsma et al. 2001). All matrix elements (with the exception of young plantations) provided continuous tree cover, which likely facilitated the observed dispersal of all but two forest specialists from unlogged forest (Tscharntke et al. 2012). In addition, all sites were located within 4 km of contiguous, intact forest that covered an area larger than the plantation estate. This expanse of high-quality forest would likely be capable of supporting source populations of forest-specialists and of supplementing populations of matrix-using species (Gardner et al. 2010). Thus, the main limiting factor for most forest birds in this landscape was suitable habitat at a site rather than access to it. However, were the scale of anthropogenic disturbance to increase in this landscape, it is probable that spatial context would become increasingly influential on the assemblage of matrix-using birds (C. Moran & Catterall 2014).

7-1-1-4 The role of land-use history and biogeography in shaping the species pool

This study did not set out to determine the contribution of the history of disturbance and biogeography on shaping the local species pool, nor the consequences this contribution may have for the resilience of forest biota to modern anthropogenic activities. However, the high levels of forest-species richness in modified elements and compositional similarity to old-growth forest compares most favorably with the broader literature, suggesting a possible influence of these factors on New Britain's lowland forest biota. The lowland forests of New Britain Island have experienced both frequent volcanic disturbances and one of the longest histories of exposure to human modification in the world (Lentfer et al. 2010). Theoretically this exposure over such a long time period may have resulted in modern floral and faunal communities with high resilience to disturbance via: (1) the loss of more vulnerable species to extinction/extirpation (Lentfer et al. 2010; Steadman et al. 1999); and (2) the persistence of remaining species because of their generalist traits, or by adaptation to disturbance through trait plasticity (Balmford 1996; T. E. Martin & G. A. Blackburn 2013; Gardner et al. 2009). Trait plasticity in response to disturbance has been recorded for modern tropical birds, for example through: diet modification (Edwards, Woodcock, et al. 2013b); shifts in foraging stratum (Bell 1982); and behavioural changes (Sol et al. 2002; Mayr & Diamond 2001). Modern plant plasticity may involve physiological adaptability to changing light levels, for example: photosynthetic response variation (Chazdon et al. 1996); and variation in leaf area, architectural form and seedling and adult growth (Tadele & Fetene 2013; Laurans et al. 2012). It is possible that these types of responses to disturbance may have been conserved over time, leading to a capacity of New Britain's lowland forest trees and birds to colonise and exploit a range of modified habitats.

In the same way, the biotic species pool of a given region may respond differently to disturbance depending on the biogeographic processes which have shaped it. For example, in a review of the Pan-tropical responses of bird feeding-guilds to anthropogenic disturbance, Gray (2007) found that carnivores and nectarivores responded in an opposing fashion in Asia compared to those in the Neotropics, possibly because of their differential exposure to regional evolutionary processes. Similarly, for more isolated land-masses such as oceanic islands, biotic communities have commonly arisen from repeated colonisation events and subsequent speciation through isolation (Keppel et al. 2009). Consequently, island species—at least historically—have generally possessed superior colonising traits such as high vagility and niche breadth (ecological tolerance) (Mayr & Diamond 2001; T. E. Martin & G. A. Blackburn 2013).

Moreover, islands such as New Britain which contain species-poor communities compared to source pools (Mueller-Dombois & Fosberg 1998; Steadman 2006) are thought to experience less niche partitioning of resources because of reduced competition, leading to reduced specialisation relative to mainland populations (Clegg 2010; Diamond 1970). For example, on islands east of Wallace's Line, lower avifaunal richness and a broader realised niche are accredited for the increased resilience observed in traditionally vulnerable trait classes such as understorey insectivores and restricted range species (T. E. Martin & G. A. Blackburn 2013; Abrahamczyk et al. 2008). Likewise, in this investigation I found no relationship between ground-dwelling or endemic forest birds and disturbance susceptibility, and a greater tolerance of habitat modification for traditionally vulnerable larger-bodied birds, and canopy-dwelling birds (Chapter 4). Therefore, the historical and biogeographic context of ecosystems may also influence the response of lowland biota to disturbance events. However, resilience is likely to be limited in the face of more intense, broadscale modern anthropogenic disturbance. For example, in the nearby Solomon Islands, Katovai and colleagues (2012) found that forests were resilient to disturbances accompanying conversion to secondary forest and fallow tree plantations but not coconut plantations nor grazed pastures.

7-1-2 Conservation Implications and Recommendations for Management

The findings from this study indicate that the combination of native timber plantations set among older secondary forest elements can support high levels of forest tree and bird species biodiversity. For forest-using birds, the high continuity of canopy cover and richness of rainforest tree species afforded by the secondary forest elements and to a lesser extent the native timber plantations, were important for their persistence across the landscape. In turn, the high dispersal of bird populations among most landscape elements enhanced the dispersal ability of many forest tree species. Therefore, land-sharing strategies similarly incorporating production land-uses that enable high canopy cover and tree species richness could be effective for conservation of tropical birds and plants while producing required yields. However, a number of factors were also identified in this study that acted to inhibit the persistence of viable populations of forest species among landscape elements. Judicious management of matrix elements at the stand-level along with careful land-use planning are, therefore, essential to ensure effective, long-term conservation outcomes in this production landscape.

Below are recommendations for conservation management of the *E. deglupta* plantation landscape at Open Bay based on evidence gained in this study. The recommendations cover both stand-level and landscape-wide management. Protocols for sustainable management of production landscapes will be more readily enacted when they impact marginally on yield (Evans 2009). It is in the best interests of conservation managers and policy-makers to attempt to work within these bounds because if sustainable management renders a production type unprofitable, the likelihood of either management guidelines being ignored, or the production type replaced by a more financially stable option (e.g. cash-crops such as Oil Palm) increases, with a subsequent loss in biodiversity. The operation at Open Bay has achieved certification status (Forestry Stewardship Council certificate, FSC-FM/CoC) and as such is bound to meet certain Forestry Stewardship Council (FSC) criteria. Hence, many of the following recommendations have been proposed within the framework of these criteria to improve their chances of adoption. Where appropriate, the applicability of recommendations for plantations in other contexts is also discussed.

7-1-2-1 Stand-level management

This study builds on growing evidence that native tree species plantations confer recruitment of a high richness of forest vegetation in their understorey (Dogra et al. 2009; Keenan et al. 1997;

Lima & Vieira 2013; Farwig et al. 2009; Haggar et al. 1997). The high levels of native plant species richness and canopy cover provided by mature *E. deglupta* plantations were found to be key drivers of forest bird species richness, and are likely to provide valuable habitat and/or connectivity for other native fauna (Davis et al. 2012). Therefore, the use of native tree species should be encouraged in tropical plantations, particularly where land-sharing strategies are considered for conservation management. There is much support in the conservation literature for the incorporation of native trees in tropical plantations to improve biodiversity outcomes and reduce the risk of exotic species invading natural forests (Erskine et al. 2006; Brockerhoff et al. 2008; Hartley 2002; Osunkoya et al. 2005; Richardson et al. 2004). Similarly, the FSC strongly advocates the use of native timber species in plantations where they can be proven to provide equal yields to exotic options (Forest Stewardship Council 2010). However, the overwhelming majority (~85%) of timber plantations in the tropics are comprised of exotic species (Montagnini 2001) and changing this paradigm requires investment in research and development. Research should be targeted at identifying native species which can facilitate successional processes and compete with exotics in terms of growth rates, yields and easily-implemented management protocols (Davis et al. 2012 and see section 7-1-3).

The high levels of tree species recruitment observed in the understorey of the mature *E. deglupta* plantations may also be attributable to the relatively low-intensity, short-term tending employed at Open Bay (Chapter 2), as well as an absence of silvicultural thinning (because of expense). These practices should be maintained. Intensive (mechanical) and prolonged weed-tending, and the canopy-opening activities of thinning, have both been identified as limiting processes in the recruitment of mid and late-successional trees in plantations (Kanowski, Catterall, Proctor, et al. 2005b). Intensive tending may be required in systems where the plantation canopy takes longer to provide adequate shade cover and can be reduced through closer spacing (Tucker et al. 2004). However, tree spacing will depend on the type of timber product being raised (e.g. pulpwood versus saw logs) and species used (Tucker et al. 2004; Haggar et al. 1998). In circumstances where management is necessarily intense and lengthy, trade-offs such as reserving larger areas for biodiversity conservation within the production landscape are recommended (Lindenmayer 2002; Hartley 2002).

Growth of native flora in the plantation understorey may also have been facilitated by the intercropping of traditional food crops alongside the *Eucalyptus* seedlings from 0–3 years, which likely enhanced soil conditioning (The Review Team 2005). Allowing free access to land and food for local inhabitants in this manner also reduces encroachment of slash-and-burn agriculture into neighbouring primary and secondary forests, which remains a central driver of deforestation in PNG (Shearman et al. 2010). However, this intercropping has involved traditional burning of plantations prior to planting, which has the potential to damage the soil seed bank (Uhl et al. 1981; Mamede & de Araujo 2008), increase the incidence of grass invasion, reduce soil fertility, and remove both remnant trees and potential seed vectors from the area (Bowman et al. 1990; Lindenmayer et al. 2000). Therefore, I recommend that fire use be minimised or removed altogether during plantation establishment, and that research investigating the effects of intercropping on soil conditioning be undertaken.

Traditional conservation practices, such as the retention of ethno-botanically valuable trees in disturbed areas (e.g. roadsides), occurs at Open Bay as in other tropical countries, and may be diversified and formalised with little impact on yield (Carnevale & Montagnini 2002). Examples here could include post-harvest retention of tree species recruited in the plantation understorey (especially of the more vulnerable late-successional and non-vertebrate-dispersed species), and along compartment boundaries, where they can enhance seed dispersal in plantations and provide habitat for fauna (Lindenmayer, Laurance, et al. 2012b; Hartley 2002). Such tree retention can also be beneficial for plantation yields through weed and grass suppression post-clearfell (Uhl et al. 1988) and through the creation of wind and fire breaks (Saulei & Swaine 1988; Bayliss-Smith et al. 2003). This may be of considerable importance in future rotations as weed invasiveness and drying conditions often increase through subsequent rounds of clearfell and burning (Parrotta et al. 1997). This form of management is analogous to retention forestry, which has proven globally effective for the combined benefits of biodiversity conservation and yield production by providing spatial and temporal continuity of pre-harvest elements across the landscape (Gustafsson et al. 2012).

7-1-2-2 Land use planning

Conservation management of the *E. deglupta* plantation landscape should, wherever possible, aim to maximise the spatial and temporal continuity of canopy cover, tree species richness and late-successional rainforest plant composition. This can be accomplished among all landscape elements. For plantation elements, highest canopy cover and plant species richness occurs in the oldest stands, thus temporally varying harvesting cycles to ensure the highest possible cover of mature plantations through time (and their presence at all times) would increase the conservation value of the landscape. This could be achieved through increasing rotation times of some plantation blocks, although this may mean harvesting at a sub-optimal stage economically (but see, Hartley 2002). Similarly, the negative effects on biodiversity of early plantation stages can be minimised through spatially varying harvesting activities in adjacent blocks (i.e. ensuring that cover of young plantations is dispersed throughout the plantation estate). This type of mosaic harvesting already occurs to a small extent at Open Bay but on a larger scale it may potentially lead to loss of revenue (Boston & Sessions 2006). In such a trade-off situation, cost-benefit analyses of competing spatial harvesting designs can be beneficial for harvest planning (Boston & Sessions 2006). These types of analyses utilise optimisation models to determine the potential economic and biodiversity trade-offs for variations of landscape management plans (i.e. extent and spatial array of plantations of different ages) and can assist managers with decision-making. However, this approach can be more difficult to implement in developing countries because of a lack of information and access to necessary resources (Rands et al. 2010; but see, Game et al. 2010).

The capacity of timber plantations to contribute to biodiversity in terms of population sizes and reproductive success will be modest compared to that of primary and secondary forest elements because of competition by the plantation species, and because of the discontinuity of resources created by clearfell harvesting (Catterall et al. 2005). Thus, spatial planning and management of the non-plantation elements comprising the managed landscape are of great importance to the maintenance of species populations (Hartley 2002). For example, secondary riparian buffers provide essential connectivity and habitat refugia within production areas (Paquette & Messier 2010). At Open Bay, the secondary riparian element was degraded (in terms of plant species composition), particularly in sites where strips had been narrowed by poor initial planning and/or poor policing of local residents harvesting timber and cutting paths to access a valuable water resource. Riparian habitats harbour a specialised flora and fauna (e.g. water-dispersed trees, kingfishers), which depend on their structural and abiotic integrity (Lamb et al. 1997). The increased protection and restoration of riparian habitats would provide for these species and expand their range and colonising potential throughout the landscape (Griscom et al. 2009) with no impact on plantation yield. Furthermore, riparian buffers ≥50 m wide on both river-banks are a requirement of both the FSC certification criteria and national logging laws in Papua New Guinea (Barnett 2010; Forest Stewardship Council 2010). One method of increasing the width of the more degraded strips at Open Bay could be through enrichment planting. Improved access to water throughout the village areas and permanent access routes to rivers would also discourage disturbance of riparian areas with no impact on yield. Finally, designating easily accessible areas as timber woodlots for building materials and fuel would reduce the need to harvest riparian understorey trees.

In-keeping with studies of regenerating selectively-logged forests throughout the tropics (Berry et al. 2010; Edwards et al. 2011), the secondary forests at Open Bay provided refuge for the majority of forest tree and bird species, as well as the more vulnerable forest-restricted species. Therefore, I recommend that old, regenerating secondary forests be recognised for their high conservation value, and that substantial areas remain protected (along with unlogged forest) from any future expansion of plantations to meet increasing timber demands. Currently, Open

Bay Timber formally protects ~ 2705 ha consisting of mangrove swamp, peat-land forest and a large lake, because of their recognition as High Conservation Value areas (HCVs) by the FSC. Informally, the company protects just 382 ha of selectively-logged secondary forest from development because of its importance as a catchment area. This leaves a large expanse of biodiverse primary and secondary lowland–hill forest open to future development. Secondary forest is more likely to be exploited than primary forest because of its accessibility by old logging roads and its perception as degraded forest (Laurance & Balmford 2013; Edwards, Larsen, et al. 2010b). For example, in southeast Asia, lack of protection has seen the rapid disappearance of secondary forests through conversion to agricultural and tree crops (Sodhi, Brook, et al. 2009a; Ansell et al. 2011). The FSC encourages protection of unlogged ('natural') forests in production landscapes by not granting certification status to any plantation enterprise converting natural forest to plantations after November 1994 (Forest Stewardship Council 2010). Were 'natural' forest to formally include old-growth secondary forests with high conservation value, such as those present in the Open Bay landscape, substantial expansion of the landscape area providing refuge for lowland forest biota would ensue, with great benefit for the long-term persistence of forest species.

7-2 Future Research

The findings from this study corroborated a commonly-held belief that native timber plantations can support a high level of plant and faunal species and therefore may represent an ideal production type for land-sharing conservation strategies in tropical forest regions. However, the extent to which contextual factors influence the ability of this study's *E. deglupta* plantation landscape to foster native biodiversity while achieving required yields remains uncertain; thus extrapolation of these findings to other regions where *E. deglupta* is native requires further research. In terms of conservation outcomes, the effects of contextual influences (e.g. species pool, landscape composition, management intensity and plantation scale) may be assessed by comparing biodiversity studies of native timber plantation landscapes throughout the tropics (e.g. E. Nichols et al. 2007). However, this will initially require more conservation research to be prioritised within native plantations (Stephens & Wagner 2007).

In terms of acceptance of native tree species by land managers as viable replacements of exotic species in plantations, further research is required to demonstrate how well native trees can compete with exotics in terms of growth and survival rates, establishment under competition, performance across a range of sites and comparative reliance on chemical inputs (Davis et al. 2012). Similarly, investment would need to be made to deliver commercial-grade stocks of seeds/seedlings and propagation protocols for 'new' species (Davis et al. 2012). In Melanesia and other parts of the tropics, much traditional knowledge of plant propagation techniques remains intact, and incorporation of local practices should be adopted to speed these processes (Trosper 2011; Chazdon, Harvey, et al. 2009a).

There is still much to be learned about the evolutionary processes that influence species resilience to disturbance. In this study, a large proportion of forest tree and bird species were capable of exploiting forestry-affected landscape elements, which may have been partly attributable to their long history of exposure to human modification of lowland rainforests (Sodhi, Lee, et al. 2009b; Balmford 1996). Further research is required to understand to what extent historical disturbance effects confer resilience in modern communities. However, it will be difficult to identify the evolution of traits in response to these influences without access to a more complete fossil record (Gardner et al. 2009). In the same way, the species pool of a given location may be more or less vulnerable to disturbance depending on biogeographic processes which have shaped it. Endemic species, by definition, represent a subset of the species pool most directly shaped by local biogeographic and historical processes. Therefore, comparing the fate of endemic species across a broad biogeographic range may assist in our understanding of the 'background' resilience of a given region. For example, it is hypothesised that island endemics, having historically required colonising and adaptive traits, may be capable of better adapting to modern disturbance than continental endemics can (T. E. Martin & G. A. Blackburn 2013), and was a pattern also found for birds in this study. Research comparing the disturbance response of endemics of closed (island) and open (continental) communities may improve our understanding of the influence of biogeographic and historical processes on modern biota.

Examining the effect of disturbance on the occurrence patterns of broadly-classified species traits and functional groups in this study allowed me to identify underlying ecological processes governing community assemblages of birds and trees in modified landscape elements. However, much variation in species occurrence patterns remained unexplained, partly because I studied traits and functional groups roughly related to composites of physiological traits (Swenson 2013; Burley et al. 2011). Ideally, traits important for dispersal, survival and fecundity should be measured directly to quantify the role of deterministic processes in shaping assemblages capable of colonising novel habitats now and into the future (Swenson 2013; e.g., Lasky et al. 2014). But this can be enormously time-consuming and costly in species-rich communities (Baraloto et al. 2010), while rainforest deforestation and degradation continue apace. This is particularly problematic in less developed tropical countries where research investment is minimal and large areas lack even baseline data, as was the case in this study.

While detailed physiological trait research is still important, it may be more effective for conservation outcomes in data-poor regions to determine direct relationships between composite traits and disturbance effects through experimental research and predictive trait-disturbance models (Shanahan & Possingham 2009). For example, following on from this study, quantifying the importance of fruiting species diversity for frugivores could be achieved through non-fatal examinations of stomach contents (Sam et al. 2014). Similarly, predictive trait-disturbance models could reveal possible interactions between traits and between disturbance effects influencing frugivore occurrence (Ewers & Didham 2006). For example, all frugivores in the study were also medium-large in size and larger birds are theoretically more exposed to hunting pressure (Owens & Bennett 2000). Therefore, modelling the effects and interaction of both hunting pressure and fruiting diversity may highlight the greater risk for these species in this context, and better inform management (e.g. the need for hunting moratoriums). Equally, incorporating phylogenetic information of communities into predictive models may account for correlations of unmeasured species traits leading to a clearer identification of the role of individual traits in disturbance response (Ewers & Didham 2006).

Above all, in terms of conservation management, the best data to inform mechanisms of declines and future persistence of species among production landscapes is demographic data. Demographic data can only be obtained through long-term population monitoring, which is sorely lacking in tropical multi-use production landscapes (Chazdon, Harvey, et al. 2009a; Gardner et al. 2009). Such data, if collected across all landscape elements, can inform important ecological questions such as: the viability of populations through space and time (e.g. the effects of time lags (Brooks et al. 1997) and soil degradation of future rotations (Lugo 1988)); population recovery (fecundity); breeding requirements; and long-term capacity to adapt to dynamic resource availability (Gardner et al. 2009; Tscharntke et al. 2012). This data can also feed into conservation planning tools (Wilson et al. 2010). For example, understanding the population viability status of species to a variety of land-uses can assist with regional land-use planning by way of identifying biodiversity costs of converting one land-use to another (Wilson et al. 2010). Within landscapes, population data can be incorporated within an adaptive management framework to assist with planning and assessment of management actions (Wintle, Bekessy, et al. 2005a). For example, this data can be used to test the effectiveness of buffer zones and their management, or the impact of restoration plantings and remnant tree retention on the demographics of target species. Such data can be invaluable for conservation decision-making but is deficient in tropical human-affected landscapes (Chazdon, Harvey, et al. 2009a).

Unfortunately, long-term studies in tropical production landscapes are rare because of the logistical and financial requirements involved (Gardner et al. 2009). However, theoretically this data is being collected in sustainably managed forests where implementation of annual monitoring and adaptive management strategies are mandated. For example, in the case of the

FSC draft guidelines for PNG, Section 8.2.2 directs “Forest dynamics are [to be] studied in harvested and unharvested forest to monitor changes in plant and animal species composition” and that “[8.4] the results of monitoring shall be incorporated into the implementation and revision of the management plan” (Forest Stewardship Council 2010). While these directives are to be applauded, very little of this data appears to be used to further ecological understanding of these systems, and the design of monitoring protocols and adaptive management thresholds is left in the hands of the resource company rather than via scientific implementation (Wintle & Lindenmayer 2008). Collaborative partnerships between research institutions and sustainable-management organisations could benefit all parties, whereby research institutions assist with threshold setting, monitoring design and data interpretation in collaboration with bodies such as the FSC, while gaining access to remote and/or inaccessible landscapes and valuable long-term ecological data. Lack of funding is a primary limitation to conducting the extensive monitoring required for adaptive management research (Walshe et al. 2007). The stability that collaborative partnerships would entail may assist with attraction of donor funding (Ahrends et al. 2011), as well as government and industry grants. Furthermore, the production of tangible results from monitoring by way of annual reporting from research institutions and sustainable-management organisations alike, could assist with the motivation of land managers to invest labour and funding for future rounds of monitoring.

Ultimately, the success of achieving dual outcomes of biodiversity conservation and production yield in tropical multi-use landscapes depends on the value of both goals to land managers and land owners. At Open Bay, a fundamental reason that the vast expanses of intact forest and native timber plantations still exist is because of local opposition to their replacement by oil palm. This type of opposition carries much weight in PNG where 85–97% of the land is owned by indigenous people (Filer 2011). The choice of local communities to support the continuing of this land-use over a more intensive and potentially financially-rewarding option is complex but certainly is largely influenced by the involvement of local communities in the functioning of the plantations, and the co-existence of traditional livelihood activities within production areas. Understanding the importance of considering the interests and well-being of local communities and their inclusion in land-management decisions for the success of conservation outcomes should be a key area of future tropical research (Ancrenaz et al. 2007). Science can play a role in informing management decisions but ultimately land-use planning and future conservation will be driven by societal values.

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APPENDICES

Appendix A Chapter 3 supporting data

Appendix Table A.1 Tree species occurring at Open Bay across all landscape elements. Trait classification and literature used for categorisations are specified for each species. NVD: non-vertebrate dispersed.

Family	Species	Successional Stage	Dispersal Mode	References
Myrtaceae	*Acmena spp.*	Mid-succession	Animal	(Conn & Damas 2006)
Meliaceae	*Aglaia spp.*	Late-succession	Animal	(Conn & Damas 2006; Wright 2005; Womersley 1995; van Steenis, Rijksherbarium Netherlands, Lembaga Biologi Nasional Indonesia, Keban Raya Indonesia, et al. 2012; Muellner, Pannell,
Simaroubaceae	*Ailanthus integrifolia*	Late-succession	NVD	(Conn & Damas 2006; Paijmans 1976)
Fabaceae	*Albizia falcataria*	Early-succession	NVD	(Paijmans 1976; van Steenis et al. 2012; Paijmans 1973)
Euphorbiaceae	*Aleurites moluccana*	Early-succession	Animal	(Manner 2006; Conn & Damas 2006; Paijmans 1976)
Apocynaceae	*Alstonia spp.*	Early-succession	NVD	(Conn & Damas 2006; Paijmans 1976)
Apocynaceae	*Alstonia scholaris*	Mid-succession	NVD	(Paijmans 1976; Datta & Rawat 2008)

Family	Species	Successional Stage	Dispersal Mode	References
Moraceae	*Antiaris toxicaria*	Early-succession	Animal	(Paijmans 1976; Conn & Damas 2006)
Moraceae	*Artrocarpus indicus*	Mid-succession (heliophilic)	Animal	(Ragone 2006; Burley, Enright & Mayfield 2011)
Phyllanthaceae	*Bischofia javanica*	Early-succession	Animal	(Conn & Damas 2006; Paijmans 1976; Datta & Rawat 2008)
Sapotaceae	*Burckella obovata*	Early-succession	Animal	(Wright 2005; van Steenis et al. 2012)
Clusiaceae/ Guttiferae	*Calophyllum inophyllum*	Late-succession	Animal	(Friday & Okano 2006; Paijmans 1976; Mueller-Dombois & Fosberg 1998; Conn 1995)
Anacardiaceae	*Campnosperma brevipetiolata*	Mid-succession (heliophilic)	Animal	(Burslem & Whitmore 1999; Paijmans 1973)
Annonaceae	*Canaga odorata*	Mid-succession (heliophilic)	Animal	(Manner & Elevitch 2006; Conn & Damas 2006; van Steenis et al. 2012)
Burseraceae	*Canarium oleosum*	Mid-succession (heliophilic)	Animal	(Paijmans 1976; Conn & Damas 2006)
Burseraceae	*Canarium indicum*	Late-succession	Animal	(Evans 2006a; Lentfer, Pavlides & Specht 2010; Burley, Enright & Mayfield 2011; Paijmans 1976)

Family	Species	Successional Stage	Dispersal Mode	References
Rhizophoraceae	*Carallia brachiata*	Mid-succession (heliophilic)	Animal	(Paijmans 1976; Siebert 2002)
Cannabaceae (Ulmaceae)	*Celtis rigescens*	Late-succession	Animal	(Lentfer, Pavlides & Specht 2010; Paijmans 1976; 1973)
Apocynaceae	*Cerbera floribunda*	Mid-succession	Animal	(Wright 2005; Paijmans 1973)
Meliaceae	*Chisocheton ceramicus*	Late-succession	Animal	(Paijmans 1976; van Steenis et al. 2012; Conn & Damas 2006; Womersley 1995)
Sapotaceae	*Chrysophyllum roxburghii*	Late-succession	Animal	(Conn & Damas 2006; van Steenis et al. 2012)
Lauraceae	*Cinnamomum mercadoi*	Late-succession	Animal	(Conn & Damas 2006; van Steenis et al. 2012)
Lauraceae	*Cryptocarya spp.(murrayi)*	Late-succession	Animal	(Wright 2005; Paijmans 1976; Mueller-Dombois & Fosberg 1998)
Urticaceae	*Dendrocnide peltata*	Mid-succession (heliophilic)	Animal	(Paijmans 1976; 1973)
Dilleniaceae	*Dillenia papuana*	Mid-succession	Animal	(Burslem & Whitmore 1999; Paijmans 1976; van Steenis et al. 2012)

Family	Species	Successional Stage	Dispersal Mode	References
Ebenaceae	*Diospyros ferrea*	Late-succession	Animal	(Swaine & Whitmore 1988)
Anacardiaceae	*Dracontomelon dao*	Mid-succession	Animal	(Paijmans 1976; Conn & Damas 2006; van Steenis et al. 2012)
Putranjivaceae	*Drypetes spp.*	Late-succession	Animal	(Swaine & Whitmore 1988)
Meliaceae	*Dysoxylum parasiticum*	Late-succession	Animal	(Paijmans 1976; Conn & Damas 2006)
Elaeocapraceae	*Elaeocarpus sphaericus*	Late-succession	Animal	(Burslem & Whitmore 1999)
Magnoliaceae	*Elmerrillia papuensis (or tsiampaca)*	Late-succession	Animal	(Wright 2005; Womersley 1995; Mack & Wright 1996)
Euphorbiaceae	*Endospermum medullosum*	Early succession	Animal	(Thomson 2006a; Burslem & Whitmore 1999; Paijmans 1976; 1973)
Myrtaceae	*Eucalyptus deglupta*	Mid-succession (heliophilic)	NVD	(World Agroforestry Centre 2013; Swaine & Whitmore 1988; Paijmans 1976; 1973)
Moraceae	*Ficus spp.*	Mid-succession (heliophilic)	Animal	(Lepš & Novotny 2001; Paijmans 1976)

Family	Species	Successional Stage	Dispersal Mode	References
Saliaceae	*Flacourtia zippelii*	Late-succession	Animal	(Conn & Damas 2006)
Himantandraceae	*Galbulimima belgraveana*	Late-succession	Animal	(Thane 1983; Conn & Damas 2006)
Clusiaceae (prev. Guttiferae)	*Garcinia latissima*	Late-succession	Animal	(Wright 2005; Paijmans 1976)
Burseraceae	*Garuga floribunda*	Late-succession	Animal	(Franklin, Drake, Bolick, Smith, et al. 1999; Paijmans 1976)
Phyllanthaceae	*Glochidion spp.*	Mid-succession (heliophilic)	Animal	(Conn & Damas 2006; van Steenis et al. 2012)
Lamiaceae	*Gmelina moluccana*	Mid-succession (heliophilic)	Animal	(Burslem & Whitmore 1999; Conn & Damas 2006)
Malvaceae (prev. Sterculiaceae)	*Heretiera littoralis*	Mid-succession	NVD	(Paijmans 1976)
Saliaceae	*Homalium foetidum*	Mid-succession (heliophilic)	NVD	(Paijmans 1976; Bell 1982)
Myristicaceae	*Horsfieldia helwigii*	Late-succession	Animal	(Paijmans 1976; Conn & Damas 2006)

Family	Species	Successional Stage	Dispersal Mode	References
Fabaceae	*Inocarpus fagifer*	Late-succession	NVD	(Pauku 2006; Conn & Damas 2006)
Fabaceae	*Instia bijuga*	Late-succession	NVD	(Thaman, Thomson, DeMeo, Areki, et al. 2006; Conn & Damas 2006)
Leeaceae	*Leea tertramera*	Early- succession	Animal	(Paijmans 1976; van Steenis et al. 2012)
Lauraceae	*Litsea spp.*	Mid-succession (heliophilic)	Animal	(Priatna, Kartawinata & Abdulhadi 2006; Paijmans 1976)
Celastraceae	*Lophopetalum torricellense*	Late succession	NVD	(Paijmans 1976; Mueller-Dombois & Fosberg 1998)
Euphorbiaceae	*Macaranga spp.*	Early-succession	Animal	(Swaine & Whitmore 1988; Priatna, Kartawinata & Abdulhadi 2006) (Lepš & Novotny 2001; Paijmans 1973)
Anacardiaceae	*Magnifera minor*	Mid-succession	Animal	(Paijmans 1976; Conn & Damas 2006)
Fabaceae	*Maniltoa schefferi*	Late-succession	NVD	(Paijmans 1976; van Steenis et al. 2012)
Chrysobalanaceae	*Maranthes corymbosa*	Late-succession	Animal	(Burslem & Whitmore 1999; Paijmans 1976)

Family	Species	Successional Stage	Dispersal Mode	References
Rutaceae	*Melicope elleryana*	Mid-succession (heliophilic)	Animal	(Paijmans 1976; Harbaugh, Wagner, Allan & Zimmer 2009; Conn & Damas 2006)
Muntingiaceae	*Muntingia calabura*	Early succession	Animal	Introduced species
Myristicaceae	*Myristica spp.*	Late-succession	Animal	(Paijmans 1976; Womersley 1995)
Rubiaceae	*Nauclea orientalis*	Early- succession	Animal	(Paijmans 1976; Conn & Damas 2006)
Rubiaceae	*Neonauclea purpurea*	Early- succession	Animal	(van Steenis et al. 2012; Conn & Damas 2006; Paijmans 1976)
Rubiaceae	*Neonauclea spp. (not purpurea)*	Early- succession	Animal	(van Steenis et al. 2012; Conn & Damas 2006; Paijmans 1976)
Tetramelaceae	*Octomeles sumatrana*	Mid-succession (heliophilic)	NVD	(Paijmans 1976; 1973)
Euphorbiaceae	*Omalanthus*	Early- succession	Animal	(Lepš & Novotny 2001)
Sapotaceae	*Palaquium warburgianum*	Mid-succession	Animal	(Paijmans 1976; Conn & Damas 2006)

Family	Species	Successional Stage	Dispersal Mode	References
Pandanus	*Pandanus*	Early- succession	Animal	(Thomson, Englberger, Guarino, Thaman, et al. 2006; Paijmans 1973; 1976)
Saliaceae	*Pangium edule*	Late succession	Animal	(Lentfer, Pavlides & Specht 2010; Paijmans 1976; Conn & Damas 2006)
Moraceae	*Paratocarpus venenosus*	Early- succession	Animal	(Conn & Damas 2006; Paijmans 1976)
Euphorbiaceae	*Pimelodendron amboinicum*	Mid-succession	Animal	(Lepš & Novotny 2001; Paijmans 1976; Conn & Damas 2006; Paijmans 1973)
Sapotaceae	*Planchonella chartaceae*	Late succession	Animal	(van Steenis et al. 2012)
Sapindaceae	*Pometia pinnata*	Mid-succession (heliophilic)	Animal	(Thomson & Thaman 2006; Burslem & Whitmore 1999; Burley, Enright & Mayfield 2011)
Burseraceae	*Protium macgregorii*	Late succession	Animal	(Paijmans 1976; van Steenis et al. 2012)
Rosaceae	*Prunus gazelle-peninsulae*	Late succession	Animal	(Wright 2005)
Fabaceae	*Pterocarpus indicus*	Early-succession	NVD	(Thomson 2006b; Burley, Enright & Mayfield 2011; Paijmans 1976)

Family	Species	Successional Stage	Dispersal Mode	References
Malvaceae (prev. Sterculiaceae)	*Pterocymbium beccarii*	Mid-succession (heliophilic)	NVD	(Paijmans 1976; 1973)
Anacardiaceae	*Semecarpus forstenii*	Late succession	Animal	(van Steenis et al. 2012)
Elaeocapraceae	*Sloanea sogerensis*	Late succession	Animal	(Swaine & Whitmore 1988; Paijmans 1976; Conn & Damas 2006)
Bigoniaceae	*Spathodea campanulata*	Mid-succession (heliophilic)	NVD	(Paijmans 1976)
Anacardiaceae	*Spondias cytherea (dulcis)*	Mid-succession (heliophilic)	Animal	(Conn & Damas 2006; van Steenis et al. 2012)
Malvaceae (prev. Sterculiaceae)	*Sterculia schumanniana*	Early-succession	NVD	(Conn & Damas 2006; Paijmans 1976)
Myrtaceae	*Syzygium effusum*	Late-succession	Animal	(Paijmans 1976; Conn & Damas 2006)
Myrtaceae	*Syzygium spp.*	Late-succession	Animal	(van Steenis et al. 2012; Paijmans 1976)
Combretaceae	*Terminalia complanata*	Mid-succession (heliophilic)	Animal	(Evans 2006b; Swaine & Whitmore 1988; Conn & Damas 2006)

Family	Species	Successional Stage	Dispersal Mode	References
Combretaceae	*Terminalia brassii*	Early-succession	NVD	(Swaine & Whitmore 1988; Conn & Damas 2006; Paijmans 1976)
Meliaceae	*Toona ciliata*	Late-succession	NVD	(van Steenis et al. 2012; Womersley 1995)
Ulmaceae	*Trema orientalis*	Early-succession	Animal	(Swaine & Whitmore 1988; Paijmans 1976)
Saliaceae (prev. Flacourtiaceae)	*Trichadenia philippinensis*	Late-succession	Animal	(van Steenis et al. 2012; Conn & Damas 2006)
Sapindaceae	*Tristiropsis subangula*	Late-succession	Animal	(Mueller-Dombois & Fosberg 1998; Bell 1982)
Lamiaceae (Verbenaceae)	*Vitex cofassus*	Early-succession	Animal	(Burley, Enright & Mayfield 2011)

Table A.1 reference list

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Appendix Table A.2 Tree species occurring in significantly different abundance among landscape elements (multivariate GLM $p_{adj} < 0.05$). NVD: non-vertebrate dispersed.

Species	Successional Stage	Dispersal Mode
Aglaia spp.	Late-succession	Animal
Calophyllum inophyllum	Late-succession	Animal
Celtis rigescens	Late-succession	Animal
Chisocheton ceramicus	Late-succession	Animal
Cryptocarya spp.(murrayi)	Late-succession	Animal
Elaeocarpus sphaericus	Late-succession	Animal
Elmerrillia papuensis (tsiampaca)	Late-succession	Animal
Flacourtia zippelii	Late-succession	Animal
Galbulimima belgraveana	Late-succession	Animal
Garcinia latissima	Late-succession	Animal
Horsfieldia helwigii	Late-succession	Animal
Lophopetalum torricellense	Late succession	NVD
Maranthes corymbosa	Late-succession	Animal
Myristica spp.	Late-succession	Animal
Pangium edule	Late succession	Animal
Protium macgregorii	Late succession	Animal
Semecarpus forstenii	Late succession	Animal
Syzygium effusum	Late-succession	Animal
Antiaris toxicaria	Early-succession	Animal
Macaranga spp.	Early-succession	Animal
Endospermum medullosum	Early succession	Animal
Leea tertramera	Early- succession	Animal
Melicope elleryana	Mid-succession (heliophilic)	Animal
Nauclea orientalis	Early- succession	Animal
Sterculia schumanniana	Early-succession	NVD
Alstonia scholaris	Mid-succession	NVD

Cerbera floribunda	Mid-succession	Animal
Dracontomelon dao	Mid-succession	Animal
Eucalyptus deglupta	Mid-succession (heliophilic)	NVD
Ficus spp.	Mid-succession (heliophilic)	Animal
Litsea spp.	Mid-succession (heliophilic)	Animal
Magnifera minor	Mid-succession	Animal
Octomeles sumatrana	Mid-succession (heliophilic)	NVD
Palaquium warburgianum	Mid-succession	Animal
Pimelodendron amboinicum	Mid-succession	Animal
Pometia pinnata	Mid-succession (heliophilic)	Animal
Pterocymbium beccarii	Mid-succession (heliophilic)	NVD
Spondias cytherea (dulcis)	Mid-succession (heliophilic)	Animal

Appendix B Chapter 4 supporting data

Appendix Table B.1 Trait categorisations of all analysed bird species

Species	**Primary Diet**	**Body Size**	**Foraging Stratum**	**Habitat Breadth**	**Species/allospecies Range**	**Subspecies Range**
Aceros plicatus	Frugivore	Large	Canopy	Forest	Melanesia	Bismarcks
Alcedo lepida	Carnivore	Small	Ground	Secondary Closed	Melanesia	New Britain Endemic
Myzomela cineracea	Carnivore	Small	All	Generalist	New Britain & Bismarcks endemics	Bismarcks
Aplonis metallica	Omnivore	Medium	Canopy	Secondary Open	Asia-Pacific	Melanesia
Aviceda subcristata	Omnivore	Large	Canopy	Generalist	Asia-Pacific	Bismarcks
Centropus violaceous	Omnivore	Large	Sub Canopy	Secondary Closed	New Britain & Bismarcks endemics	Bismarcks
Cacatua opthalmica	Omnivore	Large	Canopy	Generalist	New Britain & Bismarcks endemics	New Britain Endemic
Cacomantis variolosus	Carnivore	Small	Canopy	Generalist	Asia-Pacific	Bismarcks
Centropus alteralbus	Omnivore	Large	Midstorey	Secondary Open	New Britain & Bismarcks endemics	Bismarcks
Chalcophaps stephani	Frugivore	Medium	Ground	Secondary Open	Melanesia	Melanesia
Coracina papuensis	Carnivore	Medium	Sub Canopy	Secondary Closed	Asia-Pacific	Bismarcks
Coracina tenuirostris	Carnivore	Medium	Sub Canopy	Secondary Closed	Asia-Pacific	New Britain Endemic
Corvus orru	Omnivore	Large	Ground	Generalist	Asia-Pacific	Bismarcks
Ducula rubricera	Frugivore	Large	Canopy	Forest	Northern Melnesia	Bismarcks
Dicaeum eximum	Omnivore	Small	Canopy	Generalist	New Britain & Bismarcks endemics	New Britain Endemic
Dicrurus bracteatus	Carnivore	Medium	Sub Canopy	Secondary Closed	Asia-Pacific	New Britain Endemic
Ducula finshii	Frugivore	Large	Sub Canopy	Forest/Edge	New Britain & Bismarcks endemics	Bismarcks
Ducula subflavescens	Frugivore	Large	Canopy	Generalist	Asia-Pacific	Bismarcks
Eclectus roratus	Frugivore	Large	Canopy	Generalist	Asia-Pacific	Bismarcks
Eudynamys scolopacea	Frugivore	Medium	Canopy	Secondary Open	Asia-Pacific	Bismarcks

Species	**Primary Diet**	**Body Size**	**Foraging Stratum**	**Habitat Breadth**	**Species/allospecies Range**	**Subspecies Range**
Geoffroyus heteroclitus	Frugivore	Medium	Canopy	Forest	Northern Melnesia	Melanesia
Lalage leucomela	Carnivore	Small	Sub Canopy	Secondary Closed	Asia-Pacific	New Britain Endemic
Lorius hypoinchrous	Frugivore	Medium	Canopy	Forest/Edge	Northern Melnesia	Melanesia
Macropygia amboinensis	Frugivore	Medium	Midstorey	Forest/Edge	Melanesia	New Britain Endemic
Megapodius eremita	Omnivore	Large	Ground	Secondary Closed	Northern Melnesia	Melanesia
Mino dumontii	Frugivore	Medium	Sub Canopy	Generalist	Melanesia	Melanesia
Monarcha verticalis	Carnivore	Small	Sub Canopy	Forest	New Britain & Bismarcks endemics	Bismarcks
Myiagra alecto	Carnivore	Small	Ground	Generalist	Asia-Pacific	Melanesia
Nectarinia aspasia	Carnivore	Small	Canopy	Generalist	Asia-Pacific	Bismarcks
Pachycephala pectoralis	Carnivore	Small	Canopy	Forest	Asia-Pacific	Bismarcks
Philemon cockerelli	Omnivore	Medium	Sub Canopy	Generalist	New Britain & Bismarcks endemics	New Britain Endemic
Pitta erythrogaster	Carnivore	Medium	Ground	Secondary Closed	Asia-Pacific	New Britain Endemic
Ptilinopus insolitus	Frugivore	Medium	Canopy	Secondary Closed	New Britain & Bismarcks endemics	Bismarcks
Ptilinopus rivoli	Frugivore	Medium	Midstorey	Forest	Melanesia	Bismarcks
Ptilinopus superbus	Frugivore	Medium	Sub Canopy	Forest/Edge	Asia-Pacific	Melanesia
Reinwardtoena browni	Frugivore	Large	Midstorey	Forest	New Britain & Bismarcks endemics	Bismarcks
Rhipidura rufiventris	Carnivore	Small	Midstorey	Secondary Closed	Asia-Pacific	New Britain Endemic
Tanysiptera nigriceps	Carnivore	Medium	Ground	Secondary Closed	New Britain & Bismarcks endemics	New Britain Endemic
Todiramphus chloris	Carnivore	Medium	Sub Canopy	Secondary Open	Asia-Pacific	New Britain Endemic
Todiramphus albonotatus	Carnivore	Small	Midstorey	Secondary Open	New Britain & Bismarcks endemics	New Britain Endemic
Trichoglossus haematodus	Omnivore	Medium	Sub Canopy	Generalist	Asia-Pacific	Melanesia

Appendix B.2 Species trait categorisation method

Diet was defined as the dominant food source consumed by a species (frugivore, carnivore (insectivore and/or vertevore), and omnivore). To organise species into body size classes, we performed a correlation analysis between the body mass (g) and body length (cm) data gathered from the literature, ($r = 0.92$). We categorised species' habitat breadth according to their relative forest specialization, from purely forest occurring species to forest species capable of exploiting a range of disturbed habitats as established in field guides and the literature. The breadth of vertical stratum layers used by species was based on the literature and field observations during the study.

Species were categorised into a geographic range class which grouped those of similar location and extent of global breeding area. Location classes were defined according to species' geographic distributions as recorded in Mayr (2001) and Dutson (2012). Global breeding area was calculated using online databases of island and continental land areas (km^2) (Dahl, 1991; Lepage, 2013). We ran ANOVAs of (i) species and (ii) subspecies levels specifying breeding area (km^2) as the response, and location class as categorical predictor. Location classes which were not significantly different in breeding area were grouped together in a geographic range class (Table 1). We included 2 taxonomic levels in order to account for both historic (species) and current (subspecies) potential to disperse and colonise novel environments – particularly over water. At the subspecies level, this information is more recent and may more accurately represent dispersal limitations with respect to localized habitat modification (Moore, W. D. Robinson, Lovette & T. R. Robinson 2008).

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Appendix Table B.4 Bird trait type analyses of deviance showing differences in probability of occurrence of each trait class among landscape elements. Traits are organized from most specialized class to least specialized class (first column). Habitats are of increasing disturbance from left to right (header row). Bold font indicates elements whose 95% confidence interval does not overlap with zero, with unlogged forest as the reference category.

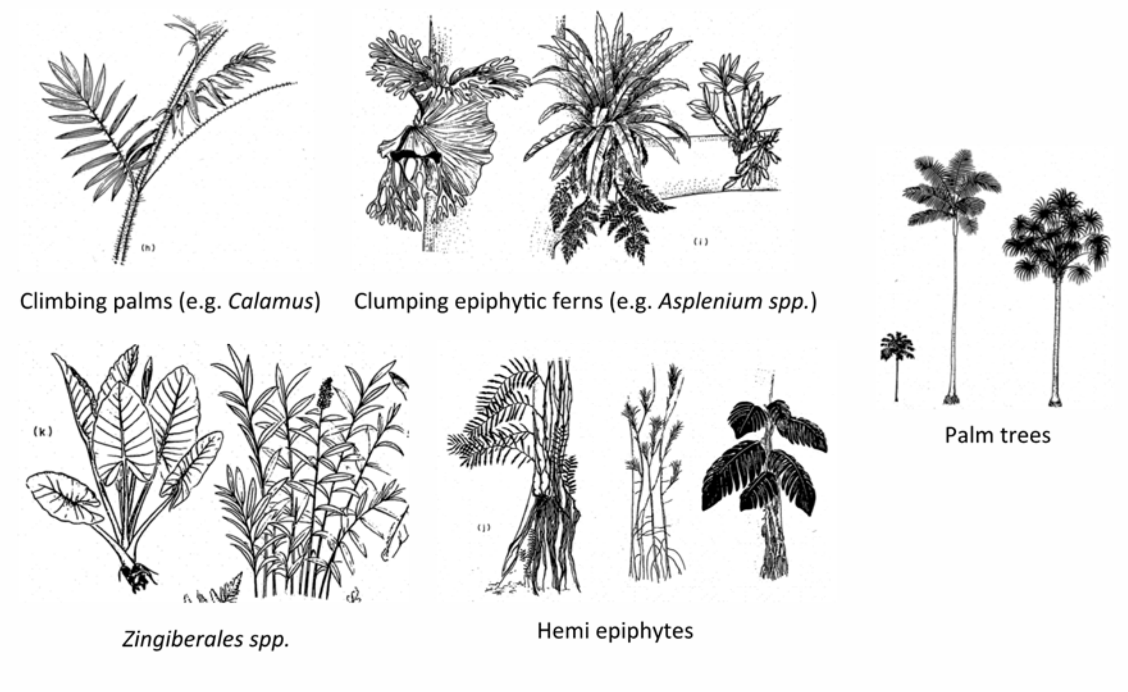
Trait	d^2	Reference Forest		Secondary Remnant		Secondary Riparian		Mature Plantations		Young Plantations	
		Mean	± *s.e.*	Mean	± *s.e.*	Mean	± *s.e.*	Mean	± *s.e.*	Mean	± *s.e.*
Diet											
Frugivores[a]	0.72	0.395	*0.022*	0.424	*0.041*	**0.263**	***0.029***	**0.188**	***0.015***	**0.013**	***0.006***
Carnivores†	0.53	0.359	*0.021*	**0.540**	***0.040***	**0.517**	***0.033***	**0.424**	***0.025***	**0.216**	***0.021***
Omnivores	0.41	0.269	*0.025*	**0.489**	***0.053***	**0.521**	***0.042***	0.261	*0.021*	**0.138**	***0.022***
Species/Allospecies Range											
NB Endemic & Bismarcks	0.45	0.378	*0.025*	**0.500**	***0.048***	0.435	*0.038*	0.333	*0.021*	**0.115**	***0.019***
Nth Melanesia[a]	0.51	0.484	*0.044*	0.667	*0.079*	0.536	*0.066*	**0.331**	***0.036***	**0.021**	***0.015***
Melanesia	0.50	0.354	*0.035*	**0.611**	***0.066***	0.393	*0.053*	**0.213**	***0.026***	**0.049**	***0.018***
Asia/Pacific	0.42	0.231	*0.018*	**0.321**	***0.037***	**0.313**	***0.029***	0.218	*0.015*	**0.076**	***0.013***
Subspecies Range											
New Britain Endemic	0.52	0.349	*0.024*	**0.556**	***0.048***	**0.566**	***0.038***	**0.469**	***0.022***	**0.153**	***0.021***
Bismarcks[a]	0.65	0.311	*0.019*	**0.404**	***0.038***	0.282	*0.028*	**0.165**	***0.013***	**0.039**	***0.009***
Melanesia	0.44	0.328	0.034	**0.519**	***0.068***	0.429	*0.054*	**0.236**	***0.026***	**0.028**	***0.014***
Stratum Layer											
Canopy	0.61	0.409	*0.022*	**0.533**	***0.033***	0.395	*0.043*	**0.288**	***0.018***	**0.125**	***0.017***
Sub Canopy	0.55	0.382	*0.024*	0.462	*0.036*	0.385	*0.046*	**0.268**	***0.019***	**0.071**	***0.014***
Midstorey	0.27	0.274	*0.033*	0.333	*0.049*	0.273	*0.064*	0.271	*0.027*	**0.063**	***0.020***
Ground	0.45	0.234	*0.027*	**0.542**	***0.045***	**0.643**	***0.059***	**0.363**	***0.026***	0.229	*0.030*
Body Size											
Large (>35 cm)	0.58	0.30	*0.023*	**0.44**	***0.048***	0.36	*0.037*	**0.16**	***0.015***	**0.035**	***0.011***
Medium[a] (20-35 cm)	0.59	0.343	*0.019*	0.392	*0.037*	0.387	*0.030*	**0.253**	***0.015***	**0.061**	***0.011***
Small (<20 cm)	0.41	0.414	*0.025*	**0.676**	***0.045***	**0.548**	***0.038***	**0.512**	***0.022***	**0.306**	***0.027***
Habitat Breadth (literature-based)											
Forest	0.69	0.438	*0.033*	0.556	*0.063*	**0.204**	***0.041***	**0.150**	***0.021***	**0.006**	***0.006***
Forest/Edge	0.53	0.444	*0.039*	0.489	*0.075*	**0.171**	***0.045***	**0.181**	***0.026***	**0.000**	***0.000***
Secondary Closed	0.58	0.361	*0.024*	**0.616**	***0.046***	**0.565**	***0.037***	0.406	*0.020*	**0.087**	***0.025***
Secondary Open	0.24	0.143	*0.026*	**0.254**	***0.049***	**0.449**	***0.040***	**0.216**	***0.023***	0.143	*0.017*
All (generalist)	0.30	0.370	*0.027*	0.453	*0.055*	**0.506**	***0.023***	0.376	*0.024*	**0.250**	***0.023***

a Best model fit (highest % deviance explained) for the trait type

† Vertivores and insectivores

Appendix C Chapter 5 supporting data

Appendix Figure C.1 Diagrams of some life forms measured (taken from Webb et al. 1976).



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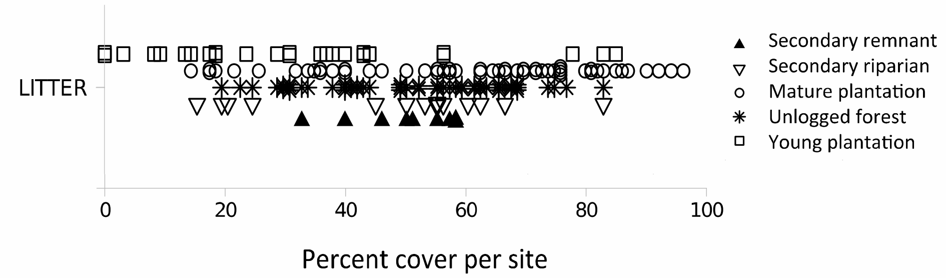


Appendix D Chapter 6 supporting data

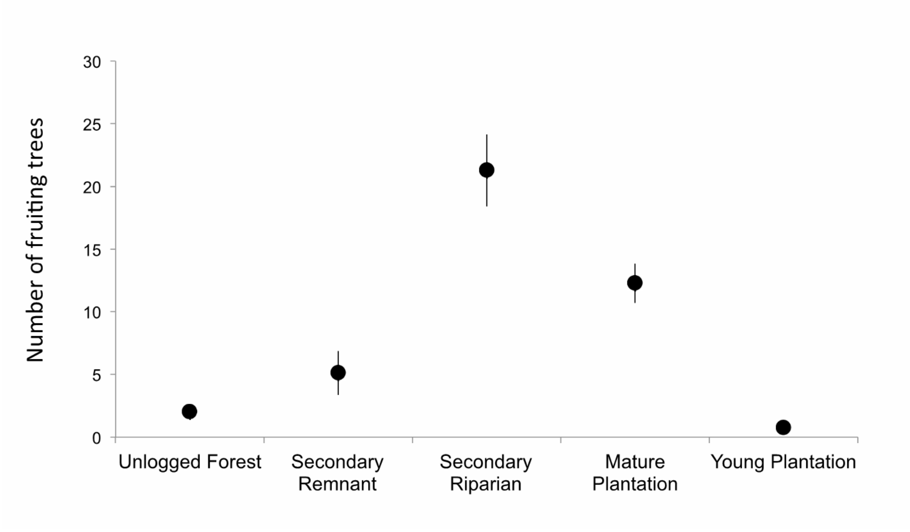
Appendix Table D.1 Model-selection results for bird species richness of forest-using and forest-specialist birds. Included are log-likelihood values (log(*L*)), degrees of freedom (*K*), AIC$_c$ values, AIC$_c$ differences (delta), and Akaike weights (w_i).

Group	Model	*K*	log(*L*)	AICc	delta	w_i
Species richness forest-using birds	CC + TrR + Tr(DBH)	5	-272.277	555.147	0.000	0.439
	CC + TrR + Tr(DBH) + IFC2km	6	-272.244	557.329	2.182	0.147
	CC + TrR + Tr(DBH) + Palm + Ginger	7	-271.176	557.484	2.337	0.136
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg	7	-271.333	557.796	2.649	0.117
	CC + TrR + Tr(DBH) + Palm + Ginger + IFC2km	8	-271.138	559.746	4.599	0.044
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg + IFC2km	8	-271.216	559.901	4.754	0.041
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg + Palm + Ginger	9	-270.420	560.695	5.547	0.027
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg + Palm + Ginger + IFC2km	10	-270.317	562.926	7.779	0.009
	IFC2km	3	-278.551	563.336	8.189	0.007
	Fern + Shr/sdlg	4	-277.724	563.840	8.693	0.006
	Palm + Ginger	4	-278.420	565.231	10.084	0.003
	Fern + Shr/sdlg + IFC2km	5	-277.640	565.874	10.727	0.002
	Palm + Ginger + IFC2km	5	-278.357	567.309	12.162	0.001
	Fern + Shr/sdlg + Palm + Ginger	6	-277.630	568.100	12.952	0.001
	Fern + Shr/sdlg + Palm + Ginger + IFC2km	7	-277.560	570.251	15.104	0.000
Species richness forest-specialist birds	CC + TrR + Tr(DBH) + Palm + Ginger	7	-195.586	406.315	0.000	0.229
	CC + TrR + Tr(DBH) + Palm + Ginger + IFC2km	8	-194.472	406.429	0.114	0.216
	CC + TrR + Tr(DBH)	5	-198.253	407.106	0.791	0.154
	CC + TrR + Tr(DBH) + IFC2km	6	-197.434	407.717	1.402	0.114
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg	7	-196.536	408.214	1.899	0.089
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg + Palm + Ginger	9	-194.292	408.458	2.143	0.078
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg + Palm + Ginger + IFC2km	10	-193.314	408.944	2.629	0.061
	CC + TrR + Tr(DBH) + Fern + Shr/sdlg + IFC2km	8	-195.852	409.189	2.873	0.054
	Fern + Shr/sdlg	4	-204.424	417.243	10.928	0.001
	IFC2km	3	-205.809	417.854	11.539	0.001
	Palm + Ginger	4	-205.030	418.456	12.141	0.001
	Fern + Shr/sdlg + IFC2km	5	-204.305	419.210	12.895	0.000
	Fern + Shr/sdlg + Palm + Ginger	6	-203.789	420.427	14.112	0.000
	Palm + Ginger + IFC2km	5	-204.970	420.540	14.225	0.000
	Fern + Shr/sdlg + Palm + Ginger + IFC2km	7	-203.726	422.594	16.279	0.000

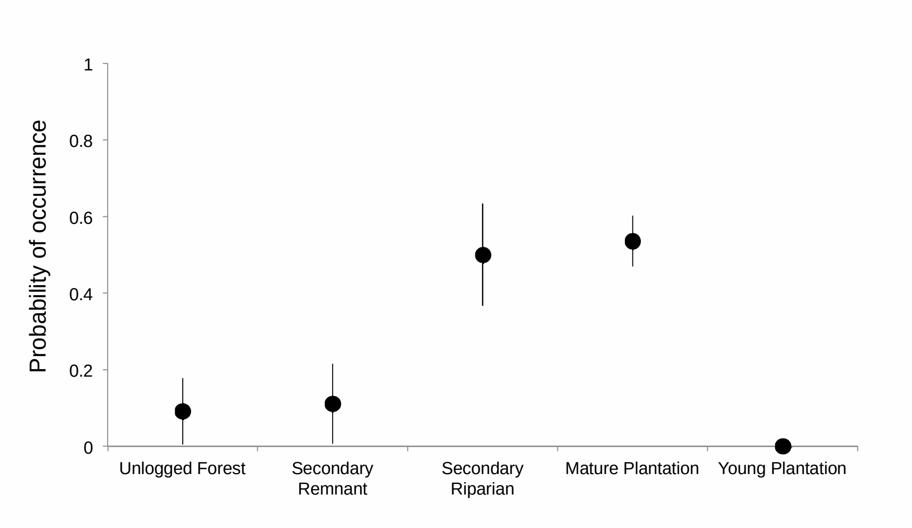
Appendix Table D.2 Model-averaging results for species richness of forest-using and forest-specialist birds.

Group	Variable	Coefficient	Standard error
Species richness forest-using birds	Tree species richness	0.368	0.121
	Tree size diversity	0.090	0.075
	Canopy cover	0.298	0.107
	Intact rainforest cover	-0.032	0.119
	Ginger cover	0.088	0.073
	Palm cover	0.085	0.083
	Shrubs/seedlings cover	0.095	0.071
	Fern cover	0.031	0.066
Species richness forest-specialist birds	Tree species richness	0.680	0.253
	Tree size diversity	0.115	0.128
	Canopy cover	1.691	0.472
	Ginger cover	0.133	0.141
	Palm cover	0.363	0.146
	Intact rainforest cover	0.263	0.173
	Shrubs/seedlings cover	0.213	0.127
	Fern cover	0.065	0.127

Appendix Figure D.1 Mean (standard error) number of trees in fruit at sites within landscape elements



Appendix Figure D.2 Probability of occurrence of arboreal termitaria at sites within landscape elements



Appendix Table D.3 Observations of nests of forest-using bird species outside of unlogged forest

Species	Landscape element(s)	Comments
Alcedo lepida, Todhiramphus albonotata, Tanysiptera nigriceps	Mature plantation, Secondary riparian, Unlogged forest	Only observed *T. albonotata* but it is likely that these other kingfishers also use these nest holes
Ducula subflavescens	Young plantation, Mature plantation	Birds observed on nest in remnant large trees
Dicrurus bracteatus	Young plantation	Birds observed on nest in a young plantation tree (fork)
Myiagra alecto	Mature plantation	Birds observed on nest
Ptilinopus insolitus	Open (village)	Bird observed on nest
Mino dumontii	Secondary riparian	Bird observed on nest
Philemon cockerelli	Mature plantation, Young plantation	Birds observed on nests. Young plantation was observed in a remnant tree.
Aviceda subcristata	Open (roadside)	Bird observed on nest of large remnant tree.
Aplonis metallica	Open (roadside), Mature plantations	Birds observed on nests
Ptilinopus superbus	Mature plantations, Unlogged forest	Birds observed on nests