Moloney, James McLellan (2005) ***The effects of habitat fragmentation on bird communities in a naturally disturbed environment: the Wet Tropics lowlands.*** **PhD thesis, James Cook University.**

Chapter 1. General introduction.

This thesis primarily examines the impacts of habitat fragmentation on the lowland bird assemblage of the Wet Tropics of northern Queensland. Bird distributions are analysed at the local and landscape scale. Landscape patterns and ecological correlates of clearing are identified, as is the distribution of vegetation types. It also examines the effects of edges on both vegetation and the bird assemblages, and examines the determinants of bird assemblages in a fragmented environment. Results are placed in theoretical and practical contexts, involving several themes that are briefly introduced below, and which relate particularly to conservation of avifauna in fragmented environments.

1.1 Rainforest conservation

Tropical forests represent the most diverse and complex land communities on earth. Although they cover less than 7% of the world's landmass, they contain two-thirds of the world's known species of plants and animals (Wilson 1988). Comprising less than 1% of Australia's landmass, the rainforests of the Wet Tropics region contain 25% of all plant genera, 17% of plant species (Australian Heritage Commission 1986), and over 700 endemic plant species (Wet Tropics Management Authority 1995). The region contains 30% of Australia's marsupial species, 60% of the bat species, 30% of the frog species, 23% of the reptile species and 62% of the butterfly species (Australian Heritage Commission 1986). The avifauna of the rainforests of the region is also the most diverse in Australia with about 95 species associated with rainforests or their edges (Kikkawa 1982). Furthermore, 54 species of vertebrate animals are endemic to the Wet Tropics (Nix & Switzer 1991). In particular, the lowlands contain the richest overall biological diversity (Driscoll & Kikkawa 1989), and wet lowland rainforest on fertile, well-drained soils (complex mesophyll vine forest) is structurally the most complex and diverse of all rainforest types (Kikkawa 1982).

Much of this biodiversity is under threat. Fragmentation of tropical rainforest through clearing, especially on lowland plains and moderately sloping uplands, provide a worldwide problem. From 1981-1990, 46 million hectares of lowland rainforest was lost, representing an average annual loss of 0.64% of what remained in 1980 (Whitmore 1997). Northern Queensland is no exception, with over half of the lowland rainforests in the region now cleared (Winter *et al.* 1987). Pressure on the now predominantly fragmented lowland rainforest continues in the form of clearing for agriculture, tourism development, and urban expansion (Crome 1993).

Much research has been conducted into the effects of a variety of human disturbances on rainforest assemblages, such as logging (e.g., Owiunji & Plumtree 1998), the presence of roads (e.g., Goosem 1997), fragmentation (e.g., Stouffer & Bierregaard 1995a), mineral extraction (e.g., Canaday & Rivadeneyra 2001), hunting (e.g., Peres & Dolman 2000), and many others. However, patterns and processes resulting from a particular type of impact often differ in different regions, which can be due to a variety of factors including the climate, the natural architecture of the rainforest, and characteristics (e.g., diversity, food and habitat requirements) of the subject taxon or taxa. Therefore, although broad trends often emerge from multiple studies, it remains important to study the responses of tropical biota to human impact at a variety of locations because results from one location may not translate to others. In addition, comparisons of results from different regions that encompass a range of environmental and taxonomic characteristics (e.g., diversity) may allow us to discover why these different patterns emerge, and to identify the characteristics of assemblages that predispose them to vulnerability to human disturbance.

1.2 Habitat fragmentation

Perhaps the most significant ongoing threat to rainforests worldwide is habitat clearing for agriculture or timber, which almost inevitably results in the fragmentation of remaining habitat. Tropical avifaunas, with their more diverse and specialized assemblages, are particularly vulnerable to fragmentation. For example, tropical studies consistently suggest strong declines in richness of rainforest birds in patches over time (e.g., Kattan *et al.* 1994). This vulnerability is due to a number of factors. Compared to temperate avifaunas, these assemblages are usually more diverse, species are more specialized in their foraging habits, and consequently they occur in lower densities (Wilcove *et al.* 1986, Turner 1996) and patchier distributions (Thiollay 1989, Diamond 1980). Furthermore, many tropical species have lower dispersal powers (Wilcove *et al.* 1986), and are less tolerant of vegetation outside the forest (Turner 1996).

Within tropical bird assemblages, some species may be particularly vulnerable to fragmentation. They include species with large home ranges (Thiollay 1996), those that require specific but scattered resources (Wilcove *et al.* 1986, Telleria & Santos 1995), habitat specialists (Bierregaard *et al.* 1992), edge-avoiding species (e.g., McIntyre 1995), specialist feeders (Lovejoy *et al.* 1986, Bierregaard *et al.* 1992), and other naturally rare species (e.g., Soule *et al.* 1988). Different feeding guilds often respond differently, with insectivorous birds (Stouffer & Bierregaard 1995a) often particularly vulnerable, and with nectarivores more resilient (Stouffer & Bierregaard 1995b). Swihart *et al.* (2003) found for mammals and amphibians that dietary generalists may be less affected by fragmentation due to their lower susceptibility to variation in availability of food resources (the niche-breadth hypothesis). Furthermore, species that are capable of using a wide range of habitats are more likely to be able to use human-altered portions of a landscape (Laurance 1991, Andren 1994).

For much of the last 40 years, landscape measures focussed on the area of a patch, and the distance from 'mainland' habitat, as a result of MacArthur and Wilson's (1967) theory of island biogeography (Galli *et al.* 1976). However, different species and guilds are affected by different vegetation and spatial characteristics at the patch and landscape scale. While patch area strongly influences bird assemblages in many if not most cases (e.g., Bellamy *et al.* 1996), bird assemblages (or components of bird assemblages) may be influenced by other spatial characteristics such as habitat shape (e.g., Temple 1986), distance to unfragmented habitat (e.g., Breininger *et al.* 1991), nearest neighbour (e.g., Jansson & Angelstam 1999) and habitat within certain radii of the focal patch (e.g., Opdam *et al.* 1985).

To understand how fragmentation affects plant and animal communities, many studies now examine how the particular characteristics of the landscape affect these communities. Most species are influenced by a combination of patch characteristics, whether vegetative (Blake & Carr 1987), patch level (geometric attributes of a single patch) (Thiollay & Meyburg 1988), or landscape (e.g., relationships to other patches) (Pereira & Itami 1991). These characteristics often impact on biological processes such as dispersal (Sieving *et al.* 1996), foraging (Stouffer & Bierregaard 1995a), predation and parasitism (Wilcove 1985, Arango-Velez & Kattan 1997, Cooper & Francis 1998, Paton 1994), reproductive success (Breininger 1999) and competition from edge species (Loyn 1987, Grey *et al.* 1997).

Research on fragmentation has grown significantly, especially in the last 15 years, and a number of studies have examined the effects of rainforest fragmentation on bird assemblages, especially in the neotropics (e.g., Stouffer & Bierregaard 1995a, 1995b, Terborgh *et al.* 1997, Willis 1980, Daily *et al.* 2001). Although previous studies have variously identified the above factors and others to as potential factors influencing bird use of fragmented landscapes, results vary significantly depending on structural characteristics of the forest, characteristics of the focal bird assemblage, and many other variables. Furthermore, the understanding of these processes is still very poor. Therefore, to rely on the research in Brazil and other hyper-diverse neotropical areas for conclusions about the influence of fragmentation on all tropical rainforests is unsatisfactory, as not only can Amazonian birds not be expected to represent all tropical forest avian assemblages (Turner 1996), but there remains much to learn about the processes structuring even the most closely-studied fragmented assemblages.

At a practical, local level, there is an urgent need to understand the processes ensuing from habitat fragmentation in the lowlands of the Wet Tropics of northern Queensland (Australian Heritage Commission 1986, Crome 1993). In a broader sense, however, the particular characteristics of the Wet Tropics lowland rainforests and their bird assemblages, and the significant differences between these rainforest assemblages and most of those that have been studied elsewhere, provide an opportunity to examine why responses to natural and human disturbance differ between locations. In other words, do assemblages that are adapted to natural disturbances such as cyclones show a greater resistance and resilience to some forms of human disturbance? Furthermore, the relatively depauperate and generalist avifauna of the Wet Tropics allows us to examine the diversity-stability hypothesis in the context of anthropogenic habitat fragmentation as a disturbance.

1.3 Natural versus human disturbance

The vulnerability of an assemblage to human disturbances may depend on the adaptation of that assemblage to natural disturbance, and the types of disturbance to which the assemblage is subjected. Physical disturbances, such as tree falls, that create gaps are well known and well studied natural features of tropical rainforests (e.g., Connell 1978), and regular gap formation regimes help structure animal and plant species composition (Denslow 1987). Furthermore, the particular disturbance regime will not only exert selection pressure on the assemblage composition, but may exert selection pressure on animal behaviours such as feeding habits and habitat selection (Jones *et al.* 2001). Apart from regular and isolated tree falls, the Wet Tropics lowlands have been subjected to at least two forms of natural disturbance – one past and one ongoing. Firstly, Pleistocene contractions led to the near disappearance of lowland rainforest (Williams & Pearson 1997), and secondly, regular cyclones continue to alter the canopy structure, thus impacting on the avifauna of the lowlands.

Past events may dictate the ability of a species to respond to current threats. For example, palaeontologic evidence suggests that Pliocene drops in sea temperature caused extinctions of marine molluscs in the Caribbean, but that subsequent and just as severe Pleistocene fluctuations has caused little further extinction. In other words, the vulnerable species had already become extinct, leaving a core of species that were relatively resilient to further fluctuations (Jackson 1995). Similarly, adaptations to historical bison (*Bison bison*) grazing are thought to explain differential resistance of North American plants to modern cattle grazing (Balmford 1996). A further example is the introduction of rats on oceanic islands, which has led to catastrophic extinctions on islands lacking native predators, but minimal species loss on some others that already contained native predators (Atkinson 1985). In these cases, previous selective pressure within populations, or the entire disappearance of vulnerable species, has left bird assemblages that are relatively resistant to the introduction of rats (Balmford 1996).

Cyclone damage, like any disturbance, varies in severity. The impact of a disturbance, however, depends on a range of factors such as the frequency of occurrence (Turner & Dale 1998), the severity of the disturbance, and the spatial extent of the disturbance in relation to the ecosystem (Whittaker 1995). Harper (1977) differentiated between minor disasters, which happen so frequently that selection pressure is exerted on the communities and organisms, and 'catastrophes', which are disturbances (such as a volcanic eruption) that happen so infrequently that populations are ill-adapted to cope. Some researchers (e.g., Waide 1991a) have suggested that habitat susceptibility to tropical storms may select for behavioural plasticity in foraging height and diet among birds. If this were the case, we may predict that these generalist characteristics would lead to resistance to human disturbances such as fragmentation. The lowlands of the Wet Tropics experience regular cyclonic disturbance and, at any time, evidence of this disturbance can be found throughout much of the region (Webb 1958). Thus, cyclone impacts may lie within the 'disaster' area of the spectrum.

The broad relationships between natural disturbance, anthropogenic disturbance, vegetation, and bird assemblages are illustrated in Figure 1.1. The vegetation and bird assemblages of the Wet Tropics lowlands result from the biogeographic history of the region (Williams & Pearson 1997), but may also be shaped by more frequent, localised, and ongoing disturbance from cyclones. Local bird assemblages are likely to be affected by the vegetation characteristics, and in turn the bird assemblages may impact on vegetation through seed dispersal and other processes. Anthropogenic habitat fragmentation is likely to impact on the resulting vegetation and bird assemblages, and indirectly on the bird assemblage via vegetation impacts.

Therefore, although the relative impacts of rainforest contractions and regular storm impact on lowland bird assemblages in the Wet Tropics are difficult to separate, both would be expected to lead to a low-diversity bird assemblage made up of habitat generalists that are not so reliant upon a continuously closed canopy. In other words, this is likely to be a robust (and simple) assemblage (Danielsen 1997). Accordingly, an assemblage that is adapted to natural disturbance may as a result be more resistant to certain types of human disturbance (Lynch 1991).

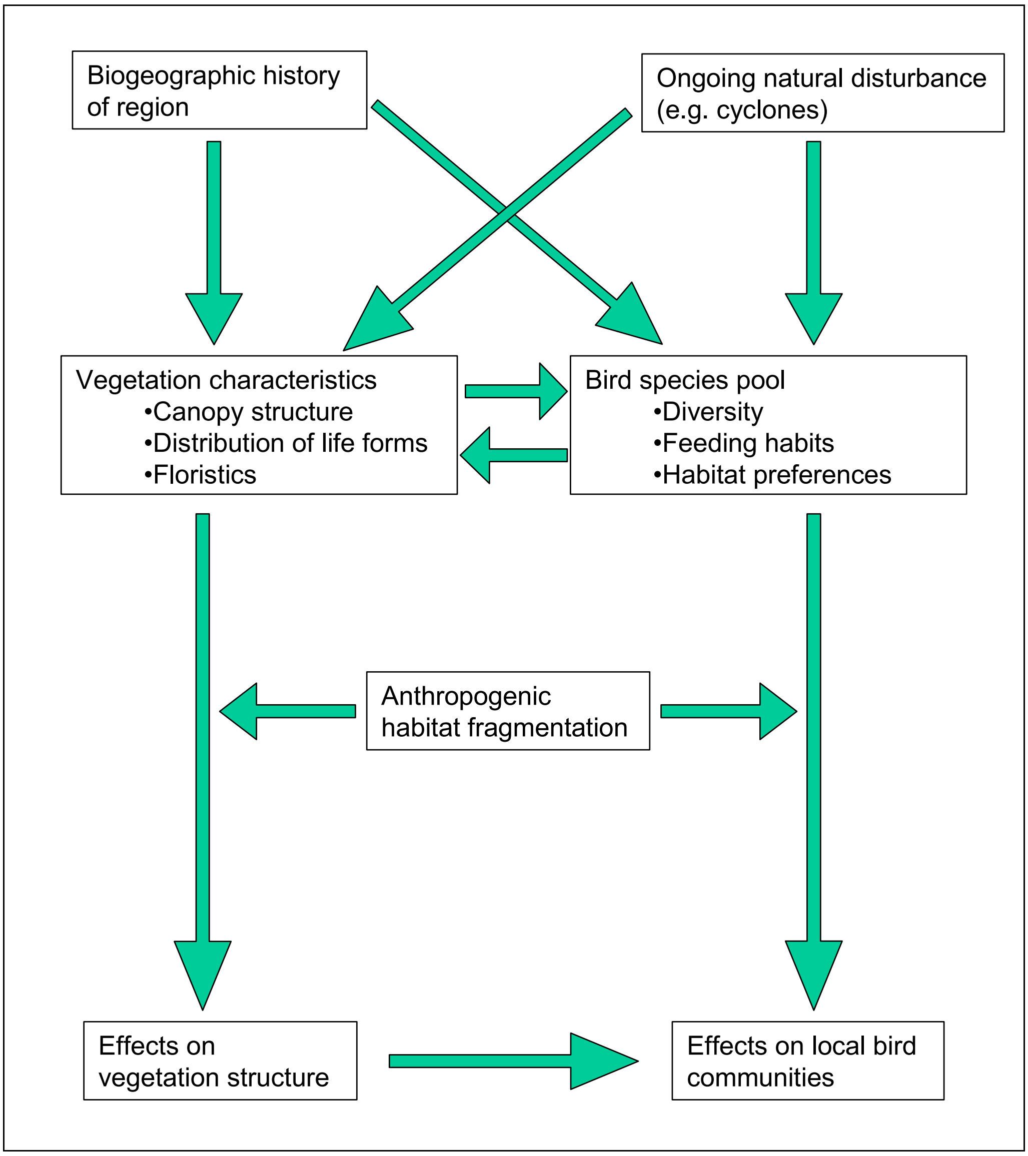

Figure 1.1 Conceptual flow chart of the potential relationship between natural and anthropogenic disturbance in Wet Tropics lowland forests.

1.4 Diversity and community stability

A crucial issue in landscape ecology and conservation biology is the understanding of how much habitat modification a biological assemblage can tolerate without significant loss of diversity or community functions, and whether the fragility of communities follows predictable patterns. The diversity-stability hypothesis has generated much debate over the last 40 years. Work in the 1950s and 1960s suggested that communities that are more diverse are more stable and more resistant to invasion (e.g., MacArthur 1955, Elton 1958). However, modelling in the 1970s suggested the contrary - that higher diversity frequently led to decreased stability (e.g., May 1972). Goodman (1975) reviewed the evidence and found little pattern, and the ensuing 25 years have seen many studies exploring the diversity-stability hypothesis (e.g., Pimm 1984, Tilman & Downing 1994). Although results from models and real communities have varied, the evidence suggests that there is a general tendency for stability to increase as diversity increases (McCann 2000).

A number of factors have clouded the stability-diversity debate, however. Firstly, there exist differing definitions of stability. Stability can be defined as resistance (ability to not change in the face of some perturbation), or as resilience (ability to return to the previous equilibrium after perturbation), or variations on these definitions (McCann 2000). These properties can have important implications for the results. Secondly, studies have examined different taxa and different numbers of trophic levels, which may influence responses. Furthermore, the response of a community will depend on what type of perturbation is inflicted on the community. Biologically diverse systems, such as complex rainforest, may be more resistant to biological invasion than other systems, as species in narrow, specialized niches may be more difficult to displace; but they may be more vulnerable to physical disturbance to the habitat (such as habitat fragmentation or storm damage), also because of the species' narrow niches. Furthermore, the nature of the diversity/stability relationship may vary depending on whether the ecosystems to be compared are all of one broad type (such as rainforest) or encompass a variety of habitats (such as woodlands, open forest and closed forest).

Species richness in rainforests varies substantially across the globe, and according to taxon. The northern Queensland rainforests contain fewer bird species than might be predicted because of Palaeozoic contractions resulting from climate change (Driscoll & Kikkawa 1989), and are particularly low in numbers of specialized rainforest species (Williams *et al.* 1996). However, because the Australian rainforest avifauna is relatively abundant and has more general resource requirements (Driscoll & Kikkawa 1989), it may be predicted that it will be more resistant to the effects of fragmentation than its counterparts in the Americas or Africa.

1.5 Aims

This project addresses the above themes by (i) examining how the size and spatial structure of forest remnants affect vegetation structure and bird assemblages, (ii) addressing questions of how the theory of diversity and stability relates to the response of assemblages to anthropogenic habitat fragmentation, and (iii) determining how these responses may also depend on natural impacts, both historical and ongoing, in this environment. Although primary data for this project comes from a single region, the results are interpreted in the context of natural versus anthropogenic disturbance by means of comparison with other studies with markedly different bird assemblages and disturbance regimes.

1.6 Thesis outline

Figure 1.2 illustrates the overall structure of this thesis. Chapter 2 describes the study region, the conservation of rainforests within it, and describes the disturbance regimes that have shaped the flora and fauna.

Chapter 3 reviews the use of landscape metrics in conservation biology, outlines in detail the methods of spatial data collection and analysis used here, describes and quantifies the spatial characteristics of the landscape, and analyses the environmental patterns of clearing in the study region. This chapter therefore addresses local rainforest conservation from a spatial perspective, including the extent and arrangement of clearing.

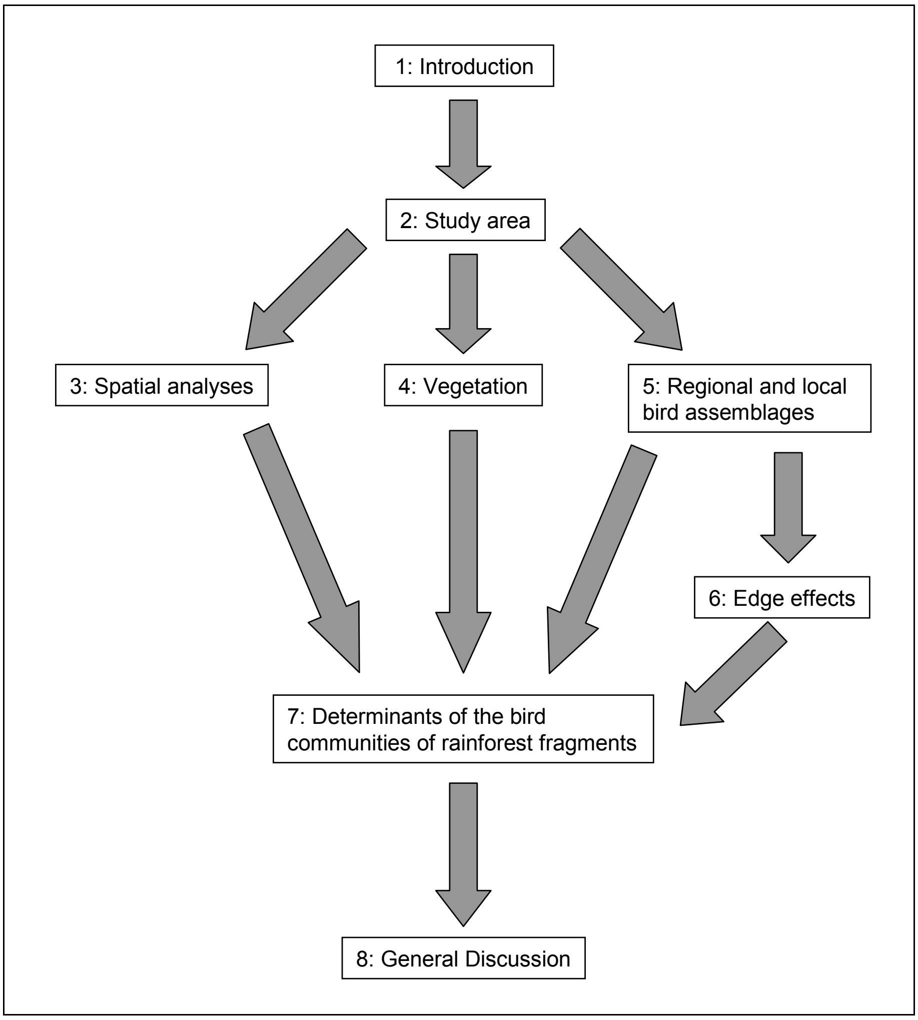

Figure 1.2 Thesis chapter structure.

Chapter 4 summarizes the vegetation structure and selected floristics of the study sites. The distribution of vegetation in the region is also analysed with respect to environmental gradients, and the results of this chapter are related to general rainforest conservation in addition to the effects of human and natural disturbance on rainforest vegetation in this region.

Chapter 5 describes the characteristics of the bird assemblages of the study sites, and compares these characteristics to bird assemblages in other rainforests in relation to the biogeographic history of the area, and the nature of disturbance regimes. It also describes a technique for identifying indicator species in a fragmented environment.

Chapter 6 examines the effect of rainforest edges on the vegetation structure and on the rainforest bird assemblage in a fragmented environment. The results are compared to results from other rainforest regions, and interpreted in the context of stability/diversity hypothesis and natural versus anthropogenic disturbance.

Chapter 7 draws together spatial and vegetation information and the characteristics of the bird assemblage, and analyses the determinants of bird assemblage structure across this fragmented environment. From a theoretical perspective, this chapter considers the relationship between natural disturbance and the response of assemblages to habitat fragmentation, and the relationship between community diversity and stability in the face of this type of perturbation. From a practical perspective, it identifies what characteristics of the landscape are important to lowland bird conservation, and thresholds above which patches are of significant conservation value.

Chapter 8 further discusses the results of the study in a theoretical and practical context, and suggests further research.

Common names of birds are relatively well known, and are therefore used throughout the text except where taxonomic groupings are relevant. Scientific and common names are given in Appendix 5, and are as per Christidis and Boles (1994).

Chapter 2. Study Area

2.1 Wet Tropics biogeographic region overview

The Wet Tropics biogeographic region of north-eastern Queensland contains the largest continuous area of rainforest in Australia, with around 800,000 ha remaining in an almost continuous strip between Townsville and Cooktown (Figure 2.1). It is the presence of this rainforest, reflecting high rainfall, which largely determines the delineation of the biogeographic region.

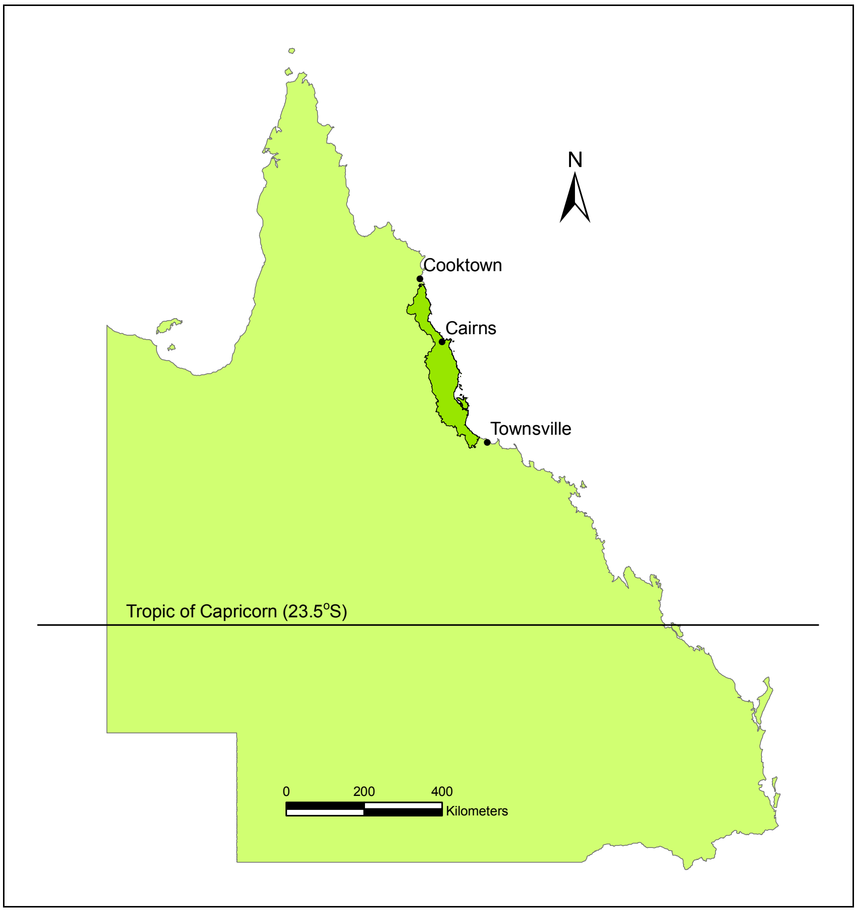

Figure 2.1 Location of the Wet Tropics biogeographic region (darker green) in Queensland.

Clearing of the Wet Tropics lowlands for agriculture began in the 1870s (Adam 1992). By the mid 1980s, approximately 20% of all rainforest in north-eastern Queensland had been cleared, but more significantly, over 50% of all coastal lowland rainforest had by this time disappeared for agriculture and grazing (Figure 2.2). The lowland clearance figure of 56.9% (Figure 2.2) includes all areas below 80 m altitude, whether on fertile, flat or gently sloping land, or the less fertile areas on granite and metamorphic soils on steep ground. Within the flat and gently undulating lowlands on more fertile soil below 80 m altitude, considerably more land has been cleared (Winter *et al.* 1987), and within the study area, less than 32% of lowland rainforest on flat areas and on gentle slopes (less than 10 degrees) remain (J. Moloney, unpub. data).

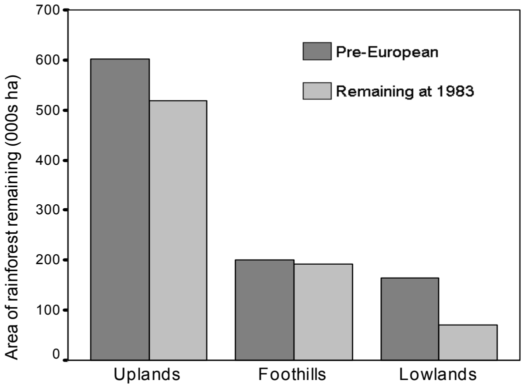

Figure 2.2 Original and standing (circa 1983) areas of rainforest in the Townsville to Cooktown region (adapted from Winter *et al.* 1987).

The majority of the current landscape of the Wet Tropics lowlands consists of isolated rainforest fragments within a mosaic of pasture or monocultures, especially sugar cane. This mosaic is almost entirely devoid of trees, and hostile to all but a few species of birds, of which few penetrate far into the rainforest. The matrix can be considered a uniform 'non-habitat' for rainforest birds, and therefore the landscape of the lowlands consists of fragments of varyingly hospitable rainforest habitat surrounded by a 'sea' of inhospitable habitat. The patterns of clearance and resulting fragmentation of the study area is addressed in detail in Chapter 3.

Over some areas of the coastal lowlands, much of the cleared vegetation comprised non-rainforest vegetation; however, in the wettest parts of the region, between El Arish and Fishery Falls (Figure 2.3), the majority of cleared vegetation was rainforest (Winter *et al.* 1987). Between Eubenangee and El Arish, and in the well-drained and fertile Mena Creek and Palmerston areas, all clearing was of rainforest (Winter *et al.* 1987). Lowland rainforest in some areas remains under pressure from clearing for agricultural expansion, tourism development, and urban expansion (Crome 1993). With over one third of remaining lowland rainforests on private land (Bell *et al.* 1987), and the majority of this area outside the Wet Tropics World Heritage Area, much of the remaining coastal lowland rainforests are under threat of further disturbance.

2.2 Study area

Three study sites were located in contiguous rainforest and 30 in fragmented patches along a 60 km stretch of the lowlands between Gordonvale in the north and Mena Creek, south of Innisfail, to the south (Figure 2.3). In the northern part of the study area, the lowlands form a flat valley running roughly parallel to the coast, ranging in width from approximately 3 km at Fishery Falls to 10 km at Mirriwini, and are bounded on the east by a series of narrow coastal ranges. The highest of these is the Malbon Thompson Range, which rises to an altitude of 1026 m at Bell Peak North. Further south, the Graham, Seymour and Moresby ranges are lower and less steep (605 m, 475 m and 245 m respectively). The western side is bounded by steep, heavily incised ranges reaching 1622 m (Mt. Bartle Frere) in the Bellenden Ker Range. South of Innisfail, the lowlands on flat alluvial soil widen to approximately 15 km, and to the west form gently undulating low foothills in the Palmerston and Mena Creek areas. Rugged mountains bound these low foothills to the north, south and west.

Study sites were located at altitudes ranging from <10 m to ≈160 m. This range was included for three reasons. Firstly, there is a lack of suitable and accessible sites at or near sea level within this area of high rainfall. Secondly, this range of altitudes is well within what is considered ecologically to be lowland habitat: lowland rainforests are commonly defined as rainforests at an altitude of <300 m (Adam 1992, Bell *et al.* 1987), as this roughly divides upland and lowland faunas (Kikkawa 1982, Winter *et al.* 1987). Thirdly, while increased altitude correlates with changing vegetation characteristics such as smaller leaf size, increased emergent eucalypts, and other sclerophylls, greater numbers of tree ferns and mossy epiphytes, and less of most other special life forms, little difference is observed up to 200-300 m altitude (Webb 1968).

A further division at 80 m altitude has been recognized by Winter *et al.* (1987) dividing the plains from the steep lower foothills. This delineation, however, is based largely on topography, and the authors note that the exception to this occurs on basalt flows in the Palmerston and Mena Creek areas, which are gently sloping transitions from lowland to foothills. In this study, all sites occurring at altitudes above 80 m were on the Palmerston basalt flow.

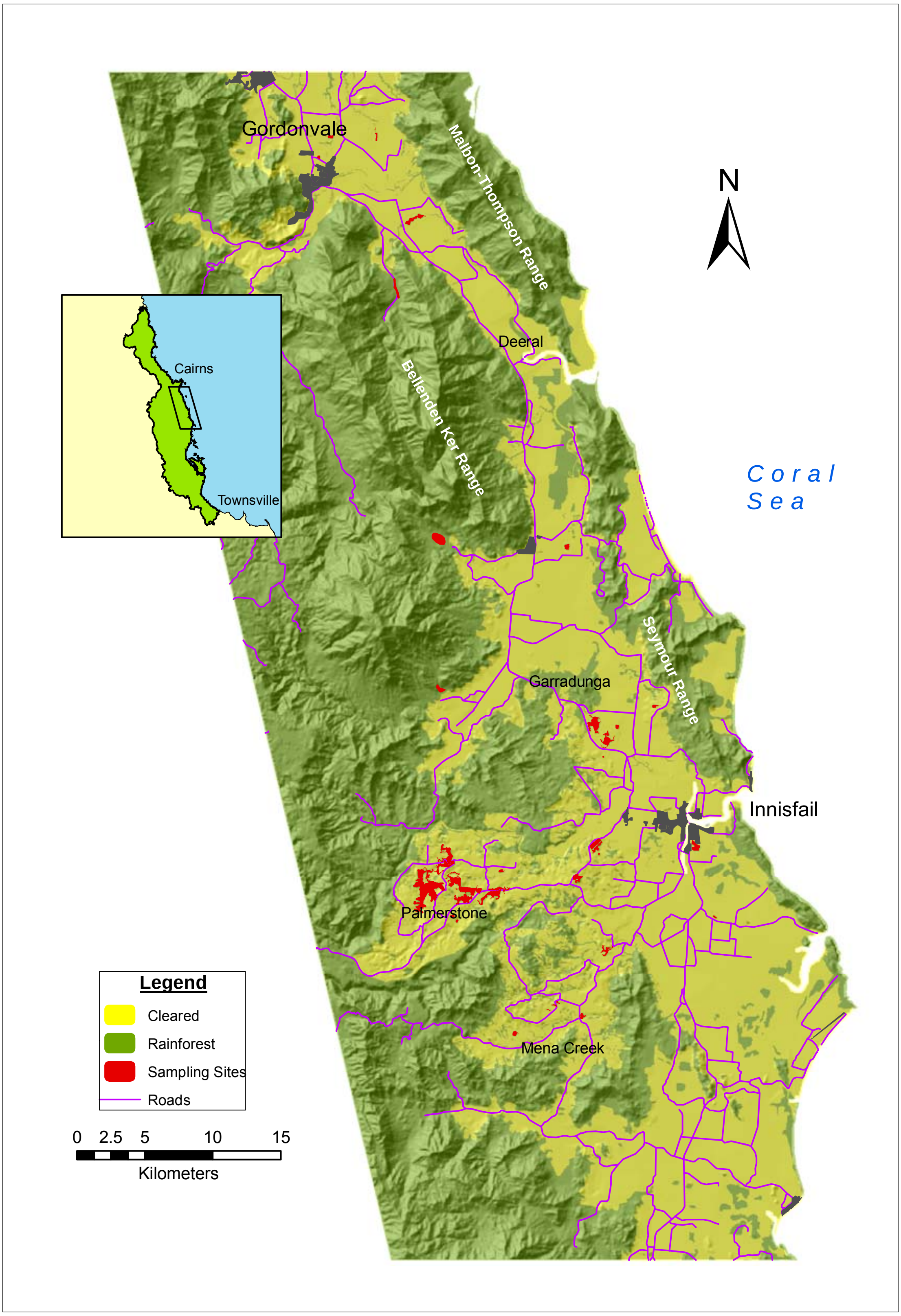

Figure 2.3 Location of the study area in the coastal lowlands of north-eastern Queensland, showing the current distribution of rainforest, and the locations of sites.

2.3 Geology and soils

The Cairns-Cardwell lowland plain lies predominantly on Quaternary alluvial and lagoonal deposits (Figure 2.4). The low coastal ranges are composed of granite (Malbon Thompson Range) and metamorphics (the Seymour and Moresby ranges). To the west of the alluvial plain, the steep, high ranges comprise granite (de Keyser 1964), whereas the lower foothills are mainly formed from metamorphics. The other major rock unit in the low foothill areas comprise Pliocene basalt flows, having emanated from vents on the Atherton Tableland and flowed down the North Johnstone and South Johnstone valleys (de Keyser 1964).

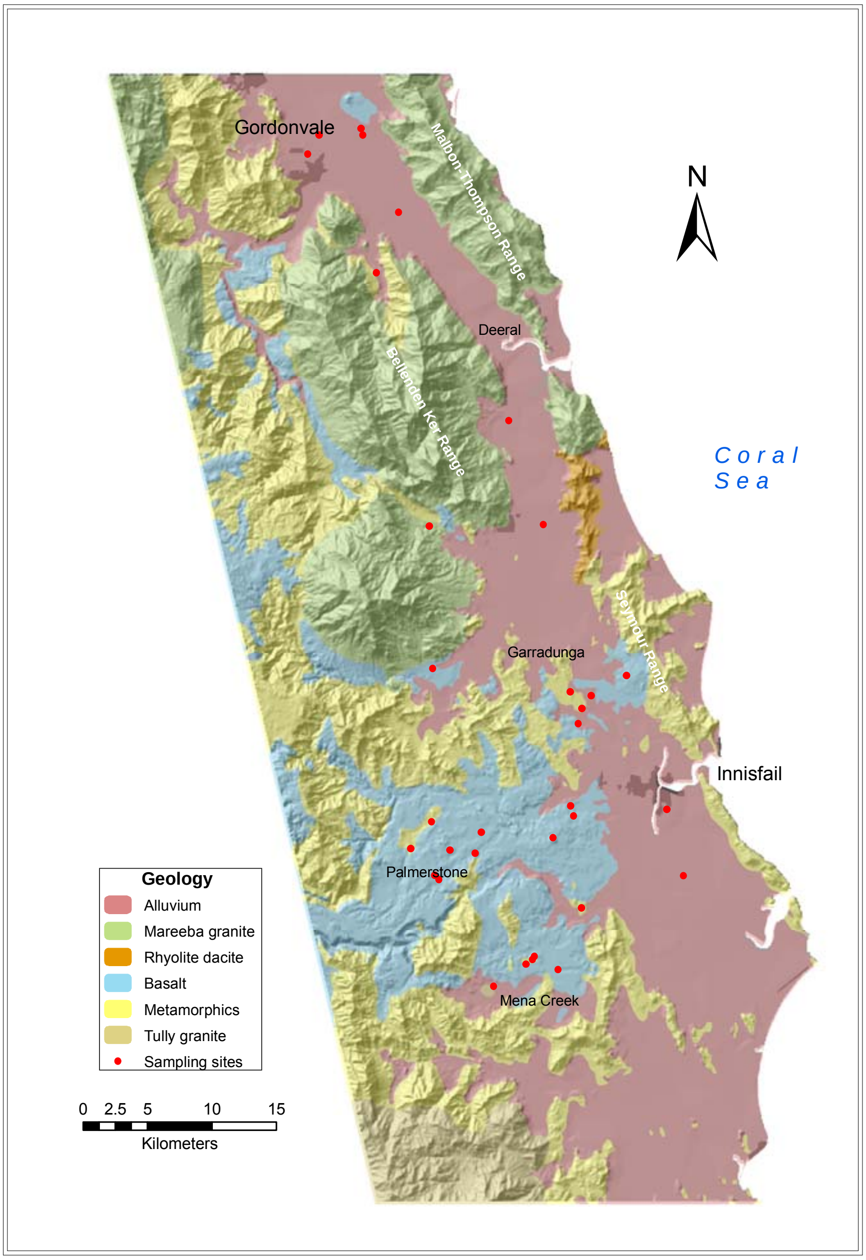

Figure 2.4 Underlying geology of the study area. Study sites are represented as points.

Lowland soils are variable, depending on underlying geology and topography, with broad soil types matching underlying geologies in 26 of 33 sites (Table 2.1). Foothill areas in particular contain soils that closely reflect local geology (Tracey 1982). These range from granite-based soils on and around the bases of the highest and steepest massifs (Bartle Frere, Bellenden Ker and the Malbon Thompson Range), metamorphic soils around some of the lower, gently sloping areas, and basalt soils down much of the North Johnstone and South Johnstone valleys (Murtha 1986, Murtha *et al.* 1996).

Table 2.1 Number of sites in each geology/soil combination.

Geology	**Soil**				
	Alluvial	Basaltic	Granitic	Metamorphic	Total
Alluvium	**8**	3		1	12
Basalt		**12**	1	1	14
Granite	1		**1**		2
Metamorphic				**5**	5
Total	9	15	2	7	33

Soils of the lowland plain (<80 m altitude) are less predictable from underlying geology, and distributions of soil types are somewhat more complex. Most comprise well-drained soils formed on alluvium, although some poorly drained soils and peats are found in the lowest areas and where drainage is impeded (Murtha 1986, Murtha *et al.* 1996). Alluvium comprises various mixtures of the parent rocks from upland and foothill areas (granites, metamorphics, and basalts), with the composition at a site determined by drainage as well as local geology (Tracey 1982).

The majority of sampling sites were located on either Quaternary alluvial deposits (12 sites) or on the basalt flows of the Palmerston and Mena Creek areas (14 sites). Of the remaining sites, two were on granite, with five on metamorphic substrate (Appendix 1, Figure 2.4). Almost half of the sites (15) occurred on basalt soils, mainly around the Palmerston foothill and Mena Creek areas (Table 2.1), while nine were on alluvial deposits. Of the remainder, seven were on metamorphic soils, while unfragmented sites at Josephine Falls (Site 31) and The Boulders (Site 32) were located on granite soils on the periphery of the main granite massif of Bartle Frere.

Soils are particularly relevant to this study, as they may significantly affect rainforest structure and distribution (Mackey 1993). The physical properties of soil have limited impact on rainforest vegetation (Tracey 1969) although poorly drained soils contain fewer woody lianes and often form simplified palm forests (Webb 1968). Soil nutrient status, on the other hand, significantly affects rainforest structure and broader vegetation types (Webb 1969, Mackey 1993). Whilst soils have less influence on leaf size than do climatic influences (Webb 1968), within the highest rainfall lowland areas, poor nutrient soils tend to lead to the replacement of mesophyll trees with notophyll trees (Mackey 1993). Soils with poorer nutrient levels may also lead to increased densities of emergent *Eucalyptus* spp. and other sclerophyllous trees, increased deciduousness and decreased numbers of robust woody lianes (Webb 1968).

In north-eastern Queensland, soil attributes such as nutrient levels broadly correlate with underlying geology (Mackey 1993). Soils vary throughout the study sites, with the most important component being the nutrient levels, which are a significant factor in determining the distributions of rainforest types (Mackey 1993). The majority of sites lie on basaltic and alluvial soils (Table 2.1), which are both eutrophic (Mackey 1993). Two sites lie on mesotrophic soils (granitic), while seven sites were found on less fertile metamorphic soil. Clearing on the basalt lava flows has been extensive because of their highly fertile soils and gently undulating topography, which is suitable for cropping (Winter *et al.* 1987).

2.4 Climate

North-eastern Queensland lies in what are known as the ‘marginal tropics’, where average daily temperatures vary by more than 5^0C throughout the year (Webb 1966, Tracey 1982). Nevertheless, the Wet Tropics region is subject to the highest average annual rainfall in Australia, with the ranges and coastal plain generally receiving at least 2000 mm (Bell *et al.* 1987), and up to 4500 mm on mountain peaks. The region is characterized by hot, humid summers and mild dry winters (Murtha *et al.* 1996).

The study area is among the wettest areas in the region, with an average of 3000-4000 mm of rain per year, most of which is concentrated in the summer months from December to April (Adam 1992). Unlike the equatorial rainforests of Papua New Guinea and Malaysia, the Wet Tropics experiences a pronounced dry season between about May and November (Bell *et al.* 1987). Lowland rainforests in this area are generally subject to a mean annual rainfall in excess of 3000 mm (Adam 1992), although sharp rainfall gradients exist throughout the area (Figure 2.5) due to local topographic influences, distance from the coast, and coastal orientation (Mackey 1993). Within the study area, the strongest gradient exists between Gordonvale and Deeral Landing (10 km south of Fishery Falls) which, although barely 20 km apart, average 1943 mm and 4019 mm annual rainfall, respectively (Figure 2.5).

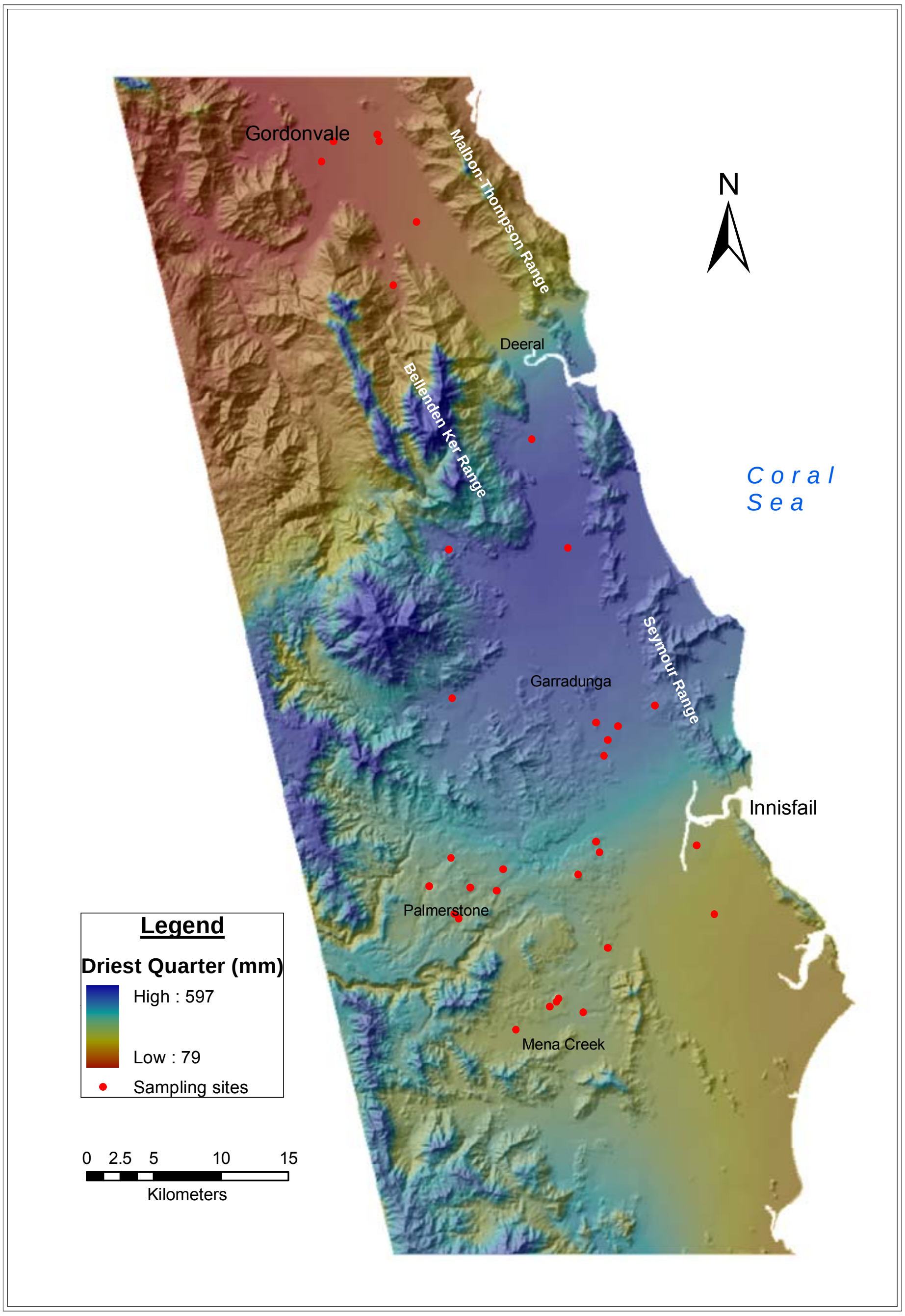

Figure 2.5 Mean driest quarter rainfall (mm) in the study area. Study site locations are indicated as points. Rainfall comes from interpolation from recordings at a series of locations throughout the region from 70 years of records (from Turton *et al.* 1999).

Rainfall gradients substantially influence rainforest flora. The best developed rainforest in the Queensland Wet Tropics, (complex mesophyll vine forest), occurs in high rainfall lowland areas on well-drained, fertile soils. Decreasing rainfall leads to smaller leaf sizes (Mackey 1993), increased deciduousness, and simpler rainforests – that is, they have fewer special life forms such as robust woody lianes, palms, plank buttresses, tree ferns, and other structures (Webb 1968). In addition, lower rainfall results in increased numbers of sclerophyllous plants (Webb

1968), probably resulting from the potential for fire to intrude into the rainforest. Thus, in the absence of other variables, lower rainfall leads to rainforests grading from complex to simple with smaller leaves, and eventually to mixed forests, which are found in the region of Gordonvale (Figure 2.5).

The study sites were located in a small area along a 60 km stretch of coast with all sites at an elevation of 160 m or less, so that temperature differences within the study area were minimal. The annual mean temperature is between 23-25°C in the area, while in the coldest month the mean minimum temperature ranges between 13 and 17°C (Nix & Switzer 1991). Rainfall differences are more pronounced. The majority of sites experience mean annual totals of between 3000 and 4000 mm, with sites 6 and 7 subjected to over 4000 mm annually. Sites 1 to 4 and Site 33 are the exceptions, with substantially less rainfall (between 2000 and 2500 mm annually). Likewise, these drier sites experience a mean driest quarter rainfall of approximately 100 mm (Nix & Switzer 1991, Murtha *et al.* 1996), compared to 225-375 mm for the remainder of the sites (Nix & Switzer 1991). The effects of rainfall differences on vegetation are examined in Chapter 4.

2.5 Vegetation

Seventeen major types of rainforest have been described and mapped at 1:100000 in the Wet Tropics, based on structural features of the vegetation (Tracey & Webb 1975). The best-developed rainforest is complex mesophyll vine forest (CMVF), which is found on the lowlands between Tully and just north of Babinda, and from Daintree to Cape Tribulation, where mean annual rainfall exceeds 2500 mm (Bell *et al.* 1987). It is estimated that some 81,000 ha remain, with only 17,300 ha as virgin rainforest within core natural forest areas, and with 40% of this on freehold, leasehold or vacant crown land (Australian Heritage Commission 1986).

Six main vegetation structural types are found in the study area. Although 42% of the lowlands in this area had been cleared by 1975 (Tracey 1982), the coverages generated and used in the present study show that this figure is now around 53%, with most of the extant rainforest found on the hillslopes. Of the extant lowland vegetation in the region, mesophyll forest types (Figure 2.6) are the most common (Table 2.2), with most sites containing this type of vegetation. The other important vegetation types in the area include closed forest with *Acacia* spp. emergents, and closed forest with *Eucalyptus* spp. and *Acacia* spp. emergents, both types of which are found mainly in the north of the region (Figure 2.7). Although ‘medium open forest and medium woodland’, and ‘medium and low woodland’ are found in significant quantities, the former is found only on swampy ground and the latter only in the extreme north-west of the study area, and no study sites were located on these forest types.

Figure 2.6 Mesophyll vine forest near Babinda (Site 32).

Table 2.2 Approximate areas of vegetation types within the study area (bounded by the 300m contour.

Vegetation Structural Type	Area (ha)	%
Mesophyll forest types	74569.91	37.2
Notopyhll forest types	1818.15	0.9
Closed forest with *Acacia* spp. emergents	13249.79	6.6
Closed forest with *Eucalyptus* spp. and *Acacia* spp. emergents	4204.32	2.1
Medium open forest and medium woodland	13709.91	6.8
Medium and low woodland	8064.37	4.0
Cleared areas	84751.36	42.3
Total	200367.81	100

Clearing has concentrated on the wetter but well-drained soils in flat or undulating areas, which are most suitable for sugar cane growing (Winter *et al.* 1987). Clearing on basalt flows such as in the Palmerston area is particularly extensive, because of the deep fertile soils on gently undulating land well suited to agriculture (Winter *et al.* 1987). Remnant patches of rainforest on basalt soils are therefore considered to be of particularly high conservation value.

Figure 2.7 Mixed forest with a rainforest understorey and *Eucalyptus* spp. and *Acacia* spp. emergents. This site (Site 4) is located near Gordonvale, in the north of the study area (see Figure 2.3).

2.6 Disturbance

Disturbance is a natural feature of tropical rainforests (Denslow 1987). Fallen trees or limbs can lead to localized microclimate changes in the understorey at and around the site of the fall. These changes may include increased light availability, increased wind speed, higher temperatures, decreased humidity, increased soil temperatures, and lower soil moisture (Denslow 1987, Brokaw 1985). Moderate, or intermediate, levels of natural disturbance from tree falls aid in the maintenance of tree diversity in tropical rainforest (Connell 1978), with the opening up of a range of microclimate niches (Ricklefs 1977, Stocker 1988), and are characteristic of tropical rainforests worldwide.

The size and frequency of gaps is an important determinant of forest structure and species composition (Denslow 1987). Larger gaps generally allow the colonization of light-demanding pioneer species (Adam 1992, Brokaw 1985); however, within smaller, less frequent gaps, primary tree seedlings from the understorey are usually favoured (Brokaw 1985, Denslow 1985). Within very small breaks in the canopy caused by limb loss from canopy trees, the gap may be filled by horizontal canopy extension from surrounding trees (Brokaw 1985).

Rainforest disturbance through the formation of gaps varies between locations. Differences in gap size distribution, frequency of gaps, and the rate of forest turnover vary considerably depending on such factors as tree species, climate, soil moisture, topography, and disturbance regimes (see Brokaw 1985 for review). In addition to clearance leading to fragmentation, the Wet Tropics lowlands have been subjected to at least two types of physical disturbance (cyclones and selective logging) which further modify the structure of the rainforest in addition to the disturbance caused by natural occasional tree-fall.

Cyclones also result in the creation of gaps in the canopy, although when intense, they have the potential to create much larger and more frequent gaps, leading to an extremely uneven canopy (Denslow 1987). Immediate effects may include defoliation (Askins & Ewert 1991), the blowing down of vines and branches (Lynch 1991), and the snapping or uprooting of large trees (Brokaw & Walker 1991, Will 1991), causing a considerable reduction in upper canopy cover (Brokaw & Walker 1991). Increased light reaching the understorey gives rise to high abundances of pioneer species throughout an area (Schowalter & Ganio 1999, Brokaw & Walker 1991), and may allow exotic weeds to penetrate (Horvitz *et al.* 1998, Hjerpe *et al.* 2001). In the lowland rainforests of north-eastern Queensland, the most common weed species are common lantana *Lantana camara* and giant bramble *Rubus alceaefolius*. This understorey growth, combined with litter from vines, snapped branches and fallen trees, often creates a deep, impenetrable understorey (Lynch 1991), and these effects may last decades (Crow 1980, Brokaw & Walker 1991, Webb 1958).

Tropical cyclone damage to rainforests is an intrinsic feature of many sub-equatorial coastal regions such as Australia's Wet Tropics. Indeed, Webb (1958) estimates that none of the lowland and foothill rainforests of north-eastern Queensland could escape some form of cyclone damage at least every 40 years. The study area has over the last century been subjected to natural disturbance from severe cyclones in 1918, 1956, and 1986 (Unwin *et al.* 1988). Even prior to Cyclone Winifred in 1986, vegetation on the coastal side of the Bellenden Ker range had characteristics of regular cyclone impacts between Cairns and Innisfail (Tracey 1982). The still-evident impacts of Cyclone Winifred are therefore not an aberration, but rather they reflect a position in the continuous cycle of disturbance. Along this area of coast, it can be expected that rapid and catastrophic changes to lowland rainforest structure are a normal, if irregular, consequence of their location. No severe cyclones have passed directly through the study area since 1986, although smaller cyclones have passed outside the study area (e.g., Cyclone Justin in 1987), resulting in strong winds and rain, but with negligible further impact on vegetation.

In 1986 cyclone Winifred (central pressure 957 hPa) crossed the coast at Innisfail, causing extensive damage, especially to lowland rainforests and remnants between Tully and Gordonvale. Damage included the smashing of the boles or crowns of most trees, the uprooting of many emergent trees, defoliation and frequent tree falls (Unwin *et al.* 1988). Many canopy and understorey stems were broken, and canopy vines were torn off and thrown to the ground. The result of this damage, in time, has been the development of vine tangles around the uneven canopy and the development of a thick understorey of disturbance-adapted plants such as *Calamus* spp. (Figure 2.8, Figure 2.9). This formation is locally known as 'cyclone scrub'; however, the effects of cyclones are by no means uniform. Aspect, slope, exposure, distance from the cyclone's centre, forest type and soil drainage are all important determinants of the degree of structural vegetation damage caused by cyclones (Unwin *et al.* 1988). Variability in the degree of damage remains evident to this day, and is addressed in detail in Chapter 4.

Figure 2.8. Mesophyll vine forest near Babinda (Site 32) showing the canopy gaps that are characteristic of much of this section of the Wet Tropics lowlands.

Figure 2.9. Mesophyll vine forest near Babinda (Site 32). Thick tangles of *Calamus* spp. are clearly evident in the understorey.

The second major disturbance that has affected the lowlands is logging. The earliest impacts on the lowland rainforests of the region were through selective harvesting of red cedar *Toona australis* from the 1870s (Frawley 1991). This initially occurred along major rivers, but soon led to the opening up of areas for agriculture and general timber harvesting in the 1880s (Birtles 1982). Saw milling accelerated in the region in the 1940s (Winter *et al.* 1991), although extraction for local uses had already occurred. Selective logging of many of the remaining lowland areas continued until the 1980s, and to this day continues on some private land (W. Brockett, pers. com.). On the Cairns-Cardwell lowlands, virtually all accessible rainforest except for some foothill areas has now been selectively logged at some time (Australian Heritage Commission 1986, Winter *et al.* 1991).

Within the study area, nearly all accessible rainforest has been selectively logged at least once (Australian Heritage Commission 1986, Winter *et al.* 1991); however, since most of the sites lie on private property, timber extraction has been haphazard, and records have often not been kept. Although some patches have been free of logging at least since the early 1900s (E. McCowatt, pers. comm.), individual trees have been removed from some other sites within the last 10 years (W. Brockett, pers. comm.). It is therefore difficult to identify the degree of selective logging as an environmental variable.

The impacts of selective logging on tropical rainforest biota have received much attention in recent years (e.g., Crome & Moore 1989, Nicholson *et al.* 1988, Johns 1991, Owiunji & Plumptre 1998). Much evidence suggests that selective harvesting, depending on the level of intensity and frequency, causes changes to the rainforest structure itself (Nicholson *et al.* 1988) and often impacts on bird assemblages (Johns 1988). The important question is whether this disturbance lies within the range of natural disturbance levels. However, the degrees of difference between the effects of natural disturbance and logging, and the interaction between natural disturbance and logging, have recently been questioned and remain unclear (Danielsen 1997).

Although selective timber harvesting has occurred over much if not most of the Wet Tropics lowlands, the region already experiences regular and severe disturbance regimes, and rates of growth are likely to be faster than in the uplands or subtropical rainforests of Australia due to higher productivity (Walker *et al.* 1996). Unwin *et al.* (1988) found no apparent interaction between previous logging and a cyclone in the degree of damage caused. They surmised that where the intensity of either disturbance is severe, then little of the mature structure would remain from either perturbation. Therefore, it is likely that the effects of selective logging in all but the most intrusive cases would have a lesser immediate impact than cyclones on bird assemblages, and rather similar effects in the longer term. Hence, the effects of past selective logging on rainforest bird assemblages may be less in the Wet Tropics lowlands than in the uplands or subtropical rainforests of Australia, or within most other tropical rainforests worldwide (see Whitman *et al.* 1998). In the absence of accurate records of selective logging and records of specific impacts of Cyclone Winifred at the local scale, these impacts cannot be included in quantitative analyses. However, residual variation in vegetation structure and selected floristics, after the effects of soils, altitude and rainfall are removed, is probably largely the result of these two impacts.

2.7 Site Selection and Sampling Design

With a few notable exceptions, such as the ‘Biological Dynamics of Forest Fragments’ project in Brazil (Laurance *et al.* 2002), few experimental, replicated experiments into landscape fragmentation have been attempted, owing to expense, labour requirements, and the required destruction of valuable habitat. Furthermore, because of the reliance of landscape measures on a few basic parameters, the number of potentially relevant landscape measures that can be related to biological processes simultaneously is limited. In the Amazonian project (Laurence *et al.* 2002), researchers have limited their attention to patch size and distance to the edge, as the major spatial variables affecting a range of plant and animal taxa (e.g., Lovejoy *et al.* 1986, Bierregaard *et al.* 1992, Zimmerman & Bierregaard 1986, Klein 1989).

In the majority of studies on the effects of fragmentation on natural processes and patterns, researchers study the existing landscape (e.g., Grant & Berkey 1999). To the greatest extent possible, they choose a range of fragments which exhibit a variety of characteristics with examples representing a wide spread along the inferred important spatial gradients, and avoiding colinearity between the most important gradients. Of necessity, the current study took this approach, with existing patches in a mainly-cleared landscape chosen on the basis of a number of factors.

Firstly, this study focused mainly on the effects on birds of the spatial arrangement of habitat. Therefore, to reduce the influence of vegetation structure (apart from the northernmost group), the sites lie in the very high rainfall areas around Innisfail where vegetation is relatively homogeneous (complex mesophyll vine forest). Secondly, as patch area is the most commonly-measured spatial variable in fragmentation studies, sites were chosen to represent a continuum of fragment sizes from 1 ha up to approximately 300 ha. Thirdly, logistics influenced the sampling design. Sites needed to be accessible by vehicle and on foot, permission granted by landholders, and sites in some cases needed to be in close enough proximity of one another to allow sampling on the same day. Three ‘control’ sites (unfragmented locations along the main Bellenden Ker massif) were also sampled for comparative purposes.

Therefore, bird and vegetation surveys were conducted in 30 fragments and three control sites (Appendix 1). Of these, 26 fragments and two control sites were located in mesophyll vine forest, while four fragments and one control site were located in the northern region of the study area, which contained mixed rainforest with *Eucalytus* spp. and *Acacia* spp. emergents. The spatial characteristics of the study sites are described in Chapter 3, while the vegetation characteristics of sites are described in Chapter 4.

Many studies have carried out equal-effort sampling in all fragments regardless of size (McIntyre 1995, Bentley & Catterall 1997, Lynch 1987). This allows for the direct comparison of abundances and diversity per unit area but, where patch area varies widely, the ability to sample the largest patches sufficiently to record the majority of the rarer species is limited, and complete species lists for the larger fragments are unlikely. Other studies (Warburton 1997, Willis 1974, Bellamy *et al.* 1996, Loyn 1987) have spent greater effort sampling larger patches proportionate to the size of the patch, thus increasing the probability of recording the rarer species. However, unless the sampling effort can be broken down into sample units standardised by area, there is no option to analyse absolute or relative abundances. This project sought not only to examine persistence in fragments, but also to examine abundances and assemblage structure. Thus it was important to sample as many of the rarer species as possible whilst still retaining a standard unit of measure. Therefore, different numbers of standard-sized sampling units were used, in common with Lescourret & Genard (1994) and Blake (1991). The number of transects per patch was proportional to the size of the patch, from two in the smallest patches to six in the largest patches (Table 2.3). This resulted in a total of 137 transects.

Table 2.3 Summary of numbers of transects at each site in relation to the size range of sites.

Size range (ha)	Transects/site	No Sites
1.2-3.5	2	8
1.7-6.9	3	3
5.6-24.5 *	4	10
20.1-294.1	6	12

* One site, although 24.5 ha in area, was extremely irregular in shape, prohibiting the sampling of six transects at 0, 50 and 100m from the edge.

Transects were 100 m in length and 50 m wide. These dimensions were chosen because within 25 m of the transect, birds can usually be seen to be within or outside the strip. The 100 m length was found to be the most suitable due to the difficulty in fitting continuous larger transects in often irregularly shaped fragments, especially the smaller ones.

In each patch, two transects followed the edges of the patch, with further pairs of transects parallel to the patch edge at various distances within the patch, following the edge contour. The position of the transects in the patch was randomly determined where possible, except where precluded by access difficulties. Transects were separated by at least 100 m from each other to maintain sampling independence. Transects were located and marked out prior to the first census. Direction within fragment interiors was carefully maintained with the aid of a compass, and distances were measured by a Fieldranger 6500 metric hip-chain. Three sites with insufficient interior area to accommodate two transects 50 m from the edge contained only one interior transect, along with two edge transects. Otherwise, pairs of transects were used.

2.8 Subregion characteristics

Partly for logistical reasons, and partly through the tendency of remnants to occur in clusters, the study sites were chosen within five sub-regions (Figure 2.10). Subregion A included five fragments and one continuous site near the town of Gordonvale (Figure 2.11). These sites experienced less rainfall than the other sites in this study (Figure 2.5), and consequently contained closed forest with emergent *Eucalyptus* spp. and *Acacia* spp. Surrounding land use consisted entirely of sugar cane. To the east, the coastal range comprised mainly Type 1a and 2a (complex mesophyll vine forest), with Types 12a and 13e (Closed forest with emergent *Acacia* spp.) on more exposed ridges. The ranges to the west contained a mosaic of mesophyll rainforest, closed forest with *Acacia* spp. emergents, and woodland (Tracey 1982).

Two fragments were located in the Deeral subregion (B) (Figure 2.12). This area had extremely high rainfall, and occurred on very low-lying land, as indicated by the presence of swampy land with dominant fan palms directly north of Site 7. A continuous site (Site 32 – The Boulders) was located immediately adjacent to the south-west corner of the map. This region is almost entirely devoted to sugar cane production apart from areas of poor drainage containing fan palm forest and Type 15a (medium open paperbark forest). The lower parts of the hills to the west of this subregion contained complex mesophyll vine forest, as did this section of the coastal range, although closed forest with *Acacia* spp. emergents was found along some of the more exposed ridges of the coast range.

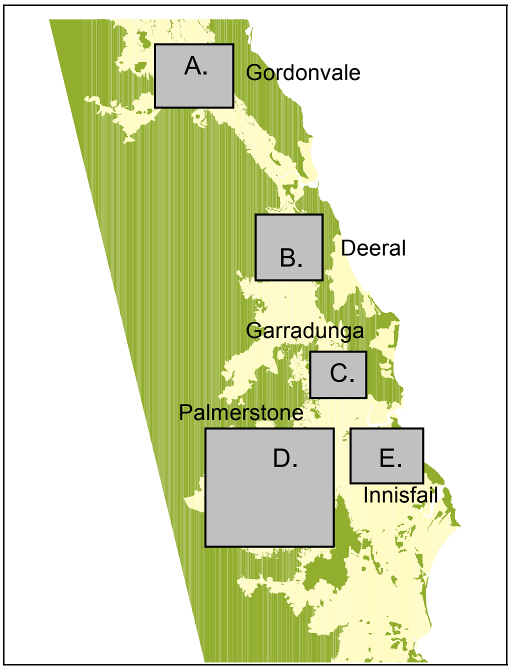

Figure 2.10 Map of study region with subregions identified.

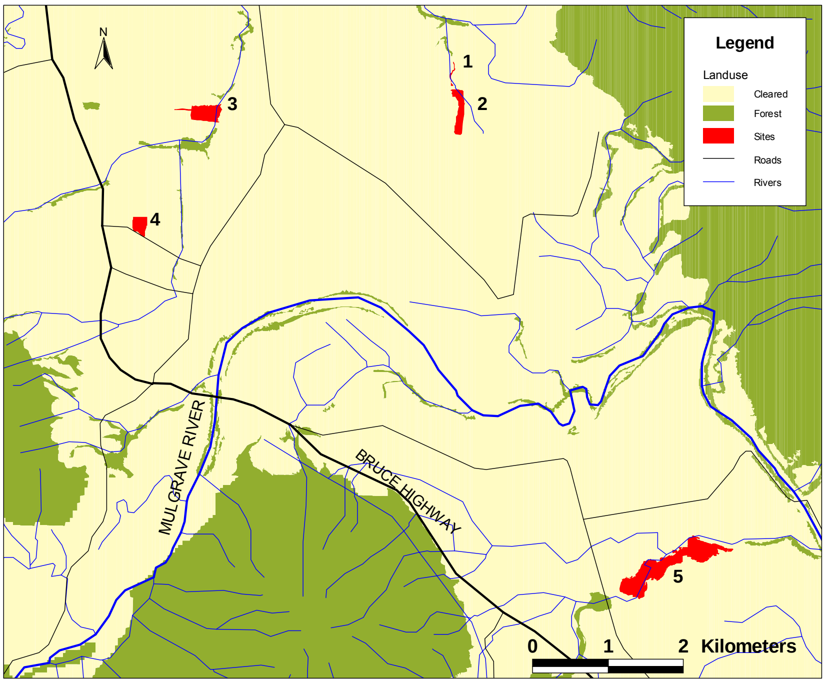

Figure 2.11 Distribution of forest in the Gordonvale subregion (A), with sites identified in red.

Subregion C (Garradunga) is a very wet area of the coast (>3600 mm per annum), and included five sites (Figure 2.13). This area was mainly devoted to sugar cane production, although banana and papayas (papaws) were also grown. Adjacent to Site 8 were some small-acre holdings (1-5 ha), and a residential estate lay on the eastern side of this site. The country here was flat to gently undulating, and broad vegetation types to both the east and west of this subregion included mainly mesophyll vine forest, with small amounts of closed forest with *Acacia* spp. emergents on more exposed ridges.

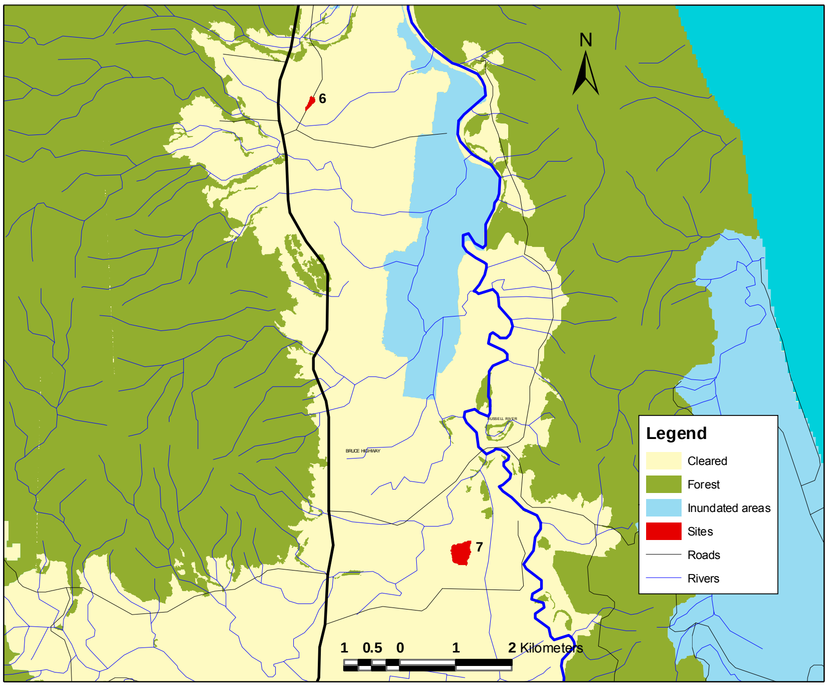

Figure 2.12 Distribution of forest in the Deeral subregion (B), with sites identified in red.

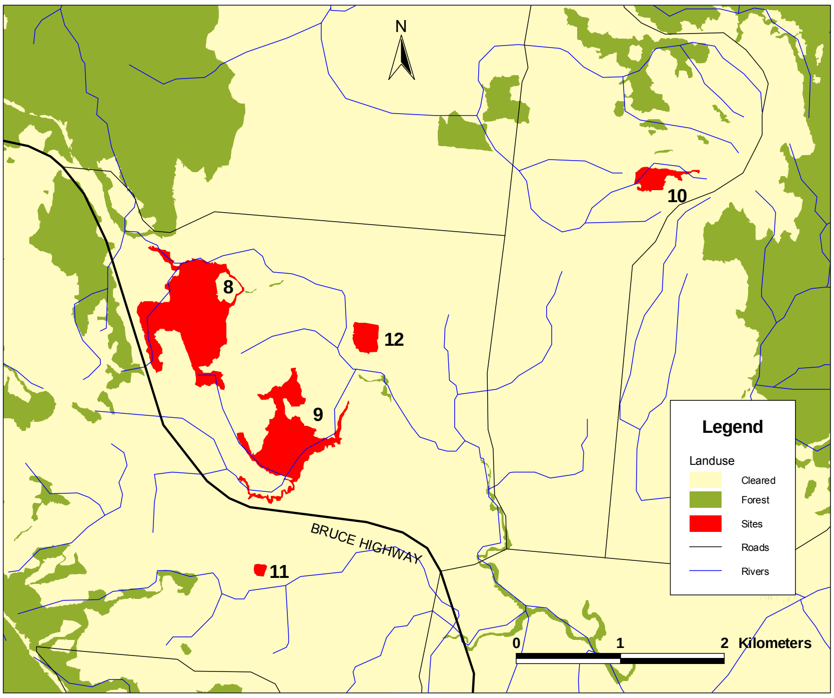

Figure 2.13 Distribution of forest in the Garradunga subregion (C), with sites identified in red.

Sixteen sites were located in the Palmerston subregion (D) (Figure 2.14), most of which lay on nutrient-rich basalt soil. This country was gently undulating, with large amounts of remnant vegetation present, largely dependent on topography. The subregion was used mainly for sugar cane growing and cattle grazing, with banana plantations present in some areas. Intact vegetation surrounding these areas consisted almost entirely of mesophyll vine forest, although the low Basilisk Range to the east of Site 25 contained closed forest with *Acacia* spp. emergents. Rainfall surrounding the sites was high, ranging from 3300 mm to 3500 mm per annum.

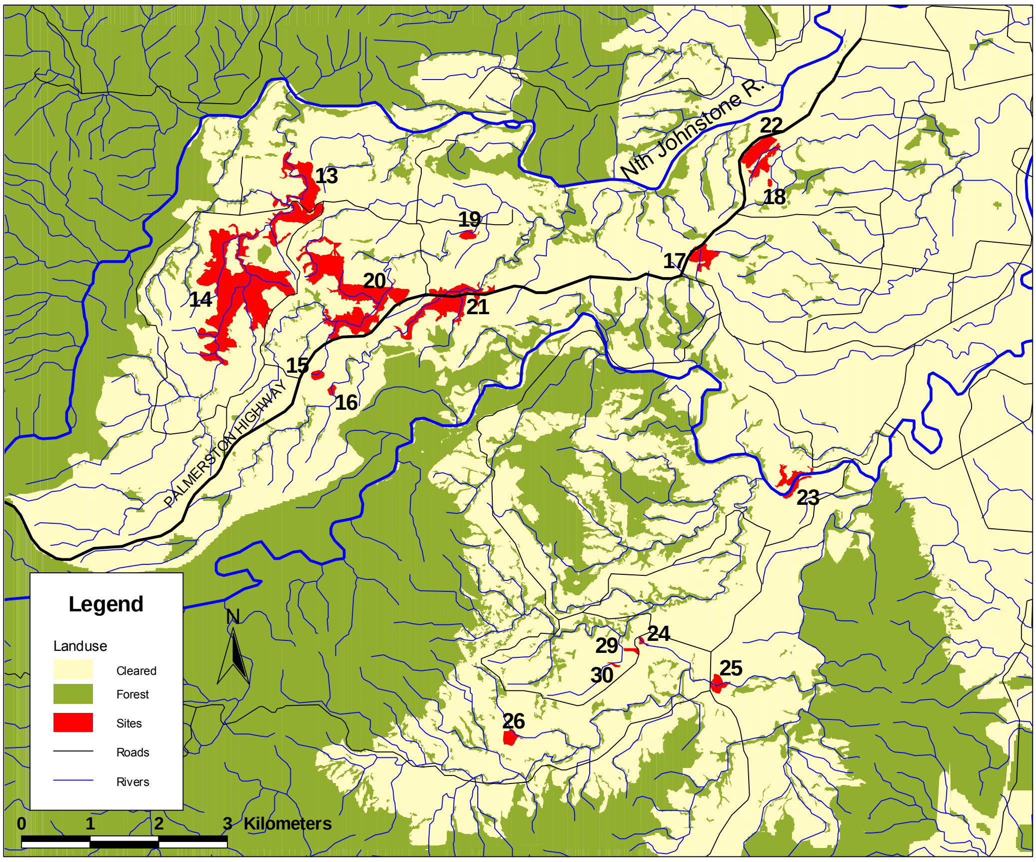

Figure 2.14 Distribution of forest in the Palmerston subregion (D), with sites identified in red.

Two sites were located in the Innisfail subregion (E) (Figure 2.15). These lay on flat, low-lying alluvial deposits. The majority of this subregion was used for sugar cane farming, although urban development was substantial. Site 27 was adjacent to the town of Innisfail, with cattle grazing on the southern and eastern sides, while sugar cane farms surrounded Site 28. Extant vegetation types in the surrounding areas included mesophyll vine forest where the soil was well-drained, and medium open paperbark forest in poorly drained areas.

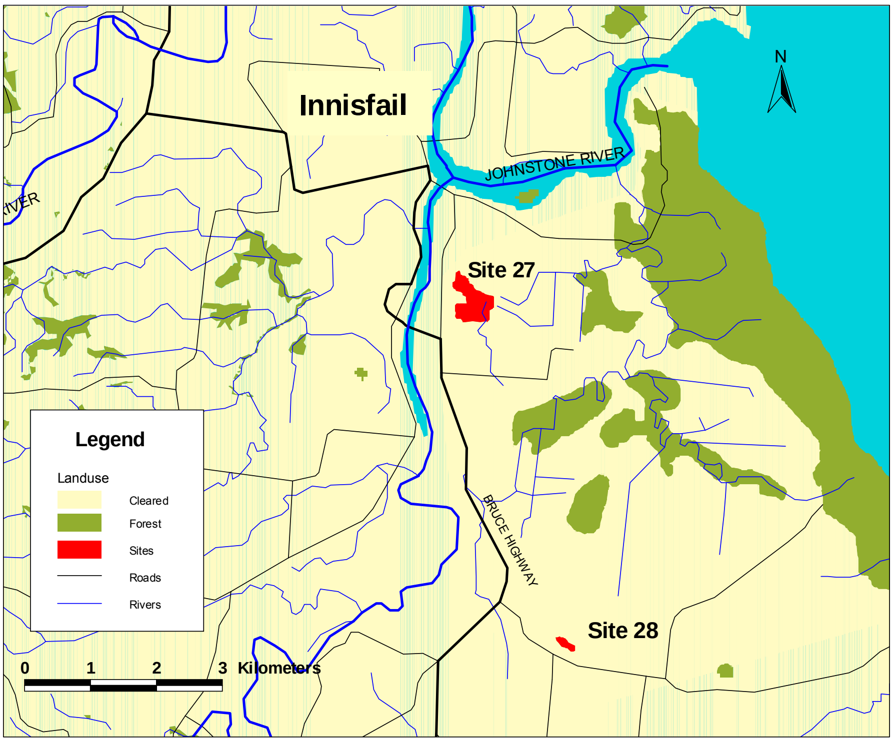

Figure 2.15 Distribution of forest in the Innisfail subregion (E), with sites identified in red.

Chapter 3: Spatial patterns in the study region: regional, subregional and site characteristics

3.1 Introduction

Two major components of landscapes that interact to influence the distribution of organisms in space are *landscape composition* and *landscape configuration*. Landscape composition represents the types of habitat within a landscape, and is described for the study area in Chapter 4; landscape configuration, on the other hand, is the amount and arrangement of these habitats in space (McGarigal & Marks 1995), and is described and analysed here.

Habitat fragmentation involves four main components: loss of the original habitat, reduction in patch size, isolation of habitat patches, and increase in the contribution of edge zones (Andren 1994, Saunders *et al.* 1991), which influence a variety of biological processes (e.g., Burkey 1993, Sieving *et al.* 1996, Breininger 1999). Examination of the effects of landscape configuration on biological patterns and processes (in this case, bird assemblage structure) requires landscape pattern quantification, but no single measure can capture the spatial characteristics that affect different processes (Davidson 1998). Where more than one aspect of the landscape configuration is of interest, or where different species are likely to be affected by different landscape characteristics, several descriptors can be used to describe relevant landscape characteristics (Haines-Young & Chopping 1996, Ritters *et al.* 1995).

Landscape-scale studies require that relevant characteristics of the landscape are quantified, but the nature and relevance of landscape measures must first be fully understood, and possibly reduced to a subset of the most biologically meaningful measures (e.g., Clark *et al.* 1999b). Sites also need to be selected in a combination that allows the most potentially important variables to be tested against response variables (in this case, the bird assemblage) while minimising colinearity between independent variables, although independent variables must still be tested for colinearity and, where necessary, excluded or combined (Hargis *et al.* 1998). Therefore, a major goal of this chapter is to review the use of landscape metrics with respect to their relationship to species distributions, to calculate a range of relevant landscape metrics to characterise study sites, and to reduce these measures to a manageable and biologically relevant subset with which to examine the spatial determinants of bird distribution.

Descriptions of general patterns of cleared and remnant land in the study area are important in providing a background and context to discuss the results of bird assemblage patterns, and to allow the analysis of the distribution of threatened habitat types. Simply calculating the extent of fragmentation in a study area provides relevant but incomplete information: the size, number, and location of remnants throughout the landscape reveal more information regarding the conservation status of the target habitat.

Within any region, remnant rainforest is unlikely to be randomly scattered. Patterns of clearing often depend on factors such as topography and soil properties (Kemper *et al.* 2000). Topography often influences rainforest structure and floristics (e.g., Clark *et al.* 1995) by affecting hydrology, soil structure or exposure (Webb *et al.* 1999), and soil nutrient levels often influence major structural and physiognomic features (Coomes & Grubb 1996, Herrera & Finegan 1997). Rainforest structure and floristics in turn influence faunal assemblages (e.g., Kikkawa 1982, Lescourret & Genard 1994). Consequently, among remnant lowland rainforest, analysis of the distribution of rainforest and patterns of clearing with respect to topography, rainfall and soil may provide an insight into which areas are well and which are poorly represented by rainforest, and by modelling the patterns of clearing, an insight may be gained into what remnants are threatened. Furthermore, it also provides a spatial and biophysical context in which to analyse bird assemblages. Therefore, a second goal of this chapter is to describe and explain the landscape configuration of the study area, and explain the patterns with respect to environmental variables.

Aims

The aims of this chapter are to:

- review the use of landscape metrics in fragmented landscapes, and discuss how these measures can best be combined and used;
- describe and quantify the landscape characteristics of the study area;
- identify redundancy in spatial measures, and thus reduce these measures to a manageable subset for further analyses; and
- model the extent of habitat loss in relation to rainfall, topography and geology.

3.2 Spatial measures as applied to faunal assemblages in landscapes

Introduction to landscape metrics

Over 60 indices of landscape fragmentation have been used to describe landscape characteristics, largely as a result of developments in remote sensing and Geographic Information Systems (GIS), and the increased accessibility of these technologies (e.g., Dale & Pearson 1997, Hargis *et al.* 1998). In many studies, researchers examine the effects of a number of spatial measures on faunal communities (e.g., Ribe *et al.* 1998, Kramer 1997, Estades & Temple 1999). In most cases, some measures correlate with each other (e.g., Bellamy *et al.* 1996), largely because most measures are derived from a small set of parameters related to patch size, shape and inter-patch distance. Consequently, as a parameter changes, measures that share that parameter also change (Hargis *et al.* 1997).

Where landscape descriptors are to be used to explain the distribution of organisms, this redundancy requires the reduction of these measures to a manageable number, often by formal data reduction techniques such as factor analysis (Ritters *et al.* 1995, Naugle *et al.* 2000). Ritters *et al.* (1995) performed a principle components analysis on 26 landscape variables, with the first six factors explaining 87% of the total variation. From these factors, they chose the single metric with the highest loading on each factor to describe the landscape. Similarly, Clark *et al.* (1999b) reduced 21 metrics from the landscape computer program FRAGSTATS (McGarigal & Marks 1995) to five variables by extracting four components of a principle components analysis which described 70% of the variation in the landscape. This technique is suitable for efficiently describing a landscape in the general sense – for example, to compare different landscapes or one landscape over time. However, if the objective is to explain animal distributions within a landscape (e.g., Clark *et al.* 1999b), this technique may be unsuitable, because variables that summarise the most spatial variation may not have any biological relationship to the animal taxa concerned. In other words, this method cannot help decide which metrics are worth measuring in the first place (Ritters *et al.* 1995).

Nevertheless, formal data reduction techniques in conjunction with partial regression may be useful in creating landscape measures that are independent of other spatial characteristics. For example, Trzcinski *et al.* (1999) examined the relative importance of forest cover and forest fragmentation on bird species distributions. They achieved this by using principal components analysis and partial linear regression to create a measure of forest fragmentation independent of forest cover.

The other major variable-reduction technique involves examining bivariate correlations between different measures, and then removing some that are highly correlated. Grant & Berkey (1999) used a between-variable correlation coefficient threshold of 0.6 to filter variables. Freemark & Merriam (1986) omitted one of those with correlation coefficients greater than 0.76, whereas other studies include habitat variables correlations as high as r=0.8 (Germaine *et al.* 1998) and r=0.97 (Howell *et al.* 2000) when these measure unique attributes of the landscape, although care must be taken in interpreting results where dependents exhibit high colinearity (Legendre & Legendre 1998). Howell *et al.* (2000), for example, tested almost perfectly correlated spatial variables simultaneously, and then assigned causality to the variable with the strongest explanatory power. On the other hand (and more justifiably) Forys & Humphrey (1999) chose the more biologically meaningful habitat variable where significant correlation between variables was found.

Therefore, these techniques should ideally take into account the measures relevant to the processes that are being examined and the conceptual relationships between measures, whilst removing redundancy. Where a sampling design contains large numbers of sampling points (>150) up to 40 variables that are believed to be of potential biological importance are sometimes retained for further analysis (Bellamy *et al.* 1996, Drapeau *et al.* 2000); however, care should be taken not to simply insert every conceivable metric into a multiple regression, and then to accept what ‘results’ emerge. The effective use of landscape measures is only possible with an understanding of the merits and limitations of each, and of how different measures relate to one another, and the study organism (Hargis *et al.* 1998).

Area measures

The most commonly measured and tested spatial variable in a fragmented or patchy environment is patch area. The influence of this characteristic may manifest itself in various interrelated ways. The size of a patch can influence the viability of populations (Ribe *et al.* 1998, Opdam *et al.* 1985, Stouffer & Bierregaard 1995a, Fritz 1980). Following the well-known species-area relationships (Wiens 1989), bird species richness often correlates with patch size (e.g., Galli *et al.* 1976, Tellaria & Santos 1995, Grant & Berkey 1999), and ordination has demonstrated that assemblages in smaller patches often diverge from pre-isolation assemblages (or unfragmented sites) more than large patches (Stouffer & Bierregaard 1995a). Where specific, more vulnerable species drop out of patches of certain sizes, or certain species better colonise patches, a nested rather than random pattern of assemblages can form across an archipelago of patches (Cutler 1991), where smaller patches contain a subset (more-or-less) of larger patches (Patterson 1987). Appropriately, patch area is virtually always included as a spatial variable when testing the influence of landscape configuration on bird assemblages.

Patch area is usually measured as the amount of uninterrupted habitat of interest that is bounded on all sides by different habitat. Other area measures include the total class area within the coverage, and the total landscape area: these measures are useful where different landscapes are compared, and especially where the total available habitat within the landscape is particularly limited (McGarigal & Marks 1995).

Isolation measures

Many forest specialist birds will avoid crossing an open matrix (e.g., Bierregaard *et al.* 1992, Turner 1996), with some species avoiding crossing open distances of as little as 100 m between forest blocks (Bierregaard *et al.* 1992, Saunders & de Rebiera 1991). This can affect the ability of species from other local areas of native vegetation to colonise a remnant (Saunders *et al.* 1991, Schieck *et al.* 1995). Therefore, even though an animal is physically capable of traversing the matrix between patches, behavioural resistance may still preclude this movement (Saunders *et al.* 1991). The matrix then becomes an effective barrier or impediment to dispersal. Some locally nomadic or within-forest migratory species may not be able to move between fragments, as is the case with some frugivores on Barro Colorado Island, Panama (Foster 1982).

Within a landscape, a patch may be isolated in many different ways, and researchers have tested a range of isolation measures for their impact on bird assemblages. The best known isolation measure, derived from island biogeography theory (MacArthur & Wilson 1967), is the distance of a patch to extensive areas of similar habitat containing a source population (Opdam *et al.* 1985, Diamond 1975). Other direct measures include the distance from a patch to the nearest patch of suitable habitat (nearest neighbour) (e.g., van Dorp & Opdam 1987), the distance to patches of certain sizes (e.g., Opdam *et al.* 1985, Delin & Andren 1999, Schieck *et al.* 1995), and the area of suitable habitat within a certain radius of the focal patch (e.g., Honnay *et al.* 1999).

All of these measures have each been shown to influence bird assemblages in some regions but not in others. For example, some studies have shown that the distance of a patch from large, unfragmented blocks can influence bird assemblages in Europe (Opdam *et al.* (1985), Western Australia (Fortin & Arnold 1997) and sub-tropical rainforests in New South Wales (Howe *et al.* 1981); however, this measure was not found to influence forest bird assemblages in at least one Victorian study (Loyn 1987).

Similarly, the nearest neighbour measure has occasionally been shown to explain distributions of birds (Jansson & Angelstam 1999), mammals (Estrada *et al.* 1994) and invertebrates (Kehler & Bondrup-Neilsen 1999), but other studies have found little influence of this factor (e.g., Loyn 1987). Nearest-neighbour measures take no account of the size of the nearest patch or the degree of isolation of that neighbour beyond the original patch in question, and assumes not only that the neighbouring patch contains a source population, but also that no boundary or edge effects are present (Turner *et al.* 1991). The nearest neighbour measure is likely to be of greater importance where most patches are medium to large, or where very small patches in the landscape are ignored by using the distance to the nearest patch of a given size (e.g., Schieck *et al.* 1995). This latter measure assumes that the larger patches are large enough to contain a source population; however, in many studies, no biological reason is given for using a particular area threshold (e.g., Opdam *et al.* 1985, Schieck *et al.* 1995, Delin and Andren 1999).

The areas of suitable habitat within certain radii of patches have been tested for their influence on avifauna. Radii that have been applied vary from 500 m (Honnay *et al.* 1999) to 3 km (Opdam *et al.* 1985, van Dorp & Opdam 1987). Again, this measure often partially explains faunal distributions in patches (e.g., Vos and Stumpel 1995, Opdam *et al.* 1985), but in other instances these concentric isolation measures may explain little variation in bird distribution or diversity (e.g., Jansson & Angelstam 1999, Grant & Burkey 1999).

The fact that habitat fragments are, by definition, isolated from large continuous tracts of habitat influences bird assemblages in the majority of cases. Thus, islands of habitat usually possess bird assemblages that differ from those in large contiguous tracts of habitat (e.g., Bierregaard *et al.* 1992). The actual degree of isolation is less often identifiable as a structuring variable of bird assemblages. While some studies of isolation have found a negative effect of spatial isolation on incidence, abundance or richness in birds (e.g., Bellamy *et al.* 1996, Lynch & Whigham 1984), other studies have shown the degree of isolation to have little bearing on bird assemblage structure over distances of 100 to 2000 m (e.g., Estades & Temple 1999, Matthysen & Adriaensen 1998, Matthysen 1999).

Edge effects

Many of the potential effects of edges on animal and plant communities are well known (see review in Chapter 6). The influence of these effects into a patch may range up to hundreds of metres, and the response of animal populations varies from avoidance to preference (Murcia 1995). Of major interest in landscape ecological studies is the question of how best to represent possible or actual edge effects when developing spatial habitat models. There are three main types of metrics, which are based on the assumed effects of edges in the landscape. They are edge, core area and shape metrics.

Edge metrics include edge per patch (perimeter), and total edge within certain radii or across the entire landscape (edge density). In themselves, these measures are of little value when examining interior species except involving second-order interactions such as predation or competition from edge species (Donovan *et al.* 1997). However, where the edge between habitat types has sufficiently different characteristics to be considered a separate type of habitat, or certain species of interest require both the patch habitat and the matrix habitat for population survival, then the extent of this habitat per patch or per unit area may be of interest. This is the case with studies into the distribution of those species that rely on this forest-open habitat interface, such as cowbirds in North America (Donovan *et al.* 1997).

Core area measures involve the calculation of the area of a patch that is believed to be unaffected by edges. Recent developments in remote sensing and GIS have allowed researchers to develop a number of core-area models (e.g., Laurance 1991, Malcolm 1994, Zheng & Chen 2000). Core areas are often calculated as the amount of habitat beyond a certain distance from the edge, for example 100 m (Foreman & Godron 1986, Jullien & Thiollay 1996). Some studies have actually found core area to be more accurate than total forest area in predicting forest-interior bird abundance (e.g., Temple 1986).

Where shape is similar, larger remnants have a larger core area that is unaffected by the biophysical changes around the edges (Saunders *et al.* 1991). Where two remnants are of an identical size, the remnant with the less convoluted shape will usually (but not always) contain a greater amount of core area (Figure 3.1). Thus, core area may be seen as an interaction between area and shape (Laurance 1991).

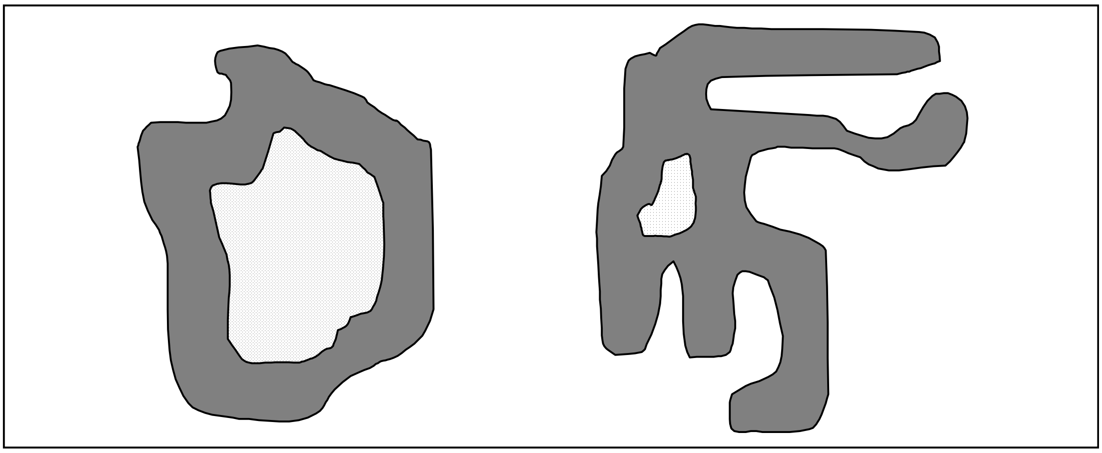

Figure 3.1 Schematic diagram of the relationship of shape to core area, where core area (stippled area) is defined by the same fixed distance from the edge, in each case.

Shape metrics have often been used in landscape ecology as explanatory spatial variables at a variety of scales (Bellamy *et al.* 1996, van Dorp & Opdam 1987, Williams & Pearson 1997). A range of metrics are employed, including the perimeter-area ratio (Graham & Blake 2001), the area-adjusted Shape Index (Williams & Pearson 1997, Bastin & Thomas 1999), and fractal dimension (McGarigal & Marks 1995).

Shape is a difficult characteristic to represent in a single measure (McGarigal & Marks 1995). Where area is also under scrutiny as an independent variable, the area-perimeter ratio is usually inappropriate, as patch perimeter usually correlates strongly with patch area, leading to a close relationship between patch area and area-perimeter ratio (e.g., Suarez *et al.* 1998). The Shape Index and fractal dimension, on the other hand, are independent of area (McGarigal & Marks 1995, Suarez *et al.* 1998) and are therefore more appropriate. Fractal dimension has the advantage of suitability for comparing shape at different map resolutions and scales, but unless differences in shape are very great, this measure is often very insensitive (Hargis *et al.* 1997).

Shape measures have been related to the probability of patch colonisation (Buechner 1989, Hamazaki 1996) and foraging strategies (Foreman & Godron 1986), but by far the most significant use of shape as a landscape metric is to represent edge effects (e.g., Kozakiewicz *et al.* 1999, Bastin & Thomas 1999). Bastin & Thomas (1999) go so far as to claim “Patch shape can affect its vulnerability to external influences. For example, small and linear patches may contain little or no ‘core’ habitat that may be required by habitat specialists”. However, shape metrics do not always reflect core area. For example, all of the convolutions in a patch may be in one half only, leaving an area of core habitat within the other half; in another patch with the same area and perimeter, convolutions may be more evenly spread, thus reducing core area. Core area measures, although dependent on area, allow for different shapes within different parts of the patch, thus reflecting the area that remains when areas subjected to edge effects are considered less suitable habitat. Where edge effects are sufficiently large to prevent excessive colinearity between the core area and patch area, this measure may often more appropriately reflect the effects of edges on the organisms in question.

Conclusion

Many studies test the influence of spatial variables on animal assemblage structure without providing any evidence or argument supporting their inclusion in the test (e.g., Opdam *et al.* 1985, Doherty & Grubb 2000). Others relate variables to known effects – for example Burel (1992) chose landscape structural variables of hedgerows based on their known impacts on carabid beetle assemblages in a very well-studied system. This approach requires substantial prior knowledge of the system, a luxury that is not always available in studies of fragmented tropical landscapes. Nor do many ecological studies at a scale of tens of hectares have the luxury of creating replicated forest plots to allow particular characteristics such as patch size to be examined in the absence of other factors, although there are some notable exceptions (Laurance *et. al* 2002, Davies *et al.* 2000).

Most multivariate approaches to the spatial determinants of organisms in fragmented habitat will of necessity be rather speculative. However, the use of multiple independent spatial measures, with sufficient knowledge of the limitations of each measure, is an appropriate strategy to investigate the effects of spatial parameters on species in a landscape.

3.3 Methods

3.3.1 Habitat coverages

The object of this exercise was to create a spatially and temporally accurate GIS coverage of forested (rainforest) and non-forested land in the study area. Background coverage was provided by mapping the study area at a coarse scale using digitised 1:100,000 maps, and then converting to a raster coverage with 20 m x 20 m grid cells. The areas around study sites required greater spatial and temporal accuracy than provided by the topographic maps, so five fine-scale (2 m x 2 m grid cells) coverages covering the sites and surrounding areas to a radius of at least 5 km were derived from scanned 1:20,000 air photos. These finer-scale coverages were mosaiced with the coarser coverage, with the 2 m resolution placed over the 20 m resolution coverage. Where overlap occurred, the 2 m x 2 m coverages were given precedence. The overall order of procedures is outlined in Figure 3.2.

Coarse-scale coverage

This coverage was digitised from 1:100,000 topographic maps (see Appendix 2) using ArcInfo (ESRI 1996) software, and stored as a vector ArcInfo coverage. The topographic maps were printed in 1989 from 1978 aerial photos, so some landscape change could be expected in the subsequent 15 years. Therefore, prior to digitisation, the topographic maps were compared to a 1995 Landsat TM coverage to check for landscape changes (usually in the form of further clearing) since the topographic map dates. The removal of some vegetation in the intervening 15 years was identified on the topographic maps prior to digitising. The digitised vector coverage was then transferred to a Unix platform and converted to a 20 m resolution grid in Arc/Info.

Fine-scale coverage

Fine-scale coverages were derived from 1992 1:25,000 colour aerial photography purchased from the department of Natural Resources (Appendix 3). Twenty-eight aerial photographs encompassed the study sites and adjacent areas within approximately 5 km. These coverages were then merged with the regional coverage to provide continuous coverage.

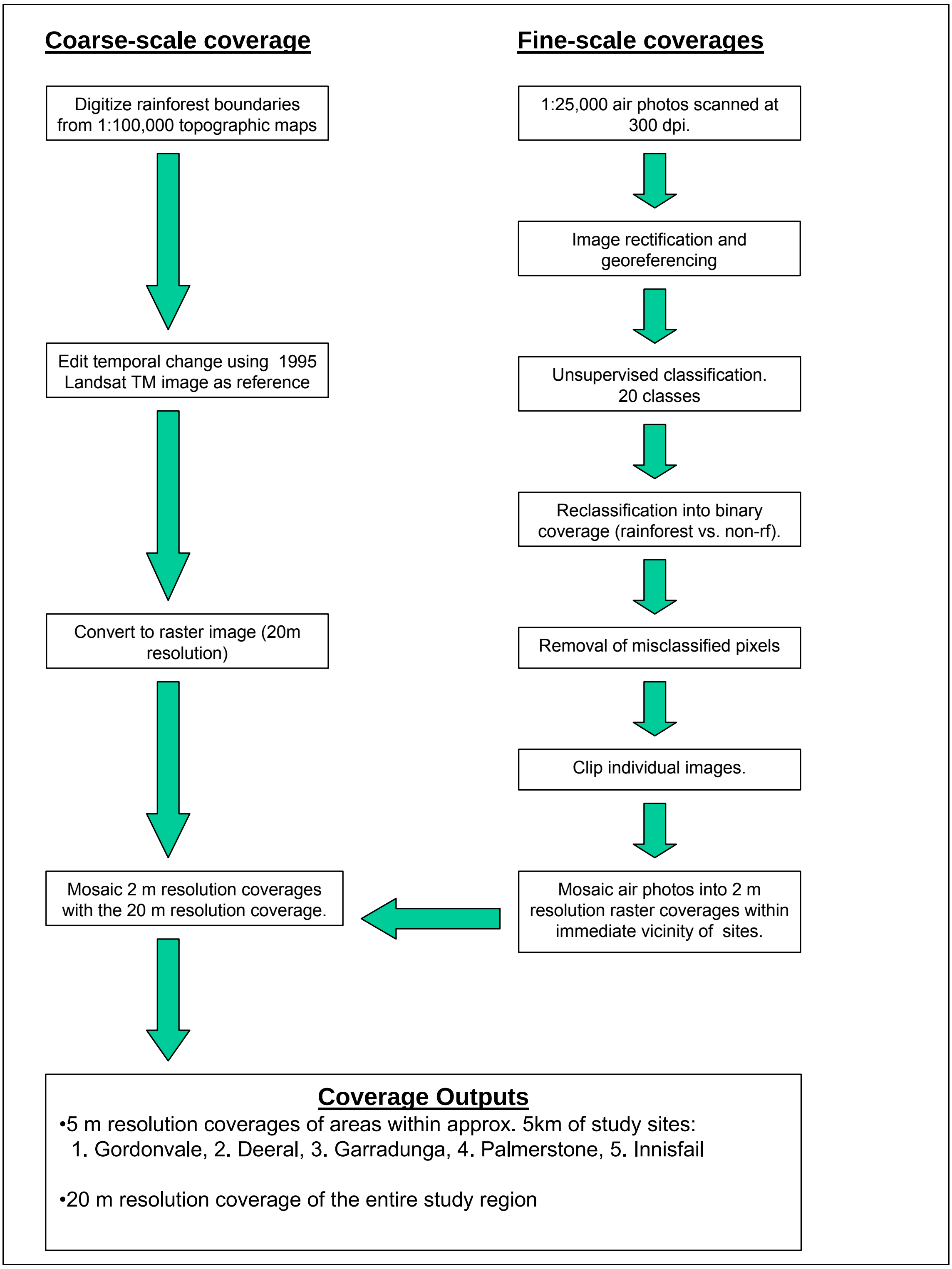

Figure 3.2 Flow chart of the development of the GIS coverages used in the spatial analysis.

Air photos were scanned on a PC using Corel Photo-Paint Version 7 and a Microtek ScanMaker III flatbed scanner. Photos were scanned in colour at 300 dpi. This resulted in a pixel size, and therefore a resolution, of 2 m. Although this resolution was considerably higher than was necessary for most analyses, it left the potential for a greater range of analyses, with resampling at the appropriate pixel size. Scanned images were saved as TIFF bitmaps that were then exported to a UNIX system, on which all image-processing analyses were completed. Images were imported into the image-processing program ERMAPPER (Earth Resource Mapping 1996) and converted into ERMAPPER datasets, from which algorithms were created for rectifying by a coverage-to-coverage rectification. The Wet Tropics stream vector coverage was overlaid on to a blank ERMAPPER algorithm to form the reference coverage from which twenty control points were generated for each image. Due to the potential for the warping of photos, and the possible effects of pitch and yaw (Burrough 1986), each image was then rectified by 2nd order polynomial (quadratic), with nearest neighbour resampling.

Statistics were calculated for each image prior to unsupervised classification, which was also performed in ERMAPPER. Each photo was classified separately due to markedly different degrees of brightness and contrast among photos. In addition, interpretation may be hampered by shading from rugged terrain (Mackey 1993), which occurs outside the study area but within many photographs. Other factors prohibiting the single classification of mosaiced images include the different reflectances of the rainforest plants, and variations in atmospheric conditions such as moisture vapour (Mackey 1993). Isoclass unsupervised classification using a maximum of 20 classes, with a maximum of 100 iterations or 95% of pixels were unchanged.

Due to the different brightness values of rainforest between photos, the reclassified values were identified as rainforest or non-rainforest by manually changing the class colours to green (rainforest) or red (non-rainforest) one at a time. Lower classes (representing darker shades on the unclassified image) represented rainforest. Therefore, class colours were changed to green until classes no longer represented rainforest. At this point, note was made of the threshold below which classes represented rainforest.

Images were then exported from ERMAPPER and imported into Arc/Info using the *imagegrid* command. Classes from 1-20 were reclassified into 2 classes (0 = non-rainforest, 1 = rainforest). Due to variations in spectral reflectance not only between photographs but also within photographs, the classification resulted in some inaccuracies. Some crop areas were incorrectly classified as rainforest, while occasional pixels within rainforest areas were misallocated as non-rainforest. This was especially the case where some areas within a photo were in direct sunlight whilst other areas, due to topography or clouds, were in shadow.

Rainforest and crops were readily differentiated visually through close examination of the aerial photographs. Spuriously classified pixels were therefore removed manually in the ArcInfo module ‘Grid’ by erasing groups of pixels that were identifiable as crops, and occasional small clusters of pixels were reclassified by using the *griddespeckle* command.

Images were then clipped to remove the occasional photograph boundary areas from around the edges of coverages, using the ArcInfo command *gridclip*. Finally, the fine-scale images were merged with the coarse-scale coverage using the *merge* command. The coarse-scale coverage was inputted last, resulting in the fine-scale coverages being given priority where overlap occurred. The final coverage of the entire region was at 20 m resolution; however, sub-regions within approximately 5 km of groups of sites were stored at 2 m resolution.

3.3.2 Calculation of spatial measures

Spatial measures were calculated using a resolution of 2 m (area) or 5 m (all other measures). The overall study area was divided into five areas corresponding to clusters of sites A - E (Gordonvale, Deeral, Garradunga, Palmerston and Innisfail) to reflect environmental differences (see Chapter 2), and to reduce the coverage sizes to allow more efficient processing.

Patch area

Patch area was calculated by the *regiongroup* command in the ARC/INFO module ‘Grid’ at 2 m resolution. This allocates a patch ID and an attribute descriptor for each contiguous group of cells. Patch area is the most studied landscape variable, so the highest resolution possible (2 m pixel size) was used. This was also possible due to the relatively small areas of coverage to be examined, and the simple calculation (Area = no. cells/2500), which limited the processing demands. Areas were defined by groups of continuous cells that were adjacent or touching diagonally (8 possible neighbouring cells).

Isolation measures

These measures were performed on aggregated coverages of 5 m pixel size due to the increased processing demands in some of the calculations:

- Nearest neighbour distance equals the distance to the nearest patch of rainforest (of any size), based on the shortest edge-to-edge distance, and was calculated using the ArcView (ESRI 1999) extension ‘Patch Analyst’ (Rempel 2000).

- Distance to continuous habitat was measured by initially identifying continuous habitat. In this study area, a threshold area of 1000 ha included the main Bellenden Ker massif and contiguous areas, the Malbon-Thompson Range and contiguous areas, and the Moresby Range south of the mouth of the Johnstone River. Distances from the nearest edge of each patch to the nearest extremity of continuous habitat were calculated using the ArcView *ruler* tool. This was also re-calculated whilst ignoring peninsulas (areas <50 m wide, usually following watercourses) to allow for the possible presence of edge effects.

- Distance to the nearest rainforest patch over 30 ha was calculated by identifying and selecting all rainforest patches above this size in the attribute table in ArcView. Distances from the nearest edge of each site patch to the nearest extremity of continuous habitat were also calculated using the ArcView *ruler* tool.

- Proportion of rainforest cover around sites within radii of 1 km, 2 km, 5 km and 10 km were calculated in ArcView using the following steps (Figure 3.3).
  1. The *regiongrouped* grid coverages with identified habitat patches were displayed.
  2. The site patches were identified in the attribute tables.
  3. Buffers were placed around each site patch, thus creating shapefiles (vector data layer) containing the buffers. Where the buffers of adjacent sites overlapped, the buffer polygons were not merged, retaining a separate polygon for each buffer around each site. Therefore, a separate shapefile was created for each different radius (four files), and each case (buffer area) was identified by the site number.
  4. In Spatial Analyst, zonal statistics were calculated for each polygon, with the relevant overlain grid coverages containing the data within these zones. In these grid coverages, rainforest =1 and non-rainforest = 0. Therefore, the sum within each zone represented the amount of rainforest within each buffered area.

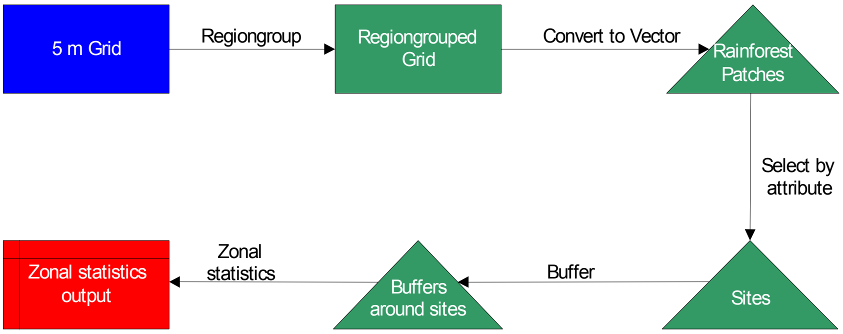

Figure 3.3 Flowchart summarising the steps involved in calculating the proportion of rainforest cover within differing radii of study sites.

These measures are not, however, independent of patch size and shape for two reasons. Firstly, a larger patch will have a larger area contained within a buffer of the same width as a smaller patch. Secondly, the patch itself contributes to both the number of rainforest pixels and the overall area of the buffer by the same number of cells. This results in a proportionally greater increase in the number of ‘positive’ or rainforest cells than in overall number of cells within the buffer, and therefore an artificially high measure of the proportion of rainforest within a buffer around a patch. Consequently, the true proportion of rainforest in the buffer was calculated by first subtracting the area of the buffered patch from the total area of rainforest within the buffer. This was then divided by the difference between the total area of the buffer and the area of the buffered patch. The result was a proportional measure of the amount of rainforest within the buffer but outside the original patch of interest.

Proportion of rainforest within the buffer = $(A_{rf}-A_p)/(A_b-A_p)$;

where,
A_{rf} = area of rainforest within the entire buffer area,
A_p = area of the buffered patch, and
A_b = total area of the buffer.

Edge measures

True edge lengths are overestimated on raster maps due to the creation of artificial right-angled borders along the edge of pixels (Hargis *et al.* 1997). Edge habitat is more accurately measured using vector data. Therefore, the 5 m grids of the subregions (Gordonvale, Deeral, Garradunga, Palmerston and Innisfail) were converted into polygon shape coverages (Figure 3.4). The ‘stepped’ effects which result from a direct outline of the external grid cells of a patch were eliminated by utilising the Douglas-Poiker algorithm with the following weed tolerance: sqrt(0.5) * cellsize. A range of edge measures were calculated as outlined below:

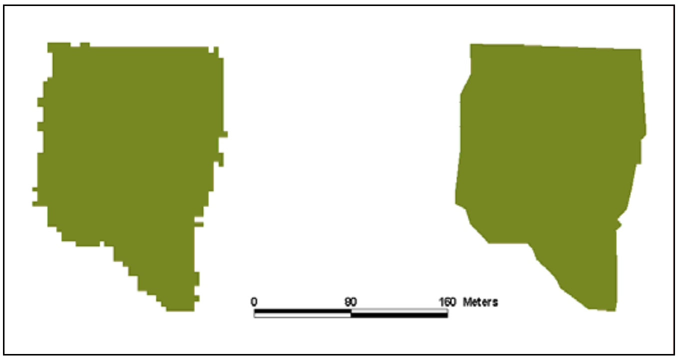

Figure 3.4 Site 4 pre- and post-conversion from raster grid to vector shape file.

- Patch edge is the perimeter of each site.

- Shape index = the perimeter of the patch divided by the square root of the patch area and adjusted for circular standard (calculated in the ArcView extension Patch Analyst).

Shape Index of a patch = edge length/($2\sqrt{\pi}$*area) (Patton 1975).

- Perimeter/area ratio = perimeter/area (calculated in Patch Analyst).

- Fractal dimension is a measure of shape complexity (calculated in Patch Analyst).

Fractal Dimension = 2ln p/ln a. Range = 1-2.

- Edge habitat within 1 km and 2 km radii measures the total length of edge within certain radii of a patch. This was calculated through the following steps in ArcView:

1. The 1 and 2 km external buffer files used in the calculation of the isolation measures were overlain with the polygon shapefiles (derived from the 5 m grids) using the *intersect* command in ArcView. The resulting shapefiles included all polygons falling within or partly within the buffer files, and each polygon was identified as rainforest/non-rainforest, by its original polygon ID number, and by the site buffer in which it fell. Where polygons occurred within the buffers of two or more sites, the polygon (or part thereof) was included in both buffer areas.
2. Using the Patch Analyst extension, the total edge for each class was calculated, with the buffer ID used as the class field. Therefore, the perimeters of all of the polygons within each buffer were summed.
3. The edge of the buffer was also included in the calculations, as for the purpose of this method, a virtual boundary is created around the class (the buffer). This of course was not a real edge, so for each site buffer, the buffer perimeter was subtracted from the total edge measure to obtain the ‘gross within-buffer edge’.
4. However, within the buffer every edge is measured twice, as the matrix (or any other non-rainforest patch) was also recognised as a polygon in the calculation. Therefore, the gross within-buffer edge was divided by two to obtain the ‘actual edge’ measure.

- Edge density within 1 km and 2 km radii (m/ha) was calculated by dividing the ‘actual edge’ by the area of the buffer.

Core area measures

The core area of all site patches was calculated in ArcView using the Patch Analyst extension. For each patch, the area of patch further than 25 m, 50 m, and 100 m, respectively, from any edge was considered core habitat.

In total, 21 spatial measures were calculated for each patch, with some of these (area, perimeter, and shape measures) calculated for all rainforest patches within the entire region (Table 3.1). From these measures, I calculated the overall percentage of lowland rainforest remaining in the entire region and within the different subregions, and calculated the density of edge within these areas.

Table 3.1 Summary of spatial measures

Type	Description
Area	Area of each patch
Isolation	Nearest neighbour distance (distance to nearest rainforest patch)
	Distance to ‘mainland’ area (with and without peninsulas)
	Distance to ‘mainland’ area (with and without peninsulas)
	Distance to area of over 30 ha (includes peninsulas)
	Rainforest area within 1 km of patch
	Rainforest area within 2 km of patch
	Rainforest area within 5 km of patch
	Rainforest area within 10 km of patch
Edge	Edge per patch
	Edge within 1 km radii of sites
	Edge within 2 km radii of sites
	Edge density within 1 km of sites
	Edge density within 2 km of sites
Core area	Core area of each patch (25 m)
	Core area of each patch (50 m)
	Core area of each patch (100 m)
Shape	Perimeter
	Shape index
	Perimeter/area ratio
	Fractal dimension

3.3.3 Relationships between spatial measures

Spearman rank correlations using all 30 patches were used to test for independence of spatial measures from one another, and to examine relationships and redundancy of variables (Grant & Burkey 1999). This was performed using SPSS 7.0 (SPSS 1996).

3.3.4 Patterns of clearing with respect to environmental variables

Geology

Patterns of lowland clearing were analysed by first selecting from a digital terrain model (DTM) of the Wet Tropics (Wet Tropics Management Authority) those areas in the study region that are less than 300 m in altitude (the generally accepted divide between lowland and upland areas). The resulting area was converted into a shape file, and used to clip a vector geology layer of the Wet Tropics to just those areas in the study area below 300 m elevation.

From this lowland geology coverage, the major rock types (granite, metamorphic, basalt, alluvium and rhyolite) were selected out one by one using the *query* command in ArcView, creating five shapefiles. Each shapefile was used to clip the main vegetation coverage of the study area, creating a coverage of rainforest and cleared areas for each substrate type. Spatial statistics were calculated for the patterns of clearing on each rock type using the Spatial Analyst extension in ArcView, and were compared between the five rock types. Statistics used were as follows:

1. Forested area
2. Total landscape area
3. Percentage of landscape uncleared
4. Mean patch size
5. Total edge
6. Edge density
7. Mean patch edge
8. Mean shape index
9. Mean perimeter/area ratio
10. Mean patch fractal dimension

Slope

A slope coverage of the whole Wet Tropics was created from the 80 m DTM using the ArcView extension 3D Analyst. In order to clip out those areas above 300 m altitude, the slope coverage was overlain with a grid coverage of the lowland areas only, where all cells were allocated a value of 1. Using the *map calculator* function in the ArcView extension Spatial Analyst, the two grids were multiplied cell-by-cell. The resulting grid contained slope values for all areas in the study area lower than 300 m.

In this output coverage, slopes ranged from 0 to 44.2 degrees, and were reclassified into 22 classes (Class 1 = 0-1.99 degrees, Class 2 = 2-3.99 degrees, etc.). This grouping of values allowed the calculation of zonal statistics. Zonal statistics allow values from a coverage to be analysed for specific areas (zones) that are defined in a second coverage. In this instance, within each class in the slope coverage, the amount of remaining forest as a proportion of the total area of each slope angle class was calculated from the binary forested/cleared coverage. This provided a useful way to identify slope thresholds, below which little forested area remains due to clearing.

The mean slopes for all cleared areas and all forested areas were calculated by using the zonal statistics of the binary forest coverage, where clearing was the input coverage (with two zonal classes – cleared and forested), and values were derived from the slope coverage.

Regression analyses were used to develop the most appropriate model to explain the relationship between slope and the proportion of habitat remaining. Exploratory analyses indicated that there were two linear relationships between these variables at different slope ranges. Therefore, a piece-wise regression was employed. Piece-wise regression assumes linear responses between independent variables and a dependent variable, but allows the nature of the relationship to change over the range of the independent variables, and was performed using Statistica 5.5 (Statsoft 1999). The piece-wise regression equation is as follows:

$$y = a + b_1 * x * (x \leq x_{bp}) + b_2 * x * (x > x_{bp})$$

where y = proportion of forest remaining within a slope angle class, x = slope angle class, x_{bp} = the slope breakpoint, a = the common intercept, and b_1 and b_2 = the slopes of the two conditional regression slopes.

Altitude

Using the same single value grid coverage of the lowlands as above, I used the *Map Calculator* to remove all areas above 300 m altitude and outside the study area from the 80 m DTM of the Wet Tropics. The resulting grid contained elevation values for all areas in the study area below 300 m. In this output image, elevation values (0 to 300 m) were reclassified into 20 classes (Class 1 = 0-15 m, Class 2 = 16-30 m etc.). As with slope, zonal statistics were calculated. Within each class in the elevation coverage, the amount of remaining forest as a proportion of the total area of each elevation class was calculated from the same binary forested/cleared coverage as above.

Modelling clearance patterns

I created 300 random point locations throughout the study area using the ArcView extension Random Point Generator (Jenness 2001), of which 164 occurred in areas below 300 m altitude. These random points were overlain against each of the forest/non-forest layers using the zonal statistics function, with each point representing a zone. This created a binary value for each point (clear or forested) representing the response variable. The same random sample points were overlain with the elevation, geology, slope and mean dry-season rainfall (Turton *et al.* 1999) coverages to create the four explanatory variables. Rainfall data for the Wet Tropics was derived from interpolation from 70-year means from a series of recording stations located throughout the region (Turton *et al.* 1999). Although rainfall models are not without some degree of error, the lowlands, with relatively intense agriculture in most areas, contain a high number of stations, resulting in reasonably accurate rainfall surfaces.

Spearman rank correlation was used to test for colinearity between the numeric explanatory variables elevation, slope, geology and driest quarter rainfall. Forward stepwise logistic regression quantified the influence of these predictor variables on habitat clearance status, with elevation and slope both log-transformed to achieve normality and homogeneity of variances. This analysis was performed using SPSS 10.0 (SPSS 1999).

3.4 Results

3.4.1 Landscape fragmentation patterns

The study area covered 198,482 ha, of which 91,668 ha (46%) was forested, mostly on the foothills and lower slopes of the escarpment. Within those areas below 300 m elevation and with a slope of less than 10 degrees, only 31.75% of the original vegetation remains. Landscape characteristics of the lowlands (excluding the large unfragmented rainforest blocks >1000 ha) and the subregions are shown in Table 3.2. The Palmerston/Mena Creek area contained the highest percentage of remnant forest, with 10% of the region uncleared. Gordonvale, Garradunga and Innisfail all contained approximately 5% forest cover, whilst the Deeral area was almost entirely devoid of remnant rainforest on the plain. The Palmerston area consequently contained a much higher density of patches larger than 10 ha than did the other subregions.

The Innisfail subregion contained the largest mean fragment area and Deeral the smallest, although the standard deviations in all areas were high, because all areas contained a range of patch sizes from very small (≈0.4 ha) to moderately large (≈20 ha). The Palmerston area contained the highest number and density of larger patches, while Deeral and Innisfail contained very few. Therefore, although Palmerston contained the largest number of medium to large fragments, and the largest fragments *per se*, the large number of very small patches dotted throughout the landscape lowered the average patch size in this subregion.

Table 3.2 Summary of fragments of rainforest remaining within each subregion. Measures include all remaining fragments (≥ 0.4 ha) within the cleared areas, and omit major unfragmented rainforest blocks (>1000 ha).

	Gordonvale	Deeral	Garradunga	Palmerston	Innisfail	Total
Total area (ha)	16,225.8	7,904.7	7,023.3	21,044.1	7,287.0	114,761.2
Total rainforest remaining (ha)	874.7	136.2	401.0	2279.5	366.2	7523.4
% forest	5.4	1.7	5.7	10.8	5.0	6.6
No. of patches	77	21	45	274	15	890
No. of patches greater than 10 ha	13	3	9	44	5	114
Denity of patches larger than 10 ha (per 1000 ha)	0.80	0.38	1.28	2.09	0.69	0.99
Mean area of patches (ha)	11.3	6.5	8.9	8.3	23.8	8.5
SD of patch areas (ha)	43.2	17.7	16.1	25.6	27.5	32.5
Mean shape per patch*	3.3	2.6	2.2	2.7	1.4	1.8

* Shape Index of a patch = edge length/(2√π*area). 1.0 = circular, >1.0 = more convoluted.

3.4.2 Landscape patterns among the sites

Sites ranged in area from 1.2 to 294.0 ha (Table 3.3). The three unfragmented sites, although occurring within a block of rainforest hundreds of thousands of hectares in area, were allocated an arbitrary area of 500 ha for later analyses. Distance to the nearest adjacent rainforest (nearest neighbour) ranged from 35 m to 1605 m, while distance to the nearest block of contiguous rainforest ranged from 101 m to 4.33 km, although the lower figure included peninsulas which often ran along creek lines for some distance out of the major blocks. Where peninsulas were ignored, the closest patch was 274 m from the main rainforest block.

The density of rainforest within surrounding radii ranged from nil (completely surrounded by cleared areas) to 71% cover, with consistently larger percentages within larger radii (Table 3.3). This resulted from the narrow nature of the flat lowland strip, which ranged in width from 3 to 10 km. Since the majority of patches lay within 3 to 4 km of large expanses of rainforest, the larger radii included larger areas of continuous rainforest as a percentage of the total area within the radius. Core areas ranged from zero to 239 ha, with means of 24 ha, 17 ha and 8 ha for edge impacts of 25 m, 50 m and 100 m, respectively. The wide range of most measures across the study sites allows broad gradients to be later analysed for effects on bird assemblages.

Table 3.3 Summary statistics of patch sites (n=30).

Spatial Variable	Min	Max	Mean ± SD
Area (ha)	1.1	294.0	33.2 ± 62.0
Distance from patch to nearest rainforest (m)	35	1605	290.8 ± 350.2
Distance from patch to continuous rainforest[1] (m)	274	4330	1848.7 ± 1101.2
Distance from patch to continuous rainforest[2] (m)	101	4330	1327.4 ± 973.3
Distance from patch to nearest 30ha patch (m)	101	3442	692.4 ± 721.3
Density of rainforest within 1km radius of patch (0-1)	0.00	0.23	0.079 ± 0.06
Density of rainforest within 2km radius of patch (0-1)	0.01	0.32	0.141 ± 0.09
Density of rainforest within 5km radius of patch (0-1)	0.05	0.64	0.323 ± 0.14
Density of rainforest within 10km radius of patch (0-1)	0.18	0.71	0.458 ± 0.14
Patch perimeter (m)	413	24667	4569 ± 638
Shape index (1 and above)	0.95	4.20	1.92 ± 0.98
Perimeter area ratio (m/m^2)	0.01	0.14	0.03 ± 0.02
Fractal dimension (1-2)	0.99	1.22	1.09 ± 0.07
Total edge within 1km radius of patch (m)	827	82871	19573 ± 19763
Edge density within 1km radius of patch (m/ha)	2.1	62.3	29.4 ± 16.4
Total edge within 2km radius of patch (m)	4172	289605	105238 ± 72009
Edge density within 2km radius of patch (m/ha)	3.0	116.6	57.8 ± 30.8
Total core area of patch 25m from edges (ha)	0.0	239.2	23.7 ± 48.8
Total core area of patch 50m from edges (ha)	0.0	189.4	16.5 ± 37.9
Total core area of patch 100m from edges (ha)	0.0	117.6	7.9 ± 22.7

[1] does not consider habitat peninsulas to be part of the main rainforest block.
[2] considers habitat peninsulas to be part of the main rainforest block.

3.4.3 Relationships between spatial measures, and variable reduction.

Correlations between spatial measures are shown in Table 3.4. Patch perimeter, perimeter/area ratio, and the three core area measures all correlated positively with patch area, as did the shape index and fractal dimension, albeit to a lesser extent. Distance to main, unfragmented blocks of rainforest weakly negatively correlated with patch area.

Distances to continuous rainforest including and excluding narrow habitat peninsulas correlated closely, and the choice of which to use was dependent on the results of the analysis of edge effects (Chapter 6). Further significant correlations occurred between these two variables and the amount of rainforest within 2, 5 and 10 km, as the main block of rainforest, where closer to the patch of interest, often contributes largely to the proportion of the surrounding area containing rainforest.

Rainforest density within 1 and 2 km both correlated with 1 and 2 km edge densities, with the two 1.0 km measures correlating most closely (Table 3.4). Where some habitat exists within a certain radius of a patch then, by definition, some edge must also be present, and the amount of edge habitat within a certain radius of a patch depends on the amount and arrangement of habitat within that radius. Therefore, the nature of the relationship between the amount of

Table 3.4 Spearman rank coefficient matrix of r values for spatial variables for all study patches (n = 30). $P < 0.05$ where $r \geq 0.35$, and $P < 0.01$ where $r \geq 0.46$. Correlation coefficients > 0.8 (unsuitable for simultaneous testing) are marked in bold.

	Area	Nearest neighbour	Dist main. no penin	Dist main. incl penin	Dist 30ha patches	Rainforest within 1km	Rainforest within 2km	Rainforest within 5km	Rainforest within 10km	Patch perim	Shape index	Perimeter area ratio	Fractal dimension	1km edge density	2km edge density	Core area (25m)	Core area (50m)
1. Nearest neighbour	-0.317																
2. Dist main-no pen	-0.402	0.208															
3. Dist main-incl pen	-0.4	0.265	**0.843**														
4. Dist 30ha patches	-0.366	0.407	0.24	0.514													
5. Rforest within 1km	0.278	-0.457	-0.318	-0.412	-0.735												
6. Rforest within 2km	0.346	-0.284	-0.61	-0.595	-0.543	0.772											
7. Rforest within 5km	0.292	-0.071	-0.712	-0.689	-0.372	0.401	0.734										
8. Rforest within 10km	0.131	-0.13	-0.464	-0.442	-0.152	0.227	0.493	**0.812**									
9. Patch perimeter	**0.963**	-0.419	-0.36	-0.403	-0.427	0.284	0.324	0.28	0.104								
10. Shape index	0.639	-0.589	-0.3	-0.431	-0.496	0.36	0.269	0.258	0.164	0.778							
11. Perimeter area ratio	**-0.826**	0.056	0.341	0.182	0.096	-0.128	-0.271	-0.211	-0.117	-0.684	-0.194						
12. Fractal dimension	0.529	-0.572	-0.25	-0.39	-0.452	0.303	0.189	0.205	0.131	0.684	**0.984**	-0.085					
13. 1km edge density	0.261	-0.406	-0.111	-0.269	-0.653	**0.85**	0.648	0.408	0.322	0.318	0.392	-0.083	0.354				
14. 2km edge density	0.163	-0.236	-0.125	-0.312	-0.599	0.752	0.717	0.557	0.507	0.198	0.258	-0.062	0.214	**0.904**			
15. Core area (25m)	**0.993**	-0.282	-0.369	-0.359	-0.34	0.268	0.326	0.255	0.111	**0.939**	0.588	**-0.858**	0.478	0.252	0.155		
16. Core area (50m)	**0.967**	-0.271	-0.393	-0.383	-0.37	0.297	0.368	0.291	0.11	**0.91**	0.562	**-0.858**	0.454	0.247	0.174	**0.976**	
17. Core area (100m)	**0.955**	-0.262	-0.387	-0.359	-0.367	0.304	0.342	0.294	0.111	**0.907**	0.597	**-0.854**	0.495	0.246	0.169	**0.962**	**0.968**

1 = distance to nearest rainforest patch of any size; 2 = distance to unfragmented habitat (ignoring riparian strips attached to these large blocks); 3 = distance to unfragmented habitat (including riparian strips); 4 = distance to patches larger than 30 ha; 5 = the proportion of land within a 1 km radius containing rainforest; 6 = the proportion of land within a 2 km radius containing rainforest; 7 = the proportion of land within a 5 km radius containing rainforest; 8 = the proportion of land within a 10 km radius containing rainforest; 10 = shape index (SI = edge length/$\{2\sqrt{\pi}*\text{area}\}$); 13 = density of edge within a 1 km radius; 14 = density of edge within a 2 km radius; 15 = core area beyond 25 m from the patch edge; 16 = core area beyond 50 m of the patch edge; 17 = core area beyond 100 m of the patch edge

habitat and the amount of edge within a certain radius will depend on differences in the above factors. In this instance, a strong relationship exists, suggesting that these other factors had a relatively minor impact on the amount of edge within 1 km radius. Although the relationship between the proportion of rainforest within 1km and the edge density within a 1 km radius was particularly strong (r = 0.85), they effectively measure two different types of habitat, and therefore may be subject to simultaneous analysis.

Rainforest areas within 5 km and 10 km correlated strongly with each other, because both of these measures are influenced by the presence of large tracts of continuous rainforest more than by patches within certain radii. Patch perimeter correlated closely with all core area measures, due to the close relationship that both have to patch area. The shape index and fractal dimension correlated very closely, indicating that these measures are virtually interchangeable because both are calculated using area and perimeter as the input variables. The perimeter-area ratio, being so strongly dependent on area, correlated strongly with all core area measures, whilst the 1 km density and 2 km density also strongly correlated. Similarly, the three core area measures all strongly correlated with one another (Table 3.4).

3.4.4 Patterns of clearing with respect to environmental variables

Geology

Patterns of clearing differed substantially between the areas with different geologies. Granite and metamorphic substrates retained far higher proportions of natural habitat, with approximately one half of rainforest cover left on basalt regions, and alluvial areas containing only 15% of natural habitat (Table 3.5). Patches on alluvial and basalt substrates were on average considerably smaller, although basalt areas contained a greater degree of variability in patch size than alluvial areas.

Table 3.5 Spatial characteristics of landscapes on different geologies.

	Alluvium	Granite	Metamorphic	Basalt	Total lowlands
Forested area (ha)	15,042.7	17,471.5	44,641.4	14,512.0	91,667.5
Total landscape area (ha)	95,235.7	18,380.7	51,214.4	33,651.6	198,482.3
Percentage of landscape forested	15.8	95.1	87.2	43.1	46.2
Number of patches	1,231	68	288	1,262	2,849
Mean patch size (ha)	12.2	256.9	155.0	11.5	32.2
Total edge (m)	1,581,993.7	529,259.9	1,371,535.6	1,169,995.0	4,652,784.2
Edge density (m/ha)	16.6	28.8	26.8	34.8	23.4
Mean patch edge (m)	1,285.1	7,783.2	4,762.3	927.1	1,633.1
Mean shape index *	1.6	1.8	1.6	1.5	1.6

* Shape Index of a patch = edge length/($2\sqrt{\pi}$*area). 1.0 = circular, >1.0 = more convoluted.

Topography

Less than 15% of original habitat remained in areas with a gradient less than 2 degrees. This figure rose sharply with slope in a linear fashion up to 9 degrees, where approximately 90% of the original habitat remained (Figure 3.5). Above 9 degrees, this relationship levelled off sharply, with a second, but very shallow linear increase in habitat remaining in the steeper slope classes. This was extremely well expressed (98.6% of variance explained) in the piecewise regression equation:

$$y = 0.1117 + 0.0909\ x\ [x \leq 8.50\ \text{deg}] + 0.0021\ x\ [\ x > 8.50\ \text{deg}]$$

where y = proportion of rainforest remaining within a slope class, x = slope class, and 8.50 degrees = the slope class breakpoint; 0.1117 = the common intercept, and 0.0909 and 0.0021 = the respective slopes of the two conditional regressions.

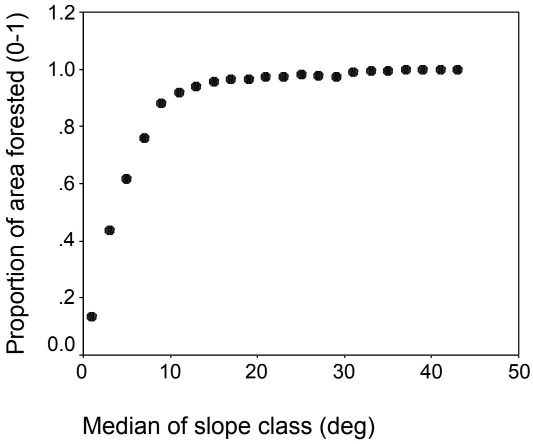

Figure 3.5 Scatterplot of the proportion of area forested as a function of slope (n = 22).

Predictors of landscape clearing

Correlation analysis revealed a significant relationship between elevation and slope (r = 0.78), although this figure lies below an often-used colinearity threshold of r = 0.8, which allows simultaneous testing against response variables (e.g., Freemark & Merriam 1986, Germaine *et al.* 1998). Nevertheless, interpretations of results of models in this instance should still be made with some caution.

The influence of environmental variables (elevation, slope and geology) on the probability of habitat clearing was explored by logistic regression. The model with the best fit included the variables *slope* and *geology*, with 81.7% correct classification (Table 3.6). The overall model failed to reject the null hypothesis of model adequacy (Hosmer-Lemeshow goodness of fit; x^2 = 0.762, df = 5, P = 0.979), suggesting a good model fit. Slope exhibited a positive relationship with the presence of remnant rainforest, whereas within geology, only the metamorphic category significantly explained variation in the data, having a positive relationship with the probability of rainforest remaining.

Table 3.6 Logistic regression predicting habitat clearance in the Wet Tropics lowlands (<300m elevation) as a function of slope, geology, elevation and driest quarter rainfall (n = 164). Beta = logistic regression coefficient, SE = Standard error of the coefficient, and significant coefficients are shown where $P < 0.05$ (Wald Chi-square test of significance).

Variable	Beta	SE	Wald	*P*
Slope	0.9	0.331	7.379	0.007
Geology			10.023	0.018
Geology (1) Alluvial	-0.639	0.634	1.051	0.305
Geology (2) Granite	7.771	17.972	0.184	0.668
Geology (3) Metamorphic	1.578	0.606	6.782	0.009
Constant	-1.845	0.638	8.364	0.004

3.5 Discussion

Landscape fragmentation patterns

The major landscape pattern to emerge from this study is that, within the study area, less than half of the area below 300 m altitude remains forested, and that remnants of rainforest are clearly distributed non-randomly. Steep granite foothills have been little affected by clearing, whereas flatter areas on alluvial and, to a lesser extent, basalt soils, contain little natural vegetation. Overall, less than 10% of rainforest remains. In the subregions, distinct variation in clearing rates indicate that topography largely determines which areas are left uncleared, as the very fertile but undulating Palmerston subregion on basalt soils contains the greatest amount of remnant habitat. Topography has often been shown to be important to the distribution of rainforest structure and floristics (e.g., Clark *et al.* 1995) by affecting hydrology, soil structure or exposure (Webb *et al.* 1999). Rainforest structure and floristics in turn strongly influence faunal assemblages (e.g., Kikkawa 1982, Lescourret & Genard 1994). Clearly, therefore, although substantial areas of rainforest are found within the 300 m elevation delineating lowland assemblages, within well-drained but relatively flat areas of the Wet Tropics lowlands, remnant rainforest remains scarce, and thus of particular conservation interest.

Intuitively, one would expect that within a study area with rainfall varying by a factor of two across locations, as is the case here, rainfall may partly determine land use and thus the area of remnant vegetation (Kemper *et al.* 2000). In this region, however, the entire study area receives adequate rainfall for sugar cane cropping, so rainfall is not a major determinant. The smaller mixed forest patches reflect both the overall lower patch sizes, and the more complete clearing of the native vegetation in the Gordonvale region, which is reflected in the smaller amounts of rainforest within 1-10 km of mixed forest patches.

From the analysis of landscape pattern and clearing, the patterns produced by fragmentation are clearly non-random. Rainforest on granite substrates remains relatively intact. There are two main reasons for this. Firstly, as was found in Chapter 2, soils correlate strongly with substrate (Table 2.1), and granite-based soils are of low fertility, making them unsuitable for sugar cane; and, secondly, granite substrates (and therefore soils) are generally restricted to the steep major massifs, and therefore are unsuitable for cropping. Areas on alluvial soils are the most suitable for cropping due to their gentle slopes and high nutrient status. Consequently, rainforest remnants on these areas are rare, and average patch size is small; larger patches on well-drained alluvial soil are comparatively rare and so are likely to be of high conservation value.

The relationship between slope and rates of clearance was best represented by two separate linear relationships in a piecewise (breakpoint) regression. Land use on very flat gradients (<4 degrees) is dominated by sugar cane farming, but at higher slopes (6-8 degrees), sugar is replaced by cattle grazing as the major human activity due to the lower suitability for sugar growing (Murtha & Smith 1994). Slopes above 9 degrees contain little or no sugar cane farming. The breakpoint of the regression represents the cut-off at which sugar production (higher land value) is replaced entirely by cattle grazing (lower land value). The two separate linear gradients relating land clearing to slope class therefore reflect quite separate land values depending whether or not the location is suitable for sugar cane.

In common with many other studies (e.g., Kemper *et al.* 2000), the logistic clearance model reflected the strong influence of slope on the probability of habitat clearance. Metamorphic geology also exhibited a negative relationship to clearance probability due to the low nutrient status of metamorphic soils (Mackey 1993); granite geology, on the other hand, while also little cleared, was excluded from the model due to its correspondence to steep terrain.

Landscape variables and site descriptions

Clearly, from the review of spatial landscape measures, the *ad hoc* testing of every possible landscape measure against the biological patterns in question may lead to spurious results. Studies of actual and simulated landscapes have shown that many measures correlate with one another, therefore becoming redundant (Hargis *et al.* 1997). This is partly because most measures are derived from a limited number of basic parameters, such as patch area and perimeter, and distance to other patches (Li *et al.* 1993, Hargis *et al.* 1998). Secondly, because of the spatial distribution of the environmental variables that lead to patterns of clearing such as soil and topographic characteristics (e.g., Kemper *et al.* 2000) landscapes usually contain some clumping of fragments, with larger fragments surrounded by greater numbers of fragments than are smaller fragments, creating extra colinearity between spatial variables.

As mentioned in Chapter 2, most fragmentation studies focus on an existing landscape (e.g., Grant & Berkey 1999), with efforts made to choose a range of fragments which represent a wide spread along the inferred important spatial gradients, and avoiding colinearity between the most important gradients. Redundant measures will always be present where a number of landscape characteristics are measured, but those that are retained for further analysis should be those that are more biologically interpretable. Importantly for this study, the major spatial variables of patch area, distance to continuous habitat, proportion of rainforest within different radii from patches, and shape index, all show low colinearity with one-another. This implies that little confusion should arise in later analyses that relate the bird assemblage to these variables.

However, obvious and expected correlations were found between spatial variables among sites in this project. Within the correlation matrix, 45 out of 188 correlation coefficients were over 0.5; however only 19 exceeded 0.8, above-which interpretation may be seriously compromised (Legendre & Legendre 1998). Patch perimeter, not surprisingly, correlated closely with patch area, and is of necessity dropped as a variable. In the absence of massive variations in shape, patch area will usually correlate with patch perimeter, while the perimeter-area ratio is also not independent of area. Area also correlated closely with the perimeter area ratio, but this is of little concern, as both the shape index and fractal dimension have been shown to be more appropriate, area-independent measures of patch shape (McGarigal & Marks 1995). The shape index is more sensitive to shape differences (Hargis *et al.* 1997) and is therefore retained.

Other strong correlations (>0.8) between closely related measures require choices to be made over which spatial variables to include and which to omit. These include close relationships between patch area and core area measures of 25, 50 and 100 m from the edge. The correlations between area and the core areas decrease with larger assumed edge effects, since the larger the edge distance, the more will be the impact of changes in the shape of a patch. Whether to retain any of the core area measures will depend partly on the results of Chapter 6, *Edge Effects*.

Further colinearity occurs between the distance to major rainforest blocks including and excluding riparian peninsulas, between the amount of rainforest within 5 and 10 km radii, and between the amount of rainforest within 1 km and edge density within 1 km. Some of these are impossible to avoid. Patches in this study were chosen (within the limitations of accessibility and landholder permission) to reflect a broad range of values along patch area, major isolation and shape gradients, with little significant correlation between these. Within these broad groups of variables, some colinearity is inevitable; however, the spatial characteristics of the 30 fragments in this study allowed simultaneous examination of measures of patch area, distance to main unfragmented rainforest blocks, amount of rainforest within different radii of a patch, patch shape, and core area.

Methodological issues and limitations

Spatial and temporal error must be addressed in nearly all exercises involving spatial analysis. In this project, the technique of digitising from 1:100,000 topographic maps may lead to substantial spatial errors due to the digitising itself, or temporal errors due to time since the publication of the maps (1985). Digitising by skilled operators normally results in accuracy of crosshair placement of ± 0.05 to ± 0.06 mm (Bernhardsen 2002) which from a 1:100,000 map will translate to an error on the ground of 5 to 6 m. If a more conservative accuracy estimate of 10 m is allowed, then over the scale of this study, this error is unlikely to greatly change the landscape measures. Analysing a recent 1995 Landsat TM and modifying the coverage manually where necessary combated temporal error.

The impact of these errors was further minimised by the merging of 2 m resolution finer scale coverages from the more recent aerial photography (1992). This resulted in increased spatial and temporal reliability within those areas (the subregions) of most importance to the bird assemblage dynamics of he study sites. Within the areas within approximately 5 km of sites, the resolution of 2 m from aerial photography provided more than sufficient spatial resolution for this study.

This chapter would benefit from a higher-resolution digital terrain model (DTM) of the region. Much remnant habitat (identified at a resolution of 20 m) lies in or around gullies or other small but steep areas that may not be recognisable at the coarser resolution (80 m) of the DTM. Therefore, a 20 or 30 m resolution (were it available) would probably provide a more reliable and precise methodology for analysing clearance patterns in the region. It is likely that many of the riparian strips of habitat, whilst appearing to be on flat ground in the 80 m DTM, would be recognised as creek-gully vegetation on a 30 m DTM. Thus, a finer-scale DTM would reveal that there is in fact more rainforest on areas of higher slope, and thus higher rates of clearance on flatter and gently-sloping areas than are recorded in this study.

Practical applications

Although the Wet Tropics uplands is one of the best-protected ecosystems Australia (since World Heritage Listing in 1988), the lowlands on flat or gently sloping land are poorly represented in protected areas. Major lowland rainforests exist in the Mission Beach area, but some of these are threatened by ongoing clearing for residential and acreage residential (FNQRPAC 2000) where they fall outside state and federal government control.

Previous authors have demonstrated pessimism regarding the conservation of the Wet Tropics lowland rainforest (e.g., Ehrlich & Murphy 1987), and this study shows that, within the heavily cleared study area, a little over 15% of rainforest on alluvial soils remains. This lies towards the lower end of estimates of 10-30% cover required to preserve species (although these figures vary and are the subject of some conjecture) (Homan *et al.* 2004). Furthermore, within this region, options for establishing a representative reserve system of rainforest habitat on alluvial rainforest are limited, as much of the remaining land exists on private property. Protected areas on alluvial soils are mainly restricted to areas of poor drainage such as Eubanangee Swamp National Park, which contains fan palm forest rather than true mesophyll vine forest.

Chapter 4. Vegetation structure in lowland rainforest patches.

4.1. Introduction

Vegetation structure influences bird assemblage structure both between and within habitat types (e.g., MacArthur & MacArthur 1961, Karr & Freemark 1983). Therefore, although the primary objective of this project is to investigate the effects of landscape configuration on bird assemblages within fragmented lowland rainforest, it is also necessary to examine vegetation structure as a possible factor influencing the avifauna. In this chapter, the major characteristics of the vegetation are described, and major patterns among vegetation characteristics are identified to allow reduction to a few summary variables for later comparison with the bird assemblage. This chapter also examines, at a relatively fine scale, the effects of environmental variables on vegetation structure.

Rainforest vegetation and bird assemblages

Vegetation structure has for most of the last century been recognized as an important influence on bird assemblages (Lack 1933). Studies from different regions have identified structural attributes of vegetation that strongly influence bird assemblages (e.g., MacArthur & MacArthur 1961, MacArthur *et al.* 1966, Karr & Roth 1971). The availability of particular substrates often influences the abundance of particular guilds or species (e.g., Gilmore 1985, Raman *et al.*1998), and the availability of fruiting or flowering plants may also influence the structure of bird assemblages (e.g., Stouffer & Bierregaard 1995b). These responses to structural differences in vegetation are reflected in the sensitivity of many species to physical disturbances such as selective logging (e.g., Johns 1992), fire damage (Barlow *et al.* 2002) storm damage (Will 1991), or secondary growth (Laurance *et al.* 1996).

In particular, structural complexity (often measured as foliage height diversity or foliage density throughout the strata) has long been considered an important factor in explaining the higher diversities often found in architecturally complex tropical forests (Karr & Roth 1971, Erard 1989), and in determining the numbers of bird species present in tropical forest habitats (e.g., Pearson 1977). More complex habitat at a particular location (greater volume and variety of substrates and resources) will, in theory, allow more complex habitat subdivision (Pearson 1977). This subdivision allows closer species packing and the coexistence of a greater range of foraging groups, leading to the presence of more species (Bowman *et al.* 1990). The horizontal diversity in foliage density (heterogeneity) also often positively influences bird diversity at a variety of scales (e.g., Roth 1976), although biogeographical effects may confound comparisons between sites in different areas (Pearson 1975).

The present study was conducted at a small spatial scale in comparison with studies that have found vegetation structure to strongly influence avian assemblages (e.g., Pearson 1977). Further, many of the studies that have shown this relationship between species richness and foliage height diversity includes multiple habitat types (Erdelen 1984). Moreover, Waide (1991a) suggests that habitat susceptibility to tropical storms, as is the case in the study region (Chapter 2), may select for behavioural plasticity in foraging height and diet. Although the major focus of this project is on the spatial dynamics of bird assemblages in a relatively homogeneous habitat (lowland rainforest), the breadth of work examining and supporting vegetation structure as a major influence in structuring bird assemblages suggests that even within a single structural type, subtle differences in vegetation structure should be examined along with spatial characteristics.

Therefore, the first major goals of this chapter were to derive measures of horizontal heterogeneity and vertical complexity, to identify vegetation differences between patches and between transects to identify any patches that were sufficiently different to require separate analyses of bird assemblages. In addition, the vegetation components that characterise these differences were identified, and these vegetation variables were reduced to appropriate meaningful summary variables for later comparison with bird assemblages.

Environmental determinants of rainforest structure

Where vegetation changes among a series of sites are examined, it is also of interest to determine what environmental variables correspond with these vegetation changes, allowing the tentative assignment of causality. There are several potentially important environmental characteristics within the study area, including rainfall, soil types and topography (Chapter 2). In this chapter, I examine the effects of these variables on vegetation groupings and gradients that may be important to lowland bird assemblages.

The sites of this study are all classified as rainforest of one type or another (Chapter 2), from complex mesophyll vine forest in the south to closed forest with *Eucalyptus* spp. and *Acacia* spp. emergents in the north of the study area (Tracey 1982). This study focuses on the factors influencing structural variations not only between but also *within* rainforest types.

Rainforest distribution and characteristics are, of course, strongly related to elements of the rainfall regime of an area (Condit 1998, Mackey 1993), or where other factors lead to the retention of moisture (Winter *et al.* 1987, Hilbert & van den Muyzenberg 1999). Over a broad scale, or when rainfall gradients are particularly strong, annual or driest quarter rainfall is often the major determinant of the presence or absence of rainforest. This has been found in a variety of locations worldwide (e.g., Swaine 1996, Mackey 1993). However, in addition to suitable rainfall and temperature, other variables may influence rainforest boundaries at a local scale, including slope (Austin *et al.* 1996), aspect (Bale *et al.* 1998) and fire regimes (Russell-Smith *et al.* 2004).

Topography affects hydrology, soil structure and exposure (Webb *et al.* 1999). Consequently, overseas studies have shown it often to be an important influence to rainforest structure and floristics, influencing palm density (Clark *et al.* 1995) and species composition (Svenning 1999, Clark *et al.* 1999a), tree diversity (Webb *et al.* 1999), canopy species composition (Newbery *et al.* 1986, Clark *et al.* 1999a) and canopy height (Webb *et al.* 1999). Steeper slopes may also lead to less discreet rainforest strata (Pascal & Pelissier 1996) and lower herb species diversity (Poulsen 1996).

There is little published work on the effects of topography on floristics or structure within the Wet Tropics. For example, Mackey (1993) modelled rainforest distribution in the region with respect to climatic and soil influences, but did not examine the effects of topography on rainforest structure or floristics. More recently, Hilbert & van den Muyzenberg (1999) utilised aspect and slope in modelling the broad distribution of rainforest types throughout the Wet Tropics from existing rainforest maps, but they did not examine more specific structural differences within rainforest types using ground surveys. Webb (1968) examined topography, but only with regard to soil processes and fire shadows. In addition, Webb's examination of environmental data was restricted to the major areas of each structural type, and at a general, broader scale. This chapter, on the other hand, examines the influence of topography on more subtle structural characteristics of vegetation at a local scale.

Soil physical properties are of limited impact to Wet Tropics rainforest vegetation, with other factors such as temperature, rainfall, altitude, and fire history all probably having greater impact on vegetation types (Tracey 1969). Soil nutrient levels, on the other hand, may influence major structural and physiognomic features of rainforest (Coomes & Grubb 1996, Herrera & Finegan 1997). In northern Queensland, at a coarse scale, rainforest structure and broader vegetation types have been found to correspond to soil nutrient status (Webb 1969, Mackey 1993). Whilst soils influence leaf size less than do climatic influences (Webb 1968), within the highest rainfall areas in the lowlands, poor nutrient soils tend to lead to smaller leaves and decreased complexity (Mackey 1993), lower densities of emergent *Eucalyptus* spp. and other sclerophylls, increased deciduousness and lower numbers of robust woody lianas (Webb 1968).

However, whether these patterns hold at a finer scale within a specific portion of the Wet Tropics lowlands is unknown. Studies in the Wet Tropics that have examined some environmental influences on rainforest structure at a broader, more regional scale than this study have encompassed a considerably wider rainfall range, and have included non-rainforest areas (Webb 1969, Mackey 1993). Within the wetter lowland section, temperature gradients are negligible and, apart from a sharp gradient in the northern part of the study area, rainfall differences are moderate. Given this climatic regime, local topography may become an important variable, and the consistent effects of cyclones along this section of coast may confound the effects of soil patterns and exacerbate rainfall differences.

Aims

The aims of this chapter are to:

- describe the vegetation characteristics of sample sites within the study area;
- identify vegetation differences between patches and between transects to identify patches that are sufficiently different to require separate later analyses;
- identify which environmental factors explain these patterns;
- reduce the large number of vegetation variables to a meaningful subset with which to analyse the bird assemblage responses; and
- derive measures of horizontal heterogeneity, and test the independence of patch area from habitat heterogeneity.

4.2 Methods

Vegetation sampling

Vegetation surveys were undertaken during August and September 1997. All vegetation data was obtained during the dry season to minimize the effects of seasonal foliage change that may occur during the wet season (August 1983).

Environmental and disturbance characteristics were described at all transects (137) within all sites (33). Along each transect, attributes of the physical environment were recorded, including dominant landform type, slope, aspect, drainage quality (well, moderately or poorly drained), and distance to the nearest waterway. The type and degree of disturbance (if any) was recorded at three locations along each transect (at approximately 0, 50 and 100 m), including evidence of canopy gaps caused by selective logging, impacts of non-native animals, evidence of fire, salinity, flood damage, presence of alien plant species, and litter or rubbish. The recording of the vegetation characteristics for each transect followed a proforma (Appendix 4) based on a variation of the Braun-Blanquet method of visual estimation. Vegetation structure was described quantitatively within a 5 m radius at three positions (start, 50 m and end) along each transect (Table 4.1), whereas the relative abundance of structural features and growth forms was estimated for the whole transect on an ordinal scale. From the information collected in the field, a subset comprising those variables that described the physical structure of the forest and the relative abundance of different growth forms was used in analyses of vegetation structure (Table 4.1).

Table 4.1 Summary of vegetation structural variables used in the overall classification and ordination of transects and patches. For the stratum and connectivity variables, data are numeric (0 = absent, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%). Other variables are represented as relative abundances (0 = not evident, 1 = uncommon and/or inconspicuous, 2 = occasional or uncommon but conspicuous, 3 = common or abundant, 4 = virtually everywhere).

Type	Name	Description
Structure	Stratum1	Vegetation density in the stratum 0-1 m
	Stratum2	Vegetation density in the stratum 1-2 m
	Stratum3	Vegetation density in the stratum 2-5 m
	Stratum4	Vegetation density in the sub-canopy
	Stratum5	Vegetation density in the canopy
	Height	Height of upper canopy (m)
	Connect	Proportion of sky visible from ≈ 1.8 m height
	Stems	Number of tree stems >2 cm diameter within 5 m radius
Structural features	Plank	Abundance of trees with plank buttress roots
	Spur	Abundance of trees with spur buttress roots
Growth forms	Sinpal	Abundance of single-stemmed palms
	Mulpal	Abundance of multi-stemmed palms
	Lianas	Abundance of woody lianas
	Grfern	Abundance of ground ferns
	Shrubs	Abundance of shrubs
	Seedli	Abundance of seedlings
	Moss	Abundance of moss
	Clipal	Abundance of climbing palms
	Fanpal	Abundance of fan palms
	Trefer	Abundance of tree ferns
	Pandan	Abundance of pandans
	Strang	Abundance of strangler fig trees
	Lichen	Abundance of lichens
	Episto	Abundance of all epiphytes
	Vines (Thorns)	Abundance of vines with thorns
Canopy Species	Acacia	Abundance of *Acacia* spp.
	Eucal	Abundance of *Eucalyptus* spp.

Environmental Variables

Environmental variables, calculated at the patch and transect levels, and tested for their influence on the major vegetation gradients, are summarized in Table 4.2. Landform is a categorical variable based on the predominant landform along each transect. Local slope was measured in degrees with the use of a clinometer, and was recorded as the maximum slope in any direction along a transect, while aspect was the direction of this maximum slope. Altitude was recorded as the mean along each transect and within each site, and was obtained from the 80m DTM of the Wet Tropics (Wet Tropics Management Authority) and analysed in ArcView. Soil nutrient levels were not measured at each site, but rather soil types and their parent materials were identified at each site from Murtha (1986) and Murtha *et al.* (1996), and a soil potential nutrient index was derived from the parent rock material (Mackey 1993), where:

Alluvium	8.0
Basalt soils	9.0
Granitic soils	7.0
Metamorphic soils	4.5

Rainfall data for the region comes from Turton *et al.* (1999), and is described in Chapter 3. Rainfall measures were estimated for all sites, with a high level of correlation existing between the different rainfall measures. Of these, the mean driest quarter rainfall was chosen to represent rainfall, as this has been shown in other areas to be a particularly strong determinant of rainforest distribution (Martin 1991).

Drainage is an ordinal variable estimated at each transect, and included the categories excellent, good and moderate. Finally, aspect, as a circular variable, was transformed into two derived variables - northness, and eastness. Northness is calculated by the cosine of the aspect, whilst eastness represents the sine of the aspect (Clark *et al.* 1999a).

Table 4.2 Environmental variables within the study area. C = Categorical variable, N = Numeric.

Variable	Type	Description
Landform	C	1 (hillcrest), 2 (summit surface), 3 (hillslope), 4 (plain), 5 (valley flat), 6 (gully)
Slope	N	0-90°
Altitude	N	Mean height above sea level of a transect or site in 10 m increments
Soil nutrient level	N	9.0 (basalt soils), 8.0 (alluvial soils), 7.0 (granite soils), 4.5 (metamorphic soils)
Dry season rainfall	N	Mean driest quarter rainfall over last 70 years (mm)
Drainage	C	1 (excellent), 2 (good), 3 (moderate)
Northness	N	Cosine (aspect)
Eastness	N	Sine (aspect)

Data Analysis

Vegetation variables were combined in matrices at three different scales: point, transect and landscape (patch). Structural variables (Table 4.1) were aggregated from the point scale to transect and patch scales by the mean, and growth form variables (Table 4.1), measured at the transect scale, were also aggregated to the patch scale by the mean. Nominal variables (landform and drainage) were aggregated by the mode.

To examine the similarity and grouping of transects and of sites, non-hierarchical k-means cluster analysis was utilized to identify similar groups of transects. This technique allows the identification of transects or sites that are sufficiently different to warrant separate later analyses with the bird assemblage. This technique was chosen because it does not require a nested structure to the data (Legendre & Legendre 1998). K-means groups were then superimposed on to a non-metric multidimensional scaling (NMDS) ordination of the transects using the same variables, and Euclidean distance measures. NMDS, which uses ranks rather than absolute values in calculating a distance matrix proved a more suitable ordination than principal components analysis (PCA), because much of the vegetation data (especially growth forms, structural features and canopy species) could not be transformed into a state of normality (Krzanowski & Marriott 1994). Ordination was employed in an effort to provide further evidence in support of the cluster analyses, to allow for the identification of gradients through the data and, using the gradients in the data, to allow the reduction of the 27 vegetation characteristics to a useable number in later analyses. In both the classification and ordination, data were standardized by column maximum, ensuring that variables with different scales of measurement received similar weighting (Jongman *et al*. 1995).

To identify the vegetation characteristics responsible for the major gradients, Spearman rank correlation between axis scores and the vegetation variables used in the ordination were calculated. Non-parametric correlation was employed because many of the growth form distributions could not be transformed to a normal distribution, and scatterplots were checked for outliers that might create false or misleading correlation coefficients.

Environmental variables, including mean driest quarter rainfall, soil type, slope, altitude, aspect and drainage, were examined for their ability to explain vegetation patterns. Regression trees were used because of non-linear relationships between the explanatory variables and the vegetation structure (represented as NMDS ordination axes). Regression and classification trees are non-linear methods of explaining variation in a univariate or multivariate response variable, by repeatedly splitting the data into more homogeneous groups using combinations of numeric and/or categorical explanatory variables (De'ath & Fabricius, 2000).

Habitat heterogeneity has long been seen as a contributing (and often confounding) component of the species-area relationship (Boecklen 1986), and can be represented in a variety of ways. These include the coefficient of variation (CV) of the mean number of vertical strata with foliage, at points along each transect (Raman *et al.* 1998), the average CV of each stratum throughout the points within each site (Karr & Freemark 1983) or the CV of distances of particular vegetation components from a central point (Roth 1976). However, techniques using CV measures, while suitable for the creation of multiple measures of horizontal heterogeneity (at each stratum separately), lose information when averaged to create a single heterogeneity measure. Where a single strong vegetation gradient exists, variation along a single factor of a PCA (August 1983) or dimension in a NMDS (Williams 1997) may prove an appropriate measure. However, in the case of more subtle variation within a single habitat type involving multiple but weaker gradients, as is the case in this study, variation explained by multiple factors may be incorporated into a single index of heterogeneity (Boecklen 1986).

Therefore, to create a univariate measure of structural habitat heterogeneity, a PCA was performed on vegetation structural data (Table 4.3) from all points ($n = 411$) among all transects ($n = 137$). Variables included in this analysis are explained in Table 4.3 (Measure 1). Component scores for all eight principal components were weighted by multiplying each axis score by the eigenvalue of that axis (Boecklen 1986), and then used to calculate average and maximum Euclidean distances among points within each transect and within each patch (Blake & Karr 1987).

Heterogeneity was also calculated on a patch basis with summary variables of total growth forms requiring damp, dark habitats, and the total requiring gaps added to the structural measures (Table 4.3, Measure 2). This could not be performed at a transect level, as the growth forms were not recorded at a scale finer than the transect; hence at a transect level, heterogeneity would not differ between the two groups of variables.

To ascertain the likely independence of patch area and heterogeneity, and to examine at what scale vegetation structural differences occur, the different measures of heterogeneity were correlated against patch area and core area measures at 50 m and 100 m using Spearman rank correlations. Heterogeneity measures were also tested for the influence of environmental variables (Table 4.2) or location within a patch (edge/interior) using regression trees.

Cluster analyses were performed using SPSS 10.0 (SPSS 1999), ordinations using PC-ord 4.0 (McCune & Mefford 1999), and regression trees using S-Plus 3.4 (Mathsoft, 1996).

Table 4.3 Variables used in Principal Components Analyses to derive measures of heterogeneity at the transect and the site level.

Measure 1: Structural variables only		Measure 2: Structural variables and specific growth forms	
Name	Description	Name	Description
Stratum1	Vegetation density (0-1 m height)	Stratum1	Vegetation density (0-1 m height)
Stratum2	Vegetation density (1-2 m height)	Stratum2	Vegetation density (1-2 m height)
Stratum3	Vegetation density (2-5 m height)	Stratum3	Vegetation density (2-5 m height)
Stratum4	Vegetation density (subcanopy)	Stratum4	Vegetation density (subcanopy)
Stratum5	Vegetation density (canopy)	Stratum5	Vegetation density (canopy)
Connect	Canopy connectedness.	Connect	Canopy connectedness
Stems	No. tree stems within 5 m radius.	Stems	No. tree stems within 5 m radius
Height	Height of canopy	Height	Height of canopy
		Typeopen	Sum of scores of growth forms associated with openings[a]
		Typedark	Sum of growth forms associated with cool, dark microclimates[b]
		Typetot	Total sum of growth forms[c]

a. climbing palms, shrubs
b. tree ferns, moss, ground ferns, climbing pandans, single palms, multiple palms, epiphytes
c. all growth forms

4.3 Results

General characteristics

The remaining natural vegetation in the study region mainly consisted of complex mesophyll vine forest and complex notophyll vine forest, which are the most well developed of Australia's rainforest types (Australian Heritage Commission 1986). Other habitat types existed in small remnants in the region, but they were uncommon in this area, having been largely cleared. The northern-most sites contained mixed forest, which consists of mostly rainforest species in the lower and mid-stories, and *Acacia* spp. and *Eucalyptus* spp. comprising most of the canopy and all emergent species.

Canopy height averaged 23.17 ± 0.78 m (Table 4.4). Many special growth forms were common in the area. Shrubs, seedlings and lichens were found at all sites, although shrubs occurred at only 80 of the 137 transects, the majority being edge transects. Plank and spur roots were found in most sites, as were woody lianas, pandans, epiphytes, multi-stemmed palms and moss. Less prevalent were vines with thorns, single-stemmed palms, tree ferns and strangler figs. Single-stemmed palms were present at most sites (21) but at only 50 transects, indicating that they were sparsely but relatively consistently distributed throughout the area. All transects within all patches contained some measure of each of the five strata, although the canopy layer (Stratum5) was less dense and more variable than lower strata.

Table 4.4 Summary statistics of structural vegetation variables across all sites (n = 33). For the stratum and connectivity variables, data are numeric (0 = absent, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%). Other variables are represented as relative abundances (0 = not evident, 1 = uncommon and/or inconspicuous, 2 = occasional or uncommon but conspicuous, 3 = common or abundant, 4 = virtually everywhere).

	Mean	CI(95.0%)	Median	Mode	SD	Min	Max	CV (%)	Transects	Sites
Stratum1 (0-4)	2.34	0.11	2.33	2	0.66	1	4	28.21	137	33
Stratum2 (0-4)	2.18	0.10	2.33	2	0.61	1	3.67	27.98	137	33
Stratum3 (0-4)	2.42	0.07	2.33	2.33	0.41	1.33	3.33	16.94	137	33
Stratum4 (0-4)	2.23	0.08	2.33	2	0.49	1.33	3.67	21.97	137	33
Stratum5 (0-4)	1.59	0.10	1.67	1	0.57	1	3.33	35.85	137	33
Height (m)	23.17	0.78	25	25	4.62	12	35	19.94	137	33
Connectivity (0-4)	2.52	0.08	2.67	2.67	0.47	1.33	4	18.65	137	33
Stem abundance (#)	24.38	1.39	22.33	16.33	8.23	10	55.66	33.76	137	33
Plank roots (0-4)	1.77	0.16	2	2	0.95	0	3	53.67	115	29
Spur roots (0-4)	1.80	0.13	2	2	0.79	0	3	43.89	121	31
Single-stemmed palms (0-4)	0.85	0.20	0	0	1.19	0	4	140	53	21
Multi-stemmed palms (0-4)	2.07	0.19	2	3	1.12	0	3	54.11	111	28
Woody lianas (0-4)	2.41	0.13	3	3	0.75	0	3	31.12	133	32
Ground ferns (0-4)	1.23	0.20	1	0	1.19	0	3	96.75	77	25
Shrubs (0-4)	1.24	0.20	1	0	1.17	0	3	94.35	80	33
Seedlings (0-4)	2.77	0.09	3	3	0.50	0	3	18.05	136	33
Moss (0-4)	1.88	0.14	2	2	0.84	0	3	44.68	128	31
Climbing palm (0-4)	2.23	0.20	3	3	1.20	0	4	53.81	111	27
Tree ferns (0-4)	0.42	0.14	0	0	0.83	0	3	197.62	30	15
Pandans (0-4)	1.91	0.21	2	3	1.26	0	4	65.97	100	28
Stranglers (0-4)	0.28	0.11	0	0	0.63	0	2	225	25	14
Lichens (0-4)	2.83	0.09	3	3	0.52	0	3	18.37	134	33
Epiphytes (0-4)	1.09	0.14	1	2	0.83	0	2	76.15	96	30
Vines with thorns (0-4)	0.93	0.15	1	0	0.90	0	3	96.77	79	23
Acacia spp. (0-4)	0.55	0.18	0	0	1.06	0	3	192.73	31	11
Eucalyptus spp. (0-4)	0.35	0.15	0	0	0.91	0	3	260	19	5

Vegetation similarities and characteristics at the transect and site levels

To identify groupings of, and gradients among transects, K-means cluster analysis and NMDS, respectively, were performed on vegetation by transects (Figure 4.1). The vegetation variables included all structural measures, structural types, and the abundance of *Eucalyptus* spp. and *Acacia* spp. (Table 4.5). The K-means grouping level was set at 4, after examining both ordination plots and hierarchical cluster dendrograms for interpretable groupings. Group 1 consisted of 21 transects from seven sites (Figure 4.3). This group consisted mainly of mixed forest, being characterised by a high but open canopy, relatively clear understorey, open canopy, abundant emergent *Eucalyptus* spp. and *Acacia* spp., and few specific growth forms (see Table 4.1). Five of these seven sites comprised Group 1 transects exclusively. The exceptions were Site 8 and Site 25, each of which contained one edge transect that fell into this group.

Group 4 consisted of all four transects from Site 7, and clearly differed from the others. This group of transects was characterised by a low, open canopy consisting mainly of palms, a clear understorey, and few specific growth forms. Most transects fell into Groups 2 and Group 3 (59 and 53 transects, respectively), and were characterised by higher foliage density throughout all strata, greater variety and abundance of specific growth forms such as plank buttresses, lianas, climbing palms and epiphytes, and a relative lack of emergent *Eucalyptus* spp. and *Acacia* spp. In other words, these transects broadly contained complex mesophyll vine forest (Tracey 1982).

Groups 2 and 3 were more closely related than the other two more divergent groups. Group 2, in comparison to Group 3, was characterised by slightly denser canopy and subcanopy, more abundant ground ferns, moss, tree ferns, pandans, strangler figs and thorny vines, and fewer *Acacia* spp. These more closely related groupings are reflected in the fact that 11 sites contained a mixture of Group 2 and Group 3 transects.

Figure 4.1 shows the substantial agreement between the cluster and ordination. The major vegetation gradient (Axis 1) describes 60.8% of total variation, and correlates negatively with the abundance of *Acacia* spp. and *Eucalyptus* spp., and positively with canopy density, and a range of structural features and growth forms (Table 4.5). Thus, Axis 1 represents a gradient from mixed, less complex forest with emergent *Eucalyptus* spp. and *Acacia* spp. and few structural features and growth forms, to complex forest containing greater amounts and variety of growth forms and structural features. Axis 2 (14.4% of variation), correlated positively with single-stemmed palms, fan palms, tree ferns, and negatively with shrubs, while Axis 3 (9.3% of variation) correlated negatively with tree ferns, shrubs and ground ferns (Table 4.5).

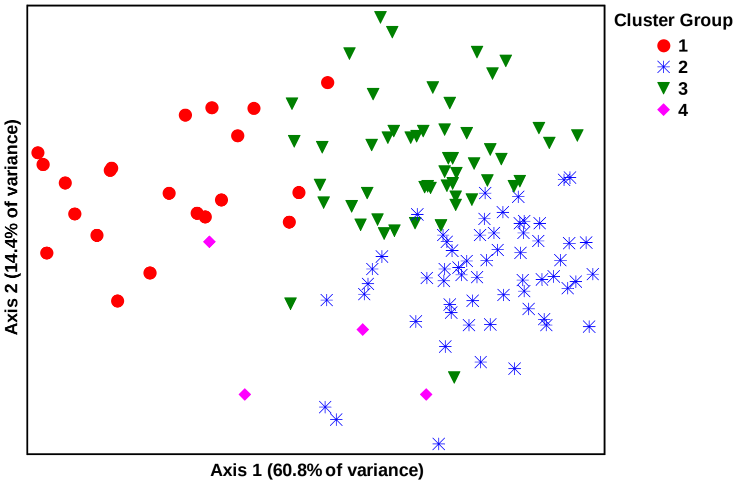

Figure 4.1 Non-metric Multidimensional Scaling plot of vegetation at all transects (n=137) based on all vegetation variables. K-means Classification groups are identified by symbols, and variables are standardized by maximum (0-1). Stress = 0.12.

Table 4.5 Spearman correlation coefficients between the three vegetation ordination axes (gradients) from the NMDS and the included vegetation components for all transects (n=137). The highest coefficients along each axis are displayed in boldface.

	Axis 1	Axis 2	Axis 3
Variance explained	60.8 %	14.3 %	9.3 %
Vegetation density in Stratum1 (0-1m)	0.334	-0.103	-0.189
Vegetation density in Stratum2 (1-2m)	0.370	-0.072	-0.061
Vegetation density in Stratum3 (2-5m)	0.170	0.041	0.085
Vegetation density in Stratum4 (sub-canopy)	0.314	0.108	0.037
Vegetation density in Stratum5 (canopy)	0.434	0.071	0.084
Height of upper canopy	-0.079	-0.256	0.182
Proportion of sky visible from ≈ 1.8m height	0.316	0.059	0.128
Number of tree stems within 5m radius	-0.067	0.287	0.134
Abundance of trees with plank buttress roots	**0.596**	-0.222	0.256
Abundance of trees with spur buttress roots	**0.574**	-0.095	0.228
Abundance of single-stemmed palms	-0.202	**0.483**	-0.117
Abundance of multi-stemmed palms	**0.463**	0.171	-0.158
Abundance of woody lianas	**0.487**	-0.238	-0.185
Abundance of ground ferns	**0.497**	0.364	**-0.534**
Abundance of shrubs	-0.226	**-0.497**	**-0.657**
Abundance of seedlings	-0.043	-0.063	0.327
Abundance of moss	**0.562**	0.114	-0.213
Abundance of climbing palms	**0.609**	-0.110	-0.264
Abundance of fan palms	-0.010	**0.387**	0.232
Abundance of tree ferns	0.389	**0.392**	**-0.415**
Abundance of pandans	**0.547**	0.326	-0.148
Abundance of strangler fig trees	0.444	-0.008	-0.084
Abundance of lichens	0.342	0.238	-0.064
Abundance of all epiphytes	**0.619**	-0.375	0.285
Abundance of vines with thorns	0.358	-0.185	-0.118
Abundance of *Acacia* spp.	**-0.637**	0.118	0.223
Abundance of *Eucalyptus* spp.	**-0.591**	-0.009	0.144

The influence of environmental variables on these major vegetation gradients (represented as NMDS axes scores) was explored by regression tree analysis. Environmental variables included in the models were landform, slope, northness, eastness, altitude, soil nutrient level, mean driest quarter rainfall, and degree of soil drainage. The regression tree is summarized in Figure 4.2, and explains 67% (naïve error) of the variation in the dependent variable. The prediction error (cross-validated error) was 70%, which indicates substantial variability in the dataset. Mean driest quarter rainfall led to a split in transects along the major vegetation gradient (Axis 1), and explained 53% of the variation along Axis 1. Regression trees (not shown) were fitted to Axis 2 and Axis 3, but explanatory power (20.1% and 16.3%, respectively) and very high predictive errors, showed that negligible relationships existed between these gradients and the environmental variables.

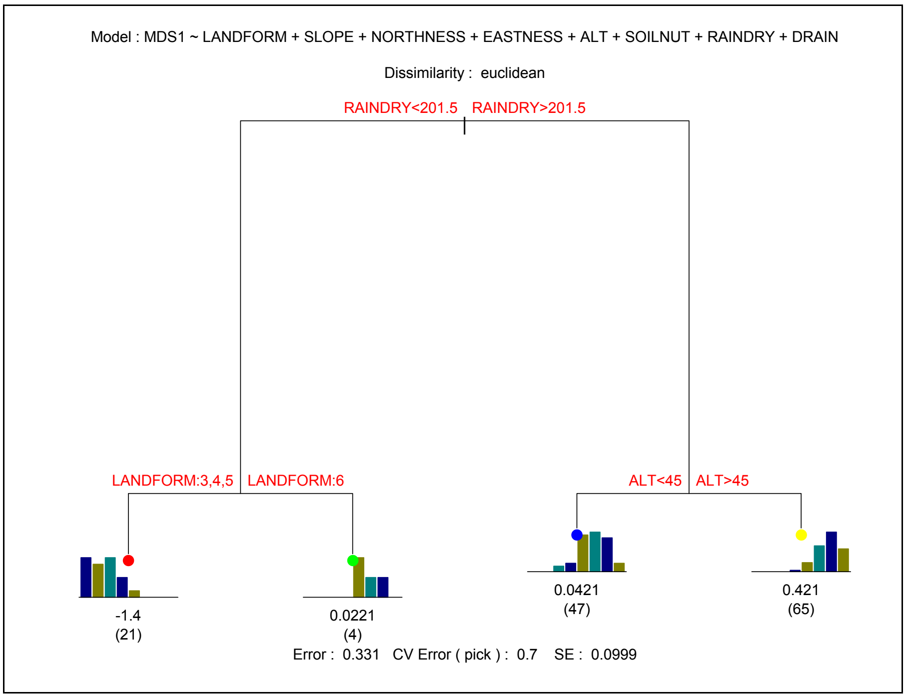

Figure 4.2 Regression tree analysis of Axis 1 of the Non-Metric Multidimensional Scaling of all vegetation variables over all transects (n = 137). Explanatory variables chosen in the model were altitude, landform, slope, soil nutrient status, mean driest quarter, drainage, and two derived aspect variables (northness and eastness). The splits are labelled with the explanatory variables determining the split, and the value of the variable at which the split occurs. Leaves are labelled with the mean response variable score (NMDS Axis 1) and number of cases in the group, and the reductions in residual SS at each split are represented by the relative lengths of the vertical lines (branches) below each split. Each histogram represents the distribution of Axis 1 at that leaf. Distance measures are Euclidean, and cross validation is by sites.

Therefore, the major vegetation gradient, representing a change from mixed rainforest with *Acacia* spp. and *Eucalyptus* spp. emergents and few growth forms to complex mesophyll vine forest (Tracey 1982) with a wide variety of growth forms, is driven primarily by a change in rainfall. This splits the transects into two, more homogeneous groups. However, within the drier sites, some differentiation occurs on the basis of topology. Among these transects, those in gullies (category 6) split out from the others, with higher Axis 1 scores. Therefore, within areas of drier rainfall, transects in or near gullies are characterized by a larger amount and variety of growth forms and structural features, and a virtual absence of *Acacia* spp. and *Eucalyptus* spp. A further split occurs within the transects in the wetter areas, with those sites above 45 m sea level containing greater abundances of growth forms that prefer moister microclimates, and denser foliage throughout the strata. However, as demonstrated by the shallow branch, this factor explains a small amount of the variability of Axis 1.

To further explain the nature of the regression tree, the relationships between NMDS Axis 1 and the environmental variables used in the splits are shown in Figure 4.3, where numeric and categorical variables are shown on scatterplots and error bar charts respectively. Mean driest quarter rainfall, the strongest explanatory variable, shows a major difference between those sites experiencing < 200 mm and those experiencing > 200 mm (Figure 4.3a). Although the split is recorded as 201.5 mm (Figure 4.2), the actual threshold can be seen in Figure 4.3a lying between 164 and 239 mm, due to the extremely sharp rainfall gradient in that area. Of further note in Figure 4.3a are the outlying transects of Site 5 (identified), with higher Axis 1 scores. Within the 25 transects within drier areas, the outliers identified in Figure 4.3a all lie in gullies, whereas all other transects are found on valley flat, plain and gentle hillslope landforms. Figure 4.3b shows that among these drier-area transects, those in gullies show significantly higher Axis 1 scores than those on other landforms (Kruskal-Wallis Test; $x^2 = 10.007$, df = 3, $P = 0.019$).

In wetter areas, the split between transects at altitudes less than and greater than 45 m above sea level was shown to be weak by the length of the branches on Figure 4.2. This is supported by Figure 4.3c, which demonstrates the weak logistic relationship between altitude and Axis 1 scores within transects in wetter areas. In higher rainfall areas, there were no significant differences in Axis 1 scores between transects on different soil types, as shown in Figure 4.3d (Kruskal-Wallis Test; $x^2 = 7.387$, df = 3, $P = 0.061$). Although soil differences do not bear any apparent relationship to Axis 1 scores, this plot is included for comparative purposes, and because this variable is widely considered important in influencing the structure of tropical rainforests.

Vegetation structure was examined at the landscape (patch) scale for groupings and gradients. After examining ordination plots and cluster dendrograms, and to allow comparison with the transect analysis, the K-means grouping level was again set at four. The clustering of sites (Figure 4.4) broadly matches the clustering of transects (Figure 4.1), with Group1 again representing the mixed rainforest with a tall, open canopy comprising *Eucalyptus* spp. and *Acacia* spp., and few special growth forms (see Table 4.1). Once again, Site 7 forms its own cluster, as was the case with the Site 7 transects in Figure 4.1. This site was characterised by a very low, relatively open canopy consisting mainly of palms, a clear understorey, and a relatively low variety of growth forms. The other anomalous site is Site 11, which had extremely dense under- and midstoreys, a low, sparse canopy with abundant palms, abundant thorny vines and climbing palms, and low numbers of stems. Unlike Site 7, however, palms at this site did not make up the entire canopy.

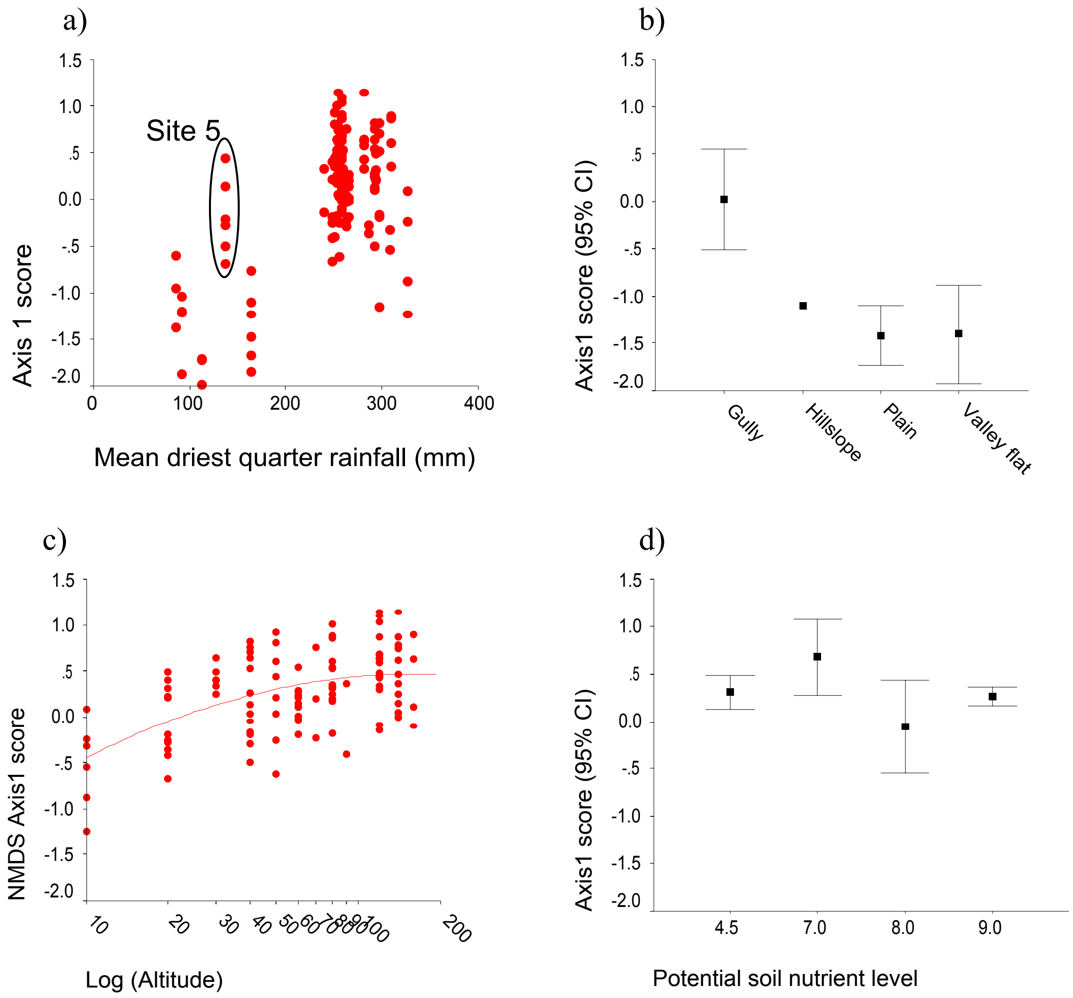

Figure 4.3 Numeric and categorical environmental variables responsible for regression tree splits, and their relationships to NMDS Axis 1 scores. They are a) mean driest quarter rainfall over all sites (split 1), b) landform type over the drier subset of sites (split 2), c) altitude within the wetter subset of sites (split 3), and d) potential soil nutrient levels within the wetter subset of sites. Refer to Figure 4.2 for numbers of cases.

The major difference between the clustering of transects and clustering of sites, is the merging of Groups 3 and 4 at the site level. Clearly, the subtle changes in canopy closure and growth forms occur at a sub-patch level, and this heterogeneity is lost upon aggregating the data to a patch (site) level. This cluster group (Group 2) comprises nearly all of the mesophyll sites. This group is characterised by dense under and mid-storeys, a less closed canopy, but one that is still more closed than that of the other cluster groups, and a high abundance of a variety of growth forms such as climbing pandans, spur and plank roots, multi-stemmed palms, and climbing palms.

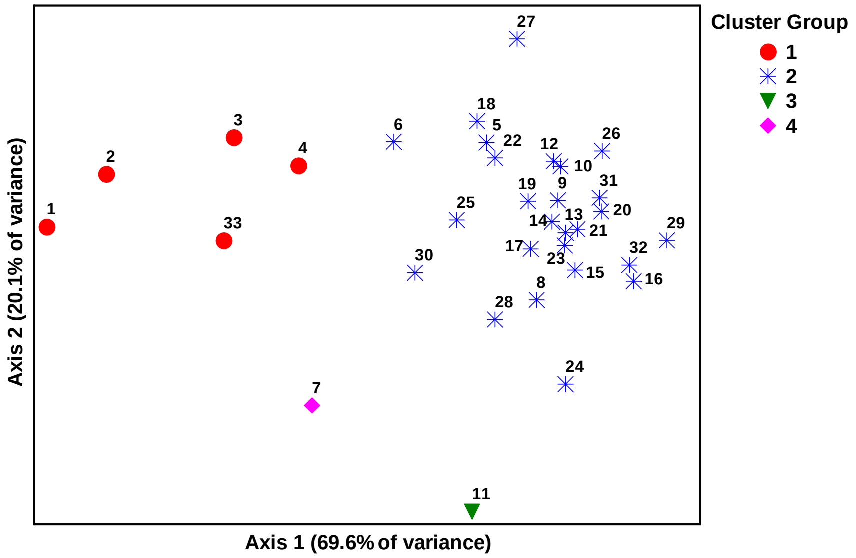

Figure 4.4 Non-metric Multidimensional Scaling plot of vegetation at all sites (n=33) based on all vegetation variables. K-means Classification groups are identified by symbol, and variables are standardized by maximum (0-1). Stress = .13

Figure 4.4 shows that, as with the vegetation analysis by transect, there is substantial agreement between the cluster and ordination. The major vegetation axis (Axis 1) describes 69.6% of total variation. This axis correlates negatively with the abundance of *Acacia* spp. and *Eucalyptus* spp., and positively with a range of structural features and growth forms (Table 4.6). Thus, in common with the analysis at the transect level, Axis 1 represents a gradient from mixed, less complex forest with emergent *Eucalyptus* spp. and *Acacia* spp. and few structural features and growth forms, to complex forest containing an increased amount and variety of growth forms and structural features. Axis 2 describes 20.1% of the variation, and correlates positively with the abundance of tree ferns, pandans, strangler figs and ground ferns (Table 4.6). Axis 2 contrasts with Axes 2 and 3 of the transect ordination, which is related to the densities of single-stemmed palms, fan palms, tree ferns, ground ferns and shrubs (Table 4.5).

The influence of environmental variables on these major vegetation gradients by site (represented as NMDS axes scores) was again explored by regression tree. The regression tree with Axis 1 scores is summarized in Figure 4.5, and explains 66.8% of the variation along this gradient. The model retains strong predictive power, represented by the cross-validated error of 0.471; a mean driest quarter rainfall threshold of 201.5 mm drives the sole significant split. A regression tree of the same environmental variables (not shown) failed to explain variation along the gradients of Axis 2 (naïve error = 31.8%, with a cross validated error of 1.26, meaning that there is no predictive power in the model).

Table 4.6 Spearman correlation coefficients between the two vegetation ordination axes (gradients) from the Non-Metric Multidimensional Scaling and the included vegetation components for all sites (n=33). The highest coefficients along axes are displayed in bold type.

	Axis 1	Axis 2
Vegetation density in Stratum1 (0-1m)	0.433	-0.150
Vegetation density in Stratum2 (1-2m)	0.447	-0.214
Vegetation density in Stratum3 (2-5m)	0.280	-0.074
Vegetation density in Stratum4 (sub-canopy)	0.469	0.250
Vegetation density in Stratum5 (canopy)	**0.599**	0.351
Height of upper canopy	-0.275	-0.310
Proportion of sky visible from ≈ 1.8m height	**0.493**	0.053
Number of tree stems within 5m radius	0.034	0.299
Abundance of trees with plank buttress roots	**0.459**	-0.337
Abundance of trees with spur buttress roots	**0.589**	-0.228
Abundance of single-stemmed palms	-0.286	0.147
Abundance of multi-stemmed palms	**0.487**	0.086
Abundance of woody lianas	**0.694**	-0.330
Abundance of ground ferns	0.423	**0.452**
Abundance of shrubs	-0.136	-0.317
Abundance of seedlings	-0.182	-0.369
Abundance of moss	**0.602**	0.222
Abundance of climbing palms	**0.777**	-0.102
Abundance of fan palms	-0.063	0.078
Abundance of tree ferns	**0.545**	**0.681**
Abundance of pandans	**0.501**	**0.588**
Abundance of strangler fig trees	**0.524**	**0.455**
Abundance of lichens	**0.446**	0.255
Abundance of all epiphytes	**0.551**	-0.204
Abundance of vines with thorns	**0.455**	-0.230
Abundance of *Acacia* spp.	**-0.668**	0.098
Abundance of *Eucalyptus* spp.	**-0.622**	-0.058

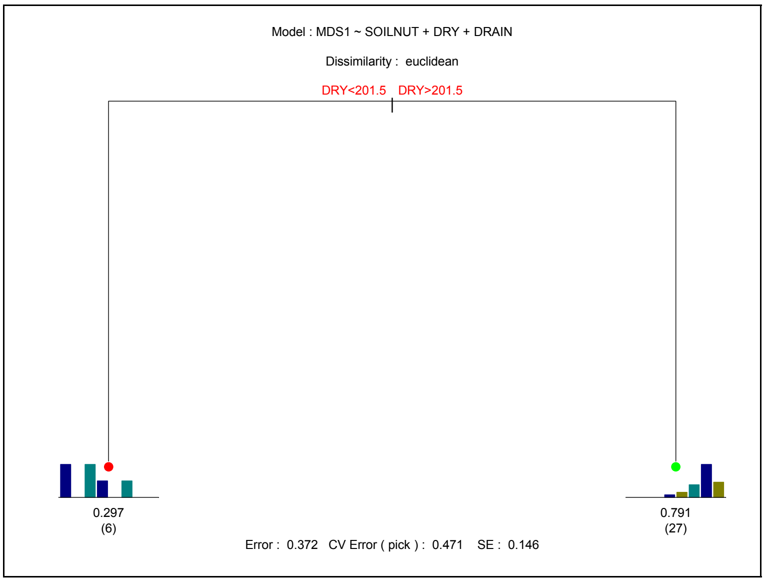

Figure 4.5 Regression tree analysis of Axis 1 of the Non-Metric Multidimensional Scaling of all vegetation variables over all sites (n = 33). Explanatory variables chosen in the model are altitude, landform, slope, soil nutrient status, mean driest quarter, drainage, and two derived aspect variables (northness and eastness). Each histogram represents the distribution of Axis 1 values at that leaf. Distance measures are Euclidean, and cross validation is by sites (see Figure 4.2 caption for detailed explanation).

The clear differences in vegetation structure between mesophyll and mixed sites (Figure 4.1) demanded that the bird assemblages be analysed separately in each habitat. Therefore, the vegetation structure among the complex mesophyll sites (Groups 2 and 3 from Figure 4.1) required reduction, if possible, to a few summary variables that represented the major structural gradients. In this instance the site differences and gradients are less clear-cut (Figure 4.6). The first three axes of the NMDS explain 90% of the variation among mesophyll sites (Table 4.7), although no particular gradient dominates, as was the case with the previous analyses of all sites and transects.

The strongest axis (Axis 2) explains 36% of the variation, and correlates positively with plank and spur buttress roots, abundance of epiphytes and numbers of seedlings, and negatively with abundance of ground ferns, abundance of tree ferns, and abundance of single-stemmed palms. Axis 1 explains 28% of the variation, and correlates with canopy closure and abundance of moss, tree ferns, strangler figs and thorny vines. Axis 3 explains 26% of the variation, and correlates with the abundance of multi-stemmed palms, fan palms and pandans, and negatively with the abundance of thorny vines. Once again, the K-means clusters correspond strongly with the site ordination (Figure 4.6).

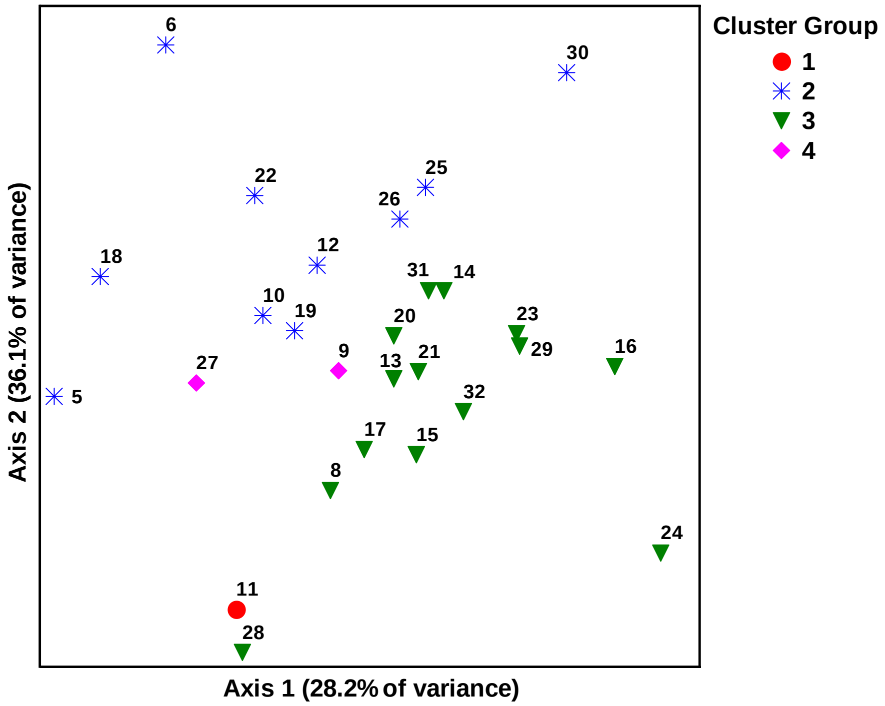

Figure 4.6 Non-metric Multidimensional Scaling plot of vegetation at all mesophyll rainforest sites (n=27) based on all vegetation variables. K-means Classification groups are identified by symbol, and variables are standardized by maximum (0-1). Stress = .11

Table 4.7 Spearman correlation coefficients between the three vegetation ordination axes (gradients) from the Non-Metric Multidimensional Scaling and the included vegetation components for mesophyll rainforest sites (n=27). The highest coefficients along each axis are displayed in bold type.

	Axis 1	Axis 2	Axis 3
Variance explained	28.2 %	36.1 %	25.7 %
Vegetation density in Stratum1 (0-1m)	-0.174	-0.184	0.244
Vegetation density in Stratum2 (1-2m)	-0.336	-0.027	0.294
Vegetation density in Stratum3 (2-5m)	-0.124	0.216	-0.017
Vegetation density in Stratum4 (sub-canopy)	**0.764**	0.083	-0.300
Vegetation density in Stratum5 (canopy)	**0.849**	0.223	0.046
Height of upper canopy	-0.101	0.463	0.127
Proportion of sky visible from ≈ 1.8m height	**0.514**	0.401	-0.182
Number of tree stems within 5m radius	0.241	0.047	-0.113
Abundance of trees with plank buttress roots	0.034	**0.570**	0.119
Abundance of trees with spur buttress roots	0.096	**0.446**	0.227
Abundance of single-stemmed palms	-0.369	**-0.510**	0.175
Abundance of multi-stemmed palms	-0.191	-0.277	**0.424**
Abundance of woody lianas	0.103	-0.007	-0.159
Abundance of ground ferns	0.387	**-0.609**	-0.043
Abundance of shrubs	-0.369	-0.147	-0.360
Abundance of seedlings	-0.144	**0.527**	0.244
Abundance of moss	**0.425**	-0.192	0.167
Abundance of climbing palms	0.106	-0.389	0.313
Abundance of fan palms	-0.248	0.001	**0.446**
Abundance of tree ferns	**0.612**	**-0.473**	0.252
Abundance of pandans	0.397	-0.375	**0.421**
Abundance of strangler fig trees	**0.681**	-0.044	0.136
Abundance of lichens	0.223	-0.118	0.200
Abundance of all epiphytes	0.191	**0.700**	0.163
Abundance of vines with thorns	**0.431**	-0.018	**-0.726**
Abundance of *Acacia* spp.	-0.346	-0.286	0.378

Structural heterogeneity

The 411 points among all 137 transects were subjected to a PCA based on the eight structural measures. Although the first three orthogonal axes summarized 66% of the total variation, all eight axes were utilized to maximize the variation, and to allow the use of the eigenvalues as a weighting mechanism. Likewise, all 11 axes derived from the PCA of the structural and growth form variables were retained for calculating distance measures, and were also weighted by their eigenvalues.

Mean relative heterogeneity within transects (represented by mean Euclidean distance measures) was 3.15 ± 0.10. Mean heterogeneity within sites was 3.57 ± 0.16 for the eight structural measures and 4.00 ± 0.16 for the structural measures combined with summary variables for morphological types. The different measures of heterogeneity were retained as vegetation variables for later analysis against environmental variables, and for use as explanatory variables in the bird assemblage analysis in Chapter 7.

Correlations between the different measures of horizontal heterogeneity and the area of patches were weak (Table 4.8). This indicates that, as far as later species-area relationships are concerned, these are most likely due to the area effect and not the effects of habitat heterogeneity.

Table 4.8 Spearman rank coefficients of heterogeneity measures against patch area and core area measures for all sites (n = 33) and mesophyll rainforest sites (n = 28). Significant correlations are marked in bold.

	Area	50m Core Area	100m Core Area
All Sites			
Mean heterogeneity (structural variables)	0.10	0.06	0.05
Maximum heterogeneity (structural variables)	0.26	0.23	0.23
Mean heterogeneity (structural variables and sums of growth forms)	0.12	0.07	0.07
Maximum heterogeneity (structural variables and sums of growth forms)	**0.36**	0.32	0.33
Mesophyll Rainforest Sites			
Mean heterogeneity (8 structural variables)	0.05	0.01	-0.01
Maximum heterogeneity (8 structural variables)	0.20	0.18	0.18
Mean heterogeneity (structural variables and sums of growth forms)	0.05	0.01	-0.01
Maximum heterogeneity (structural variables and sums of growth forms)	0.34	0.33	0.34

At the patch scale, sites 30, 8, 24, 26, 20 and 25 were the most heterogeneous (measured by the maximum Euclidean distance between points within each site), while sites 11 and 6 were the most homogeneous. Regression trees were employed to seek relationships between heterogeneity measures and environmental variables, but they found no identifiable relationship between measures of heterogeneity and any of the environmental variables, including whether the transect was an edge or interior transect. By transect, only 13% of the variation in mean heterogeneity calculated from the structural variables, and by site 26% of the variation in structural variables, could be explained by the environmental variables. The cross-validated (predictive) error of 1.26 inferred that that there is little or no predictive power in the model. In other words, vegetation structural heterogeneity appeared little affected by the measured environmental variables.

4.4 Discussion

General characteristics

This thesis focuses primarily on bird assemblage responses to spatial arrangement of the rainforest habitat, so study sites were chosen partly for their relative homogeneity. However, vegetation will always differ to some degree between sites, with characteristics dependent on any of the environmental factors mentioned in the introduction, or due to localized stochastic processes such as treefalls (Denslow 1987). Nevertheless, outside the major delineation between the mixed forest of the northern sites and the mesophyll sites in the southern areas, few strong vegetation gradients were expected. Although the study area lies on a range of soil types, slopes range from 0 degrees to 20 degrees, and average annual rainfall ranges from 1995 mm (86 mm in dry season) to 3965 mm (309 mm in dry season), subtle structural differences caused by these factors were expected to be masked by the effects of storm damage.

Throughout the Wet Tropics lowlands, and particularly within the study area, cyclones have strongly altered aspects of rainforest structure. The frequency of canopy gaps, and the often-dense understorey and mid-storeys with abundant *Calamus* spp. and other disturbance-adapted plants demonstrate this. This contrasts with anecdotal descriptions from landholders of clearer understoreys beneath closed canopies at some sites prior to the 1986 cyclone (W. Brockett, G. Wolsey, pers. comm.). Virtually the entire area from Mena Creek in the south to north of Babinda was subjected to this most recent severe storm, although localized effects within this area are haphazard and difficult to quantify with respect to variables such as slope, aspect, and position in relation to the path of the cyclone centre.

Among all transects, vegetation is present to some degree in all five strata, but the strata are not clearly defined, again probably because of the impact of cyclones. The effect of an individual cyclone ranges from foliage loss (Askins & Ewert 1991) to the snapping or uprooting of large trees (Will 1991) causing a considerable reduction in upper canopy cover (Brokaw & Walker 1991). This is reflected in the low canopy density relative to all other stratum densities (Table 4.4). Many of the growth forms that require darker, more humid microclimates, such as ground ferns, epiphytes and moss were widely (present along most transects) but very sparsely (low relative abundance) distributed. This may suggest (especially within a fragmented environment) that the potential exists for these growth forms to be far more abundant if the cyclone regime allowed the development of more consistently suitable microclimates.

Vegetation similarities and characteristics at the site and transect levels

As expected, the northern group of five sites differed substantially in structure and floristics from the remainder. This was found at both the transect and the patch scale. Although these sites contained a rainforest understorey and midstorey, the canopy was dominated by *Eucalyptus* spp. and *Acacia* spp., and they lacked the range of growth forms characteristic of complex rainforests. The other strongly divergent site was Site 7, with a very low canopy composed largely of single-stemmed palms. These six sites were therefore removed from major quantative analyses of the bird assemblages in later chapters, and the five northern sites were analysed separately where appropriate.

Site 11, although splitting out at the site level, did not differ substantially from the major group of mesophyll sites along the major axis that separated these from the northern sites. Although it contained a very low canopy and significant numbers of single-stemmed palms, the canopy mainly consisted of rainforest trees, and a range of growth forms were evident. Therefore, this site was retained for further analysis with the bird assemblages.

The major vegetation differences occurred at a landscape (site) scale, as evidenced by the similarities in the general trends between site and transect groupings and ordination. In both cases, the mixed sites and Site 7 clearly differed. The major difference between the analyses at the two scales was that, at the site scale, two large groups of mesophyll sites merged. This was most likely due to relatively small levels of internal heterogeneity that were evident in 12 of the 27 sites, which contained transects in both Group 2 and Group 3 of the transect analysis (Figure 4.1). Group 2 was characterised by a slightly denser canopy and subcanopy, and more abundant ground ferns, moss, tree ferns, pandans, strangler figs and thorny vines, while Group 3 was characterised by greater numbers of multi-stemmed palms, fan palms, and *Acacia* spp.. Group 3 contained a higher proportion of edge transects (48%) than did Group 3 (39%), which may have contributed to the within-patch variation among mesophyll sites, although this is somewhat speculative. Overall, though, the small within-patch variation revealed by both the ordination and classification was expected, as these sites were chosen for their relative homogeneity.

Environmental variables

Of the measured environmental variables, rainfall explained the major delineation in vegetation structure between mesophyll vine forest and mixed rainforest. However, this value (driest quarter mean = 201.5 mm) is imprecise, as there exists a very sharp rainfall gradient in the Fishery Falls area (Figure 2.3, Figure 2.5). The threshold value of rainfall that explains the present distribution of the rainforest types lies in the range of (164-239 mm). This general result is unsurprising, since other studies have demonstrated strong effects of rainfall gradients on rainforest flora in a range of locations (e.g., Swaine 1996, Dumetz 1999, Mackey 1993). Condit (1998) has even documented significant decreases in the abundance of some rainforest species in Panama because of decreasing rainfall and lengthening dry seasons.

In this study, however, the total mean annual rainfall levels (>2000mm) in this area are all within a range that in other areas is adequate for the presence of rainforest. For example, some Guinean-Congolian rainforests of Central and West Africa receive as little as 1600 mm annually with strong seasonality (Mabberley 1992), and environmental modelling of rainforest distribution in the Wet Tropics has predicted that these areas should in the absence of human interference support closed forest (Hilbert & van den Muyzenberg 1999).

The presence of mixed forest in the north of the study area is most likely due to the presence, and then subsequent cessation some 50 to 100 years ago, of Aboriginal burning practices (Stocker & Unwin 1989). Sclerophyll plants are usually unable to germinate where rainforest is present due to their need for light; however, they are generally fire tolerant, whereas rainforest tend to be sensitive to fire (Webb 1968). Therefore, prior to European settlement of the area, these burning practices allowed the sclerophyll communities to dominate, whereas since the cessation of burning, the more aggressive rainforest has in many areas of this region encroached upon sclerophyll communities (Stocker & Unwin 1989). Rather than directly limiting the extent of rainforest through insufficient moisture, the lower rainfall in the north of the study area likely helped to create a rainforest community that at times of water stress (such as droughts) was sufficiently dry to allow fire to penetrate this rainforest, destroy most of the rainforest plants, and allow sclerophyll communities to emerge. Therefore rather than directly limiting the extent of rainforest, rainfall differences may have limited the distribution of these rainforest types given the fire regime that was present. In this northern part of the study area, further lack of fire will probably lead to the eventual succession of the *Eucalypt* spp. and *Acacia* spp. canopy by rainforest species, as has been found in other areas of northern Queensland (Harrington & Sanderson 1994, Russell-Smith *et al.* 2004).

Unsurprisingly, within the drier sites, only topography (in the form of a gully) was shown to influence the distribution of rainforest types. Topography has often been shown to be important to rainforest structure and floristics (e.g., Clark *et al.* 1995, Poulsen 1996) by affecting hydrology, soil structure or exposure (Webb *et al.* 1999). In this instance, it seems that the moister microclimate in the broad stream gully at Site 5, or the sheltering effects of the topography itself, may have protected this vegetation from fire intrusion.

Within the wetter sites, only altitude, of the environmental variables, explained differences in the mesophyll rainforest structure, with rainforest at higher elevations (>45 m) containing higher Axis 1 values (increased buttress roots, multi-stemmed palms, moss, climbing palms and epiphytes). This trend may have been because most of these sites lie on rich basalt soils. Alternatively, it may be due to drainage, not under normal circumstances, but during extreme events, which were not picked up during these surveys.

Variable reduction

A major aim of this chapter was to summarise multiple vegetation characteristics into a few meaningful variables to with which to compare characteristics of the bird assemblage. As the mixed forest clearly differed from the mesophyll vine forest, it was appropriate in later analysis to relate the mesophyll sites to the bird communities separately, and to seek summary vegetation variables from within these 27 sites.

Within the mesophyll sites, structural patterns were unclear, with three gradients summarising similar proportions of the overall variation. The most explainable Axis (Axis 1) represented a gradient from high to low canopy closure. Higher scores on this axis represent a thicker and more closed canopy, and a higher abundance of moss, tree ferns, strangler figs and thorny vines. In this case, the open canopy of some sites (resulting primarily from storm damage) will lead to understorey conditions (hotter and less humid) that are unsuited to the growth of moss and tree ferns (Hylander *et al.* 2005), and strangler figs are thought to be particularly vulnerable to the effects of high winds (Pavelka & Behie 2005). The other two major vegetation gradients are more difficult to explain, possibly due to the deliberate selection of sites containing relatively similar vegetation, which makes strong, interpretable relationships less likely.

Structural heterogeneity and sub-transect (point) patterns.

Structural heterogeneity was calculated primarily as a vegetative variable with which to compare the bird assemblage, but considerable heterogeneity was found within transects as well as within patches. Not surprisingly, transects, with their smaller spatial scales, were less heterogeneous than patches, but heterogeneity within transects remained considerable. This may be because remnant habitat (and this area is no exception) frequently includes streams or gullies and the areas around them, due to their unsuitability for some forms of agriculture. This results in very small-scale (tens of metres) variation in landform, which can then influence vegetation structure. Conversely, treefall gaps, which are characteristic of tropical forests, and often are in the range of 80-220 m^2 (Schemske & Brokaw 1981) will also create heterogeneity along a transect where the transect passes through the gap.

Conclusions

The major vegetation difference in the study area, not surprisingly, consisted of the mesophyll vine forest across most sites, and mixed forest (rainforest with *Eucalyptus* spp. and *Acacia* spp. emergents and a lack of specific growth forms) in the five northernmost sites. These two groups of sites were therefore separated in later analyses. This major difference was mainly due to an interaction between rainfall and burning, rainforest growing beneath existing sclerophyll plants following the cessation of indigenous burning. If fire remains absent, rainforest species will eventually succeed the *Eucalypt* spp. and *Acacia* spp. canopy.

Among the mesophyll rainforest sites, variation was modest, in line with the site-selection goal of minimising vegetation heterogeneity. The main vegetation differences occurred at a landscape (site) scale rather than at the transect scale. Within the mesophyll sites, cyclone disturbance has resulted in many cases in a broken canopy, dense understorey and mid-storeys, ill-defined strata, and abundant *Calamus* spp. and other disturbance-adapted plants.

Nevertheless, the mesophyll transects formed two major groups, with one group characterised by denser canopy and subcanopy and higher abundances of ground ferns, moss, tree ferns and pandans, all of which prefer humid, darker conditions. Other within-site variation in the mesophyll sites was probably due to subtle edge effects.

Among the drier sites, topology influenced the diversity of growth forms, probably due to a combination of shelter from fire and wetter microclimate. Of the wetter sites, those above 45m in altitude contained greater complexity, most likely due to better drainage in these areas.

Chapter 5: Characteristics of the lowland bird assemblage

5.1 Introduction

Bird species distributions and habitat preferences in the Wet Tropics are reasonably well known (Williams *et al.* 1996). During the last 30 years, a number of studies have examined broad habitat associations of rainforest bird assemblages (Crome 1990), foraging ecology (Crome 1978, Frith 1984), and niche occupation and diversity (Driscoll & Kikkawa 1989, Kikkawa 1990). Crome (1978) examined bird foraging ecology in lowland rainforest, while Frith (1984) examined a similar question in upland rainforest. Other studies have looked at the association between birds and vegetation structure (Kikkawa 1968, 1982), and altitudinal distributions of birds (Boles & Longmore 1989, Henriod 1998). Recent studies have examined broad patterns of diversity throughout the Wet Tropics (Williams *et al.* 1996), and the determinants of patterns of vertebrate endemism throughout the region (Williams & Pearson 1997).

However, most quantitative knowledge is confined to specific locations popular for research and bird watching such as the upland areas around Paluma (e.g., Frith 1984), the Atherton Tablelands and Kirrama, and a few lowland areas such as Daintree and Mission Beach (Crome 1978). Ecological studies of birds at the landscape scale in the Wet Tropics have been conducted exclusively in upland areas (Isaacs 1994, Crome *et al.* 1994, Laurance *et al.* 1996, Warburton 1997). This chapter introduces the lowland bird assemblages of the wettest section of the Wet Tropics lowlands, examines diversity, assemblage structure and guild structure, compares these patterns to other locations, and seeks to explain some of these patterns.

The lowland avifauna

The avifauna of the rainforests of the Wet Tropics of Queensland is among the most diverse in Australia with about 95 species associated with rainforests or their edges (Kikkawa 1982). Although this richness is high compared to temperate areas, most other mainland tropical rainforest areas of the world have much larger species pools: for example, 370 species in a 1 km^2 plot in Panama (Karr 1977) and 175 species in 2 km^2 in Gabon (Erard 1989). Even elsewhere in the Australasian biogeographic region, Bell (1982) recorded 165 species within 2.5 ha of rainforest in Papua New Guinea. Furthermore, Australian rainforests contain relatively few species that specialise in rainforest habitat (Brereton & Kikkawa 1963, Driscoll & Kikkawa 1989).

The depauperate nature of this assemblage is probably due not only to the relatively small area of rainforest in the Wet Tropics, but also to species sifting, which has resulted from periodic contractions of the Wet Tropics rainforests to a few small refugia (Williams & Pearson 1997). There is much evidence from pollen records (Kershaw 1993, 1994), primitive angiosperm distributions (Webb & Tracey 1981) and charcoal remains (Hopkins *et al.* 1993) that Pleistocene climate change caused rainforests in the Wet Tropics to repeatedly contract to upland refugia, followed by later expansions into lowland areas (and other upland areas). These contractions, at least in the case of some reptile taxa, isolated some populations sufficiently for genetic differences to be apparent (Moritz et al. 2000). Since the larger upland isolates contain greater numbers of rainforest species and endemics (Williams & Pearson 1997), and allopatric speciation is unlikely to have occurred in these isolates (Schneider & Moritz 1999), the patterns of endemism in these areas suggest that the smaller isolates were probably subject to greater numbers of extinctions (Williams & Pearson 1997).

Although Williams *et al.* (1996) found no significant difference in bird species richness between uplands (>300m) and lowlands (<300m), the assemblages are quite distinct. Within the Wet Tropics rainforests, 25 species are restricted to upland areas and 10 species are restricted to the lowlands (Kikkawa 1982). Nine endemic species are restricted to upland areas, while only four occur in the lowlands. Notably, all four (Lesser sooty owl, Pied monarch, Macleay’s honeyeater, and Victoria's riflebird) also occur in upland regions. These patterns are believed to be due to the different origins of the upland and lowland assemblages. Upland endemic species are considered vicariant relicts from a connection with upland New Guinea fauna, while non-endemics are allied to temperate Australian rainforests (Kikkawa *et al.* 1981). Bird assemblages of upland areas, therefore, are derived from persistence in isolated populations (Williams *et al.* 1996). The lowland avifauna, on the other hand, is more closely related to Cape York and New Guinea lowland rainforests (Williams *et al.* 1996). Lowland rainforests virtually disappeared during Pleistocene contractions, and their bird species largely resulted from later dispersal from Cape York and New Guinea.

Kikkawa *et al.* (1981) suggested that vagility is greater for non-specialist rainforest species than rainforest specialists, and many of the lowland species are believed to have dispersed southwards from Cape York and New Guinea. Therefore, we might expect that lowland assemblages in the Wet Tropics should be broader in their habitat preferences, not only in comparison to assemblages in more temporally stable lowland rainforest areas on other continents, but also in comparison to upland assemblages in the Wet Tropics. Evidence in Central America has shown that hurricane disturbance can lead to the replacement of interior specialists with edge species and species of secondary growth (Will 1991). Therefore, it might be expected that the regular impact of cyclones over much of the lowlands of the Wet Tropics, will further select for a more generalist assemblage.

Density and extinction vulnerability

Tropical forests generally contain more rare species than are found in similar temperate habitats (Karr 1977), and the proportion of rare species increases with richness (Pearson 1977). Rarity is generally believed to predispose species to local extinctions in fragmented landscapes (Wiens 1989), and there are many examples that support this (e.g., Jones & Diamond 1976, Telleria & Santos 1995, McCoy & Mushinsky 1999). For some species, this is due to specialised requirements such as old or dead trees for nesting (Zarnowitz & Manuwal 1985), large tree trunks (e.g., Jones & Diamond 1976), rare trees (Telleria & Santos 1995), or specific but uncommon prey items (Lovejoy *et al.* 1986, Bierregaard *et al.* 1992). Others, such as forest raptors, require large home ranges, and so are sparsely distributed (Jullien & Thiollay 1996). Birds that best persist in small fragments tend to be the more common generalists (Patterson 1987).

Conversely, Karr (1990) found on Barro Colorado Island (14.8 km^2) that natural rarity did not predispose species to local extinction. However, Barro Colorado is considerably larger and contains greater habitat heterogeneity than sites in the other studies mentioned above, and some succession of habitats has occurred on the island since isolation. Patterns between rarity and local extinction in this case may be confounded by the differing availability of different habitats over time. Edge species, those species only found in areas of multiple tree-falls, and those that occasionally enter primary forest from secondary growth habitat, may naturally be rare in continuous forest (Karr 1977). These species, however, are unlikely to be adversely affected by forest fragmentation, as a major effect of the fragmentation process is the creation of larger amounts of both edge (Wiens 1989) and regrowth (Laurance *et al.* 1996). Although little evidence is available in tropical forests, Lescourret & Genard (1994) found in fragmented temperate forests that while large stands favoured high species richness, forest fragmentation actually favoured naturally rare, albeit edge-requiring species.

Patterns of rarity and local extinction are also influenced by the niche flexibility of some species. Some rarer species may be able to increase their density where potential competitors are absent (Feinsinger *et al.* 1982) and therefore be more able to persist in fragments than naturally more common competitors that, due to other factors such as breeding success or through chance, do not persist.

Therefore, the existence or nature of any significant relationship between density and extinction vulnerability depends on the habitat and resource requirements of species, the extent and variety of habitats within fragments, the nature of the pool of potentially competing species, and the ability of species to broaden their niche in response to the absence of competitors. It is expected, therefore, that the rarity/patch occupancy relationship ought to be stronger when examined only for habitat specialists compared to habitat generalists, and rainforest specialists that are rare in unfragmented habitat are less likely to readily occupy patches than similarly rare habitat generalists.

Aims

The aims of this chapter are to:

- describe the bird assemblages of the study sites, their abundance and richness, and their guild structure;
- compare diversity and assemblage structure: (i) between rainforest and mixed forest in the study area, (ii) within the Queensland Wet Tropics, and (iii) in other tropical regions;
- examine whether species density in unfragmented rainforest affects the abilities of species to occupy fragments; and
- examine whether more spatially or temporally variable species are less able to persist within a fragmented landscape.

Relationships between the avifauna and site characteristics are dealt with in Chapter 7.

5.2. Methods

Bird Counts

Strip transects (100m × 50m) were employed because they have the advantage of covering a relatively large area of forest, and are considered by many to be the most time- and labour-efficient way to census forest birds (Grieser-Johns 1996). This is especially important in diverse tropical rainforests, where many species have patchy distributions, and the thick foliage limits the distance over which a stationary observer can identify species. They can also be quantified to allow estimates of relative abundance.

Mist netting and point counts, although useful in many circumstances, were not utilised in this study. Although free from observer bias, and easily standardised to allow quantitative measures and estimates, mist netting does not provide an unbiased estimate of abundance (Bierregaard & Stouffer 1997). Canopy species and species that rarely fly are under-represented in the sample (Stouffer & Bierregaard 1995a), and net avoidance may also create bias between individuals and species (Pyke & Recher 1984). Although point counts are frequently used in forest habitats (Lynch 1987, Blake 1991, Rumble & Gobeille 1998), and allow the observer to remain stationary and therefore cause fewer disturbances to birds, they have some disadvantages in rainforest habitats. For example, there is less chance of using visual records to support calls of which the observer is unsure, as the observer cannot move; and point counts cover smaller areas, so rarer species are less likely to be identified in larger forest patches (Lynch 1987).

A major concern of strip or line transects is the movement of birds in response to the observer (Karr 1981). Cyclone impacts resulted in all sites being in some stage of succession, with some sites containing an extremely thick understorey (Chapters 2 and 3). To allow easy, silent movement along transects, foliage was cleared along narrow tracks with hedge clippers and secateurs prior to the first census along each transect. Due to the rapid regeneration of colonising species such as *Calamus* spp., further cutting was necessary prior to later survey periods.

In a rainforest, the observer must rely more on calls than visual identifications, so it was therefore particularly important that surveys be done not only when birds were active, but were calling. The most intense period of calling was in the morning, with a smaller and shorter peak in the afternoon. Transects were sampled in the morning between sunrise and approximately 9.30 a.m., with 15 minutes of searching, and in the afternoon between 3.30 p.m. and sunset with 10 minutes of active searching. Only morning surveys were used for abundance measures. The afternoon surveys were conducted to record additional species in patches that may have gone unnoticed during morning surveys.

On fine days, six transects could be sampled each morning between sunrise and 9.30 a.m., and six between 3.30 p.m. and sunset. However, in overcast conditions or where sites were some distance from each other, fewer transects could be sampled. Most bird species decrease their activity during rain or high winds (Karr 1981), so surveys were postponed in such conditions to avoid their confounding effects.

Each transect was sampled twice (morning and afternoon) during each of three sampling periods, making a total of six censuses per transect. The first sampling period was in the late wet season (14-3-97 to 23-5-97). The second sampling period was the mid dry season (17-8-97 to 30-10-97). The third sampling period was the mid wet season (24-1-98 to 21-2-98). Seasonal sampling ensured that winter and summer migrants were included. I made all observations and identifications to minimise observer bias. All bird species identified by sight or call were recorded, and whether they were inside or outside the transect was noted. The few difficult visual identifications were confirmed with a field guide in the field (Slater *et al*. 1995). When a bird was located visually but identification took some time, the stopwatch was stopped, before being switched on once again when searching continued. A morning transect took between 15 and 25 minutes to complete, and an evening transect between 10 and 20 minutes. Where sighted, the vertical position of each bird in the vegetation was recorded, and the distance of the first record of each species from the start of the transect was also recorded from the hip chain. In addition, the distance of each sighted bird from the centre line of the transect was estimated and recorded.

The Little bronze-cuckoo *Chrysococcyx malayanus* and Gould's bronze-cuckoo *Chrysococcyx m. russatus* have virtually identical calls, and are therefore difficult to separate. All visual records, however, were of Gould's bronze-cuckoo, and literature suggests that this subspecies predominates in the lowlands of this area (Nielsen 1996). Therefore, all were assumed to be *Chrysococcyx m. russatus*.

Where richness within sites (patches) is compared with independent variables, it is necessary to ensure that most of the species are recorded. Therefore, species-accumulation curves were calculated for all sites, with samples arranged in chronological order, whether they were morning or afternoon samples. Thus, patches with different numbers of transects (six samples per transect) contain different total numbers of samples.

Species-accumulation curves were therefore generated in PC-Ord 4.0 (McCune & Mefford 1999), and most sites approached an asymptote prior to the end of sampling (Figures 5.1a-d). It should be noted, however, that due to the sampling during different seasons, the smoothing algorithm (500 random subsamples for each subsample size) (McCune & Mefford 1999) will tend to overestimate the total richness, so final richness estimates from rarefaction were not generated. Furthermore, this method will disguise any flattening of an untransformed curve that might be the case in the last couple of samples. In fact, among the smaller sites, only Site 28 (Figure 5.1a) accumulated an additional species (Rainbow lorikeet) in the last two samples. Among the sites with three transects (Figure 5.1b), no new species were recorded during the final two samples.

All sites containing four transects, except Site 7, reached a richness plateau by sample 21 of 24 (Figure 5.1c). Site 7 continued to accumulate species up to and including the last sample, with five new open-country species in the last three samples, although with its fan-palm-dominated vegetation, Site 7 was sufficiently different to warrant removal from later analyses. Furthermore, the Bush hen and White-faced heron are both rare rainforest vagrants in the region

(7 and 1 records, respectively), so they were excluded from most analyses. Of the sites containing six transects, only Site 9 failed to reach an asymptote by the 33rd of 36 samples, with a Pheasant coucal (an open country species) recorded in the 34th sample (Figure 5.1d).

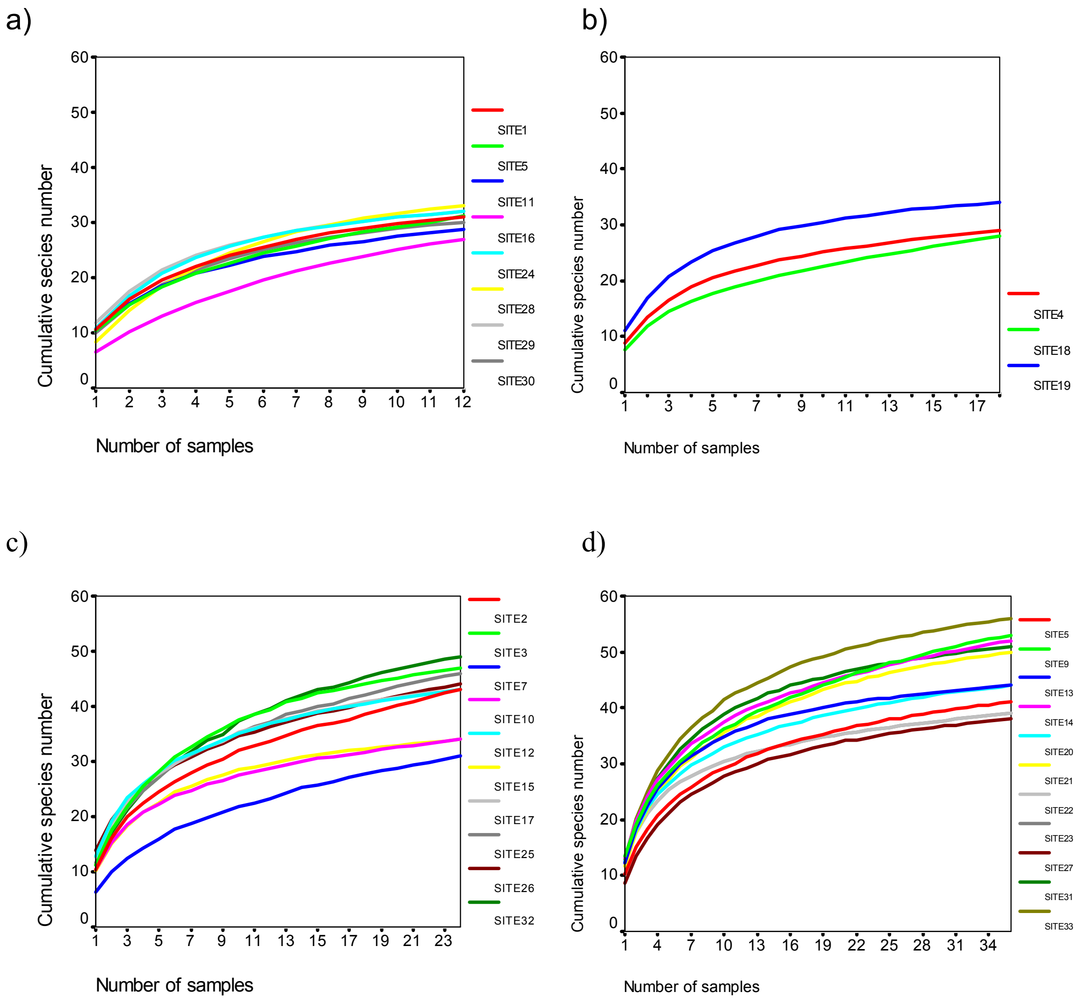

Figure 5.1 Bird species accumulation curves for sites containing (a) two transects; (b) three transects; (c) four transects; and (d) six transects. Curves have been smoothed by subsampling (McCune & Mefford 1999).

Therefore, whilst sites with different numbers of transects were subjected to between 12 and 36 samples over the three sampling periods, the species-accumulation curves are quite similar between sites with different sample numbers, with most sites failing to provide any new species in the final few samples. The patterns reflect the increasing size of the sites and justify the incorporation of greater numbers of transects the larger sites.

Guild Delineation

Bird habitat preferences, feeding habits, migratory habits and other life history characteristics were derived primarily from the literature (Crome 1978, Frith 1984, Laurance *et al.* 1996, Crome *et al.* 1994, Blakers *et al.* 1984, Wieneke 1992, Nielson 1996, Reader's Digest 1986, National Photographic Index of Australian Wildlife 1982, 1985, Boles 1988, Longmore 1991, Crome & Shields 1992, Strahan 1996) and through direct observation. Guild allocations for individual species are described in Appendix 7. It must be noted, however, that migratory status is not known for all species. Furthermore, some populations of a species may migrate, while other populations of that same species may remain resident. Thus, there exists a degree of uncertainty regarding this characteristic.

Foods were categorised into six broad types: i) vertebrates, ii) insects, iii) invertebrates other than insects, iv) fruit, v) nectar, and vi) seeds. Where quantitative data are available, I have included any species in a guild if it gains >10% of food from that source, in common with Brash (1987). However, no quantitative data exists for the majority of tropical birds in Australia, so a species was considered to feed on a particular food type if seen to do so frequently. Where authors describe feeding on a particular food type as 'occasional' then it was assumed to comprise <10% of the total diet, and was therefore discounted.

From these food types, eleven feeding groups were derived, including seven exclusive groups, as follows: i) vertebrate carnivores, ii) insectivores (insects and other invertebrates), iii) mixed carnivores (vertebrate and invertebrate prey), iv) mixed feeders (animal and plant diets), v) frugivores, vi) granivores, vii) mixed plant eaters (more than one plant type). Some species were identified as viii) partial insectivores, ix) partial frugivores, x) partial granivores or xi) partial nectarivores. No species was totally nectarivorous, as all Australian nectar feeders require insects as a protein source (Gilmore 1985).

Habitat preference categories range in a progression from species of open country to rainforest specialists. Habitat 1 = open country (grassland and open woodland), Habitat 2 = variety of open and forested habitats, but not in rainforest, Habitat 3 = only in woodland and open forest, Habitat 4 = variety of habitats, including rainforest, Habitat 5 = mainly in rainforest and other thick vegetation, and Habitat 6 = rainforest only, or dependent on rainforest plants.

Abundance and richness calculation

Although all records were incorporated in overall patch richness analyses, only the morning records within the strip transect were used for quantitative analysis because, in the absence of mark-recapture, one cannot assume that individuals observed in the afternoon censuses have or have not been recorded in the more complete morning census. Richness-per-unit-area measures utilised both morning within-transect data and morning-afternoon combined within-transect data.

Species' relative densities were calculated over all sites, for fragmented sites only, and for contiguous sites. A species density was calculated by adding all 'within strip' records, and then dividing this by the number of 0.5 ha transects, and multiplying by two to achieve a per hectare density. For residents, densities were averaged over the three sample periods, whereas for migrants that appear outside of their peak season, only the season of highest density was included.

Mesophyll rainforest versus mixed forest assemblages

Bird assemblage differences between mesophyll and mixed forests were compared throughout all sites, using the non-parametric Multi-response permutation procedure (MRPP), which is analogous to MANOVA (Zimmerman *et al*. 1985). To examine which species were most characteristic of the mixed forest sites and mesophyll forest sites, an indicator analysis was performed on both groups of sites (mesophyll and mixed forest) using the method of Dufrene & Legendre (1997). For each species, this technique combines site fidelity and site specificity into an indicator value for each group. In addition, sites were also classified by species presence/absence (all records) using K-means cluster analysis, with K-means groups displayed on a detrended correspondence analysis (DCA) ordination scatterplot for visual representation to examine whether all mixed forest sites grouped out from the mesophyll sites. All of the above tests were conducted using PC-Ord (McCune & Mefford 1999).

To further examine species assemblage differences between forest types, but in the absence of fragmentation effects, the unfragmented sites were analysed separately. However, as the unfragmented sites included two mesophyll site and only one mixed forest site, bird assemblages were compared at the transect level, using only the records within the transect to maintain independence. Abundances were aggregated by mean across all sampling periods for each transect, and then compared between those in the two mesophyll rainforest sites (Josephine Falls and The Boulders) and those at the mixed forest site (Behana Creek). Mean species richness per transect was compared between mesophyll and mixed forest control sites using t-tests and, where necessary (frugivores and mixed carnivores), variables were log transformed prior to analyses to obtain normality. Differences in the abundances of individual species between mixed and mesophyll rainforest were tested by Mann-Whitney U test using SPSS 10.0 (SPSS 1999).

Natural density and patch occupancy

To test whether naturally rarer species are less able to occupy isolated patches of rainforest, the density of each species in the three unfragmented sites was calculated as the mean density of each species over all samples within the total area of contiguous habitat sampled (8 ha). In the case of migrants such as the Buff-breasted paradise-kingfisher (latitudinal migrant) or Rufous fantail (altitudinal migrant), only samples in which these species were expected to be present were included.

All species recorded within transects in unfragmented sites were sorted by density, and split into two groups (a rarer and a more common). The mean numbers of patches occupied by each group were then compared using Mann-Whitney tests. In order to test whether this pattern applied to all feeding and habitat guilds, the same procedure was applied to each guild separately.

5.3. Results

Overall Richness and Abundance

In total, from 171 hours of sampling 102 bird species were identified within or on the edge of the rainforest study sites from 16869 records (Table 5.1). Of these species, 95 were recorded in mesophyll rainforest sites, while 77 were recorded in mixed forest sites. Ninety-four species were recorded within strip transects, with slightly lower overall species richness and overall abundance in the mid-wet season sample. Overall, 40.7%, or 6858 records, were obtained within transect strips during the morning censuses and 10949 records (64.9%) within transects during both the morning and afternoon censuses. Eighty-seven species were recorded within transects during the morning counts (85.3% of total richness) and 94 (92.2%) within morning and afternoon censuses combined.

Table 5.1 Richness and abundance of birds over all sampling periods.
Sample 1: Late wet season (April-May 1997); Sample 2: Dry season (August-September 1997); Sample 3: Mid wet season (January-February 1998)

	Total	Total	Records within Transects		Richness within Transects	
Season	Records	Richness	AM	AM & PM	AM	AM & PM
Late wet	5602	86	2405	3952	70	82
Dry	5975	84	2373	3761	72	75
Mid wet	5292	75	2080	3236	66	70
Combined	16869	102	6858	10949	87	94

The majority (83) of species were resident, 73 of which were non-nomadic (Appendix 7). Ten residents were nomadic and all of these, with the exception of the Brown honeyeater, were largely frugivorous (e.g., Wompoo fruit-dove, Superb fruit-dove). Of the 19 probable migrants, three were rare passage migrants (Black-faced monarch, Shining bronze-cuckoo and Satin flycatcher). Seven species were long-distance migrants, while nine were short distance migrants. Some of these were upland and foothill species (e.g., Brown gerygone, Lewin's honeyeater, Shining bronze-cuckoo, and Bridled honeyeater), which all occurred at very low densities. Therefore they were considered to be occasional altitudinal migrants, compared with more regular and common altitudinal migrants such as the Rufous fantail.

Species Abundance and Prevalence

For each species, the number of sites occupied (see Appendix 6) ranged from one to all 33 (mean ± SE = 12.72 ± 1.08, median = 9). Six species were recorded at all 33 sites (Black butcherbird, Figbird, Graceful honeyeater, Varied triller, Yellow-bellied sunbird and Yellow-spotted honeyeater). Thirteen species were found at one site only, and of these, 11 were species that are not usually associated with rainforests. The two exceptions were the Cassowary, which is naturally very rare, and the Little kingfisher, which is a stream specialist and uncommon throughout much of its range (Nielsen 1996). This distribution of species by the numbers of sites occupied was positively skewed (Figure 5.2). The majority of species were recorded at nine or fewer sites, while 25% of species were found in three or fewer sites. Species richness by site ranged from 23 to 56 species (mean ± SE = 39.3 ± 3.2).

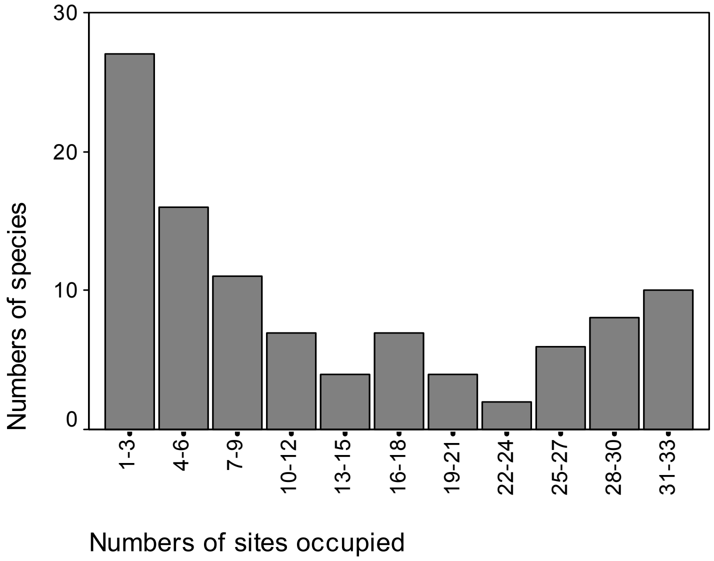

Figure 5.2 Frequency of bird species by numbers of occupied sites.

The bird assemblages were dominated numerically by a relatively small number of species. The seven most abundant species (Graceful honeyeater, Yellow-spotted honeyeater, Little shrike-thrush, Metallic starling, Large-billed scrub-wren, Figbird, and Spectacled monarch) comprised over 50 % of total numbers. Of these, all but the Metallic starling are locally resident (Appendix 7). Conversely, the 26 rarest species (of the 87 species quantitatively sampled) comprised less than 1% of the total numbers of individuals. Most of the rarest species are upland species (e.g., Lewin's honeyeater, Grey-headed robin) or open-country species (e.g., Crimson finch, Black-faced cuckoo-shrike).

Habitat and Functional Guild Summaries

Fifteen of the species recorded in the study sites were obligate rainforest species (14.7%). These species comprised 12% of the total density in the contiguous sites, but only 7% in fragments (Table 5.2). Habitat 4 and Habitat 5 species (variety of habitats including rainforest, and mainly in rainforest and other thick vegetation, respectively) together comprised 53% of species numbers, but these groups comprised the great majority of records (85%).

Habitat groups 1, 2 and 3 comprised 32.3 % of species, but a relatively low proportion of total records (5.17 %), indicating that these birds of the open country are sparsely distributed throughout the study area, averaging 6.5 sites per species. Within the continuous habitat, no Habitat 1 or Habitat 2 individuals, and very few Habitat 3 individuals, were recorded.

Table 5.2 Prevalence and abundance of birds grouped by habitat guild.
Habitats: 1 = open country, 2 = variety of open and forested habitats, but not in rainforest, 3 = only in woodland and open forest, 4 = variety of habitats, including rainforest, 5 = mainly in rainforest and other thick vegetation, 6 = rainforest only, or dependent on rainforest plants.

Habitat	Number of species	Mean nos sites	Density/ha in continuous	Density/ha in patches	Total density/ha all sites	Total number of records
1	14	7.9	0.0	0.9	0.8	461
2	9	6.0	0.0	0.5	0.4	207
3	10	4.8	0.04	0.5	0.4	204
4	25	19.8	15.9	15.9	15.9	7595
5	29	14.1	17.9	15.6	15.9	6783
6	15	12	4.7	2.6	2.9	1619
Total	102	12.7±1.1	38.6	36.1	36.4	16869

The majority of species in the study area were either insectivores or omnivores (33 and 31% of species, respectively), while mixed carnivores and frugivores were moderately diverse (13 and 10% of species, respectively) (Table 5.3). Insectivores, omnivores and frugivores were the most abundant groups, while, although diverse overall, mixed carnivores were relatively sparsely distributed throughout the study area. Vertebrate carnivores were very sparsely distributed, as were granivores, which are almost entirely birds of open country, and only prevalent at edges of patches.

Table 5.3 Prevalence and abundance by birds grouped by feeding guild. For these purposes, mixed carnivores are defined as birds that eat both vertebrate and invertebrate prey, omnivores are species that eat plants and animals, and mixed herbivores pursue more than one type of herbivory.

Guild	Number of species	Mean nos sites	Density/ha in continuous	Density/ha in Patches	Total density/ha all sites	Total records
Vertebrate carnivores	2	4.5	0.0	0.0	0.0	14
Insectivores	34	13.4	14.6	11.8	12.2	4816
Mixed carnivores	13	8.5	0.5	0.4	0.4	391
Omnivores	32	13.5	14.5	13.5	13.6	7566
Frugivores	10	16.2	7.3	8.9	8.7	3203
Mixed herbivores	6	15.3	1.7	1.2	1.2	657
Granivores	5	7.2	0	0.3	0.3	222
Total	102	12.7 ± 1.1	38.6	36.1	36.4	16869

Mesophyll rainforest and mixed forest assemblages

Across all sites (n = 33), substantial differences were found in the bird assemblage between mesophyll rainforest sites and mixed rainforest sites (MRPP, $P < 0.001$). At the five cluster level, the mixed forest fragments, along with two rainforest patches with poor drainage (Site 7 and Site 28) comprised a separate group that diverged most significantly from the unfragmented sites (Figure 5.3). The unfragmented mixed forest site, however, was similar in assemblage structure to the two mesophyll rainforest control sites. Thus, bird assemblages in unfragmented mixed forest sites were similar to those of unfragmented mesophyll rainforest, whereas the bird assemblages of fragments of mixed forest diverged in their structure, from either unfragmented sites of either rainforest type, or fragments of mesophyll vine forest.

The indicator analysis summary in Table 5.4 shows that a number of species strongly characterized mixed forest but not mesophyll vine forest, including the White-throated honeyeater, Yellow honeyeater, Spotted turtle-dove, Peaceful dove, Willy-wagtail, Leaden flycatcher, Brown-backed honeyeater and Brown honeyeater. These are all either open-country or woodland species. On the other hand, the species that characterized the mesophyll vine forest were mostly species strongly and commonly associated with rainforest or other dense habitats, such as the Orange-footed scrubfowl and Macleay’s honeyeater; the exception was the Little shrike-thrush, which favours a range of wooded habitats including rainforest.

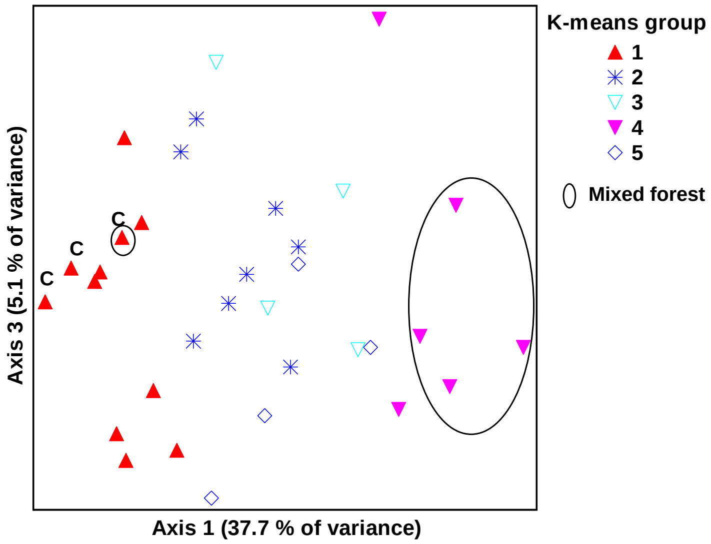

Figure 5.3 Ordination biplot depicting two axes of the DCA (detrended correspondence analysis) of total bird presence/absence among sites. C = Unfragmented (control) sites.

Some species that were found in insufficient numbers to demonstrate significant preferences were nevertheless found in numerous mesophyll sites but no mixed sites, suggesting a preference for mesophyll sites. These included the Eastern whipbird, Red-necked crake, Chowchilla, and Azure kingfisher, all of which are rainforest specialists.

Table 5.4 Significant indicator value results for bird species within mesophyll vine forest and mixed forest as per Dufrene & Legendre (1997), based on presence/absence.

Species	Group	Indicator value (IV)	Randomized mean IV	S.D	*P*
White-throated honeyeater	1	100	17.3	7.4	0.001
Yellow honeyeater	1	67.9	22.8	9.21	0.004
Spotted turtle-dove	1	65.4	24.8	9.61	0.014
Peaceful dove	1	65.4	25.3	9.91	0.017
Willy-wagtail	1	63.1	26.9	9.33	0.017
Leaden flycatcher	1	58.9	29.6	9.96	0.038
Brown-backed honeyeater	1	56.6	15.6	6.38	0.007
Brown honeyeater	1	36.7	13.1	5.5	0.041
Orange-footed scrubfowl	2	89.3	47.2	7.41	0.001
Little shrike-thrush	2	62.5	52.2	2.06	0.014
Spectacled monarch	2	62.5	52.2	2.06	0.014
Grey whistler	2	61.7	48.9	7.07	0.033
Macleay’s honeyeater	2	58.4	47.4	7.65	0.047

Another group of species appeared in at least 12 of the 28 mesophyll sites, and were recorded in the unfragmented mixed forest site, but were completely absent from the mixed forest fragments. These included the Brown cuckoo-dove, Wompoo fruit-dove, Silvereye, Spotted catbird, Pied monarch, Brush turkey, Pale-yellow robin and White-eared monarch. The presence of these and other, rarer species (Chowchilla, Yellow-breasted boatbill, Victoria's riflebird, Black-faced monarch, Barred cuckoo-shrike and Noisy pitta) in unfragmented mixed forest and their complete absence from fragmented mixed forest, indicated that these species largely drive the difference between mixed fragment assemblages and all other sites, including the unfragmented mixed forest site (see Figure 5.3).

Sites in unfragmented mesophyll rainforest contained similar overall species richness to the unfragmented mixed forest (57 vs. 56 species), but there were substantial differences in composition (MRPP, $P < 0.001$ for both abundance and presence/absence per transect). Figure 5.4a and 5.4b illustrate the separation of transects between mixed forest and mesophyll rainforest in DCA ordination space.

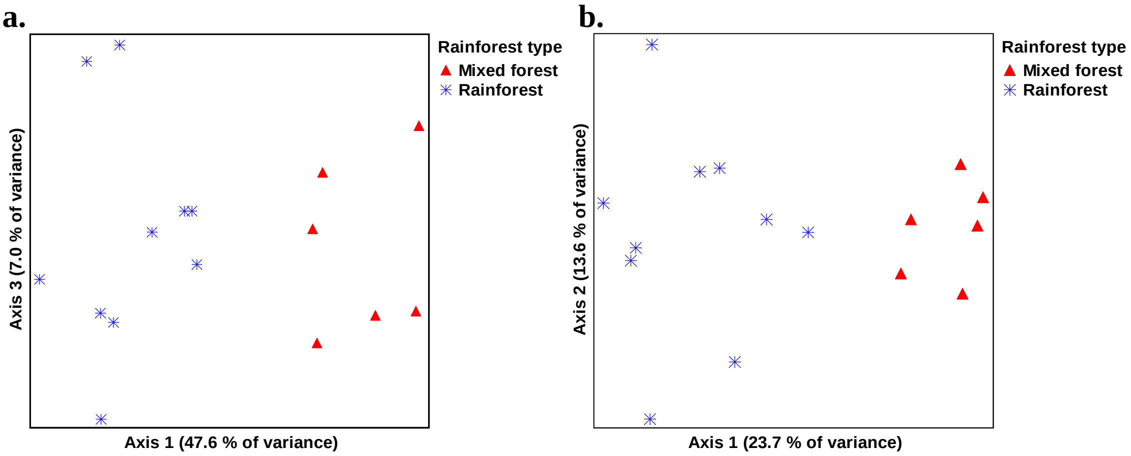

Figure 5.4 Ordination biplot depicting the two major axes of DCAs of (a) bird abundance per transect, and (b) bird presence/absence per transect, among unfragmented (control) sites.

Among unfragmented (control) sites, the mixed forest contained higher abundances per transect than did the mesophyll rainforest (Table 5.5). Habitat 4 and 6 species were more abundant in mixed forest, although the difference in abundance of Habitat 5 species was insignificant. When the closed forest specialists (Habitat 5 and 6 species) were pooled, no significant difference in abundance was evident. Mixed carnivores were more abundant in mesophyll rainforest, while partial nectarivores were more abundant in mixed forest.

Table 5.5 Mean abundances of birds grouped by habitat and feeding guilds/ha within continuous sites in mesophyll rainforest and mixed forest. Means are compared using t-tests. Habitat 4 = variety of habitats, including rainforest, Habitat 5 = mainly in rainforest and other thick vegetation, Habitat 6 = rainforest only, or dependent on rainforest plants (n = 16).

	Mixed forest transects	Mesophyll transects	
Bird group	Mean ± SE	Mean ± SE	*P*
All species	42.78 ± 2.24	33.60 ± 2.18	0.02*
Habitat 4 species	21.00 ± 1.46	12.26 ± 0.78	0.00**
Habitat 5 species	15.78 ± 3.36	17.46 ± 2.22	0.67
Habitat 6 species	5.88 ± 0.72	3.86 ± 0.50	0.03*
Habitat 5 & 6 spp.	21.66 ± 3.30	21.34 ± 2.04	0.93
Frugivores	8.22 ± 2.74	5.20 ± 1.54	0.25
Insectivores	15.22 ± 1.92	12.40 ± 1.20	0.21
Mixed feeders	16.12 ± 1.42	13.40 ± 0.98	0.13
Mixed carnivores	0.22 ± 0.14	1.6 ± 0.34	0.01*
Mixed herbivores	3.00 ± 1.02	0.94 ± 0.22	0.10
Partial frugivores	20.66 ± 2.12	16.66 ± 1.58	0.15
Partial insectivores	29.34 ± 1.34	27.46 ± 1.60	0.43
Partial granivores	5.88 ± 1.14	3.26 ± 0.42	0.07
Partial nectarivores	17.22 ± 1.82	11.26 ± 0.74	0.02*

Among control sites, no significant difference in species richness was found between mixed forest and mesophyll rainforest transects (Table 5.6). Habitat 4 species were richer in mixed forest, while the Habitat 5 group was richer in mesophyll rainforest. When the closed forest specialists (Habitat 5 and 6 species) were pooled, the mesophyll rainforest transects were found to be more species rich. Mixed carnivores were more species rich in rainforest, while partial nectarivores were richer in mixed forest.

Twelve species showed preferences for mixed forest (Table 5.7). Of these, half are species found only in dense forest, while the other half occur in a variety of habitats, including rainforest (see Appendix 7). Half of these species were insectivores, while only one frugivore was found to be more abundant in unfragmented mixed forest (Superb fruit-dove). Five species demonstrated significant preference for rainforest (Table 5.7), and all except the Sulphur-crested cockatoo are closed forest specialists. All of the species that significantly favoured mesophyll rainforest are mixed feeders.

Table 5.6 Mean richness of birds grouped by guilds per transect (0.5 ha) within continuous sites in mesophyll rainforest and mixed forest. Means are compared using t-tests. Habitat 4 = variety of habitats, including rainforest, Habitat 5 = mainly in rainforest and other thick vegetation, Habitat 6 = rainforest only, or dependent on rainforest plants (n = 16).

Bird group	Mixed forest transects Mean ± SE	Mesophyll transects Mean ± SE	*P*
All species	11.00 ± 0.19	10.60 ± 0.20	0.21
Habitat 4 species	5.28 ± 0.20	3.97 ± 0.12	<0.01**
Habitat 5 species	3.50 ± 0.22	4.93 ± 0.20	<0.01**
Habitat 6 species	2.17 ± 0.22	1.70 ± 0.18	0.13
Habitat 5 & 6 spp.	5.67 ± 0.34	6.63 ± 0.17	0.01*
Frugivores	1.39 ± 0.18	1.17 ± 0.13	0.33
Insectivores	4.78 ± 0.33	4.20 ± 0.24	0.17
Mixed feeders	4.11 ± 0.20	4.03 ± 0.27	0.85
Mixed carnivores	0.11 ± 0.07	0.80 ± 0.13	<0.01**
Mixed herbivores	0.56 ± 0.19	0.40 ± 0.10	0.43
Partial frugivores	4.50 ± 0.35	5.07 ± 0.18	0.14
Partial insectivores	8.83 ± 0.22	9.03 ± 0.30	0.64
Partial granivores	1.39 ± 0.16	1.40 ± 0.19	0.97
Partial nectarivores	3.83 ± 0.21	3.13 ± 0.20	0.04*

Table 5.7 Mean abundances of individual species (/ha) within continuous sites in mesophyll rainforest and mixed forest. Only those species demonstrating a significant preference for one habitat type (α ≤ 0.05) are shown. Means are compared using Mann-Whitney U-tests (n = 16).

	Mixed forest (Mean ± SE)	Mesophyll rainforest (Mean ± SE)	*P*
Prefer Mixed Forest			
Dusky honeyeater	3.44 ± 0.40	0.26 ± 0.22	<0.01
Fairy gerygone	1.34 ± 0.52	0.06 ± 0.06	0.01
Grey whistler	2.78 ± 0.64	1.34 ± 0.20	0.03
Large-billed gerygone	0.78 ± 0.26	0.00 ± 0.00	<0.01
Pale-yellow robin	0.66 ± 0.18	0.14 ± 0.08	0.01
Rainbow lorikeet	2.12 ± 0.74	0.00 ± 0.00	<0.01
Scaly-breasted lorikeet	2.22 ± 1.02	0.00 ± 0.00	0.02
Silvereye	1.66 ± 0.42	0.40 ± 0.10	0.01
Spangled drongo	0.78 ± 0.20	0.20 ± 0.14	0.03
Superb fruit-dove	0.44 ± 0.14	0.06 ± 0.06	0.02
Varied triller	1.12 ± 0.22	0.46 ± 0.18	0.05
Yellow-breasted boatbill	0.78 ± 0.20	0.00 ± 0.00	<0.01
Prefer Rainforest			
Black butcherbird	0.22 ± 0.14	1.14 ± 0.32	0.04
Orange-footed scrubfowl	0.00 ± 0.00	0.74 ± 0.26	0.02
Sulphur-crested cockatoo	0.00 ± 0.00	0.46 ± 0.18	0.05
Macleay’s honeyeater	0.34 ± 0.14	1.14 ± 0.24	0.04
Yellow-spotted honeyeater	3.00 ± 0.54	4.80 ± 0.40	0.02

Some species were not common enough to show a significant difference in abundance between the unfragmented rainforest and mixed habitats, but were found in one vegetation type but not the other. During the dry season (sample 2), the mesophyll sites at Josephine Falls and The

Boulders contained low numbers of upland visitors, including the Bridled honeyeater, Fan-tailed cuckoo, Grey-headed robin, Golden whistler and Brown gerygone. Furthermore, some patchily distributed closed-forest specialists were recorded in the unfragmented mesophyll sites but not in the mixed habitat (Chowchilla, Red-necked crake, Eastern whipbird and Azure kingfisher). The mixed site contained open-country (grassland and open woodland) species including the Scarlet honeyeater, Northern fantail, White-throated honeyeater, Lovely fairy-wren, Leaden flycatcher and Rainbow bee-eater.

Natural density and patch occupancy

Species found in higher densities within continuous habitat averaged significantly higher rates of patch occupancy than the rarer species (Figure 5.5a). However this pattern did not consistently hold across all groups. Mixed herbivores, partial granivores, and partial nectarivores showed no relationship between density and patch occupancy, while obligate frugivores showed a weaker relationship (Figure 5.5g-h).

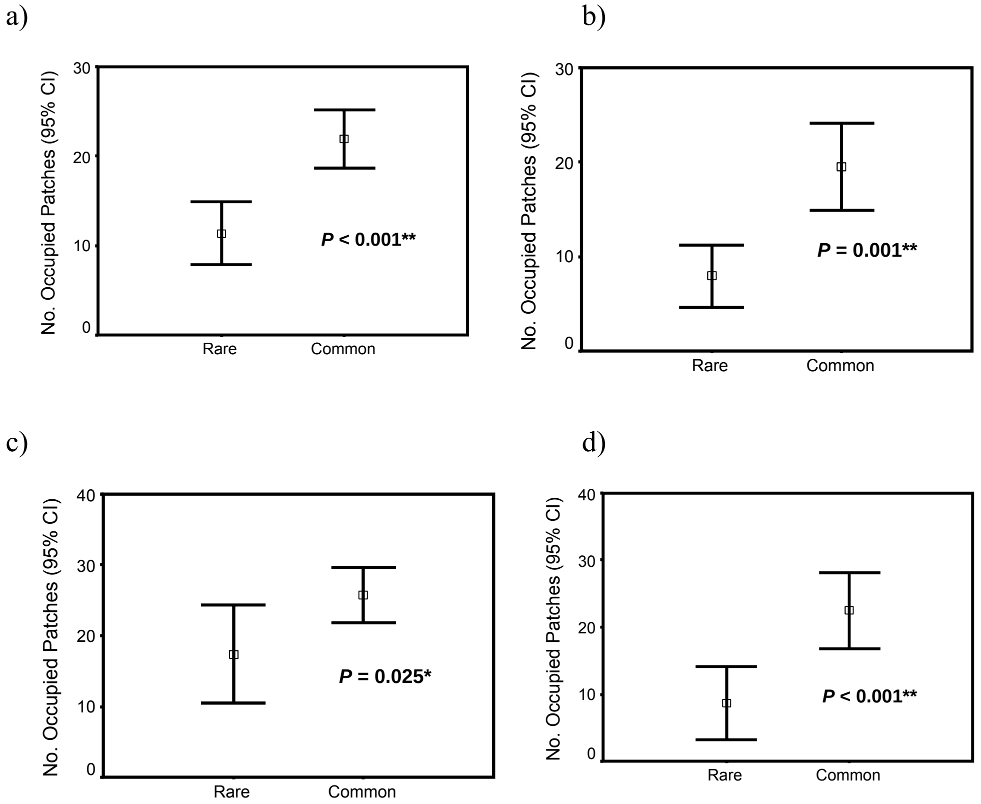

Figure 5.5 Numbers of patches occupied by rare and common species within continuous habitat. a) All species, b) Rainforest specialists (Habitat 5 and Habitat 6 species), c) Habitat generalists (Habitat 3 and 4 species), d) Obligate insectivores, e) Partial insectivores, f) Obligate frugivores, g) Partial frugivores, h) Omnivores, i) Mixed herbivores, j) Partial granivores, and k) Partial nectarivores. *P* values and asterisks indicate levels of significance from Mann-Whitney U tests for differences in patch occupancy (continued over page).

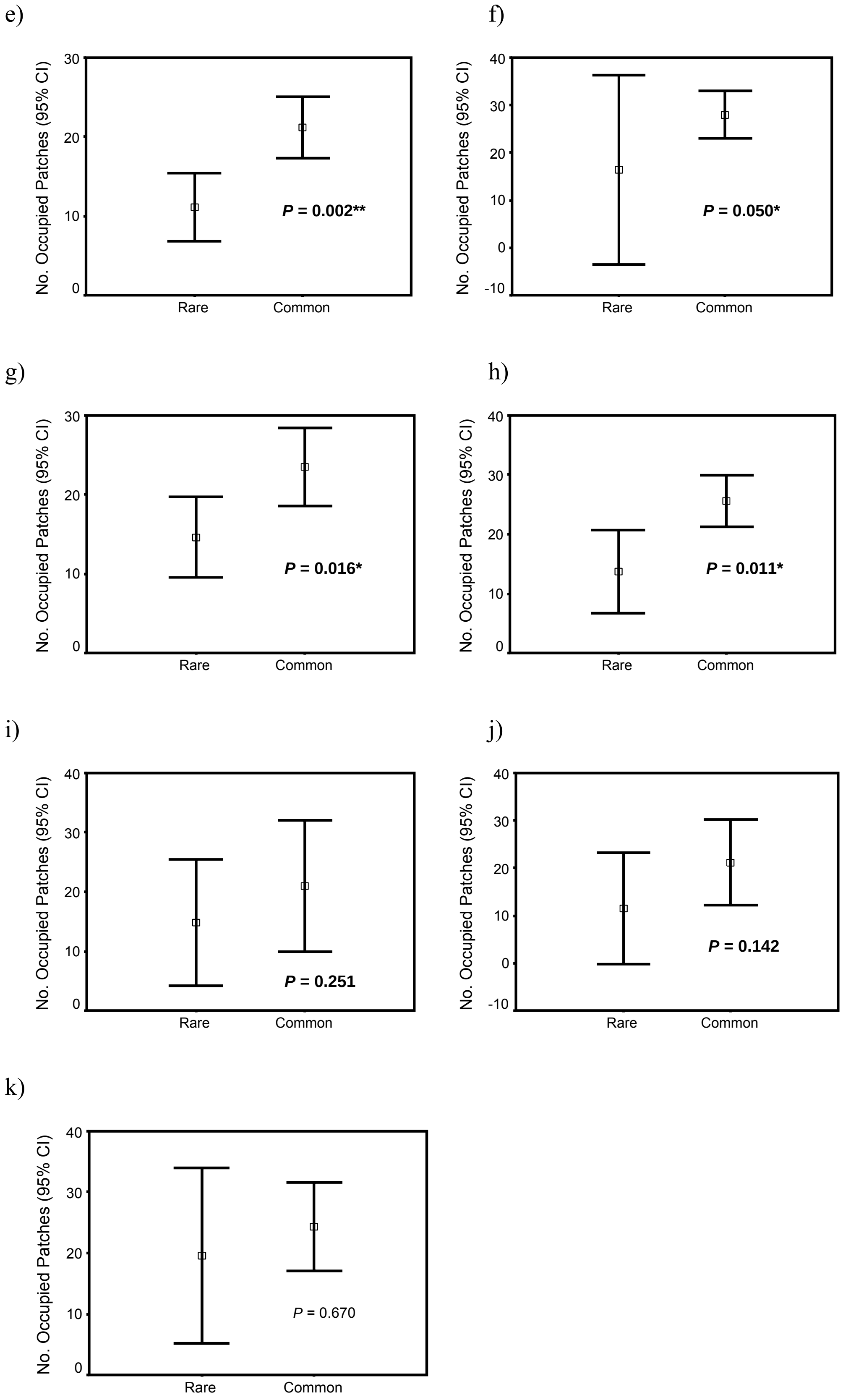

Figure 5.5 (continued).

5.4: Discussion

Sampling issues

There are difficulties associated with rainforest bird censuses. Visual-acoustic censuses provide a far more complete sample of the avifauna than mist-netting, but biases can arise due to the different detectability of species (Laurance *et al*. 1996). Also, differences in foliage density between transects (and especially between mesophyll rainforest and mixed forest) may create bias towards those species that favour a more open understorey. However, due to the strong reliance on calls (over 90% of observations were either made on the basis of calls or were visual identifications supported by calls), foliage density differences were unlikely to significantly impact on the census results. All quantitative censuses were conducted between sunrise and 9.30 a.m., when the majority of individuals are active and calling, to further minimise bias.

Species richness comparisons between different studies or regions are often complicated by different sized sample areas because of the species/area relationship, and by richness enhanced by habitat diversity (β diversity). Thus, care must be taken when comparing richness and diversity measures from different studies, or even from locations within the same study where sampling areas differ in size. This is relevant to this study with respect to richness comparisons between sites, and when comparing overall species richness to other studies. Furthermore, even in sites of similar area and heterogeneity, differing temporal sampling regimes may affect comparisons as migratory, rare or vagrant species are added to lists (MacNally & Horrocks 2002). However, strong patterns exist within the bird assemblages in this study, and major differences between this and other tropical rainforest assemblages are described. Further, equal-area transect-based sampling within this study provides a sound basis for comparisons among sites.

Nearly all sites in this study exhibit species-accumulation curves that flatten out within the final two or three samples. This indicates that, at least within the sample periods, the great majority or all of the species within a patch (at the time of census) were recorded, except for nocturnal species which would not be recorded during daylight sampling. Estimates of species richness were supplemented by the recording of species within sites but from outside transects. Although missed species would lead to inaccurate richness estimates, it is unlikely that such errors were great. The larger sites are more likely to contain species that remain unobserved due to the lower proportion of the area that was sampled. From the perspective of species-area curves, however, this would lead to a more conservative relationship. Nevertheless, the fact that the species-abundance curves of larger sites tend to flatten out suggests that most species were recorded, even allowing for the influx of new migrants in the final sampling period.

Some non-passerine orders, such as Falconiformes, are naturally rare due to large area requirements (Leck 1979, Loyn 1987, Lamberson *et al.* 1994, Jullien & Thiollay 1996). To sample the large areas of tropical rainforest necessary to quantitatively analyse these and some other rare species such as the Papuan frogmouth and Cassowary would require great time and resources, and would generally only be suitable over areas of thousands of hectares rather than the hundreds of hectares of this study (Jullien & Thiollay 1996). Therefore, whilst presence/absence results concerning this group may be used with some caution, density estimates cannot be accepted with any confidence, and are therefore not analysed further in this study. Also, the nocturnal habits of the Papuan frogmouth (Caprimulgiformes) preclude reliable daytime observation.

Therefore, at the landscape scale of this study, records of the cassowary, the three raptors, passage migrants such as the Satin flycatcher, and probable local vagrants with few records (e.g., white-throated gerygone) were unsuitable for quantitative analyses. Their natural rarity in the lowland area suggests that their presence and detection would result more from chance than landscape processes.

Upland and introduced species

This chapter describes a lowland rainforest assemblage that differs strongly from tableland assemblages (see Warburton 1997, Frith 1984). This lowland assemblage, however, contained only eight species restricted to lowland regions, although a further 28 species generally reach their highest abundances in lowland regions (Nielsen 1996, Wieneke 1992, Henriod 1998). Conversely, at least 19 species are almost totally restricted to areas above 400m altitude (Nielsen 1996, Wieneke 1992, Henriod 1998). The low number of species that are restricted to lowland rainforests in the region may be explained by the temporal variability of lowland rainforest habitat due to climate change (Williams *et al.* 1996). Few species appear to have exclusively colonised lowland rainforests from Cape York and Papua New Guinea in comparison to the numbers of species that have persisted in upland areas throughout climate fluctuations.

Six species recorded in this study are predominantly upland species (e.g., Chowchilla, Eastern whipbird, Black-faced monarch), and relatively sparsely distributed in certain lowland areas (Nielsen 1996, Henriod 1998). This study has shown that these species show little propensity to utilise lowland fragments. Likewise, the seven occasional altitudinal vagrants (e.g., Bridled honeyeater, Lewin's honeyeater, Brown gerygone) were rarely seen in fragments. This contrasts with the Atherton Tableland study of Warburton (1987) that found these species to range from presence in all upland fragments, to commonly using the larger fragments but only some of the smaller fragments.

The different patterns of these species in lowland and upland areas may be due to three factors. Firstly, most of these species are uncommon in the lowlands, and this study has shown that rarity predisposes a species to local extinction. This is reinforced by the fact that of the species within this group, the two most commonly recorded in this study (Chowchilla and Eastern whipbird) were those that utilise the most patches, albeit less than in upland areas (Warburton 1997). Secondly, microclimate conditions are possibly harsher in and between lowland patches than in tableland patches due to higher temperatures and canopies that are more open. Thirdly, many of these species only occasionally venture down to the lowlands (generally during winter), thus reducing the likelihood that individuals will be pushed into searching for new habitat through intraspecific competition.

Introduced bird species pose a significant threat in many parts of Australia, and although impacts are in most cases restricted to urban areas, concerns continue regarding the spread of some species into natural areas (Pell & Tidemann 1997). In northern Australia, the Common myna, Spotted turtle-dove, and Common house-sparrow *Passer domesticus* have colonised some larger towns, although only the Common myna and Spotted turtle-dove were found in the study sites. The two Common myna records were from Site 1, which is a narrow linear site close to the town of Gordonvale. The Spotted turtle-dove was found at all of the mixed forest fragments (but not the unfragmented mixed forest site), and along the edges of Sites 7, 22, 24, 27 and 28 which, although mesophyll rainforest, are those sites closest to the towns of Innisfail and South Johnstone. Moreover, only 38 records indicated that even very close to towns, they are only sparsely distributed along forest edges, and rarely if ever venture into the interior. Records of both species were from fragment edges close to houses and intensive land use (sugar cane or banana plantations).

Introduced avian species presently in northern Queensland are therefore unlikely to threaten rainforest systems. In this study, none were found in rainforest interiors, and only the Spotted turtle-dove was found in the interior of mixed forest (and only in a single patch close to the town of Gordonvale). The major reason stems from the habitat preferences of the species that have been introduced into Australia. Duncan *et al.* (2001) found the likelihood of the success of an introduction depends largely on the suitability of the abiotic environment for the exotic species at the introduction site. Although the Common myna and Spotted turtle-dove originate from the tropics (southern Asia), the Common myna, even in India, is a species primarily of human-modified habitats and open woodland (Pell & Tidemann 1997), and the Spotted turtle-dove, while frequenting human-modified and a range of natural habitats, avoids wet rainforest within its natural range (Ali & Ripley 1972).

Overall Richness and Abundance

The rainforests of northern Queensland lack the overall richness of rainforest bird assemblages found in many other rainforest habitats worldwide, and are particularly low in numbers of specialised rainforest species (Driscoll & Kikkawa 1989). This study demonstrates that this pattern of low diversity applies at both the local and landscape scales. Although richness comparisons can be confounded by factors such as species/area relationships, habitat heterogeneity, the overall extent of habitat outside the sampling sites, and the time spent sampling the organisms (MacNally & Horrocks 2002), some generalised comparisons may still be made between the species richness and guild structure here and in other rainforest regions.

This study revealed a total of 102 species, with 95 species in mesophyll forest and 77 in mixed forest, in a sampling area of approximately 50 ha of mixed forest and 450 ha of mesophyll rainforest (68.5ha within transects contained 94 species in total). Also of note is the large overall study area from which samples were obtained (70 km × 20 km). Almost without exception, other mainland studies from tropical forests outside Australia show considerably higher species richness, often within far smaller areas.

The most diverse rainforest assemblages occur in South America. For example, 328 species have been recorded in a 110 ha plot in western Amazonia (Terborgh 1985), 189 species in southern Brazil (Anjos & Bocon 1999), and over 400 species in a 40 × 20 km area of Amazonia (Stouffer & Bierregaard 1995a). In Colombian rainforest, Renjifo (2001) recorded 165 species in 24 sites within a 12 km × 18 km (216 km^2) area, and 2 km^2 of French Guianian rainforest yielded 227 forest species (Erard 1989).

Similarly, Central American studies have revealed exceptionally high bird richness, even in small sample areas. In Panama, Karr (1977) recorded 165 species in a 2 ha plot and 370 species in 1 km^2 from a regional rainforest pool of some 500 species, while Robinson *et al*. (2000), also in Panama, recorded 252 species in a 104 ha plot. Terborgh (1985) recorded 64 species from a 1.2 ha plot in Costa Rica, but Daily *et al*. (2001) also in Costa Rica, recorded 209 species in eight small (>25 ha) forest fragments within a 15 km radius. Estrada *et al.* (1993) found 165 species in 30 forest patches in Mexico, while Graham and Blake (2001) recorded 169 species in 17 small patches and one large patch in the same region. In Nicaragua, Cody (2000) estimated a richness of 298 species in 1 km^2, and El Salvador, with rainforest of less than half the area of those in northern Queensland, contains 125 rainforest specialists (Komar 1998).

Africa and Asia, while not as diverse as the Neotropics, also have greater bird species richness than north Queensland. Erard (1989) recorded 175 species in 2 km^2 of Gabonese rainforest, while in Uganda, 197 species were found in a single 428 km^2 forest block (Owiunji & Plumptre 1998). In peninsula Malaysia, 193 species of forest birds were recorded along three 5 km transects (Johns 1992) and Bornean studies have revealed 195 species in a 33 ha plot of primary forest (Lambert 1992) and 223 species in primary and selectively logged forest (Grieser-Johns 1996). At a regional level, Bell (1982) recorded 165 species within a 2.5 ha plot of homogeneous lowland rainforest in Papua New Guinea.

Clearly, these levels of species richness are much greater than those of the Wet Tropics lowland rainforests. Of the 102 species recorded in the present study, only 57 were recorded in the two unfragmented mesophyll rainforest sites, and 70 species in forest interiors in all mesophyll sites. In fact, only 44 of the 102 species would be considered forest specialists (Habitat 5 and 6 species). In comparison, of the 400 species recorded in Central Amazonia, few were non-rainforest species (Stouffer & Bierregaard 1995a).

Most tropical forest regions with similar or lower richness than north Queensland occur on islands, such as Isabel (3995 km^2) in the Solomon Islands (Kratter *et al.* 2001). Although low by tropical rainforest standards, diversity within this study area was comparable to many other areas of northern Queensland. Crome (1978) recorded 74 species in a 9 km^2 tract of lowland rainforest near Mission Beach, 50 km South of Innisfail (Crome 1978). Laurance *et al.* (1996) recorded 61 species in 60 ha of primary rainforest and regrowth on the Atherton Tablelands, of which 48 species were recorded in the primary rainforest (approximately 30 ha), while Warburton (1997) recorded 60 species in 33 sites on the Atherton Tablelands.

The relatively high diversity in this study compared to that found in other studies in the rainforests of northern Queensland may partly be due to the presence of altitudinal vagrants (e.g., Grey-headed robin), altitudinal migrants (e.g., Rufous fantail) and open-country species (e.g., Magpie-lark). In the cooler, dry season, upland species including the Bridled honeyeater, Lewin's honeyeater, Brown gerygone, Golden whistler, and Grey-headed robin were recorded in unfragmented sites (in very low densities). Although they probably contribute little to lowland assemblage processes, their presence adds to the overall richness at the study sites.

Species richness in the study area is enhanced by the occurrence of open-country species around patch edges, and in the mixed forest patches. The high numbers of open-country and woodland species may be due to the proximity of large areas of open woodland and mixed forest near

Gordonvale at the upper end of the study area. This woodland block extends continuously up the Mulgrave Valley, creating an almost continuous corridor of open forest of 150,000 ha. Furthermore, the distance between the western extent of this block and large areas of open woodland on the western side of the Wet Tropics is only 5 km. Thus, there exists a more-or-less continuous connection between the mixed forest and large source populations of open-country and sclerophyll species. This may facilitate colonisation of the study area by non-rainforest species.

Species abundance and rarity

Birds in Australian rainforest tend to occur in higher densities (per species) compared to sclerophyll forest habitats (Kikkawa 1974). This differs from other continental rainforest areas where richness is high but distribution is patchy. For example, there is a very strong preponderance of rarity in Neotropical forests, where 90% of species each represented less than 2% of the total captures, and the most abundant species accounted for only 10% of all captures (Bierregaard & Stouffer 1997). In the present study, 72% of species each accounted for less than 2% of the total abundance within unfragmented forest.

In the north Queensland lowland rainforests, the rarest species are usually either open country species that utilise the edges, or some of the specialist rainforest species. The more common species are mostly habitat generalists that use other vegetation as well as rainforest (e.g., Yellow-spotted honeyeater). The lower rarity in this region may reflect a generalised form of density compensation arising from the disappearance of many lowland species following Pleistocene contractions of the rainforests in the region (Williams *et al.* 1996).

Guild structure

Relatively few species in northern Queensland are rainforest specialists, in contrast with other continents. For example, of 189 species recorded by Anjos & Bocon (1999) in southern Brazil, 125 (66%) were species primarily of forest interiors and, within a Costa Rican fragmented landscape, 149 (71%) of 209 species occurred only in rainforest (Daily *et al.* 2001). Conversely, in the present study only 15 species were rainforest obligates, and 44 species (43%) occurred only in rainforest and other thick vegetation. Furthermore, three of the former and 12 of the latter group were predominantly upland species or occasional vagrants to the lowlands.

Lowland regions contain fewer rainforest obligate species than upland areas in the Wet Tropics. Warburton (1987), for example, found at least 28 rainforest obligates in his Atherton Tableland study, compared with 15 in the present study. Furthermore, the present study found considerably higher diversity of non-rainforest species. These differences may be due to the proximity of other vegetation types, to biogeographic factors, or to the effects of cyclones on lowland rainforests.

The constant existence of upland rainforest refugia throughout the Pleistocene period, resulting in the persistence or evolution of a number of endemic species and subspecies (Willams et al. 1996), has also allowed these and some other upland species to remain rainforest specialists. Conversely, rainforest in the lowlands all but disappeared during these periods of climate change, leaving species that were more generalist in their habitat requirements. Although only 43% of all species recorded here were rainforest specialists, 86% of the 14 predominantly upland species or occasional vagrants from upland areas were rainforest specialists.

As postulated in the introduction to this chapter, the Papuan influence on the lowland avifauna has also produced a generalist assemblage, whereas many of the upland species have ranges that extend down the east coast of Australia (e.g., Topknot pigeon and Australian king-parrot) and are possibly thermally restricted to the uplands. This is supported by the fact that a number of species (e.g., Golden whistler, Grey-headed robin) migrate to certain lowland area only during the cooler months (Nielsen 1996).

Comparisons of feeding-guild structure between different studies can be problematic, due to the differing size and heterogeneity of study areas, and the different methods used to define feeding guilds (Erard 1989). Nevertheless, this study clearly describes the absolute and relative lack of specialist insectivores in this region in comparison with many other tropical rainforest assemblages. In the present study, obligate insectivores comprised 33.3% of species (34 species), compared to 45% (85 species) in southern Brazil (Anjos & Bocon 1999), 70% of species in Gabon (Erard (1989), and 35.8% (152 species) of insectivores out of a regional species pool of 424 species in Nicaragua (Gillespie 2002). Eighty-four understorey insectivores alone have been recorded in a study area in the central Amazon (Stouffer & Bierregaard 1995a) and 97 (46.8%) in the Peruvian Amazon (Terborgh 1980). Beehler (1981), however, recorded only 30 obligate insectivores (29%) in Papua New Guinea.

Lowland insectivorous and frugivorous guilds are comparable in absolute richness to those of tableland guilds in the Wet Tropics. Of the 61 species recorded in a smaller, more restricted study of rainforest and regrowth in the Atherton Tablelands, Laurance *et al.* (1996) recorded 27 obligate insectivores (44%), all of which were species of thick vegetation. As many of the insectivores recorded in the present study were species of open country, and were recorded along patch edges (e.g., Willy wagtail), it is more appropriate to use only the species of control sites (which contained no edge habitat) in comparisons with upland assemblages. Within unfragmented sites, of the 57 species recorded, only six (10%) were obligate frugivores, and 20 (35%) were insectivores. When rare upland migrants are removed, only 16 species of obligate insectivores remain.

Likewise, the 10 obligate frugivores that were recorded in this study (10% of the total number of species) is a considerably lower number than that found in many other mainland rainforests. For example, 28 species (15%) of frugivores were recorded in southern Brazil (Anjos & Bocon 1999), while 21 obligate frugivores comprise 12.7% in a small plot in the Papua New Guinean lowlands (Bell 1982), and 21 in the Peruvian Amazon (Terborgh 1980).

Clearly, the Wet Tropics lowlands contain not only fewer feeding specialists than do most other rainforests throughout the world, but also contain fewer insectivores than are found in upland rainforests of northern Queensland. The lower degree of specialist insectivory of lowland species may be due to species sifting from Pleistocene rainforest contractions. Alternatively, this may result from lower dry-season moisture availability in the lowlands (Crome 1978) causing greater seasonality in insect abundance. In this case, obligate insectivory may prove to be a handicap.

Overall, these patterns are likely to be due largely to biogeographical factors. Firstly, the northern Queensland rainforests are of limited extent in comparison to other continental regions. Secondly, these forests are a significant distance from other large rainforest areas, namely those in Papua New Guinea assemblages (Williams *et al.* 1996), and colonisation over these distances is likely to favour habitat generalists, as these are usually more effective dispersers (Kikkawa *et al.* 1981). Thirdly, the Pleistocene rainforest contractions to small upland refuges would have particularly affected the lowland assemblage, as these rainforests would have virtually disappeared (Williams & Pearson 1997). Within the lowland areas, specific habitat guilds (rainforest specialists) are likely to have been more vulnerable to these contractions, due to their relative inability to utilise other habitats in the virtual absence of rainforest outside riparian zones. Specialist feeding guilds (and obligate insectivores in particular) have been shown to be particularly vulnerable to a range of anthropogenic impacts (Stouffer & Bierregaard 1995a, Patterson 1987, Canaday 1996), so these specialists may also have been less able to persist in the lowlands in the face of environmental changes.

A second influence, in the form of regular cyclonic disturbance on the vegetation of the area, may also enhance this pressure towards an avian assemblage of generalists, as in Central America, where frequent exposure to hurricanes is thought to select for more generalist and ecologically resilient assemblages (Will 1991, Lynch 1991). These two impacts, although over different spatial and temporal scales, may interact to produce the contemporary avian assemblage of the lowland region, although there is no way to separate the two types of impact.

Insectivores in particular have demonstrated a vulnerability to various types of anthropogenic disturbance from fragmentation (e.g., Stouffer & Bierregaard 1995a) and other disturbances (Canaday & Rivadeneyra 2001). In the Wet Tropics, and especially in the lowland areas, this broad feeding guild appears to demonstrate vulnerability to natural change over far larger spatial and temporal scales.

Mesophyll rainforest versus mixed forest assemblages

Perhaps unsurprisingly, bird assemblages in mixed forest (rainforest under- and mid-storeys with sclerophyll emergents) differed from those in mesophyll rainforest. This was apparent both within continuous forest, and within all sites. Less expected was the relative similarity of mixed forest to continuous forest when compared to the differences between continuous mesophyll forest and patches of mesophyll. This infers that even major changes in vegetation type have less (although still significant) impact on bird assemblages than do the effects of fragmentation.

That mixed patches diverge significantly from other patches indicates that the richness of the rainforest bird assemblage declines in patches of mixed forest to a greater degree than in mesophyll forest patches. This may be due to larger area requirements of rainforest specialists in ‘suboptimal’ mixed forest (leading to a steeper dropping out of species in isolated mixed forest patches).

The bird assemblage within mixed forest sites would likely have been substantially different 50 or 100 years ago. At this time, *Eucalyptus* spp. and *Acacia* spp. would have been present, whilst Aboriginal burning would have suppressed the emergence of a rainforest understorey. Only since the cessation of traditional burning has the rainforest understorey encroached upon these sclerophyll areas (Stocker & Unwin 1989). Were burning regimes reintroduced to some of these areas, it is likely that the mixed assemblages would diverge further from the mesophyll rainforest assemblages. However, in the continued absence of fire (and rainfall patterns similar to those today), the rainforest plants (and therefore rainforest birds) would continue to recolonise this habitat.

Clearly, bird assemblages in this very wet section of the Wet Tropics lowlands are composed of generalists, both with respect to feeding strategies and to habitat preferences, providing an illustration of how disturbances at different spatial and temporal scales can drive the structure of a bird community. Although this assemblage contains few endemic species, and even fewer endangered species, it represents an integral part of a disappearing ecosystem type, and an understanding of the patterns of faunal assemblage structure is integral to understanding how human impacts may affect the lowland rainforests.

Chapter 6. Edge effects

6.1. Introduction

Habitat fragmentation not only leads to habitat reduction and patch isolation, but also results in an increase in the proportion of habitat that adjoins other habitat types (Wiens 1989). This often exposes the organisms within one habitat to some of the conditions of the adjoining habitat (Murcia 1995). Some organisms benefit from the presence of edges, whilst others are adversely affected. For the latter, the presence of this suboptimal habitat means that the effective size of a patch of habitat is smaller than the actual size, with significant conservation and land management implications. Studies into the effects of habitat fragmentation should therefore address the impact of edges on the organisms of interest.

Forest edges, and especially tropical rainforest edges, are associated with higher temperatures and lower humidity than within the rainforest (Murcia 1995, Kapos *et al.* 1997). These effects can be particularly pronounced in human-fragmented rainforests, where the surrounding matrix (pasture or crops) is more open and less complex than the rainforest fragments. This contrast results in microclimate gradients from the forest edge towards the forest interior, in a generally perpendicular direction from the edge. These changes may include increased solar radiation, increased air temperature, increased wind and, in tropical rainforests, decreased humidity and soil moisture (Lovejoy *et al.* 1986, Laurance 1991, Matlack 1993, Murcia 1995, Saunders *et al.* 1991), and the possible penetration of fertilisers and pesticides (Fox *et al.* 1997).

These abiotic changes can result in significant biological changes, such as changes in vegetation structure and floristics. Tree mortality frequently increases close to edges, often from soil changes (Lovejoy *et al.* 1986), and some rainforest plants may demonstrate lower densities near the edge (Murcia 1995). On the other hand, the creation of an edge can increase the incident light, resulting in increased plant growth of particular (usually pioneer or disturbance-adapted) species (Murcia 1995). Therefore, closer to edges of tropical rainforests, the canopy and subcanopy are often less continuous, heavy lianas, climbing rattans and other disturbance-adapted species may become more common (Laurance 1991), and the understorey consequently becomes denser (Murcia 1995). Other effects may include increased numbers of stems at or near forest margins (Williams-Linera 1990).

Despite the great number of studies dealing with microclimate changes and subsequent effects on vegetation structure and floristics, consistent patterns have failed to emerge. Murcia (1995) reviewed work on edge effects, and found a variety of results. For example, the influence of these effects into rainforest commonly ranges from 15 m to 50 m from the edge; however, on the Atherton Tablelands, wind damage has extended up to 500 m from edges following a cyclone in 1986 (Laurance 1991). The nature, intensity and perpendicular distance of edge effects into a forest block may be affected by such factors as the size and shape of the rainforest patch (Williams-Linera *et al.* 1998), and the age of the edge (Williams-Linera 1990, Kapos *et al.* 1997). Other factors that may influence the extent of these effects include the orientation of the edge and the rainforest structural type (Turton & Freiburger 1997). Edge structure itself affects the nature and extent of microclimate and vegetation structural changes in tropical forest fragments (Didham & Lawton 1999). For example, older edges may be more 'sealed' by vegetation, thus lowering microclimate changes along the edge-interior gradient (Turton & Freiburger 1997).

Bird assemblages respond to the presence of habitat edges in a variety of ways. Temperate forest edges commonly show increased bird species richness and abundance compared to forest interiors (e.g., Hansson 1994). However, tropical rainforest edges often contain decreased richness (Lovejoy *et al.* 1986, Terborgh *et al.* 1990, Restrepo & Gomez 1998, Dale *et al.* 2000). These differences may be due to the higher natural frequency of large gaps in temperate forest, less closed canopies (resulting in less microclimate contrast between the forest interior and exterior) in temperate forest, or lower habitat specificity in most temperate bird species.

Some species may avoid edges because of the increased risk of predation (Burkey 1993, Huhta *et al.* 1998), changes in microclimatic features (Murcia 1995), lower abundances of resources (Lovejoy *et al.* 1986), or from competition for resources from outside species (Loyn 1987). Conversely, other species may benefit from increased resources at forest edges (Stouffer & Bierregaard 1995b). For example, increased plant growth near edges may result in increased numbers of insects such as leaf eaters and light-loving butterflies (Lovejoy *et al.* 1986), which then attract insectivorous birds (Lovejoy *et al.* 1986, Murcia 1995). Understorey insectivores have often been found to avoid edges (Stouffer & Bierregaard 1995a, Restrepo & Gomez 1998), whilst nectarivores may benefit from increased flowering at forest edges (Stiles 1975, Stouffer & Bierregaard 1995b, Restrepo & Gomez 1998). This factor is considered to be important in the persistence of nectarivores in relatively small fragments (Stouffer & Bierregaard 1995b). It is therefore prudent to focus not only on the effects of edges on avian richness and abundance, but also to examine the effects on feeding guilds, habitat guilds, and individual species.

Studies of the effects of rainforest edges in northern Queensland have until now been confined to upland areas. Turton & Freiburger (1997) examined the effects of edges on the microclimate of a rainforest remnant on the Atherton Tablelands, while Laurance (1991, 1994) studied the effects of edges on vegetation and small mammal assemblages in rainforest patches, again on the Atherton Tablelands. Other studies have examined lizard (Conroy 1999) and small mammal (Williams & Marsh 1998) assemblages across the rainforest/open forest upland ecotone, while Goosem (2000) examined the effects of roads as edges on small mammal assemblages.

Laurance *et al.* (1993) and Hausmann et al. (2005) found no evidence of increased nest predation near the edges of upland patches; however, no studies have so far examined the effects of edges on bird assemblage structure in Australian tropical rainforests. While a small number of studies have focussed on bird use of rainforest edges in South America (Lovejoy *et al.* 1986, Stouffer & Bierregaard 1995a, 1995b, Restrepo & Gomez 1998) and Africa (Dale *et al.* 2000), the Australian rainforest bird fauna may respond differently. The extent of edge effects on a particular bird assemblage depends on a range of factors. These include climate, canopy architecture, soil characteristics, and the manner in which these abiotic changes affect vegetation and, in turn, avifauna. Other potential factors include the nature of the rainforest biotic assemblages (such as how adapted the species are to different abiotic conditions), the abundance and nature of predators or competition from the adjacent habitat and the degree to which these species permeate the rainforest, and the history of the assemblage. Not least, edge effects depend also on the surrounding habitat use and the extent to which habitat use influences the above factors.

Aims

This chapter examines the effects of sharp, artificial edges between rainforest and agricultural land on the vegetation and bird assemblages within fragments of lowland rainforest habitat. Specific objectives of this chapter are to:

- compare vegetation structure between patch edges and interiors;
- compare bird richness and abundance between patch edges and interiors;
- determine what species or guilds show attraction to or avoidance of edges;
- identify which spatial variables explain the relative bird richness and abundance at patch edges (compared to interiors);
- compare the dissimilarity between unfragmented bird assemblages and edge assemblages, with that between patch interior bird assemblages and the unfragmented assemblages;
- identify which spatial or vegetation characteristics of a patch determine the degree of dissimilarity between edge and interior bird assemblages.

6.2 Methods

Vegetation

Vegetation variables were obtained for each transect as described in Chapter 4. I incorporated 26 measures of vegetation structure and specific floristics (the abundance of edge, gap or marginal rainforest species) into the analyses. In order to examine differences in vegetation structure between the edges and interiors of fragments, data were examined at the transect level. All sites contained transects along the edge except for the three control sites, which contained only interior transects.

Substantial structural and floristic differences exist between mixed forest in the drier area, and mesophyll rainforest on well-drained soils in the wetter section of the study area (see Figure 4.4). Therefore, to avoid confounding the major vegetation trends due to these broad differences, variation in plant structure between edges and forest interiors were examined separately for the mesophyll rainforest and mixed forest.

Transects were grouped on the basis of their distance from the edge (Edge, 50 m, ≥100 m [interior]). Vegetation structure was compared between the edge and interior of fragments by Multi-Response Permutation Procedure (MRPP) (Biondini *et al.* 1985) using PC-Ord 4.0 (McCune & Mefford 1999). This technique is a non-parametric method for testing for differences in predefined groups, performing a similar function to a multivariate ANOVA, but with very relaxed data structure requirements. Differences in individual structural characteristics between edge and interior transects were tested by Mann-Whitney U tests.

Foliage complexity in the understorey, upper storeys, total complexity, and mean and maximum heterogeneity were calculated as described in Chapter 4. These measures were aggregated by mean for the edges of each patch and all non-edge transects of each patch, and then subjected to paired comparisons for mixed forest and rainforest separately as with raw vegetation measures using Mann-Whitney U tests. All univariate statistics in this chapter were performed using SPSS 10.0 (SPSS 1999).

Bird abundance and richness

Bird surveys were undertaken as described in Chapter 5 over three seasons in 30 fragments and three control sites. Due to probable activity (and therefore sightability) differences between morning and afternoon, and the narrower activity period in the late afternoon, only the morning transects were used in the examination of edge effects. For these analyses, only those patches with both edge and interior transects could be used, leaving a total of 22 patches. Known vagrant species, raptors, and rare species with fewer than six individuals recorded in morning transects over all sample periods (usually vagrants), were removed from these analyses.

In a fragmented environment, where the presence and abundance of species may be influenced by a range of landscape factors such as the size of the patch, it is often inappropriate to pool all edge transects and all interior transects. Therefore, differences in bird abundance and richness between patch edges and interiors were tested by pairwise analyses using relative densities at the edge and interior of each patch. In order to allow paired comparisons by patch, bird abundances from all sample periods were aggregated by the mean for each transect. For each patch, all of the edge transects and all interior transects were further aggregated, again by the mean, resulting in overall density measures for each species at the edge of each patch, and within the interior of each patch. Overall abundances and species richnesses per hectare were then calculated and compared patch-by-patch using Wilcoxon signed-rank tests. Similarly, edge versus interior abundance and richness of feeding and habitat guilds were tested, allowing the use of paired comparison tests across all fragments (Sallabanks *et al*. 2000).

In order to investigate what variables determine the magnitude and nature of edge effects on richness and abundance, the relative richness of edge transects was calculated for each patch by dividing the richness per unit area of the edge by the richness per unit area of the interior as follows:

Relative edge richness = $(R_{edge}+1)/(R_{int}+1)$,

where R = richness per unit area for a given effort.

Trends in the relative densities of birds along patch edges were analysed with respect to major landscape (Chapter 3) and vegetation (Chapter 4) characteristics of patches using stepwise multiple linear regression using SPSS 10.0 (SPSS 1999). Stepwise regression is a combination of forward and backward procedures, finding the optimum model by adding those variables with the highest partial correlation to the model, but removing those model variables that, once new variables are added, add little to the model. Stepwise methods are widely used in landscape ecology to explain dependent variables (e.g. Germaine et al. 1998, Tellaria & Santos 1997). Landscape measures included area, nearest neighbour, distance to major rainforest blocks, forest cover within 1 km and 5k m radii, distance to 30 ha rainforest patches, and the length of forest edge within a 2 km radius of patches. Summary vegetation variables included edge architecture (sharp or concave), and NMDS Axis 1 and NMDS Axis 2 (from the ordination of vegetation variables by site in Chapter 4). Axis 1 described 69.6% of the variation, and represented a gradient from mixed, less complex forest with emergent eucalypts and acacias and few structural features and growth forms, to complex forest containing an increased amount and variety of growth forms and structural features. Axis 2 described 20.1% of the variation, and correlated positively with the abundance of ground ferns, tree ferns, pandans, and strangler figs (Table 4.6).

Bird assemblage responses

To examine the effects of edges on bird assemblage structure, dissimilarity matrices were calculated between all patch interiors and edges aggregated by time and by paired transects ($n = 54$) for both presence/absence and abundance, using PC-Ord 4.0 (McCune & Mefford 1999). In the case of the abundance matrix, species (column) values were standardised by z-score to remove some of the effect of more abundant species, and in both cases the Bray-Curtis distance measure was used. Thus, the measure is sensitive in heterogeneous data sets and gives less weight to outliers (McCune & Mefford 1999).

To test for the influence of vegetation and spatial variables on the dissimilarity between bird assemblages of fragment edges and interiors, the bird assemblage dissimilarity between patch edges and patch interiors was recorded on a patch basis (the mean dissimilarity in the case of large patches with 6 transects). This resulted in $n = 22$, since 22 patches contained both edge and interior transects, with each value representing the mean dissimilarity between the edge and interior assemblages of a single patch. This, control sites were not used in this analysis. Data was, where appropriate, log transformed to a state of normality prior to a stepwise multiple regression analysis using the vegetation and spatial variables outlined above.

To test whether patch edge or patch interior assemblages were more divergent from unfragmented control site assemblages, the same dissimilarity matrices were used, but in this case the mean dissimilarity of each patch’s edge assemblage and interior assemblage from those of the control sites was recorded. The difference in levels of dissimilarity of edge and interior assemblages from unfragmented forest assemblages was then compared by paired t-test using SPSS 10.0 (SPSS 1999).

6.3 Results

Vegetation

Among mesophyll rainforest sites, significant differences in overall vegetation structure were found at differing distances from the edge (MRPP, $P = 0.0001$). In order to identify which groups were responsible for these differences, pairwise post-hoc comparisons were performed between the three groups by MRPP, but using Bonferroni corrections ($\alpha = 0.05/4 = 0.0125$). Edge transects differed significantly from 50 m transects and interior transects ($P < 0.0003$ and 0.0001, respectively). On the other hand, no significant differences were apparent between 50 m transects and interior transects ($P = 0.5743$). Interior and 50 m sites were therefore grouped for further analyses.

Within the rainforest sites, significant differences were found between edges and interior transects (MRPP, $P < 0.0001$). These differences were caused by greater numbers of stems, shrubs (in particular, *Lantana camara*), and by lower abundances of ground ferns, moss, pandans, and climbing palms at the edge (Table 6.1). On the other hand, among mixed forest sites there was little evidence of changed vegetation structure between the edge and the interior of patches ($P = 0.150$). The only (weak) trends consisted of greater abundances of woody lianas and greater pooled abundances of growth forms associated with openings within interiors. It should be noted, however, that the relatively small number of mixed rainforest sites (five) may have contributed to the lack of significance in comparison with the mesophyll vine forest (28 sites). The stark clarity of these differences, however (Table 6.1), suggests that the broad differences are genuine, rather than an artefact of the different sample sizes between mesophyll vine forest and mixed rainforest.

The structural features that significantly differed in abundance between mesophyll rainforest edges and interiors are illustrated in Figure 6.1. The density of stems was significantly higher within the edge zone than within the interior of fragments (a), as were the density of shrubs (c) and the introduced weed *Lantana camara* in particular (g). Ground ferns (b), moss (d), pandans (e), *Calamus* spp. (f), and the total abundance of growth forms favouring darker, cooler, more humid places (h) were significantly more abundant in the interiors of patches. Among the mixed forest sites, there were marginally more woody lianas in patch interiors and, unexpectedly, a greater abundance of growth forms associated with openings within patch interiors. This last result may, however, been due to the large number of shrubs within the unfragmented mixed forest site (counted as ‘interior’ transects).

Table 6.1 Vegetation structural measures at edges and within interiors of rainforest and mixed forest, respectively. Columns represent mean ± SE, and p-values of Mann-Whitney U tests.

	Mixed Forest			Mesophyll Rainforest		
Variable	Edge	Interior	*P*	Edge	Interior	*P*
Vegetation density in the stratum 0-1m	1.58 ± 0.24	1.82 ± 0.12	0.225	2.44 ± 0.09	2.44 ± 0.07	0.853
Vegetation density in the stratum 1-2m	1.29 ± 0.10	1.48 ± 0.08	0.161	2.34 ± 0.08	2.30 ± 0.06	0.674
Vegetation density in the stratum 2-5m	2.00 ± 0.14	2.06 ± 0.10	0.570	2.53 ± 0.06	2.46 ± 0.04	0.355
Vegetation density in the sub-canopy	2.08 ± 0.14	1.97 ± 0.12	0.510	2.35 ± 0.07	2.25 ± 0.06	0.381
Vegetation density in the canopy	1.21 ± 0.11	1.21 ± 0.09	0.926	1.72 ± 0.09	1.68 ± 0.07	0.81
Height of upper canopy	25.83 ± 0.63	26.36 ± 0.70	0.788	22.54 ± 0.65	23.68 ± 0.55	0.121
Proportion of sky visible from 1.8m height	2.33 ± 0.19	2.15 ± 0.13	0.347	2.68 ± 0.07	2.54 ± 0.05	0.233
Number of tree stems within 5m radius	22.33 ± 2.58	21.55 ± 1.11	0.590	25.79 ± 1.01	23.16 ± 1.01	0.031*
Abundance of trees with plank buttress roots	1.00 ± 0.38	0.36 ± 0.20	0.176	1.89 ± 0.12	2.16 ± 0.08	0.086
Abundance of trees with spur buttress roots	1.00 ± 0.38	0.45 ± 0.25	0.242	2.00 ± 0.07	2.09 ± 0.06	0.383
Abundance of single-stemmed palms	0.50 ± 0.33	1.27 ± 0.30	0.105	0.5 ± 0.14	0.78 ± 0.13	0.119
Abundance of multi-stemmed palms	1.00 ± 0.38	0.73 ± 0.30	0.563	2.09 ± 0.16	2.45 ± 0.10	0.07
Abundance of woody lianas	1.00 ± 0.33	1.82 ± 0.23	0.046 *	2.54 ± 0.09	2.61 ± 0.07	0.585
Abundance of ground ferns	0.50 ± 0.33	0.64 ± 0.28	0.685	0.96 ± 0.18	1.47 ± 0.14	0.025*
Abundance of shrubs	0.88 ± 0.44	1.82 ± 0.30	0.086	1.59 ± 0.18	0.94 ± 0.13	0.004*
Abundance of seedlings	3.00 ± 0.00	2.91 ± 0.09	0.394	2.76 ± 0.07	2.80 ± 0.06	0.694
Abundance of moss	1.00 ± 0.42	1.36 ± 0.24	0.405	1.59 ± 0.12	2.27 ± 0.08	<0.001**
Abundance of fan palms	-	-	-	0.17 ± 0.10	0.28 ± 0.10	0.437
Abundance of tree ferns	-	-	-	0.33 ± 0.10	0.59 ± 0.12	0.169
Abundance of pandans	1.50 ± 0.46	0.55 ± 0.28	0.083	1.93 ± 0.17	2.28 ± 0.14	0.064*
Abundance of strangler fig trees	0.25 ± 0.25	0.00 ± 0.00	0.241	0.33 ± 0.10	0.30 ± 0.08	0.841
Abundance of lichens	2.13 ± 0.35	2.55 ± 0.16	0.353	2.96 ± 0.03	2.86 ± 0.07	0.448
Abundance of all epiphytes	0.25 ± 0.25	0.27 ± 0.19	0.795	1.26 ± 0.12	1.30 ± 0.09	0.982
Abundance of thorny vines	0.25 ± 0.25	0.64 ± 0.24	0.191	0.89 ± 0.12	1.13 ± 0.11	0.173
Abundance of *Calamus* spp.	-	-	-	2.39 ± 0.15	2.84 ± 0.06	0.019*
Abundance of *Lantana camara*	1.25 ± 0.49	1.09 ± 0.31	0.862	0.87 ± 0.16	0.14 ± 0.07	<0.001**
Abundance of *Acacia* spp.	2.75 ± 0.16	2.45 ± 0.16	0.210	0.22 ± 0.10	0.23 ± 0.09	0.852
Abundance of *Eucalyptus* spp.	2.50 ± 0.33	2.55 ± 0.16	0.699	-	-	-
Sum of growth forms associated with cool, dark microclimates	4.50 ± 0.76	6.09 ± 0.55	0.168	9.59 ± 0.46	11.77 ± 0.38	0.001**
Sum of scores of growth forms associated with openings	0.88 ± 0.44	2.18 ± 0.30	0.030 *	3.96 ± 0.25	3.80 ± 0.15	0.356

Complexity of the lower two strata (measured as the sum of the foliage density rating of each of the strata height) did not change significantly between the edge and interiors of both rainforest and mixed forest fragments (Table 6.2). Similar results were gained for the total complexity of the lower three strata (<5 m height), the top two strata (subcanopy and canopy), and the total foliage complexity. Likewise, habitat heterogeneity did not differ significantly between the edges and interiors of fragments (Table 6.2). This was true for the mean and maximum heterogeneity within transects in both rainforest and mixed forest.

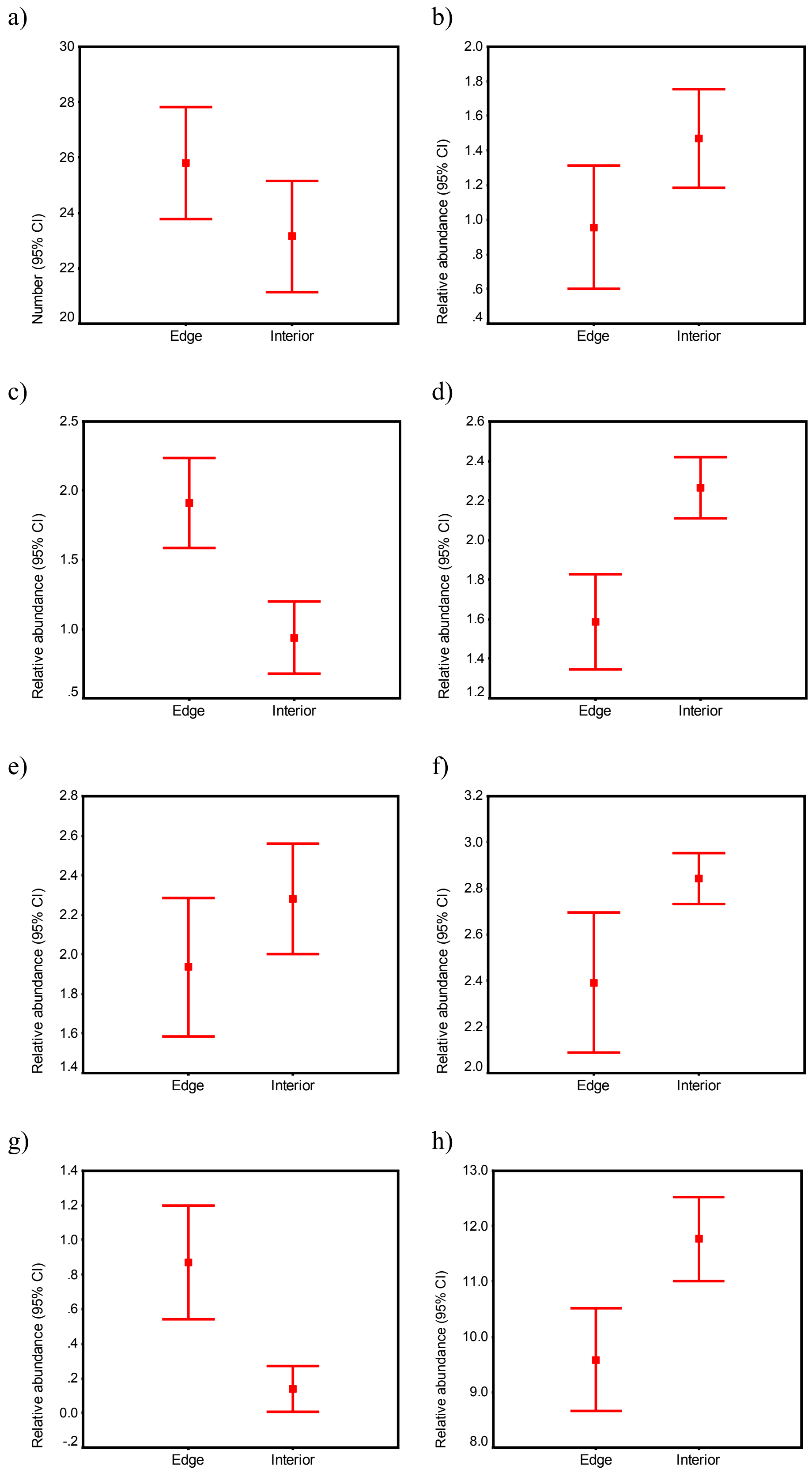

Figure 6.1 Structural vegetation measures as a function of location within mesophyll rainforest patches (Mean ± 95% CI). a) Number of stems, b) Relative abundance of ground ferns, c) Relative abundance of shrubs, d) Relative abundance of moss, e) Relative abundance of pandans, f) Relative abundance of *Calamus* spp., g) Relative abundance of *Lantana camera*, h) Relative abundance of growth forms associated with cool, dark microclimates.

Table 6.2 Vegetation complexity and heterogeneity measures at edges and within interiors of rainforest and mixed forest. Columns represent mean ± SE, and p-values of Mann-Whitney U tests. Complexity refers to foliage density, whereas heterogeneity refers to the variation in overall structure among sample points within a site or transect (see Chapter 4 for details).

	Mixed Forest			Mesophyll Rainforest		
Variables	Edge	Interior	*P*	Edge	Interior	*P*
Bottom 2 strata complexity.	2.88 ± 0.27	3.31 ±0.18	0.152	4.78 ± 0.15	4.73 ± 0.12	0.744
Total complexity for lower 3 strata	4.88 ± 0.35	5.36 ± 0.22	0.129	7.31 ± 0.16	7.19 ± 0.14	0.517
Top 2 strata complexity	3.29 ± 0.18	3.18 ± 0.18	0.840	4.06 ± 0.15	3.93 ± 0.11	0.598
Total vertical foliage complexity	8.17 ± 0.32	8.55 ± 0.28	0.545	11.38 ± 0.18	11.12 ± 0.17	0.492
Mean heterogeneity from PCA distances using structural variables.	2.75 ± 0.32	2.70 ± 0.19	1	3.40 ± 0.211	3.25 ± 0.124	0.762
Maximum heterogeneity from PCA using structural variables.	3.60 ± .46	3.51 ± 0.26	1	4.39 ± 0.279	4.13 ± 0.179	0.571

Bird richness and abundance

Eighty-seven species of birds were recorded from the morning transects. After removing raptors, vagrant species and very rare species, 72 species remained for analysis. Total bird densities did not differ between edge and interior transects (Table 6.3); however, significant differences in the composition of bird assemblages were found between edge and interior transects. Habitat 1 and Habitat 2 species (open country species) were found at higher densities at the edge, as were obligate and partial frugivores, obligate granivores, and partial nectarivores. Interior transects contained higher densities of rainforest specialists (Habitat 6 species), obligate insectivores and species that occur mainly in the understorey (below 5m). Habitat 5 species showed tendencies ($P = 0.056$) for higher relative densities in patch interiors. In other words, open country species tended to favour edges, species found in a variety of open and closed habitats showed no discernable preference, and species of closed habitats tended to prefer patch interiors.

Of the 54 species that contained ten or more records within the morning transects, 17 showed preferences for either patch edges or patch interiors (Table 6.4). Of those preferring interiors, half were species that spend their time primarily within the understorey and mid-storey. These were the Large-billed scrub wren, Little shrike-thrush, Spectacled monarch and Pale-yellow robin. These species are also, along with the Rufous fantail, obligate insectivores. The Black butcherbird, although commonly seen in the canopy, spends much time within the mid-storey, while the Orange-footed scrub-fowl is a ground-dwelling omnivore.

Table 6.3 Densities of different guilds at patch edges and interiors on a patch-by-patch basis. Comparison is by Wilcoxon sign-rank test (n = 22).
Habitat guilds: 1 = open country, 2 = variety of open and forested habitats, but not in rainforest, 3 = only in woodland and open forest, 4 = variety of habitats, including rainforest, 5 = mainly in rainforest and other thick vegetation, 6 = rainforest only, or dependent on rainforest plants.

	Denser at edge	Denser in interior	Ties	Wilcoxon Z score	*P*	Preference
Total	13	9	0	-0.325	0.745	
Habitat 1 species	16	1	5	-3.278	0.001	Edge
Habitat 2 species	11	0	11	-2.949	0.003	Edge
Habitat 3 species	6	3	13	-1.365	0.172	
Habitat 4 species	14	8	0	-1.624	0.104	
Habitat 5 species	5	16	1	-1.913	0.056	
Habitat 6 species	4	14	4	-2.311	0.021	Interior
Obligate frugivores	15	6	1	-2.486	0.013	Edge
Partial frugivores	15	6	1	-2.366	0.018	Edge
Obligate insectivores	6	16	0	-2.387	0.017	Interior
Partial insectivores	9	13	0	-1.055	0.291	
Mixed feeders	12	7	3	-0.966	0.334	
Vertebrate feeders	7	13	2	-1.815	0.069	
Mixed carnivores	7	13	2	-1.144	0.253	
Mixed herbivores	9	9	4	-0.633	0.527	
Obligate granivores	9	1	12	-2.055	0.040	Edge
Partial granivores	9	11	2	-0.635	0.525	
Partial nectarivores	14	8	0	-2.147	0.032	Edge
Understorey species[1]	3	19	0	-3.852	<0.001	Interior

[1] Species that are found in the lower and mid-storey vegetation, but rarely in the canopy.

Table 6.4. Densities of different species at patch edges and interiors on a patch-by-patch basis. Comparison is by Wilcoxon sign-rank test (n = 22).

Species	Denser at edge	Denser in interior	Ties	Wilcoxon Z score	*P*	Preference
Large-billed scrub wren	0	16	6	-3.522	<0.001	Interior
Orange-footed scrub-fowl	0	17	5	-3.627	<0.001	Interior
Rufous fantail	2	16	4	-3.347	0.001	Interior
Metallic starling	3	17	2	-3.253	0.001	Interior
Little shrike-thrush	4	17	1	-2.996	0.003	Interior
Spectacled monarch	2	17	3	-2.777	0.005	Interior
Rainbow lorikeet	0	8	14	-2.53	0.011	Interior
Black butcherbird	5	17	0	-2.385	0.017	Interior
Pale-yellow robin	1	8	13	-2.088	0.037	Interior
Yellow-bellied sunbird	16	2	4	-3.502	<0.001	Edge
Forest kingfisher	8	0	14	-3.008	0.003	Edge
Dusky honeyeater	12	2	8	-3.008	0.003	Edge
Yellow oriole	13	3	6	-2.742	0.006	Edge
Spangled drongo	14	4	4	-2.445	0.014	Edge
Helmeted friarbird	9	2	11	-2.334	0.020	Edge
Willy wagtail	6	0	16	-2.214	0.027	Edge
Spotted turtle-dove	5	0	17	-2.06	0.039	Edge
Rainbow bee-eater	9	4	9	-2.032	0.042	Edge
Silvereye	6	3	13	-1.956	0.050	Edge

Species showing a preference for edges included the Yellow-bellied sunbird, Spangled drongo, Rainbow bee-eater and Silvereye, all of which inhabit a wide range of habitats. Others, including the Willy wagtail and Forest kingfisher, are open country specialists, while the Metallic starling, although a rainforest specialist, is a highly mobile migrant frugivore.

Bird species richness did not vary significantly between edge and interior habitat (Table 6.5), although habitat and feeding guilds again demonstrated significant preferences. Habitat 1, Habitat 2 and Habitat 4 groups were more species rich at edges, whereas Habitat 5 and Habitat 6 groups were more species rich within interiors. Of the feeding guilds, only granivores demonstrated higher richness at the edge, whilst no other guilds were significantly more species rich in either edges or interiors. Insectivores, however, showed tendencies ($P = 0.095$) for higher relative densities in patch interiors.

Table 6.5 Preference of different guilds (measured as richness) for patch edges and interiors on a patch-by-patch basis. Comparison is by Wilcoxon sign-rank test (n = 22).
Habitat guilds: 1 = open country, 2 = variety of open and forested habitats, but not in rainforest, 3 = only in woodland and open forest, 4 = variety of habitats, including rainforest, 5 = mainly in rainforest and other thick vegetation, 6 = rainforest only, or dependent on rainforest plants.

	Richer at edge	Richer in interior	Ties	Wilcoxon Z score	*P*	Preference
Total	11	10	1	-0.209	0.835	
Habitat 1 species	14	2	6	-2.867	0.004	Edge
Habitat 2 species	11	1	10	-2.997	0.003	Edge
Habitat 3 species	8	3	11	-1.702	0.089	
Habitat 4 species	17	5	0	-2.778	0.005	Edge
Habitat 5 species	2	19	1	-3.844	<0.001	Interior
Habitat 6 species	4	15	3	-2.869	0.004	Interior
Frugivores	12	8	2	-0.937	0.349	
Insectivores	7	12	3	-1.671	0.095	
Mixed feeders	13	9	0	-1.486	0.137	
Mixed carnivores	8	10	4	-1.360	0.174	
Mixed herbivores	7	9	6	-0.235	0.814	
Granivores	9	1	12	-2.040	0.041	Edge

Multiple regression analysis demonstrated that the relative species richness at the edges of patches (mean richness per hectare at a patch edge divided by the mean richness per hectare at the interior of the same patch) was partly explained (26.8% of variation) by a negative relationship with patch area and a positive relationship with the amount of habitat within 5 km of the patch (Table 6.6). In effect, larger patches tended to contain lower relative richness at the patch edge, whereas larger amounts of rainforest within 5 km of patches led to higher relative numbers of species at the edge. On the other hand, the relative total abundance of species at the edges of patches could not be significantly explained by the spatial or vegetation measures.

Table 6.6 Results of stepwise multiple regressions of relative species abundance and richness at patch edges (with respect to values in patch interiors) on spatial and vegetation variables (n = 22).

Dependent variable	Adjusted R^2	Significant Predictors	Slope	Coeff	T	P
Relative total richness	.268	Log Area	-	.560	-2.735	.013
		Mean outside patch 5km	+	.508	2.480	.023
Relative total abundance	Nil	-	-	-	-	-

Assemblage responses

Edge architecture and fragment area were significant in explaining the degree of dissimilarity between edge and interior assemblages (Table 6.7). Major vegetation MDS axes, mean rainforest cover outside the focal patch, and the density of 'edge habitat' within 1 km of the focal patch were excluded from the model. However, when patches with blunt and sharp edges were treated separately, the relationships to patch area of the avian edge/interior dissimilarities were quite different. Edge/interior dissimilarity in fragments where edges were blunt demonstrated a close log-linear relationship to fragment area (r^2 = 0.7491). On the other hand, dissimilarity in fragments where edges were sharp showed no significant relationship with fragment area (Figure 6.2).

Table 6.7 Results of stepwise multiple regression of mean dissimilarity of bird assemblages at patch edges from corresponding patch interiors (n = 22).

Dependent variable	Adjusted R^2	Significant Predictors	Slope	Coeff	T	P
Assemblage dissimilarity	.518	Log Area	+	.413	2.425	.027
		Sharp edge	+	.655	3.843	.001

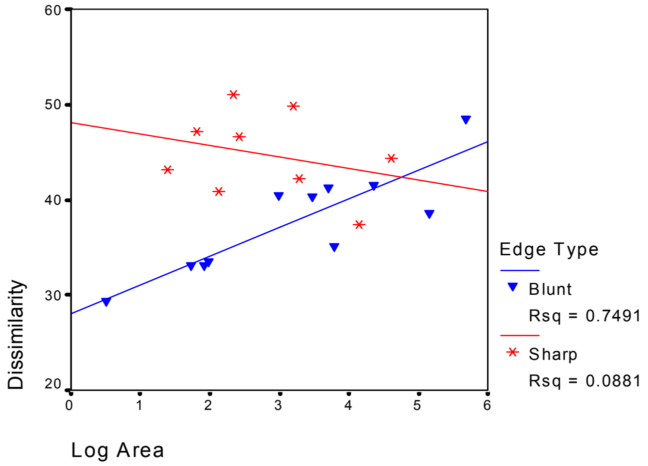

Figure 6.2 Scatterplot showing multivariate dissimilarity as a function of log fragment area (ha). Sites are identified by edge architecture, and regression coefficients are displayed.

Figure 6.3 shows that bird assemblage structure at rainforest patch edges based on species abundances consistently diverged from control sites to a greater degree than those in the interiors of the same patches (t = 3.657, df = 18, *P* = 0.002). Bird assemblage structure at rainforest patch edges based on species presence/absence also diverged to a greater degree than interior assemblages (t = 2.520, df = 18, *P* = 0.021).

Trends in mixed forest were inconclusive. Although assemblages at the edge of mixed forest patches based on both species abundance and species presence/absence were in all cases more dissimilar from the mixed forest control site than those in patch interiors, this was not statistically significant for species abundance (t = 2.466, df = 2, *P* = 0.133) or presence/absence (t = 3.625, df = 2, *P* = 0.068). This lack of significance, however, was possibly due to the small sample of mixed forest patches with both edge and interior transects (only three patches).

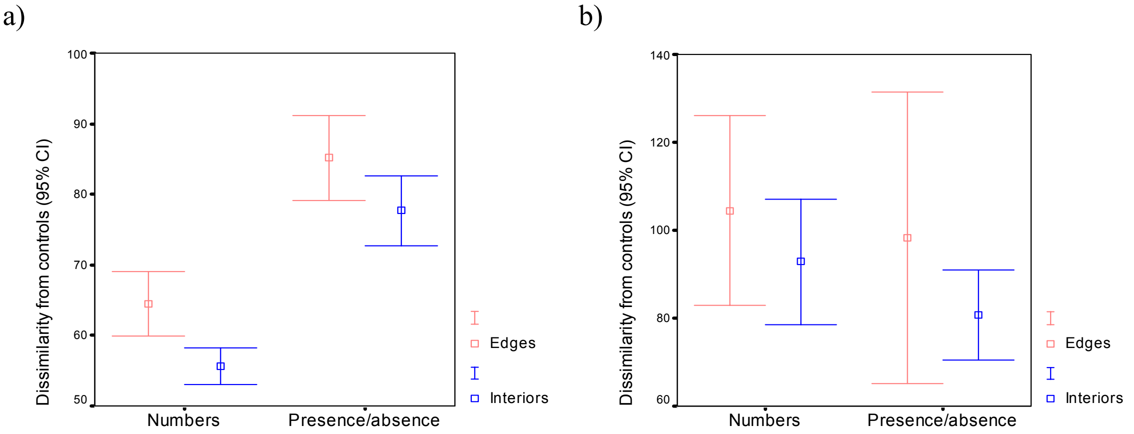

Figure 6.3 Mean dissimilarity from control sites of bird assemblages at edges and bird assemblages in interiors, in a) mesophyll rainforest, and b) mixed forest. Error bars represent 95% confidence interval.

6.4 Discussion

Vegetation

Within the mesophyll rainforest sites, there were marked differences between edge and interior vegetation, in common with other rainforests worldwide (e.g., Lovejoy *et al.* 1986, Williams-Linera 1990, Murcia 1995). The increase in numbers of stems near edges, probably because of microclimatic conditions (Murcia 1995), concurs with some previous studies (e.g., Williams-Linera 1990), as does the increase in density of shrubs (Williams-Linera 1990) and weed species near edges (Fox *et al.* 1997). Across this region, the majority of shrubs comprised giant bramble *Rubus alceifolius* or *Lantana camera*, both of which are opportunistic colonisers requiring large amounts of light. *Rubus alceifolius* was more common at edges, but successfully colonised the occasional treefall, whereas *Lantana camera* was only found at edges. Therefore, although both shrubs are exotic, in this region only *Rubus alceifolius,* with its ability to penetrate into the rainforest itself, appears to be a significant pest in the mesophyll rainforest areas. In the mixed forest, on the other hand, lantana was able to penetrate into the forest interior.

No differences in canopy connectedness and foliage density were evident between edge zones and interiors, except for a thin curtain of vines along some (probably older) edges. This is in stark contrast to the majority of studies finding decreased canopy cover in close proximity to edges (Murcia 1995, Oosterhorn & Kappelle 2000) and in the case of the Atherton Tablelands of north Queensland, up to 500 m from the edge (Laurance 1991). Furthermore, unlike many other studies (e.g., Miller & Lin 1985, in Williams-Linera 1990), these fragments showed no evidence of change in either overall complexity (foliage density) or heterogeneity between edges and interiors. This study also found no detectable difference in the density of the disturbance-adapted *Calamus* spp. (lawyer vine) between edge zones and patch interiors, in contrast to the increased densities found closer to the edges of patches on the Atherton Tablelands (Laurance 1991).

The lack of change in physical structure and *Calamus* spp. densities identified in this study probably results from the exposure of the study area (and most north Queensland lowland areas) to cyclones. The Atherton Tablelands are a mid-elevation (600-900 m) plateau approximately 30 km from the coast, and is partly protected from prevailing coastal winds by higher peaks (> 1400 m altitude). Cyclone Winifred in 1986 therefore caused damage only near forest margins on the Atherton Tablelands, but most lowland rainforests of the study area were very severely damaged by this storm, with little evidence of a gradient of impact away from edges at the time (Unwin *et al*. 1988). Likewise, even 10 years after the cyclone, little evidence of a gradient of structural impact was present. Therefore, rather than lacking the usual damaged canopy in close proximity to edges, the lowland rainforests of this region have broken canopies virtually everywhere.

Although levels of structural complexity were constant from edges to interiors, edge zones (0-20 m) contained lower abundances of moss, ground ferns and pandans, all of which require cool, moist habitats in which to thrive. This suggests that, although the canopy is consistently broken up throughout the lowland forests, there nevertheless exist microclimate differences within the edge zone. The microclimate changes from edges in the lowlands appear to be caused primarily by outside conditions permeating horizontally from the edge, rather than by secondary effects from canopy damage in turn causing microclimate changes (vertical permeation) for often great distances on the Atherton Tablelands (Laurance 1991).

The distance that edge effects penetrate often depends on the particular structural or microclimate variable concerned. For example, in central Amazonian fragments, edge effects ranged from 0 m (canopy density) to 184 m (air temperature) (Didham and Lawton 1999), and Laurance (1991) detected effects up to 500 m from the edge on the Atherton Tablelands, attributing this to damage from cyclones and heavy winds. This study, however, found no significant effects on vegetation beyond 50 m, and found no evidence of structural differences (canopy closure, density of understorey etc.) between edges and interiors. Conversely, central Amazonian rainforests exhibited a five-fold increase in canopy gaps near edges (Kapos *et al.* 1997) and even in central Amazonia, strong winds create an altered canopy up to 200 m from forest edges.

There is the possibility that edge processes affect vegetation structure over a distance beyond those measured (0 to 400 m from edges). However, this possibility is unlikely as none of the 26 structural measures demonstrated a consistent trend in values from 50 m to 400 m from edges, which would be expected were the effects of edges to penetrate beyond these distances.

In contrast to the mesophyll rainforest sites, the mixed forest shows little evidence of edge effects on vegetation structure. The sparser foliage throughout all strata (Chapter 4) suggests that temperature and light availability would be higher, and humidity lower, than those found in mesophyll rainforest. In other words, the microclimate of this type of forest might be closer to that of areas external to the forest than would be the mesophyll rainforest. This is further evidenced by the lower abundance and variety of growth forms that require cool, moist microclimates (Chapter 4). A less marked change such as this would suggest there to be less likelihood of a gradient in conditions from the edge to the interior of this forest type, leading to fewer vegetation changes.

Bird richness and abundance

Bird assemblages respond to the presence of habitat edges in a variety of ways. Temperate forest edges often contain higher species richness than forest interiors (e.g., Hansson 1994) whereas tropical edges are commonly less species-rich than forest interiors (e.g., Lovejoy *et al.* 1986). These differences may be due to the higher natural frequency of large gaps in temperate forest, less closed canopies (resulting in less microclimate contrast between the forest interior and exterior) in temperate forest, or lower habitat specificity in temperate bird species. Furthermore, rainforest edges surrounded by other natural habitat types such as woodland or open forest often contain elevated species richness due to the presence of multiple habitats (e.g., Lopez de Casenave *et al.* 1998), whereas patch edges surrounded by agriculture are frequently less species rich compared to patch interiors (e.g., Lovejoy *et al.* 1986).

Unexpectedly, this study found that neither total richness nor abundance differed between edges and interiors of lowland rainforest or mixed forest fragments, thus contrasting with most other tropical rainforest studies of edge effects in South America (Terborgh *et al.* 1990, Lovejoy *et al.* 1986, Restrepo & Gomez 1998), Africa (Dale *et al.* 2000, Beier et al. 2002), and Asia (Raman & Sukumar 2002). For example, in Central Amazonia, 10m from edges, the catch from mist nets was reduced by 60% compared with 1 km into the forest, and at 50 m from edges, the catch was still reduced by 22% (Lovejoy *et al.* 1986). Species richness was also affected, with 28 species caught at 10 m, 47 at 50 m and 50 at 1 km (Lovejoy *et al.* 1986).

It should be said that some of the above studies (Lovejoy *et al.* 1986, Restrepo & Gomez 1998, Dale *et al.* 2000) utilised mist nets to sample the avifauna, and thus would be biased towards understorey species, which are often vulnerable to a range of disturbances (e.g. Canaday). However, other studies utilised point counts and territory mapping (Terborgh *et al.* 1990, Beier et al. 2002, Raman & Sukumar 2002), thus sampling species across a wider range of vertical strata, and found similar patterns. Therefore, tropical forest edges surrounded by a matrix of pasture or crops generally tend towards lower species richness and abundance than forest interiors, a response that differs from those of temperate forests.

The response to the presence of edges of this avian assemblage was therefore intermediate between the usual responses of bird assemblages in other tropical rainforests (decreased richness and abundance at edges) and temperate forests (increased richness and diversity). Three factors that help to determine the degree of edge effects are probably the cause of this pattern: they are the vegetation contrast between edges and interiors, the nature of the forest bird assemblage, and the number of available species in the matrix.

Firstly, the relatively low differences in vegetation between patch edges and interiors, brought about by regular disturbance from cyclones, results in a lowered difference in vegetation structure and microclimate between edges and interiors. Bird assemblages often respond to differences in vegetation structure and floristics (e.g., MacArthur & MacArthur 1961, Kikkawa 1982, Laurance *et al.* 1996), and therefore lower contrast in vegetation structure between edges and interior may partly result in the lower contrast, and consistent richness and abundance, between bird assemblages at edges and interiors in this study.

Secondly, as outlined in Chapter 5, bird assemblages in the Wet Tropics of northern Queensland are less diverse and specialised than those found in most other tropical rainforest areas. For example, in central Amazonia over 400 bird species have been recorded within nine 10-ha rainforest fragments within a 40 km radius (Stouffer & Bierregaard 1995a), whereas this study recorded 102 species in 33 fragments of rainforest and mixed forest. Of these, only 15 were rainforest specialists, while a further 29 occurred mainly in rainforest, but also in other dense vegetation such as vine thicket and gallery forest. In other words, the lowland bird assemblage consists largely of habitat generalists and feeding generalists. Generalists are more likely to be able to adapt not only to change with time, but also across environmental gradients.

Thirdly, the study area contains a wide variety of open-country species around patch edges and in the mixed forest at the northern part of the study region. This woodland block extends up the Mulgrave valley, creating an almost continuous corridor of open forest. Furthermore, the distance between the western extent of this block and large areas of open woodland on the western side of the Wet Tropics is only 5 km. Thus, there exists a more-or-less continuous connection between the mixed forest and large source populations of open-country and sclerophyll species that can utilise rainforest edges, thus compensating for the decrease in forest specialists. Many other tropical areas subjected to rainforest fragmentation, such as in central Amazonia (Lovejoy *et al*. 1986) contain few open-country species that can colonise edges.

Assemblage responses

In contrast to the overall abundance and richness patterns, species composition differed between the edges and interiors of patches. Birds of open country favoured patch edges, and rarely ventured into patch interiors. Therefore, patch edges effectively provide a separate habitat. Over most of the study area, nearly all cleared vegetation was rainforest (Winter *et al*. 1987), and the present surrounding matrix (sugar cane) is generally devoid of even the open-country species. These factors suggest that these species have only been able to colonise much of the area as a result of fragmentation. The presence of perches along edges, and adjacent open strips between the rainforest patches and the sugar cane, provide a narrow ‘corridor’ of habitat that provides the necessary resources for a range of open-country and woodland species. Forest kingfishers, for example, are sit-and-pounce predators that are able to use rainforest edge trees as perches from which to prey on arthropods and small reptiles in the open areas just outside the patches. Open-country granivores such as the Spotted turtle-dove and Peaceful dove are also able to perch in edge trees and descend to feed on grass seeds just outside forest fragments.

Only rainforest obligates and species of dense habitat showed avoidance of edges, both in numbers and richness. This may be due to sensitivity that rainforest specialists exhibit to microclimates or resource levels at the edge, or could result from competition from species that are more common at the edge, such as the Spangled drongo, which is commonly aggressive towards other birds (Edden & Boles 1986). Specific analyses of causality, however, may require further studies of specific resource abundances measures (e.g., Restrepo *et al.* 1999) or bird removal experiments (e.g., Grey *et al.* 1997).

The individual species more commonly found at edges were generally those of open country except for the Silvereye, Yellow-bellied sunbird, and the Yellow oriole, which are found in a variety of habitats, including rainforest. Of the eight species that favoured patch interiors, only one (Pale-yellow robin) is a true rainforest obligate, but four others are found mainly in rainforest vegetation and other thick vegetation (Black butcherbird, Large-billed scrubwren Orange-footed scrubfowl, Spectacled monarch), while three habitat generalists occur in greater densities in forest interiors (Little shrike-thrush, Rufous fantail and Rainbow lorikeet). Although this seems at odds with the overall preference of rainforest obligates for patch interiors, I interpret this partly as due to the low numbers and low patch occupancy of many of these species, in common with Dale *et al.* (2000). Although many of these species were more abundant in patch interiors, their complete absence in many patches precluded statistical significance. Examples include the Spotted catbird (denser at two patch edges, denser at seven patch interiors, and absent in 13 sites), Chowchilla (0, 4, 18), and Emerald dove (1, 5, 16), all of which are dense-habitat specialists. The Little shrike-thrush and Rufous fantail, although habitat generalists, are understorey insectivores, a group commonly shown to be vulnerable to edges (e.g., Stouffer & Bierregaard 1995a).

The reason for frugivores favouring patch edges may be increased abundance of fruiting trees or increased fruiting by some species near the edge (McDiarmid *et al.* 1977), although this relationship is uncertain. Higher abundances of fruit at edges does not always translate to greater frugivore abundance (Restrepo et al 1999), and fruit abundance and avian frugivore abundance may vary seasonally (Restrepo & Gomez (1998), further complicating efforts to assign causality. Obligate granivores and nectarivores also favoured edges, whereas obligate insectivores and species of the understorey were particularly vulnerable to the effects of edges, in common with results from other studies (e.g., Stouffer & Bierregaard 1995a).

The relative richness at edges (compared to the interior) decreased in larger patches, and increased in patches with higher amounts of rainforest within 5 km. This is perhaps unsurprising, as ‘interior species’ are often those species that drop out first in smaller patches, possibly due to the lower proportion of interior habitat as compared to edge habitat (Wiens 1989). On the other hand, larger amounts of rainforest surrounding the focal patch appear to benefit some of the species that favour edges more than species of the forest interior. This may be due to the relationship between the amount of habitat within 5 km and the amount of edge within 2 km of the patch (Pearson's correlation coefficient = 0.63). Possibly, at this scale and degree of fragmentation, the proximity of other habitat benefits species of the edge that are able to use the edge along multiple patches in close proximity as one continuous habitat, unlike many of the interior species. Previous studies have found that interior species, and especially understorey species, are often unable or unwilling to cross an open matrix (Stouffer & Bierregaard 1995a). Therefore, in common with the theory of island biogeography, some species (often interior species) become extinct in smaller patches, whereas less isolated patches appear to allow some species (often edge species) to more readily colonise.

Larger patches also contained greater dissimilarity between patch edge and interior assemblages. This may also be due to the fact that some species that require larger patches also avoid the edges; that is, edge assemblages remain reasonably constant with patch area, whereas interior assemblages diverge significantly from edge assemblages with increasing patch area. Fragmentation increases the proportion of edge to interior habitat; therefore the size and shape of fragments may also affect bird species or assemblages due to the differing proportions of edge and core interior habitat. Very narrow or small fragments are likely to consist solely of edge-affected habitat, and will therefore contain largely edge assemblages and fewer interior species (Wiens 1989). Galli *et al.* (1976), for instance, found that woods of 0.2 ha contained edge birds only, while forest interior species began appearing at 0.8 ha. Likewise, Temple (1986) found narrow fragments to contain fewer interior species.

Initially, it was expected that bird assemblages of blunt edges (edges with shrubs, grass, climbers and other pioneer plants) would diverge from patch interior assemblages to a greater extent than would the assemblages of sharp edges (near vertical edge, with few shrubs) due to an influx of non-rainforest species that can utilise edge resources. Somewhat surprisingly therefore, in the absence of area factors, assemblages of sharper edges were found to be more dissimilar to their respective patch interiors than were assemblages of blunt edges. Gascon *et al.* (2000) describes the tendency for Amazonian edges to become blunter over time as tree mortality increases at the absolute edge. Although this process decreases the overall area of the patch, it also leads to increased amounts of vines and thicker foliage, which can 'seal' the edge, so within these edge zones (25 m from the edge) conditions are more similar to interior zones (Kapos *et al.* 1997, Didham & Lawton 1999). Therefore, although sharp edges may contain fewer edge species, they may contain significantly fewer interior species within 25 m of the edge than the blunt edges due to the hotter, drier conditions along these edge zones. It seems that, at least in this region, sharper edges are responsible for more significant edge effects, but older, blunter edges have the effect of decreasing the overall area of the patch.

Conclusions

Bird observations within an edge zone do not necessarily infer the type of use of that zone. For example, birds that forage actively close to the edge may avoid the edge for nesting purposes. In a broad sense, however, this study does provide strong evidence of impacts on vegetation structure and bird assemblage activity within close proximity of edges and that these effects are milder than those trends found in other rainforest areas, which provides a solid starting point for future studies of edge processes.

To determine how specific processes that are altered by the presence of forest edges in this region, and their effects on microclimate, plants and animals, a range of observational and manipulative studies is required. The influence of aspect, degree and type of disturbance, the age of edge, and surrounding habitat type may all influence to some degree these processes. Further studies of edge effects should include studies of the movements of individual species within (and between) patches, and more detailed research into microclimate trends between forest edges and interiors. Manipulative experiments (e.g., species removal, use of playback calls) and measures of specific resources will also provide more detailed evidence of edge effects in the region.

When incorporating the effects of edges in conservation measures such as the design of reserves in fragmented landscapes (e.g., Laurance 1991), some factors need to be considered. For example, not all edges are necessarily detrimental to forest fragments (Restrepo *et al.* 1999). Here, in the absence of detailed knowledge of seed dispersal and other specific processes, the similarity of avian assemblages of patch edges and interiors to unfragmented assemblages is used as a surrogate for degree and direction of impact. This study shows that assemblages of edge zones differ more substantially from those in unfragmented rainforest than do assemblages in interior zones, implying that edges here are in fact detrimental. However, this study also supports the assertion that edge effects change over time (Restrepo *et al.* 1999). Furthermore, strong physical disturbance and largely generalist bird assemblages may result in a lessening of edge effects both in the distance from the edge that is impacted and the degree of impact to both the vegetation and the avifauna, by those disturbances.

Chapter 7. Determinants of bird assemblage diversity and composition

7.1 Introduction

This chapter synthesises information on bird assemblages and site characteristics in order to explain the major factors that influence assemblage composition. Therefore, the results from Chapter 3 (the spatial characteristics of the study area), and Chapter 4 (the vegetation of the study sites) are here related to those from Chapter 5 (the bird community).

The impact of human-induced habitat fragmentation on biotic communities has become a major focus of ecological and conservation research (e.g., Loyn 1987, Klein 1989, Bierregaard *et al.* 1992). Of major interest in fragmentation studies are the effects of patch and landscape characteristics on the organisms of interest. Most species are influenced in some manner by a combination of patch characteristics, whether vegetative (e.g., Blake & Carr 1987), patch level (geometric attributes of a single patch) (e.g., Thiollay & Meyburg 1988), or landscape (e.g., relationships to other patches) (e.g., Pereira and Itami 1991). A large number of studies have now been undertaken at a range of scales and locations, in a variety of habitats, and using a variety of methods.

When habitat becomes fragmented, the area of habitat becomes smaller, remnants become more isolated, and edge zones become more influential (Andren 1994, Saunders *et al.* 1991). These patch and landscape characteristics (defined in detail in Chapter 3) can impact on biological processes including dispersal (e.g., Sieving *et al.* 1996), foraging (Bierregaard *et al.* 1992), predation and parasitism (e.g., Wilcove 1985, Arango-Velez & Kattan 1997, Cooper & Francis 1998), reproductive success (Breininger 1999), competition from edge species (Loyn 1987, Grey *et al.* 1997) and many others.

Patch-level characteristics include area, perimeter, shape and vegetation within the patch. Area is particularly important and is the most commonly measured landscape variable, especially with regard to island biogeography theory (MacArthur & Wilson 1967) and reserve selection (e.g., Diamond 1975). It affects species differently, depending on a species' area requirements (e.g., Thiollay 1989), the habitat heterogeneity within the patch, the potential population size of a species within a patch, the presence or abundance of scattered resources (Wilcove *et al.* 1986), and the frequency with which species can travel between patches. Patch area is particularly important in influencing bird species richness and abundance (e.g., Galli *et al.* 1976, McIntyre

1995), and assemblage composition may also change with patch size. Smaller patches, for example, often contain larger proportions of edge species at the expense of interior species (Galli *et al.* 1976, McIntyre 1995, Bellamy *et al.* 1996).

Where edge effects are in evidence, patch area may interact with patch shape to affect bird species or assemblages. Very narrow fragments are likely to consist solely of edge-affected habitat, and will therefore contain largely edge assemblages and fewer interior species (Wiens 1989, Galli *et al.* 1976, Temple 1986). Core area measures combine edge effects, patch shape and area, and can be accurate predictors of assemblage responses to fragmentation. Temple (1986), for example, found core area (area further than 100 m from the edge) to be a better predictor of the presence and abundance of fragmentation-sensitive birds than was total patch area.

Even where sites in a landscape are chosen for their vegetation similarity, virtually all landscapes will contain some degree of heterogeneity among sites, thus necessitating the incorporation of vegetation structure as a variable or series of independent variables. Vegetation structure varies between patches because of local climate, topography, soil, and land-use history (Chapter 4). Structural attributes such as tree density, foliage density, canopy height and closure, the availability of particular vegetation substrata, and horizontal heterogeneity often influence habitat use by birds (e.g., Roth 1976, Karr 1971).

Landscape-level characteristics include measures of isolation, the surrounding habitat type, and the size and arrangement of surrounding habitat in the matrix. In this study, the surrounding matrix consisted of either sugar cane or pasture, both of which provide few or no resources to forest birds. Therefore, the particular land use surrounding patches was not considered in this study.

Isolation can affect bird assemblages, as many forest specialist birds will rarely cross open areas (Bierregaard *et al.* 1992). Therefore, more isolated patches often (but not always) contain lower bird richness or diversity. Various components of isolation have been shown to influence bird assemblages, including distance to primary unfragmented habitat (Breininger *et al.* 1991, Bierregaard *et al.* 1992), and distance from the focal patch to the nearest patch of the same habitat type (e.g., Jansson & Angelstam 1999); however, many other studies have found little influence of this factor (e.g., Loyn 1987). Lower proportions of suitable habitat within a certain distance of the patch concerned may sometimes lead to lower species diversity (Vos and Stumpel 1995, Opdam *et al.* 1985) but, again, this is not always the case (Jansson & Angelstam 1999, Grant & Berkey 1999).

Lynch & Whigham (1984) found that patch isolation indices were more efficient predictors of local abundance of many species than was patch area: for example, the occurrence of long-tailed tits decreased with distance to the nearest patch of suitable habitat within a matrix of pine plantations (Jansson & Angelstam 1999). However, the degree of isolation frequently has little bearing on bird assemblage structure over distances of 100 m to 2 km (e.g., Estades & Temple 1999, Matthysen & Adriaensen 1998, Matthysen 1999).

Studies of fragmentation frequently focus not only on what landscape characteristics influence bird assemblages, but on what types of species are the most vulnerable. Again, conflicting results have been found; however, some general trends have emerged. Birds that best persist in small fragments tend to be the more common generalists (Patterson 1987), whereas specialist feeders such as antbirds and other specialist insectivores that rely on scattered resources and require larger home ranges seem particularly vulnerable (Lovejoy *et al.* 1986, Bierregaard *et al.* 1992). Other species that require scarce resources such as rare trees (Telleria & Santos 1995), cavities in old or dead trees (Zarnowitz & Manuwal 1985) or large tree trunks (e.g., Soule *et al.* 1988, Thiollay 1989) are also often adversely affected. Many studies (e.g., Diamond 1984, Soule *et al.* 1988, Tellaria & Santos 1995) have shown that rare species are usually the most affected by habitat fragmentation. However, some studies have found little evidence to support this (Karr 1982a, Karr 1990). Lescourret & Genard (1994), for example, found that although large stands contained higher species richness, rare species were actually favoured by fragmentation. In this case, however, the rarer species of the region (the French Pyrenees) largely consisted of edge species, which are usually favoured in these circumstances.

Usually forest interior species are more heavily affected by fragmentation, tending to decline in smaller patches to be replaced by edge species (e.g., McIntyre 1995, Bellamy *et al.* 1996). In agricultural and suburban landscapes, losses of species are often the result of intrusion of edge species such as cowbirds (Wilcove 1985, Brittingham & Temple 1983) or noisy miners (Loyn 1987). In some instances, migratory species have proven to be more vulnerable to fragmentation than resident species (Lynch 1987, Blake & Karr 1987).

Certain functional guilds are often sensitive to landscape-level alterations (Canaday 1996). For example, dietary specialists are often found to be more vulnerable to fragmentation, as they are more susceptible to variation in availability of food resources (the niche-breadth hypothesis) (Swihart et al. 2003). In particular, terrestrial and understorey insectivores have repeatedly been identified as highly sensitive to forest fragmentation both in the Neotropics (Willis 1974, Karr 1982b, Leck 1979, Stouffer & Bierregaard 1995a) and North America (Galli *et al.* 1976, Sieving *et al*. 1996). Nectarivores, however, may be more able to persist in fragments due to increased flowering around patch edges (Stouffer & Bierregaard 1995b).

Body size may often correlate with extinction proneness in fragments, especially for large predators that require large territories (Leck 1979, Loyn 1987, Lamberson *et al*. 1994, Jullien & Thiollay 1996). Galli *et al*. (1976) found among isolated forest patches in New Jersey that the Red-shouldered hawk (*Buteo lineatus*) utilised only the largest forest patches. Within specific functional guilds, the larger species are sometimes more adversely affected by fragmentation. This has been found for frugivorous birds (Restrepo *et al*. 1999, Renjifo 1999) and for understorey insectivores (Terborgh 1974).

Although results vary between studies, and for many of the above-mentioned trends there are conflicting results, it is generally accepted that tropical assemblages are more vulnerable to fragment area than temperate assemblages. Tropical avifaunas usually show more pronounced patterns with strong declines in richness of rainforest birds in patches over time, both in total numbers and as a proportion of the original richness (Willis 1974, Leck 1979, Kattan *et al*. 1994). These patterns of local extinction in tropical rainforest birds are particularly strong because of a number of factors. Compared to temperate avifaunas, these assemblages are usually more diverse, species are more specialised in their foraging habits, and consequently tropical rainforest species occur in lower densities (Wilcove *et al*. 1986, Turner 1996) and patchier distributions (Thiollay 1989, Diamond 1980). Furthermore, many tropical species have lower dispersal powers (Wilcove *et al*. 1986), and are less tolerant of vegetation outside the forest (Turner 1996).

I predicted that rainforest specialists would be more heavily influenced by patch-level factors such as patch area, shape and vegetation differences, as they are less likely to cross non-rainforest habitat (Stouffer & Bierregaard 1995a). In fact, they may so rarely cross open areas that the actual degree of isolation may not be such a huge factor – rather extinction within a patch may be the greater issue. Habitat generalists, on the other hand, may be more influenced by landscape-level factors such as isolation, because although they should be able to cross open areas to some degree, cane paddocks are still a hostile environment for them, so the distance to colonise may still differentially affect their ability to colonise a patch. In common with many other rainforest areas in the world, I predicted that insectivores would be particularly influenced by area.

Chapter 4 demonstrated the distinction in the study area between the two major vegetation types, namely mesophyll rainforest, and mixed rainforest with eucalypt emergents. Chapter 5 showed that bird assemblages differed substantially between these vegetation types, and Chapter 6 showed that edge effects were more pronounced in the mesophyll rainforest and almost absent in mixed forest, and that habitat specialists in particular avoided edges. Due to the potentially differing responses of mixed forest bird assemblages to landscape and vegetation factors, and the small number of mixed forest patches in this study, only the mesophyll rainforest bird assemblages are analysed in this chapter. This chapter, therefore, examines how patch-level vegetation, and patch and landscape-level spatial factors, influence bird use of isolated rainforest patches.

Aims

The aims of this chapter are to:

- evaluate the influence of spatial and vegetation characteristics of patches on overall bird abundance and diversity within the fragmented Wet Tropics lowlands;
- determine the influence of these factors on the relative abundance of individual species;
- determine whether patterns in abundance or richness are related to specific feeding or habitat preferences of species.

Particular attention is paid to whether these results conform to our current knowledge of bird assemblages elsewhere and, if not, why this may be the case.

7.2 Methods

Study sites

Study sites are described in Chapter 2. In this chapter, 25 of 26 mesophyll patches and both control sites are examined for relationships between bird assemblages and landscape and vegetation characteristics. Site 7, which largely consisted of poorly drained fan palm forest, was omitted from the analysis due to the anomalous nature of its vegetation and avifauna.

Independent variables

Spatial characteristics of each patch (patch area, patch perimeter, shape index, perimeter area ratio, fractal dimension, and core area beyond 25 m, 50 m and 100 m from the edge) were measured as outlined in Chapter 3. Within the rainforest sites, substantial correlations were evident between some of these descriptors (Table 7.1). A threshold of $r = 0.8$ was used to determine whether independent variables were suitable for simultaneous examination as predictors (Germaine *et al*. 1998). Where correlation coefficients between two independent variables exceeded 0.8, the variable with the clearest biological interpretation was retained

Table 7.1 Spearman rank coefficient matrix for all final spatial variables for all patches (n = 27). *P*=.05 where r = 0.39. Variables retained for analysis, and correlation coefficients above 0.8, are indicated in bold face.

	Area	**Nearest Neighbour**	Dist main. No penin	**Dist main Incl penin**	**Dist 30 ha Patches**	**Rforest within 1 km**	Rf within 2 km	Rf within 5 km	**Rf within 10 km**	Patch perimeter	**Shape Index**	Perimeter area ratio	1km edge Density	**2km edge density**	Core area (25 m)	Core area (50 m)
Nearest neighbour	-0.542															
Dist main-no pen	-0.472	0.266														
Dist main-incl pen	-0.462	0.427	**0.805**													
Dist 30 ha patches	-0.375	0.746	0.174	0.504												
Rforest within 1 km	0.300	-0.723	-0.324	-0.351	-0.603											
Rforest within 2 km	0.326	-0.571	-0.678	-0.545	-0.220	0.651										
Rforest within 5 km	0.261	-0.235	-0.698	-0.626	-0.163	0.257	0.672									
Rforest within 10 km	0.184	-0.204	-0.532	-0.496	-0.172	0.226	0.592	**0.913**								
Patch perimeter	**0.964**	-0.581	-0.395	-0.450	-0.449	0.289	0.279	0.246	0.160							
Shape Index	0.780	-0.598	-0.315	-0.495	-0.588	0.383	0.282	0.292	0.216	**0.882**						
Perimeter area ratio	**-0.813**	0.323	0.371	0.172	0.037	-0.137	-0.225	-0.115	-0.102	-0.685	-0.333					
1 km edge density	0.247	-0.608	-0.068	-0.187	-0.534	0.772	0.466	0.302	0.309	0.317	0.397	-0.084				
2 km edge density	0.076	-0.461	-0.034	-0.168	-0.337	0.598	0.527	0.432	0.528	0.138	0.262	0.025	**0.872**			
Core area (25 m)	**0.990**	-0.498	-0.426	-0.402	-0.333	0.282	0.279	0.203	0.146	**0.939**	0.718	**-0.852**	0.232	0.055		
Core area (50 m)	**0.982**	-0.482	-0.453	-0.426	-0.312	0.257	0.275	0.214	0.153	**0.924**	0.683	**-0.870**	0.202	0.039	**0.992**	
Core area (100 m)	**0.965**	-0.490	-0.445	-0.402	-0.331	0.269	0.237	0.217	0.160	**0.927**	0.714	**-0.852**	0.197	0.031	**0.971**	**0.976**

(e.g., Forys & Humphrey 1999). Patch area was retained, as this factor has proven to be an important predictor of faunal diversity and community structure in the majority of studies worldwide. Patch perimeter, and core areas beyond 25 m, 50 m and 100 m from edges all correlated closely with patch area (r = 0.964, 0.990, 0.982 and 0.965, respectively), and were therefore unsuitable for inclusion in the major analyses. Of the shape measures, the perimeter/area ratio correlated closely with area (r = -0.813), but the area-independent 'shape index' is a more appropriate measure of patch shape in any case.

Measures of landscape configuration around each site were calculated (Chapter 3), including nearest neighbour, distance to the nearest main block of rainforest including and excluding any riparian peninsulas, distance to the nearest patch at least 30 ha in area, the density of rainforest within 1, 2, 5 and 10 km of the focal patch, and the density of edge habitat within 1 km and 2 km of the focal patch. Again, some of these measures correlated significantly (Table 7.1). Distances to main blocks of rainforest with and without peninsulas correlated highly with one-another (r = 0.843). I chose to use distance to main blocks of rainforest with peninsulas, as only three groups of species, and eight individual species, favoured interiors over edges, and of the two, this variable correlated less with other variables. Densities of edge habitat within 1 km and 2 km of the focal patch correlated very strongly with one-another (r = 0.872). Of the two, density within 2 km was retained, due to the consistently lower correlations with other variables. The spatial variables that were included (Table 7.1) were tested for normality and homogeneity of variances, and power transformed where necessary.

Vegetation variables were subjected to a non-metric multidimensional scaling (NMDS) ordination as described in Chapter 4, and reduced to three ordination axes describing 90% of the variation. High scores on Axis 1 described a thicker canopy, with tree ferns and stranglers, higher overall abundances of growth forms requiring cool, dark microclimates, greater overall foliage complexity, and greater heterogeneity. High scores on Axis 2 described higher abundances of root buttresses, lower densities of single-stemmed palms and ground ferns, more seedlings, and lower amounts of damp-requiring species. High scores on Axis 3 describe lower densities of thorny vines, and higher densities of multiple palms, fan palms and pandans.

Bird richness and abundance

Bird richness was calculated by aggregating all records from all seasons for each patch. I included all records within and outside the strip transects (but within patches) during both morning and afternoon surveys, and incidental records. Very rare vagrants such as a perching Straw-necked ibis, and raptors, which due to their sparse distribution and large home ranges require a different sampling regime, were excluded from the analysis.

The calculation of abundances was based on records within the 0.5 ha strip transects obtained during the morning surveys only, and very rare species and raptors were again excluded. Abundances were calculated by aggregating interior transects and edge transects separately by the mean over all seasons, and scaled up (×2), to be expressed as densities/ha for edge zones and interior zones per patch. By multiplying the edge zone density and interior zone density by the total area within the edge and 50 m core zones respectively, and then dividing the sum by the total patch area, the total density per patch was calculated.

Analyses

Multi-response permutation procedure (MRPP) is a non-parametric test for assemblage differences between groups of sites (Zimmerman *et al*. 1985), and was used to test for differences in bird assemblages between fragmented and control sites. Differences were tested using species presence/absence, and species abundance, and analyses were repeated with rare species removed from presence/absence and abundance matrices. Rare species were those present in fewer than three sites, those which had fewer than six morning records within transects, respectively. Distributions of sites were illustrated on detrended correspondence analysis (DCA) ordination plots.

To assess differences in species composition between sites, K-means cluster analyses and DCA were used to classify and ordinate sites based on species presence/absence and on species abundances. DCA creates a non-linear rescaling of the ordination axes of a species data matrix, and avoids the common arch effect of correspondence analysis (CA) by segmenting the first axis (Jongman *et al*. 1995). DCA is recognised as particularly suited to the analysis of species presence/absence and abundance (Jongman *et al*. 1995). Correlations of DCA axes with landscape variables were used to identify gradients represented by the ordination axes

To determine the factors affecting the distribution of bird species, canonical correspondence analysis (CCA) was performed using bird site-by-species data matrices (presence/absence data and abundance data) and the 10 final environmental variables. CCA is a commonly used ordination technique that constrains the ordination axes by linear combinations of the explanatory variables (Jongman *et al*. 1995). I assessed the effects of individual variables by calculating the intraset correlations (Jongman *et al*. 1995), and the significance of the axis-environment relationships was tested by a Monte Carlo permutation test (199 runs). CCA can be used in conjunction with DCA to infer whether the measured environmental variables account for the major variations in the species data. The above multivariate analyses were conducted in PC-Ord 4.0 (McCune & Mefford 1999), except for the K-means cluster analyses, which were performed using SPSS 10.0 (SPSS 1999).

Species were separated into habitat and feeding guilds as described in Chapter 5. To determine which vegetation and spatial variables accounted for the greatest amounts of variation in the total species richness and guild richness of patches, stepwise multiple regressions (see Chapter 6) were conducted using SPSS 10.0 (SPSS 1999). I also sought to explain variation in total abundance and the abundance of habitat and feeding guilds in this way. Individual species densities as a function of patch size were explored by Spearman rank-correlations.

7.3 Results

Assemblage responses

Within mesophyll rainforest sites, substantial differences were found between bird assemblages (presence/absence) in continuous habitat and in fragments (MRPP, $P = 0.002$), suggesting that unfragmented sites contained a distinct assemblage. When very rare and common species were removed from the analysis, patch assemblages were still found to significantly differ from assemblages in unfragmented sites (MRPP, $P = 0.005$).

The results of the K-means classification and DCA ordination of sites based on presence/absence are shown in Figure 7.1, while correlations between DCA axes and patch descriptors are shown in Table 7.2. Axis 1 describes a negative gradient of patch area and rainforest within 1 km, and to a lesser extent correlates positively with distance to the nearest 30 ha patch and to continuous rainforest. Axis 2 correlates with the density of edge within 2 km and vegetation NMDS1 (canopy connectivity). NMDS1 also correlates with the degree of habitat heterogeneity within the site ($r = 0.623$), indicating that at least one transect in sites with high vegetation NMDS1 values contain a very closed canopy and large numbers of ferns and other forms associated with damp, dark microclimates. Axis 3 describes only 7.1% of variance, and loosely correlates with the distance to 30 ha patches vegetation NMDS1 scores.

The cluster analysis revealed similar patterns, with the cluster that contained the control sites (group 4) generally containing the larger sites (>40 ha). Sites 17 and 26 were exceptions, as they were 24 ha and 10 ha respectively; however, both sites had high vegetation heterogeneity values, with at least one transect with vegetation characteristics similar to undisturbed rainforest (closed canopy, high abundances of vegetation types that thrive in dark, moist interior rainforest). Sites 5 and 28 differed significantly from other sites. Site 28, in common with the general trend throughout the ordination, was among the smallest sites (2.6 ha). Site 5, however, was somewhat anomalous in that it was somewhat larger (32 ha) than others with similar bird assemblages (Figure 7.1).

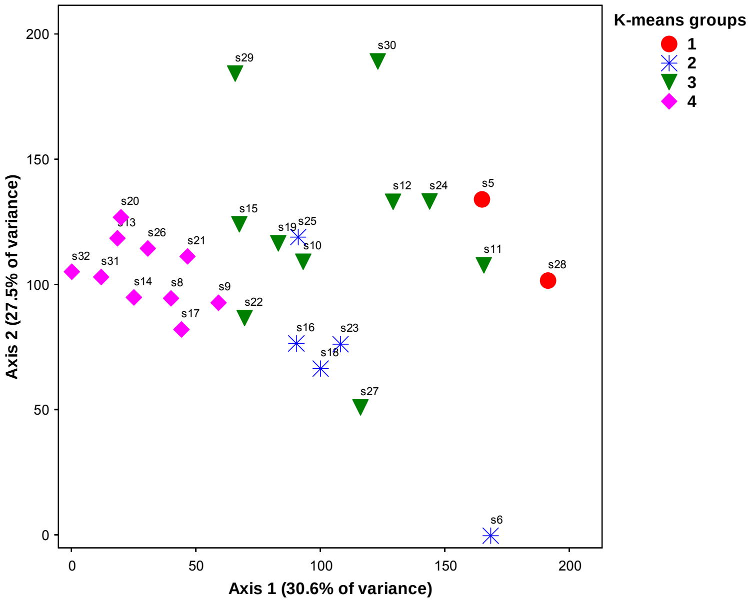

Figure 7.1 Ordination biplot depicting the first two axes of the DCA of total bird presence/absence among rainforest sites. N = 27.

Table 7.2 Pearson correlations of patch variables with DCA Ordination Axes. The strongest correlations with each axis are shown in bold face. N= 27.

	Axis 1 (30.6%)	Axis 2 (27.5%)	Axis 3 (7.1%)
Vegetation NMDS Axis 1	-.351	**.422**	**.341**
Vegetation NMDS Axis 2	-.128	-.088	-.126
Vegetation NMDS Axis 3	-.175	-.080	-.082
Patch area	**-.747**	-.078	-.011
Distance to continuous rainforest	**.468**	.054	-.092
Distance to nearest 30 ha patch	**.508**	-.204	**.228**
Density of rainforest within 1 km	**-.709**	.132	-.097
Density of rainforest within 10 km	-.448	.162	.106
Density of edge within 2 km	-.181	**.413**	.069
Shape index	.246	-.040	-.102

A constrained ordination (CCA) of bird presence/absence by site revealed two significant axes ($P \leq 0.05$, Monte Carlo tests) that explained 17.3% (Axis 1) and 6.9% (Axis 2) of the variation in the species data (Table 7.3). Axis 3, on the other hand, explained little variation and lacked significant ordinal structure ($P = 0.35$). Axis 1 was defined primarily by a combination of patch area and the proportion of forest cover within 1 km of a patch. To a lesser extent, the density of rainforest within 10 km of patches also correlated with Axis 1. Axis 2 is positively associated with vegetation NMDS2 (higher abundance of plank buttress roots, abundance of epiphytes and seedlings, and fewer ground ferns, tree ferns, and single-stemmed palms).

Although the variables explained only a small part of the variance in bird species, some species-environment associations are apparent from the biplot (Figure 7.2). The presence of a number of rainforest specialists (Buff-breasted paradise-kingfisher, King parrot, Superb fruit-dove, Chowchilla, White-eared monarch, Yellow-breasted boatbill, Barred cuckoo-shrike, Sulphur-crested cockatoo and Spotted catbird) was positively associated with patch area. The Red-necked crake, Azure kingfisher, Brown gerygone and Black-faced monarch (also species of dense habitats) were more closely correlated with the degree of isolation represented by forest cover within 1 km of a patch, while the Grey-headed robin and Victoria's riflebird were associated with both area and rainforest within 1 km. Species such as the Peaceful dove, Yellow honeyeater, Magpie-lark, Leaden flycatcher and Bar-shouldered dove (all open-country species) were negatively associated with the major patch area/isolation gradient.

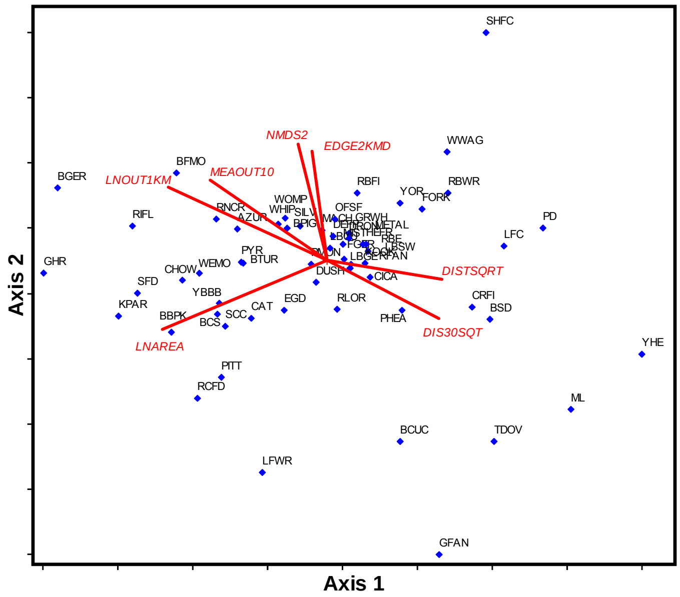

Figure 7.2 Bird species distributions in relation to site characteristics. CCA ordination diagram with species identified by code (Appendix 5). Environmental variables are identified by vector. EDGE2KMD = the length of edge within a 2 km radius of the patch, LNAREA = log patch area, LNOUT1KM = log area of rainforest within a 1 km radius of the patch, and DIS30SQT = the square- root of the distance to the nearest block of rainforest of at least 30 ha area.

On the basis of abundance, the overall bird assemblages of fragmented sites again differed from those of continuous sites (MRPP, $P = 0.019$), supporting the suggestion from the presence/absence analysis that unfragmented sites contain distinct assemblages. This pattern remained when very rare species were removed from the analysis, with patch assemblages differing significantly from unfragmented assemblages (MRPP, $P = 0.028$).

Table 7.3 Eigenvalues, variance in species data, and variance in species-environment correlations for the Canonical Correspondence Analysis of bird presence/absence against environmental variables. The p-values from the Monte Carlo tests, which tested the significance of the eigenvalues and the species-environment correlations, are indicated in brackets. The intraset correlations of environmental variables with the first three axes of the CCA are also included. The strongest intraset correlations for each axis are shown in bold face. N= 27.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.173 ($P = 0.01$)*	0.069 ($P = 0.05$)*	0.049 ($P = 0.35$)
% of variance explained	23.4	8.8	2.8
Cumulative % explained	23.4	32.2	34.9
Pearson Correlation, Spp-Envt*	0.965 ($P = 0.01$)*	0.937 ($P = 0.05$)*	0.893 ($P = 0.34$)

Variable	Correlation coefficient, r		
Vegetation NMDS Axis 1	-0.361	0.283	**-0.603**
Vegetation NMDS Axis 2	-0.145	**0.577**	-0.075
Vegetation NMDS Axis 3	-0.155	-0.291	0.004
Patch area	**-0.818**	-0.340	0.103
Distance to continuous rainforest	0.572	-0.095	-0.225
Distance to nearest 30 ha patch	0.554	-0.289	-0.193
Density of rainforest within 1 km	**-0.787**	0.362	0.237
Density of rainforest within 10 km	**-0.582**	0.398	0.078
Density of edge within 2 km	-0.075	**0.539**	**-0.721**
Shape index	0.196	0.279	0.528

Ordination of sites based on species abundances (Figure 7.3) reveals slightly different patterns to the ordination of presence/absence data, although a positive association between the abundance and presence/absence matrices remained evident (Mantel test statistic = 4.8990, $P < 0.001$). DCA Axis 1 explains 35.3% of the variance, and correlates strongly negatively with the amount of rainforest within 1km of the patch, patch area, and to a lesser extent to the amount of rainforest within 10 km of the patch (Table 7.4). Axis 1 correlates positively to the distance to the nearest patch at least 30 ha in area. Axis 2 explains 14.4% of the variation in the data, and represents a vegetation gradient from broken canopy with fewer vegetation types adapted to damp, dark areas, to denser, more continuous canopy, with more of these vegetation types (vegetation NMDS1). Axis 3, although explaining only 5.6% of the variance in the abundance data, correlates strongly with vegetation NMDS3 (lower abundances of thorny vines, and higher abundances of multiple palms, fan palms and pandans).

A constrained ordination (CCA) of abundance by site revealed only one significant axis ($P = 0.005$, Monte Carlo test), explaining 28.5% of the variation in the species data (Table 7.5). This axis (Axis 1) was defined by a combination of patch area and the proportion of forest cover within 1 km of a patch, and to a lesser extent, the density of rainforest within 10 km of patches, the distance to the nearest 30 ha patch, and the distance to unfragmented rainforest.

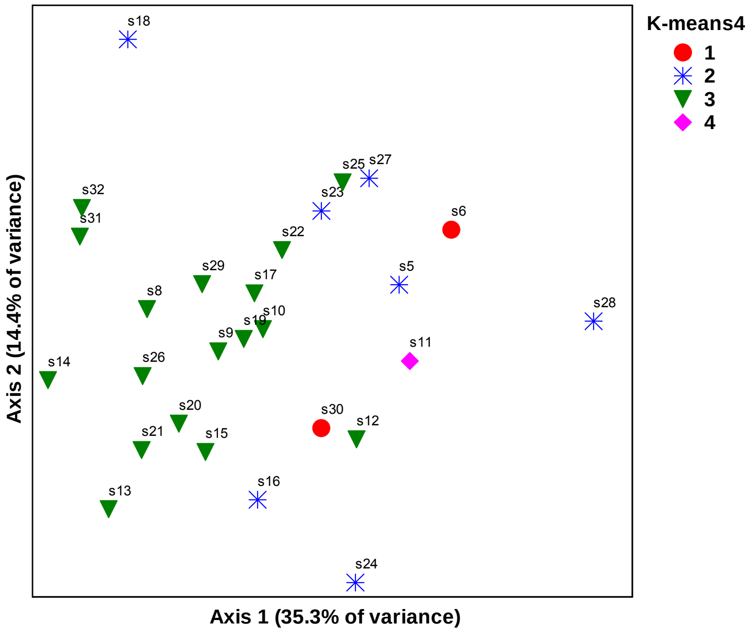

Figure 7.3 Ordination biplot depicting the first two axes of the DCA of total bird abundance among rainforest sites.

Table 7.4 Pearson Correlations with Ordination Axes. The strongest correlations with each axis are shown in bold face. N= 27.

	Axis 1 (35.3%)	Axis 2 (14.4%)	Axis 3 (5.6%)
Vegetation NMDS Axis 1	-.292	**-.532**	.135
Vegetation NMDS Axis 2	-.162	.246	.066
Vegetation NMDS Axis 3	-.123	.116	**.561**
Patch area	**-.622**	.074	-.099
Distance to continuous rainforest	**.513**	-.035	.036
Distance to nearest 30 ha patch	**.617**	-.122	.156
Density of rainforest within 1 km	**-.779**	.017	-.128
Density of rainforest within 10 km	-.508	-.314	.059
Density of edge within 2 km	-.256	-.417	-.070
Shape index	.178	.176	.115

From the biplot, species-environment associations are apparent (Figure 7.4). The abundance of a number of species was positively associated with patch area and the amount of rainforest within I km, including the Brown gerygone, Brush turkey, Buff-breasted paradise-kingfisher, Grey-headed robin, Grey whistler, Macleay's honeyeater, Pale-yellow robin, Sulphur-crested cockatoo, Superb fruit-dove, Victoria's riflebird and White-eared monarch. The Black-faced monarch and Azure kingfisher are more abundant in patches with higher amounts of rainforest within 1km and closer to 30 ha patches. Open-country species including the Bar-shouldered dove, Brush cuckoo, Forest kingfisher, Spotted turtle-dove, Leaden flycatcher, Magpie-lark, Peaceful dove and Yellow honeyeater were negatively associated with the major patch area/isolation gradient.

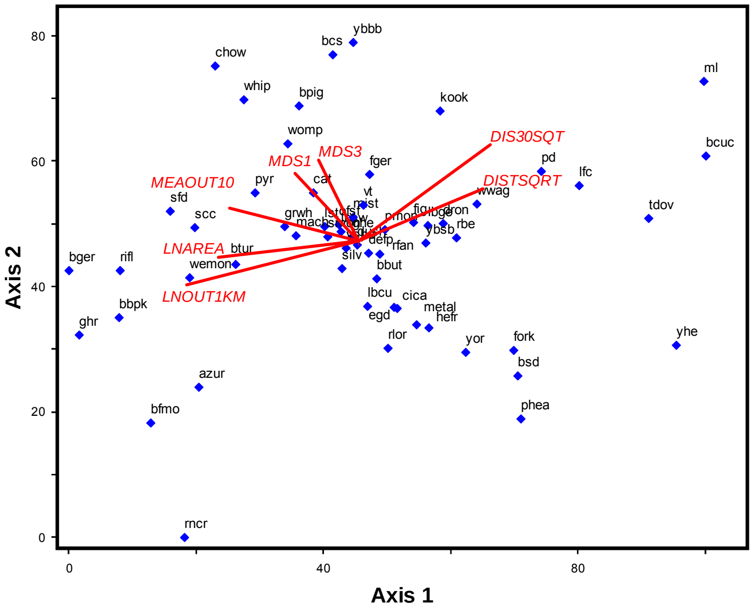

Figure 7.4 Bird species abundance in relation to site characteristics. CCA ordination diagram with species identified by code (Appendix 5). Environmental variables are identified by vector. LNAREA = log patch area, LNOUT1KM = log area of rainforest within a 1 km radius of the patch, MEAOUT10 = area of rainforest within 10 km radius of the patch, DISTSQRT = distance to unfragmented rainforest, DIS30SQT = the square-root of the distance to the nearest block of rainforest of at least 30 ha area, MDS1 = first axis of vegetation ordination by site, and MDS3 = third axis of vegetation ordination by site.

Table 7.5 Eigenvalues, variance in species data, and variance in species-environment correlations for the Canonical Correspondence Analysis of bird abundance against environmental variables. The p-values from the Monte Carlo tests, which tested the significance of the eigenvalues and the species-environment correlations, are indicated in brackets. The intraset correlations of environmental variables with the first three axes of the CCA are also included. The strongest intraset correlations for each axis are shown in bold face. N= 27.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.260 (*P*= 0.005)	0.128 (*P*= 0.460)	0.116 (*P*= 0.075)
% of variance explained	28.5	3.5	6.7
Cumulative % explained	28.5	32.0	38.7
Pearson Correlation, Spp-Envt*	0.947 (*P*= 0.010)	0.911 (*P*= 0.150)	0.820 (*P*= 0.910)
Variable	Correlation coefficient, r		
Vegetation NMDS Axis 1	-0.322	0.339	**-0.530**
Vegetation NMDS Axis 2	-0.254	-0.042	-0.192
Vegetation NMDS Axis 3	-0.199	**0.410**	**0.566**
Patch area	**-0.706**	-0.082	0.141
Distance to continuous rainforest	0.632	0.262	0.142
Distance to nearest 30 ha patch	**0.668**	**0.487**	0.276
Density of rainforest within 1 km	**-0.865**	-0.223	-0.068
Density of rainforest within 10 km	**-0.652**	0.164	-0.226
Density of edge within 2 km	-0.224	0.400	**-0.662**
Shape index	0.175	-0.228	0.392

Guild responses

Across all rainforest sites, species richness was explained by a variety of site characteristics (Table 7.6). Variance in total species richness was significantly explained by patch area, which proved to be the dominant predictive variable with regard to the richness of most feeding guilds. The exceptions to this trend were obligate granivores, which demonstrated no significant response to any of the measured variables, and nectarivores, which were positively associated with patch area and patch shape.

Table 7.6 Species richness responses of the bird assemblage and of habitat and feeding guilds. Guilds were tested with stepwise multiple regression, and models were accepted at $P \leq 0.05$. Habitat guilds: 1 = open country, 2 = variety of open and forested habitats, but not in rainforest, 3 = only in woodland and open forest, 4 = variety of habitats, including rainforest, 5 = mainly in rainforest and other thick vegetation, 6 = rainforest only, or depend on rainforest plants. N = 27.

Dependent variable	Adjusted r^2	Significant Predictors	Slope	Coeff	t	P
Total	.733	Patch area	+	.862	8.509	.000
Habitat 1 species		Nil				
Habitat 2 species		Nil				
Habitat 3 species		Nil				
Habitat 4 species	.659	Patch area	+	.910	7.215	.000
		Rainforest within 10 km	-	-.419	3.321	.003
Habitat 5 species	.711	Patch area	+	.677	5.566	.000
		Rainforest within 1 km	+	.286	2.352	.027
Habitat 6 species	.777	Patch area	+	.808	8.707	.000
		MDS1 (thicker canopy)	+	.325	3.506	.002
Habitat 1-3 species	.187	Rainforest within 1 km	-	.470	-2.554	.018
Habitat 5-6 species	.800	Patch area	+	.843	9.583	.000
		MDS1 (thicker canopy)	+	.271	3.083	.005
Obligate frugivores	.381	Patch area	+	.636	4.124	.000
Partial frugivores	.733	Patch area	+	.862	8.501	.000
Obligate insectivores	.481	Patch area	+	.708	5.011	.000
Partial insectivores	.730	Patch area	+	.861	8.450	.000
Mixed feeders	.741	Patch area	+	.866	8.674	.000
Mixed carnivores	.366	Patch area	+	.625	3.999	.000
Mixed herbivores	.589	Patch area	+	.777	6.181	.000
Obligate granivores		Nil				
Partial granivores	.447	Patch area	+	.684	4.692	.000
Partial nectarivores	.686	Patch area	+	.928	7.631	.000
		Patch shape	+	.322	2.644	.014

No relationship was demonstrated between richness of the non-rainforest guilds and the measured spatial and vegetation site characteristics. Habitat 4 species richness exhibited a marked trend towards larger patches and, to a lesser extent, away from those patches that were surrounded by higher amounts of rainforest within the broader area (10 km). In other words, the habitat generalists were influenced by a combination of patch and landscape variables.

Rainforest specialists (Habitat 6 species) were positively associated with patch size, and were the only guild that was sensitive to vegetation variables, being positively associated with thicker canopy and higher abundances of plant forms requiring darker, moister microhabitats.

Across rainforest sites, total species abundance per unit area was independent of the measured spatial or vegetation variables, in contrast to overall richness per patch, which increased with patch area. The overall abundances of all habitat guilds were independent of the measured variables except for the rainforest specialists, which were positively associated with both patch area and a thicker, more continuous canopy (Table 7.7). When pooled, the density of species restricted to dense vegetation (Habitat 5 and 6 species) was explained by patch area alone. Frugivore abundance was explained by a negative relationship to MDS3 (abundance of palms), while mixed carnivores and herbivores showed no significant relationship with the measured spatial and vegetation variables. Mixed feeder abundance was weakly related to the amount of rainforest within 1 km, whilst obligate granivores were negatively related to MDS2 (less ferns, moss and other damp-loving vegetation forms, and more seedlings). Nectarivore abundance positively related to the amount of edge within 2 km of the patch.

Table 7.7 Species abundance responses of the bird assemblage and of habitat and feeding guilds. Guilds were tested with stepwise multiple regression, and models were accepted at $P \leq 0.05$. Habitat guilds as in Table 7.6. N = 27.

Dependent variable	Adjusted r^2	Significant Predictors	Slope	Coeff	T	P
Total		Nil				
Habitat 1 species		Nil				
Habitat 2 species		Nil				
Habitat 3 species		Nil				
Habitat 4 species		Nil				
Habitat 5 species		Nil				
Habitat 6 species	.315	Patch area	+	.445	2.734	.012
		MDS1 (thicker canopy)	+	.383	2.352	.027
Habitat 1-3 species		Nil				
Habitat 5-6 species	.171	Patch area	+	.450	2.522	.018
Obligate frugivores	.236	MDS3 (Greater palms)	-	-.515	-3.006	.006
Partial frugivores	.130	MDS3 (Greater palms)	-	-.404	-2.210	.036
Obligate insectivores		Nil				
Partial insectivores		Nil				
Mixed feeders	.154	Rainforest within 1km	+	.432	2.392	.025
Mixed carnivores		Nil				
Mixed herbivores		Nil				
Obligate granivores	.385	MDS2 (More buttress roots, less dark-loving species, more seedlings)	-	-.537	-3.494	.002
		Patch area	-	-.381	-2.476	.021
Partial granivores		Nil				
Partial nectarivores	.197	2km edge density	+	.451	2.792	.010

Individual species' responses

A number of species showed positive relationships between abundance and patch area (Table 7.8). Of these, most were rainforest obligates or species of thick vegetation, such as the Superb fruit-dove, Victoria's riflebird and White-eared monarch. Of the rainforest specialists, only the Shining flycatcher showed a negative relationship between abundance and patch area. Of the habitat generalists, the Little shrike-thrush, Dusky honeyeater and Sulphur-crested cockatoo were more abundant in larger patches, whereas the Yellow oriole and Yellow-bellied sunbird were more abundant in smaller patches. The sole non-rainforest species to respond to patch size was the Leaden flycatcher.

Table 7.8 Spearman rank correlations between species density per patch and patch area. Only species with correlations with *P* < 0.1 are listed. Habitat guilds as in Table 7.6. N = 27.

Species	r	*P*	Feeding Strata	Habitat Guild	Feeding Guild
Superb fruit-dove	0.43	0.03	Upper and middle	6	Frugivore
Grey-headed robin	0.50	0.01	Low and ground	6	Insectivore
Grey whistler	0.54	0.00	All	6	Insectivore
Pale-yellow robin	0.57	0.00	Middle, lower, ground	6	Insectivore
Spotted catbird	0.68	0.00	All	6	Omnivore
Macleay's honeyeater	0.45	0.02	All	6	Omnivore
Victoria's riflebird	0.65	0.00	All	6	Omnivore
Buff-breasted paradise-kingfisher	0.43	0.03	Middle and lower	6	Mixed animal prey
Brown gerygone	0.46	0.02	All	5	Insectivore
Large-billed scrubwren	0.37	0.05	Middle and lower	5	Insectivore
Shining flycatcher	-0.34	0.08	Lower	5	Insectivore
Spectacled monarch	0.38	0.05	Middle and lower	5	Insectivore
White-eared monarch	0.46	0.02	Upper	5	Insectivore
Australian brush-turkey	0.50	0.01	Ground	5	Omnivore
Yellow-spotted honeyeater	0.48	0.01	All	5	Omnivore
Yellow oriole	-0.35	0.07	Upper and middle	4	Frugivore
Little shrike-thrush	0.54	0.00	Mainly middle and lower	4	Insectivore
Dusky honeyeater	0.35	0.07	All	4	Omnivore
Sulphur-crested cockatoo	0.70	0.00	Upper	4	Omnivore
Yellow-bellied sunbird	-0.43	0.03	All	4	Omnivore
Leaden flycatcher	-0.33	0.09	Upper and middle	3	Insectivore

Insectivores, although comprising 37% of the 71 species that were analysed quantitatively, made up 47% of the species that were denser in larger patches. Only one frugivore (Superb fruit-dove) demonstrated a positive relationship between density and patch size, although density of the Yellow oriole (a habitat generalist) was negatively associated with larger patches. No granivores showed significant relationships with patch area. Of the 16 rainforest species (habitat guilds 4, 5 or 6) that favour ground, lower or mid-storeys, six were positively associated with patch size, while only three species that do not venture below the mid-storey (out of 12) demonstrated this relationship.

7.4 Discussion

Species/area and density/area patterns

Many studies have revealed positive species/area relationships in forest patches in temperate (e.g., Freemark & Merriam 1986) and tropical (e.g., Warburton 1997, Daily *et al*. 2001) regions. Other studies, however, have failed to find this relationship. For example, Graham & Blake (2001) recorded 160 species in Los Tuxtlas, Mexico, but many forest species of the region were not recorded due to natural rarity, the disturbed nature of most sites, and because unfragmented interior areas were not included in their study. Therefore, the lack of a significant species/area relationship may have been because some of the most area-sensitive species were not recorded. Also, many of the species in that area were open-country birds, which may be more tolerant to fragmentation. Similarly, in a study of Ghanian forest fragments, Beier *et al*. (2002) failed to detect 21 target species in fragments ranging up to thousands of hectares, and concluded that even these large tracts may have lost many species. In species-rich areas such as Los Tuxtlas and Ghana, species-area effects appear to operate at a much larger scale (Graham & Blake 2001, Beier *et al*. 2002) than in less species-rich and more generalist assemblages such as those in northern Queensland. Indeed, in diverse environments some fragmentary processes may occur at a scale above that which is examined in most landscape ecological studies.

In the present study, all known lowland rainforest species (excluding rare vagrants) were recorded at some stage, and a strong species-area relationship was recorded. It can therefore be assumed that, within this region, fragmentation effects mainly occur at a scale within that of this study. This assumption is further supported by the fact that of the 57 species recorded in the two unfragmented sites combined, 75% were recorded in Site 21 (78 ha), 74% were recorded in Site 14 (294 ha), and 72% were recorded in Site 13 (100 ha). These patterns suggest firstly that although species assemblages in the unfragmented sites were significantly different from those of fragmented sites, the unfragmented sites formed the end of a richness and composition continuum rather than representing outliers. Secondly, these patterns imply that in the lowlands of northern Queensland, unlike some other tropical regions, most fragmentation effects on birds (including the species-area relationship) can be assessed at this landscape scale.

The strength of the species-area relationship found in this study may be a conservative estimate, due to the sampling of smaller proportions of larger patches than that of smaller patches. This is unlikely to be a major issue, however, for three reasons. Firstly, the patch-level species-accumulation curves (Chapter 5) tend to flatten out, unlike those of Graham and Blake (2001), indicating that few rare or cryptic species were missed in larger patches. Secondly, birds could be recorded for some distance from the sampling transects, thus reducing the areas of patches that were 'unsampled'. Finally, I undertook all sampling, and was familiar with calls of the common and rarer species, unlike some of the field assistants in the study of Graham and Blake (2001).

Although the sampling regime of Warburton's (1987) upland study in the Wet Tropics of northern Queensland differed somewhat from the present study (Warburton sampled opportunistically throughout patches until the species number in a patch reached an asymptote), both studies involved more sampling in larger patches across different seasons. Furthermore, species richness in nearly all patches in the current study also reached asymptotes. Therefore, some comparisons can be made between richness in lowland versus upland patches. Warburton (1987) derived a slightly steeper and more closely correlated ($r^2 = 0.88$) species-area gradient in the Atherton Tablelands of northern Queensland than was found in the rainforest sites in this study ($r^2 = 0.72$) (Figure 7.5). Small lowland patches (this study) tend to contain more species than small upland patches (Warburton 1987), probably because of the higher numbers of generalist and open-country species found in the lowlands, although with increased patch area this gap in species richness narrowed. This may be due to the higher proportion of rainforest specialists in upland rainforests than in lowland rainforests (Chapter 5), as species of open country often show a weaker relationship with area than do forest specialists (Blake & Karr 1987, McIntyre 1995).

The relationships between population density and area, and faunal group density and area have received substantial attention over a number of years (e.g., Bowers & Matter 1997, Matter 2000, Connor *et al.* 2000). There is a range of population density and assemblage density responses of birds to patch size: densities may be higher in larger fragments (e.g., Blake & Karr 1987), relatively constant across different patch sizes (e.g., Lescourret & Genard 1994), or higher in smaller patches (Terborgh *et al.* 1997).

Density compensation (increased relative abundance of species in isolated islands or patches) is a common feature of isolated habitats (MacArthur *et al.* 1972, Dos Anjos & Bocon 1999). In this study, no significant relationship was found between patch size and the overall bird densities. However, larger patches contained lower mean population densities (Pearson correlation coefficient -.464, $P = .015$, n = 27). Although this result could be a result of competitive release (MacArthur *et al.* 1972), it is more likely due to the increased proportion of edge habitat in smaller patches. Additionally, many of the species that persist in smaller patches are those that favour (or at least are unaffected by) edge habitat. In this case, the pattern appears may be due to a combination of fragmentation and edge effects.

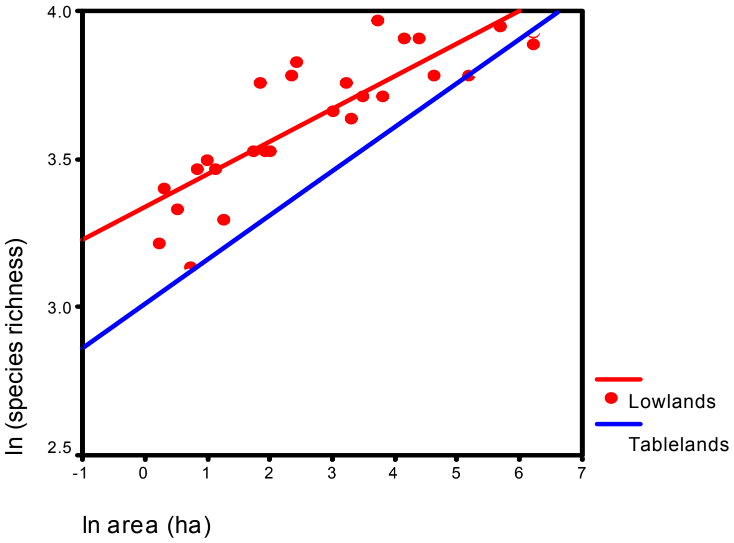

Figure 7.5 Species-area relationships for birds in lowland (the present study) and upland (Warburton 1987) fragments in northern Queensland. Note that the line-of-best-fit for Warburton's study is taken the regression equation, as specific data points were unavailable.

Assemblage responses

Clearly, substantial differences exist in composition and abundance between bird assemblages in rainforest fragments and those in unfragmented habitat. These differences seem due to both the loss of primarily upland species in virtually all fragments, and to the presence of open-country species around the edges of all patches, but not within continuous forest interiors. Across all sites (including the unfragmented sites), major differences in assemblages were driven by a combination of patch area and the degree of local isolation (proportion of rainforest within 1 km from the focal patch).

Patches with the most similar assemblages to unfragmented sites (group 1) were >40 ha except for Sites 17 and 26, which had at least two transects with high canopy closure (further indicated by high degrees of heterogeneity). Thus, within moderately-sized patches (25 ha and 10 ha, respectively), undisturbed canopy resulted in a fuller rainforest assemblage. However, very small sites such as Site 29 and Site 30 (4 ha and 1 ha, respectively) even when canopies were relatively undisturbed, were too small to contain strong rainforest assemblages. Site 5 (32 ha) was an anomaly because it should have contained a greater number of rainforest specialists than were recorded. This difference is probably due to the lack of rainforest in the local vicinity (within a 1 km radius), and to the location of this site towards the drier, northern end of the study area. Therefore, although the vegetation structure of Site 5 is complex mesophyll vine forest because of its position largely within a creek gully (see Chapter 4), most of the rainforest in the vicinity comprises mixed rainforest with sclerophyll emergents, which are likely to contain fewer rainforest specialists as potential source populations.

That patch area and isolation both partly explained much of the variation in bird assemblages across sites was not surprising, as smaller patches often diverge from pre-isolation assemblages (or unfragmented sites) more than large patches (e.g., Stouffer & Bierregaard 1995a). Likewise, the potential impact of isolation on bird assemblages is also well established (e.g., Bierregaard *et al*. 1992, Turner 1996).

Perhaps of greater interest is that the density of rainforest within 1 km was consistently more important than other measures of isolation in influencing the bird assemblage structure. Different species will use the landscape in different ways, with some species utilising multiple patches within a home range, some species very rarely crossing the matrix, and some species dispersing readily across the matrix but incorporating the home range within one patch. The influence of rainforest density within 1 km suggests that many species among this assemblage can and do cross the matrix, and that local extinction and recolonisation may be a common occurrence. This also infers that some populations use the landscape in a metapopulation manner (Hanski 1999).

The vegetation differences (in the form of canopy connectivity) formed a secondary gradient in the assemblage, indicating that, although not the major determinant of assemblage structure, forest disturbance (from cyclones) contributes towards the absence of some rainforest specialists. Many species of birds are influenced by subtle changes in vegetation structure within primary forest (e.g., Karr & Freemark 1983, Kikkawa *et al*. 1980), and although few studies have examined localised response to cyclone damage, those at a broader-scale have revealed substantial changes to avifaunas in the neotropics (Will 1991). More localised studies examining such localised disturbances as natural canopy gaps (Schemske & Brokaw 1981, Levey 1988) fire damage (Barlow *et al*. 2002), secondary growth (Laurance *et al*. 1996) and logging (Grieser-Johns 1996, Johns 1992) have also revealed avian sensitivity.

Although the overall variation in species data was best explained by a combination of patch area and the amount of rainforest within 1 km of the focal patch, this canonical axis explained only 17.3% and 28.5% of the presence/absence and abundance variation, respectively. Therefore, it is possible that obscure and unmeasured factors influence the assemblage along with natural stochasticity. Additional spatial and vegetation patterns often exist beyond the known and tested gradients (Legendre & Fortin 1989). Nevertheless, these constrained results lend weight to the non-constrained ordination regarding the determinants of bird assemblage structure.

Guild responses

The lack of any influence of the measured vegetation or other variables on the species richness or abundance of open country species (Habitat 1, 2 or 3) is consistent with both temperate (Galli *et al.* 1976, Bellamy *et al.* 1996) and Neotropical (Graham & Blake 2001, Stouffer & Bierregaard 1995a) studies. In the present study, some open country species were found along edges of all patches (except for the unfragmented sites), regardless of patch size or degree of isolation, probably because of the greater propensity of non-rainforest species to travel across open habitat (Sieving *et al.* 1996). Those species more intermediate in the degree of habitat specialisation (Habitat 4 and Habitat 5 species) were influenced in their species richness by both patch and landscape variables, which broadly concurs with the results of Graham & Blake (2001). These groups, however, showed no relationship between abundance and the landscape variables, suggesting that while some species may be lost, others may maintain or increase their densities in larger or less isolated patches.

Rainforest specialists, on the other hand, were strongly associated with both the degree of canopy closure and patch area, concurring with other tropical studies (e.g. Stouffer & Bierregaard 1995a, Graham & Blake 2001). These and other authors have suggested that forest specialists are less likely to move through the matrix, and will therefore be more strongly influenced by patch-level rather than landscape-level variables. With regard to canopy closure, a number of disturbance studies have shown that rainforest specialists frequently show the greatest vulnerability to intrusions such as tropical storms (Waide 1991b, Lynch 1991) and logging (e.g., Sekercioglu 2002), and often avoid areas of regrowth (Crome *et al.* 1994, Raman *et al.* 1998). Swihart *et al.* (2003) reviewed the characteristics of species that lead them to be more robust, and found that species that are capable of using a wide range of habitats are more likely to be able to use human-altered portions of a landscape (Laurance 1991, Andren 1994). These, along with the present study, suggest that species that are particular in their preference for a habitat type may also be specific in their preference for vegetation structure within that habitat type.

Almost all feeding guilds exhibited greater species richness with increased patch area, except for obligate granivores, which showed no relationship with landscape or vegetation variables. This may be an artefact of many absences (granivores were present at 16 patches) and the low numbers of species (only five obligate granivores were recorded, with a maximum of three within any one patch), because statistical inference can be difficult to obtain regarding rare or locally-rare species (Beier *et al.* 2002). Furthermore, all of the obligate granivores (Bar-shouldered dove, Chestnut-breasted mannikin, Double-barred finch, Peaceful dove and Spotted turtle-dove) are open-country species, and are therefore less likely to be sensitive to patch or landscape variables. Furthermore, these species were almost exclusively recorded at patch edges, as the higher density of shrubs and grasses at patch edges provide more food (small seeds) than patch interiors. No obligate nectarivores are found in the region, but for partial nectarivores, species richness positively correlated with larger patch area and a more convoluted patch shape. Patch shape (which when corrected for area reflects greater edge length) appears to reflect the preference of partial nectarivores for patch edges (Chapter 6), probably because these areas have higher abundances of flowers than patch interiors (Stouffer & Bierregaard 1995b). Thus, whilst area is the most important predictor of richness, increased edge length at a particular patch size also benefits nectarivores.

It was not expected that obligate and partial insectivores would be no more abundant in larger patches than in smaller ones. This result may be due to two factors. Firstly, although a certain number of insectivores clearly are lost in smaller patches, not all insectivores are rainforest specialists. Some habitat-generalist and open-country insectivores, such as the Spangled drongo, Willy wagtail and Rainbow bee-eater, are more common at patch edges than within interiors, and smaller patches generally contain greater proportions of edge habitat in relation to interior habitat, so these species may benefit from the higher edge-interior ratio in smaller patches.

The lower frugivore abundance in patches where single-stemmed palms were more abundant probably reflects the lower abundance and variety of canopy trees in these often poorly drained patches. Fruit in the rainforest is patchy in both space and time, and frugivores therefore rely on a variety of large rainforest trees (Estrada *et al.* 1993). The lack of strong relationships between abundance of other feeding guilds and the vegetation or landscape variables (compared to the strong area trends with richness) again tentatively suggests that density compensation may operate at this level.

Among individual species, trends broadly corresponded to those of the guilds, with species from the rainforest specialist and insectivore guilds comprising the majority of species that exhibited lower densities in smaller patches. This, again, concurs with previous studies (Stouffer & Bierregaard 1995a). The sole anomaly was the Shining flycatcher which, although a rainforest specialist insectivore, showed a negative relationship with patch area. This species, however, is essentially a bird of mangroves and streams (Nielsen 1996) and since smaller patches tend often to lie along or around streams, the stream itself will, proportionally, dominate smaller patches to a higher degree. A few habitat generalists were positively associated with patch size, including the Little shrike-thrush, Dusky honeyeater and Sulphur-crested cockatoo. In the case of the Little shrike-thrush, its understorey habits may predispose it to poor dispersal between patches. Sieving *et al.* (1996) demonstrated that many understorey birds will enter scattered cover but many will completely avoid open areas (which formed the matrix in the present study). The distribution of the Sulphur-crested cockatoo, however, is more difficult to explain. Smaller patches may have been subjected to more recent logging, resulting in fewer senescing trees containing tree holes for nesting. Alternatively, the older trees and branches in fragments may be more subject to windthrow than those in unfragmented patches, or larger patches may have more chance of containing fruit or seed bearing trees.

Data issues

Two major issues regarding the sampling of patches of rainforest are (i) whether species richness can be estimated with confidence (e.g., Soberon & Llorente 1993, Field *et al.* 2002), and (ii) whether the time since fragmentation is sufficient to have allowed the assemblage in each patch to reach a new equilibrium (e.g., Daily *et al.* 2001). The first issue has been addressed in Chapter 5, but the issue of temporal lag will briefly be addressed here.

When studying fragmentation processes, it is useful to know whether the assemblage is still in a state of significant transition resulting from the fragmentation process, or whether the assemblage has roughly stabilised. If the former is the case, then the results cannot be assumed to hold up in the future, and it may lead to a misleadingly favourable estimation of the capacity of patches to maintain faunal assemblages (Daily *et al.* 2001). Proof of a stabilised assemblage is difficult to obtain unless a study has followed patches from initial isolation through to relaxation at a new equilibrium. Furthermore, although species diversity may reach an equilibrium number, stochastic recolonisation will, at the landscape scale, usually ensure that there is a continual species turnover. Therefore, although diversity may relax around a new equilibrium, there is no such thing as a final assemblage within a patch. In comparing richness and assemblage structure between rainforest patches, however, we should remain confident that at least the bulk of species loss has occurred.

Species extinction (and therefore assemblage relaxation) in habitat fragments may take well over half a century to occur (e.g., Brooks *et al.* 1999, Robinson 1999) or may occur in a matter of years or a few decades (Stouffer & Bierregaard 1995a, Terborgh *et al.* 1997, Stratford & Stouffer 1999). The rate of species relaxation in patches or islands depends on the patch size, degree of isolation, and demographic and behavioural characteristics of the focal species. Those studies that have found very slow declines have involved relatively large areas, such as the 1500 ha Barro Colorado Island, in Panama (Robinson 1999) and 400 ha to 8600 ha in Kenya (Brooks *et al*. 1999). At smaller scales (1-200 ha), most studies have demonstrated a rapid loss of species within the first 5-10 years, with the rate of species loss considerably slower thereafter (e.g., Bierregaard & Stouffer 1997, Terborgh *et al*. 1997). In short, the available evidence suggests that smaller patches tend to lose species (and approach equilibrium) at a faster rate than larger patches (Laurance *et al*. 2002, Brooks *et al*. 1999, Terborgh *et al*. 1997).

In the present study, observation of 1:100,000 topographic maps (c. 1978) and Landsat TM imagery (c. 1995) indicated that little change had occurred in the ensuing 15 years, and in the flatter subregions most of the clearing had occurred much earlier. In summary then, we cannot be entirely sure that all assemblage relaxation had occurred by the time of this study; however, comparisons with other studies over similar scales indicate that the rapid and most substantial loss of species in these fragments in all likelihood occurred prior to this study.

Conservation implications

The sensitivity of this bird assemblage to both area and isolation emphasises the importance of patch arrangement as well as patch size. Few patches contain the diversity of rainforest specialists that make up a full ‘unfragmented’ assemblage. Therefore, not just area *per se*, but also isolation (in particular the amount of rainforest within 1km), may also influence bird assemblages found in fragments. Since the amount of edge increases with forest fragmentation (Andren 1994), and many open-country and habitat generalist species were in this study found only or nearly always at edges, the abundances and local range of many open-country species in this region will have increased due to fragmentation. Therefore, habitat conservation and augmentation should focus not only on adding pieces to already-existing patches but also, where possible, on areas in close proximity to larger patches.

Although larger patches of disturbed rainforest, with a significant proportion of rainforest within 1 km, are required for the persistence of many rainforest specialists (Figure 7.1, Table 7.2), smaller fragments may allow these species to persist where the canopy remains relatively undamaged, as is the case with Site 17 (Pin Gin Hill). Although the entire region experiences frequent natural disturbance from cyclones, the exact pattern of future disturbance is impossible to predict. Therefore, from a conservation perspective, a precautionary approach (assuming that all patches will be subjected to periodic canopy damage) would require patches greater than 40 ha to sustain bird diversity (in the expectation of further natural disturbance). Thus, the 20 ha patch that sustained a near complete suite of interior species due to its undisturbed canopy (Site

17) may lose many of these sensitive species if a future cyclone damages its canopy substantially.

In relatively species-poor tropical rainforests such as those of the current study, birds are more resistant to disturbance than those in more diverse regions such as West Africa (Beier *et al.* 2002), Central America (Graham & Blake 2001) and South America (Stouffer & Bierregaard 1995a). Consequently, smaller, isolated patches may be of greater conservation value (with regard to the bird assemblage) than would be the case if species here were more specialised and the assemblage more diverse.

Chapter 8. Summary and General Discussion

8.1 Introduction

Clearing and fragmentation of habitats, especially rainforests, is a continuing worldwide problem, and much ecological research has been focussed on the patterns of faunal response to this process. Understanding the problem requires geographically dispersed studies to test or develop general theory, as the rules that seem to apply in one location may well not apply in a different landscape or biogeographical region.

The Wet Tropics rainforests of northern Queensland are, in comparison to most other continental rainforest areas, essentially a small isolate, with an area of approximately 783,000 ha (Williams *et al,* 1996). Most upland areas, except for the Atherton Tablelands, while subjected to periodic logging in the past, have been relatively free from clearing and are now well protected. Conversely, much of the lowland forest has been cleared, and in the study area, only 44% of natural vegetation remains (Accad *et al.* 2003), mostly on non-cultivable slopes. Most of the remaining forest on flat or moderate slopes exists as isolated patches.

This project sought primarily to examine the effects of habitat fragmentation on bird assemblages in the Wet Tropics Lowlands. However, the processes that shape and influence faunal assemblages at a landscape level cannot be examined in isolation, as they are strongly affected by the regional processes that determine species pools. Responses to local features such as edges, treefalls, and natural or anthropogenic changes in vegetation structure occur within the constraints of the regional and landscape template. Thus, any interpretation and discussion of bird assemblage responses to landscape-scale processes should consider the regional processes that have shaped the assemblage.

8.2 Major findings

Spatial characteristics and vegetation of the study region

Spatial indices were used to characterise the lowland landscape and subregions, and were reduced to a manageable set with which to analyse the response of bird assemblages in later chapters. Clearing in the region has focused on alluvial and basalt soils with a slope less than 8°, and remnant rainforest on well-drained alluvial soils is particularly scarce. Therefore, these remnants are most at risk and most in need of protection and study. In the study area, only 5-10% of the remnant forest lies within conservation reserves (Morgan 2001).

Vegetation consisted of complex mesophyll vine forest in 28 sites, and mixed forest (rainforest with *Eucalyptus* spp. and *Acacia* spp.) in the five northernmost sites. The mixed forest sites also differed by way of the lack of a range of growth forms characteristic of the mesophyll rainforests. Ordination and classification confirmed the separation of the mesophyll and mixed forest at both the site and the transect level, and the two groups of sites were therefore treated separately in analyses of bird assemblages. Among the mesophyll rainforest sites, variation was modest, in line with the site-selection goal of minimising vegetation heterogeneity. The main vegetation differences occurred at a landscape (site) scale rather than at the transect scale. Within most mesophyll sites, cyclone disturbance has resulted in a broken canopy, dense understorey and mid-storey, ill-defined strata, and abundant *Calamus* spp. and other disturbance-adapted plants. Nevertheless, the mesophyll transects formed two major groups, with one group characterised by denser canopy and subcanopy and higher abundances of ground ferns, moss, tree ferns and pandans, all of which prefer humid, darker conditions. Other within-site variation in the mesophyll sites appeared to be due to subtle edge effects.

Differences in the mean driest quarter rainfall explained the major delineation in vegetation structure (between mixed forest and mesophyll rainforest). The presence of mixed rainforest in the northern sites is likely to be the result of the regrowth of rainforest beneath existing sclerophyll plants following the cessation of indigenous burning in the late 19th or early 20th centuries. Continued absence of burning over much of this northern area, will probably lead to the succession of the *Eucalypt* spp. and *Acacia* spp. canopy by rainforest species, as has been found in the western edge of the Wet Tropics (Harrington & Sanderson 1994) and on Cape York (Russell-Smith *et al.* 2004). Among the drier sites, topology influenced the diversity of growth forms, probably due to a combination of shelter from fire and wetter microclimate. Of the wetter sites, those above 45m in altitude contained greater complexity, most likely due to better drainage in these areas.

Bird assemblages of the region

It is well known that the bird assemblages of the rainforests of northern Queensland, including the lowland assemblage, are less diverse than those of most other mainland tropical rainforest regions (Driscoll & Kikkawa 1989, Williams & Pearson 1997). The study area, however, contains somewhat higher richness in comparison to many other (mainly upland) Wet Tropics rainforest areas. This was largely due to the influx of altitudinal vagrants and migrants and greater numbers of open-country species in and around the edges of this fragmented lowland forest than in many other rainforest areas of the Wet Tropics (e.g., Warburton 1997). However, the lowland study area contains fewer obligate rainforest species than are found in most other continental rainforests worldwide (e.g., Anjos & Bocon 1999, Stouffer & Bierregaard 1995a), and fewer than are found in upland rainforest in northern Queensland (Warburton 1987). Furthermore, among the rainforest specialists there were fewer feeding specialists, such as obligate insectivores.

These patterns seem largely due to biogeographical factors, such as the limited extent of northern Queensland rainforests in comparison to other continental regions, the distance from source areas such as Papua New Guinea (which would favour colonisation of habitat generalists) (Kikkawa *et al.* 1981), and the Pleistocene rainforest contractions to upland refuges, which would have particularly affected rainforest specialists and particular feeding guilds such as obligate insectivores and frugivores. The regular cyclonic disturbance on the vegetation of the area may also enhance the pressure towards an avian assemblage of ecologically resilient generalists, as has been suggested for some parts of Central America (e.g., Will 1991).

Bird assemblages in the mixed forests differed from those in mesophyll rainforest in having more habitat generalists and fewer rainforest specialists. While this pattern was observed among continuous sites (albeit without mixed replicates, so care must be taken), the assemblages within mixed patches diverged to a far greater extent from those of continuous forest than did those in mesophyll patches. This suggests that even major differences in vegetation type have less influence (although still significant) on bird assemblages than do the effects of fragmentation. This stronger divergence of mixed forest patch assemblages from all other sites (mesophyll fragments and all unfragmented forest) suggests a degree of interaction between fragmentation and the suboptimal nature of mixed forest (with respect to rainforest specialists at least), where quite large tracts may be required to sustain a characteristic rainforest assemblage.

In mixed forest areas, absence of fire will allow the continued development of a more mature rainforest canopy, and eventually the complete suppression of sclerophyll plants. Therefore, mixed forest assemblages, at least in unfragmented areas, are likely to converge towards the mesophyll rainforest assemblages. In mixed forest patches, however, this may not prove to be the case, as the eventual development of mature, complex rainforest may be limited by the ability of many rainforest plants to colonise these areas.

Effects of edges

Significant differences were found in vegetation structure between edges and interiors of mesophyll rainforest patches, with edges containing increased numbers of stems, greater density of shrubs, and lower abundances of moss, ground ferns and pandans. However, no differences in canopy connectedness, foliage density or heterogeneity were evident between edge zones and interiors, contradicting other studies (e.g., Laurance 1991, Williams-Linera 1990). This study also found no detectable difference in the density of the disturbance-adapted *Calamus* spp. (lawyer vine) between edge zones and patch interiors, in contrast to the increased densities found closer to the edges of patches on the Atherton Tablelands (Laurance 1991). This indicates that, although natural disturbance has opened up the canopy across most of the lowland forests in the study area, there nevertheless exist microclimate differences across the edge zone. Microclimate changes appear to be caused primarily by outside conditions permeating horizontally from the edge, rather than by secondary effects of canopy damage (vertical permeation) for often great distances (Laurance 1991). It is possible that the degree of severity of cyclone disturbance is such that ‘interior’ forest is severely damaged, like edge areas. In contrast, on the Atherton Tablelands, less cyclone damage meant that clearer structural gradients existed from the edge into rainforest interiors (Laurance 1991).

Bird richness and abundance did not significantly differ between the edges and interiors of lowland rainforest or mixed forest fragments, unlike results from other tropical studies (e.g., Restrepo & Gomez 1998). This result may be partly due to the lack of vegetation contrast between edges and interiors (compared to rainforest fragments in some other regions). Other contributing factors may include the more generalist nature of the bird assemblage (again, compared to those in most other rainforest areas), and species replacement from the large number of non-rainforest species that use the edges.

In contrast to the overall abundance and richness patterns, significant turnover of species occurred between the edges and interiors of patches. Richness of open-country birds was higher at patch edges, and many of these species rarely ventured into patch interiors. The rainforest obligate guild, on the other hand, demonstrated lower species richness and density at edges, which may be due to sensitivity to microclimate changes near the edge, fewer resources in this zone, or interactions with open-country species. Frugivores, obligate granivores and nectarivores all favoured patch edges, whilst obligate insectivores and understorey species avoided them.

The lesser responses of this bird assemblage to edges compared with those of other rainforest assemblages may be due to two main factors. Firstly, the regular disturbance to this area by cyclones can limit the strong and extensive microclimate gradients found in other regions (e.g., Laurance 1991, Murcia 1995). Secondly, the more generalist nature of the lowland rainforest avifauna of the Wet Tropics may predispose many of these species to greater resilience to subtle changes in habitat that characterises rainforest edges.

Determinants of bird assemblages

A strong species/area relationship was found across patches, although the smallest patches were more species rich and the slope of the species/log area curve was less steep than for a nearby upland assemblage (Warburton 1987). This possibly results from the higher numbers of generalist and open-country species found in the lowlands.

The major determinant of assemblage structure was a combination of patch area and the proportion of rainforest within 1 km of the focal patch. The degree of canopy connectivity, which is largely influenced by cyclone disturbance, also contributed (to a lesser extent) to assemblage structure. This conclusion concurs with studies of avian sensitivity to other sources of disturbance in tropical rainforests (Schemske & Brokaw 1981, Grieser-Johns 1996). Canonical correspondence analysis, however, revealed that unmeasured variables, or natural stochasticity, also influenced assemblage structure to a significant degree.

Different guilds are affected by different characteristics of the landscape, and to differing degrees. Open-country species were minimally affected by landscape characteristics, as has been found elsewhere (Bellamy *et al.* 1996, Graham & Blake 2001). Species richness of the intermediate habitat guild (found in wide ranges of habitats) was influenced by both patch and landscape variables, although no relationship between their respective abundances and the measured landscape variables was evident. Rainforest specialists, on the other hand, were heavily influenced by patch-level rather than landscape-level variables. Richness of this habitat guild was positively related to both patch area and the degree of canopy closure. Of the feeding guilds, only the obligate granivores were less species-rich in larger fragments, probably because this guild comprised entirely open-country species.

The overall results were less pronounced than has been the case in some studies from other regions, with smaller patches maintaining a higher proportion of species than is the case in other areas. For example, no species were lost in fragments of over 100 ha in this study, whereas in West Africa (Beier *et al.* 2002) and the Brazilian Amazon (Stratford & Stouffer 1999), many species were lost in similarly sized fragments, again, probably because of the substantially lower number of specialists in the northern Queensland forests, and because the rainforests of northern Queensland are less diverse to begin with. In effect, most of the species that might have been lost from anthropogenic habitat loss have already disappeared from previous natural disturbance, resulting in a ‘ghost of extinctions past’.

8.3 Influence of natural disturbance

Past events can exert selective pressure on current species (Jones *et al.* 2001, Whittaker 1995) or can, through species sifting or “extinction filters” (Balmford 1996) change the composition of the resulting assemblage. However, the resulting assemblages usually are not random. Past pressures may favour species that are more resistant to predators (Atkinson 1985), that are resistant to fluctuations in ocean temperatures (Balmford 1996) or that have persisted by means of their less specialised habitat or food preferences. In the Wet Tropics, for example, climatic changes (cooling and drying) in the Pleistocene have caused rainforest contractions to mountain tops, resulting in changes in the overall avian assemblage in rainforests across the entire Wet Tropics biogeographic region. Williams and Pearson (1997) determined that these rainforest contractions led to a nested rather than random pattern of endemic vertebrate diversity across the subregions of the Wet Tropics, and that endemic vertebrate richness within subregions could be explained by the probable spatial extent of refugial areas during these contractions. Hence, processes at regional scales have created not only regional assemblages, but have strongly influenced assemblages at the subregion and local scales.

Past events may also influence the ability of a species or assemblage to respond to contemporary threats that are similar to those that ancestral assemblages faced. Examples include sea temperature impacts on Caribbean molluscs (Jackson 1995), and plant resistance to cattle grazing in North America (Balmford 1996). The presence of land crabs on some Pacific islands may explain the different impacts on bird communities on Pacific islands from the introduction of exotic rat species (Atkinson 1985). In this case, the avifaunas that had evolved in the presence of land crabs would have already lost the species that would have been vulnerable to rat predation, so the resulting bird species were less affected. Danielsen (1997) suggested that bird assemblages in paleoecologically unstable areas might be more resistant to human impacts such as selective logging and fragmentation. He separately analysed data from South American and African fragmentation studies, and concluded that there is some evidence that birds of stable areas are more vulnerable.

Although the lowland assemblages of the Wet Tropics exhibit negative responses to habitat fragmentation, they were shown in this study to be more resistant to fragmentation than assemblages in many other parts of the world, both in their response to edges and in the structure of the patch assemblages. This is illustrated by the relatively small distances at which edge effects occur in the Wet Tropics Lowlands, the lower proportion of species lost around edges, and the smaller scale at which fragmentation effects occur, in comparison to other regions (e.g., Beier *et al.* 2002, Stratford & Stouffer 1999). Therefore, it seems that not only have regional disturbances influenced the composition of the regional lowland assemblage, but the specific generalist characteristics of the resultant lowland species pool (derived from regional processes) make this bird assemblage more resistant to anthropogenic impacts at the landscape scale. Thus, one type of change (Pleistocene contractions) may have filtered out those species that would otherwise have been highly vulnerable to quite different human disturbances, leaving an avifauna that is relatively resistant to habitat fragmentation.

Tropical storms may also impart selective pressure on to animal assemblages. Waide (1991b) suggested that the existence of many generalist species on small Caribbean islands might be related to their exposure to repeated hurricanes, which occur every 10-60 years, so that succession is a continual process. Furthermore, the island assemblages demonstrate greater resilience to tropical storms (return to pre-hurricane patterns) than those of mainland forest (Waide 1991b). This conclusion should be treated with caution, however, for two reasons. Firstly, it is unclear and very difficult to ascertain how much of the loss of species and broad niches on these Caribbean islands is due to island biogeography processes and competitive release (Cox & Ricklefs 1977), and how much is due to the selection for generalist traits by storm activity. Secondly, the effects of hurricanes may be stronger on islands where, since the hurricane will likely affect the whole island, re-colonisation by displaced species is less likely. In contrast, in the Wet Tropics lowlands, birds can recolonise disturbed patches from neighbouring, unaffected areas.

Lewis (2001) suggested that the pre-adaptation of butterfly assemblages to hurricanes may impart resistance to selective logging in Belize, and a similar resistance has been suggested for birds in that same country (Mallory & Brokaw 1997, in Lewis 2001). However, to actually demonstrate selective pressure on bird assemblages from tropical storms would be extremely difficult, as many other processes combine to determine the nature of regional and local avifauna. To date, though, no research has explicitly addressed the impacts of cyclones on Australian bird assemblages. In common with Lewis (2001), therefore, it is possible to only speculate on the selective pressures that might be exerted by cyclonic disturbance on the lowland avifauna; however, these storms do indirectly influence the bird assemblages of the lowlands through changes to vegetation. There was strong evidence of 11-year-old cyclone damage to the vegetation at most study sites, and given the sensitivity of many birds to vegetation structure (e.g., Karr 1971), cyclones, like the Pleistocene contractions, may over large temporal and spatial scales lead to the development of an avifauna that is somewhat less specialised, and therefore more resistant to other forms of disturbance.

Conversely, at a smaller scale, cyclone influence would seem to interact with fragmentation by increasing the area required to support bird assemblages similar to those of unfragmented forest. Although this project found that bird assemblages diverged significantly from 'intact' assemblages in smaller patches (especially below approximately 40 ha), Site 17 (25 ha) and Site 26 (10 ha) proved to be the exception. These two patches contained some areas of unusually high canopy connectivity (due probably to shielding from the most recent cyclone), suggesting that cyclone effects may still have some deleterious effect on the ability of patches to maintain rainforest interior assemblages. Thus, cyclone activity may, at different temporal scales, both reduce and worsen the effects of fragmentation.

8.4 Diversity and stability

This project allows consideration of a particular subset of the diversity-stability question: that is, is a more diverse bird assemblage more stable (represented by the deviation from unperturbed assemblage structure) than less diverse bird assemblages in the face of habitat fragmentation. Diversity does not seem to beget stability in the face of habitat fragmentation for rainforest bird assemblages: in fact, the relatively depauperate assemblage of the Wet Tropics Lowlands is more resilient than most other, more diverse tropical rainforest avifaunas (e.g., Stratford & Stouffer 1999). In the Wet Tropics, traits that characterise less diverse assemblages (greater average abundance per species, wider niches etc.) also allow species to resist physical changes to the rainforest, including fragmentation, by switching diet, by using a wider array of microclimates or habitat, or by using smaller areas of forest.

The two issues outlined above (natural/human disturbance and diversity/stability) are in this case related, because at least one of those natural disturbances (the Pleistocene rainforest contractions) has been partly responsible, through species sifting, for the less diverse bird assemblage that is now found in the lowlands of the Wet Tropics (Williams *et al.* 1996). However, it is well known that some forms of disturbance result in higher diversity (Mackey & Currie 2001). Furthermore, climate change and rainforest contraction has failed to result in a depauperate assemblage in the Amazon (Nores 1999), and may even have led to a great deal of speciation in once-isolated rainforest areas, and subsequently high regional and local diversity (Haffer 1997). In the Wet Tropics, however, the degree of speciation resulting from this process is uncertain (Moritz *et al.* 2001), and in any case would have been mostly restricted to the upland areas (only four of the 13 endemic birds of the region are found at lower elevations).

Therefore, although the major focus of this project was on the response of the lowland bird assemblage to anthropogenic habitat fragmentation at the landscape scale (1 ha – 10 km^2), to interpret the results and understand the processes that cause these patterns, it has been necessary to examine processes at very different spatial and temporal scales. On the one hand, rainforest contractions that occurred over thousands of years across the entire Wet Tropics biogeographic region have resulted in an assemblage of species that are relatively generalist in their food and habitat requirements, and are therefore more resistant to habitat fragmentation. On the other hand, cyclonic disturbances have occurred at intervals of decades, with swathes of up to 60km affected at a time, substantially influencing vegetation structure and the nature of edge effects and fragmentation.

8.5 Conservation implications and concluding remarks

Much of the Wet Tropics lowlands has been cleared for agriculture and (more recently) urban expansion, and some scientists have expressed pessimism about our chances of saving the biological integrity of the Wet Tropics lowland rainforest (e.g., Ehrlich & Murphy 1987). This study has shown that rainforests on gently sloping basalt and alluvial terrain have been very heavily cleared, and on the most heavily-impacted areas (on alluvial soils), a little over 15% of rainforest remains. While the exact percentage of original habitat required to maintain populations and biodiversity is highly dependent on the particular environment and taxa, and remains the subject of some conjecture (Homan et al. 2004), this lies at the lower end of the range of estimates (10-30%).

Conservation goals in human-fragmented habitats often include restoring and maintaining species assemblages to resemble those found in continuous habitats (e.g., Castelletta *et al.* 2005, Terborgh *et al.* 1997). By identifying the landscape characteristics that lead to the presence of more ‘complete’ avian assemblages (those that differ least from those found in unfragmented habitat), managers can better identify which remnants are more likely to be viable. This study showed that larger patches (>40 ha) of disturbed rainforest are required for the persistence of many rainforest specialists, and that this size represents something of a threshold below which bird assemblages more rapidly diverge from those of unfragmented rainforest. Patch isolation (in particular the amount of rainforest within 1km), also influences the bird assemblages found in fragments. Therefore, habitat conservation and augmentation should focus equally on adding pieces to already-existing patches but, where possible, this should also be focussed on areas in close proximity to larger patches.

The bird assemblages of edge zones differ more substantially from those in unfragmented rainforest than do assemblages in interior zones, with open-country species utilising edges and some rainforest specialists avoiding them. However, the shallowness of the edge zone (50 m) means that only in the narrowest or smallest patches would edge effects be a major influence on the conservation value of a patch.

This study clearly demonstrated that we cannot extrapolate the results of other studies (e.g., those from the Brazilian Amazon) to this region. Whilst edge effects and loss of specialist rainforest species are consequences of fragmentation in the Wet Tropics lowlands, these effects are milder than those found in the majority of overseas studies. In other words, in northern Queensland (with regards to the avifauna at least), smaller patches would be required to contain a given proportion of species than would be the case in many other regions such as Africa (Beier *et al.* 2002), Central America (Graham & Blake 2001) and South America (Stouffer & Bierregaard 1995a).

Some areas of the Wet Tropics lowlands remain under threat from residential and tourism development, and bird assemblages suffer negative consequences from the fragmentation of remaining habitat. Furthermore, there are few protected areas in the lowlands, especially on the nutrient-rich alluvial and basalt soils. However, as this relatively species-poor assemblage is more resilient than those from diverse regions, so smaller, isolated patches may be of greater conservation value (with regard to the bird assemblage) than might be the case in other regions where assemblages are more diverse and, importantly, species are more specialised. Thus, the loss of sensitive species resulting from natural disturbances that have helped shape the bird assemblages of the Wet Tropics lowlands may provide a greater opportunity to preserve relatively intact bird assemblages in remnants, and thus contribute to the maintenance of the ecological integrity of the lowland rainforests of the Wet Tropics.