1. INTRODUCTION

I have been trying to understand the ecology of the rainforests in the Wet Tropics bioregion of north Queensland since 1986 when I started first year biology at James Cook University. I remember, as a child, driving past places like Mount Elliot, looking up into the mysterious, cloud-draped rainforests and wondering what was up there. I have been fortunate enough to not only find out what is up there but to have made a career out of it. I have now been to many mountaintops and steamy lowland forests and the contents of this report describe some aspects of the things I have found.

During the past fifteen years, I have been attempting to understand the patterns and processes of rainforest biodiversity in the Wet Tropics and, more recently, how global climate change is likely to affect these rainforests. The Wet Tropics bioregion lies along the tropical northeastern coast of Queensland, between Cooktown in the north and Townsville in the south (Figure 1). It covers an area of approximately 1.8 million hectares, of which about one million hectares is rainforest. The Wet Tropics World Heritage Area (WTWHA) protects nearly 900,000 hectares of the region, primarily rainforest. The region is characterised by a series of disjunct mountain ranges running roughly parallel to the coast, with most of the mountains being covered in tropical rainforest.

Rainfall within the rainforest areas varies from about 1,500 millimetres up to as much as 9,000 millimetres annually, although this is highly variable from year to year. Rainfall is strongly seasonal with most of the annual rainfall falling between December and February.

When the Rainforest Cooperative Research Centre (CRC) first commenced in 1995, I conducted a review of what was known about the distribution and biodiversity of vertebrates in the region (Williams *et al.* 1996). At that stage, our distributional knowledge was surprisingly limited even for the better-known groups of vertebrates. We analysed the available data at the best resolution possible at the time, which was the presence/absence of species in each mountain range or subregion (Figure 2). These data and analyses were surprisingly informative considering the low resolution of the data, which lead me to include regional analyses of biodiversity in my PhD research and a number of publications on various aspects of ecology in the Wet Tropics (Williams 1997; Williams and Pearson 1997; Williams and Hero 1998, 2001; Graham *et al*. 2006). However, it was always recognised that we needed to move beyond subregional species richness and compile/collate/collect point locality data on species distributions and abundance.

It was always considered important but too costly and time consuming to conduct systematic surveys across the region that would include the most important gradients. The contents of this report are based on systematic, standardised surveys that were funded and conducted under a variety of research projects. Standardising the techniques has meant that the samples from the different studies that I have conducted could be combined to finally have reasonable coverage of the region, albeit more than ten years later. It is now possible to move to continuous spatial analyses rather than simple subregional comparisons.

In this report I present one step in this direction, that is, my best estimate of the distribution of most species of terrestrial rainforest vertebrate in the Wet Tropics, excluding bats. The backbone of this report is the maps of species richness and species distributions. They are not yet complete; many species do not yet have sufficient data to allow a realistic or reliable map and thus the maps presented here vary in their reliability, dependent on the amount and quality of the data input. However, I hope that these maps are useful at many levels. Biodiversity at its simplest level is the number of species in a place and this is what the combination of these maps is trying to estimate – which species are in which places.

The Wet Tropics bioregion presents a unique opportunity to examine ecology and biogeography because the rainforests have been protected under World Heritage listing since 1988 and there is an extensive ecological and biophysical research base. Webb (1987) stated that the Australian Wet Tropics is one of the "most significant regional ecosystems in the world" as a key to understanding the origins of angiosperms, past climatic sifting and to understanding links with temperate Australia, Asia and South America.

Considerable knowledge has become available on regional climate (Nix 1991), vegetation distribution (Tracey and Webb 1975; Goosem *et al*. 1995; Stanton and Stanton 2005), distribution of rainforest fauna (Winter *et al*. 1984; Winter 1988; Nix and Switzer 1991; McDonald 1992; Williams *et al.* 1996), patterns of phylogeography (Joseph *et al*. 1995; Schneider *et al*. 1998; Moritz *et al*. 2000; Hugall *et al*. 2002; Bell *et al.* 2004; Schneider and Williams 2005) and historical paleodistribution of vegetation and climate (Nix 1991; Kershaw 1994; Hilbert *et al*. 2001; Graham *et al.* 2006). Broad distributions and habitat preferences of many rainforest animals of the Wet Tropics have been well documented (Kikkawa 1976, 1982, 1991; Kikkawa and Pearse 1969; Kikkawa and Williams 1971; Kikkawa *et al*. 1981; Schodde and Calaby 1972; Driscoll and Kikkawa 1989; Crome and Nix 1991; Ingram 1991; Williams *et al*. 1996).

The regionally endemic upland species are considered to be relicts of either an older connection with the upland fauna of New Guinea or from an older, cool temperate Australian fauna (Kikkawa *et al*. 1981). In contrast, the lowland rainforest of the Wet Tropics has a higher affinity with the rainforests of Cape York and New Guinea, with dispersal from the north over the paleohistory of the region being an important process (Kikkawa *et al*. 1981). Phylogeographic patterns based on molecular population genetics suggest that vicariant evolution in historical rainforest refugia has been an important influence on the fauna (Schneider and Williams 2005). However, the species are old (at least several million years) and the influence of the more recent Quaternary climate/habitat fluctuations has been via processes of non-random extinction and recolonisation rather than recent allopatric speciation (Schneider and Williams 2005).

Data describing the detailed distributions of individual species within the region has been very patchy. While earlier studies have provided valuable basic information on species distributions, analyses of macro-ecological patterns of species richness and assemblage structure have been hampered by coarse resolution in the datasets with distribution data being limited to the scale of subregions (mountain ranges) (Winter *et al.* 1984; Winter 1988; McDonald 1992; Williams *et al*. 1996; Williams and Pearson 1997; Moritz *et al*. 2000; Williams and Hero 2001). Williams *et al.* (1996) suggested that in order to move beyond analyses based on coarse distribution data, it would be necessary to (a) compile point locality data rather than subregional (mountain range) species lists; (b) collect abundance data rather than presence/absence data; and (c) explicitly examine the elevational gradient in more detail.

The elevational gradient is the primary ecological gradient driving patterns of species richness and composition in the Wet Tropics biogeographic region (Williams and Pearson 1997). Attempts have been made to expand knowledge on the elevational distribution and relative abundance of bird species; however, data has previously been restricted to a small number of species (Crome and Nix 1991; Wieneke 1992) or incompletely sampled mountain ranges within the region (Gill 1970; Kikkawa 1982; Boles and Longmore 1989). The comprehensive dataset used to produce these maps has been and is continuing to be used in a number of recent studies.

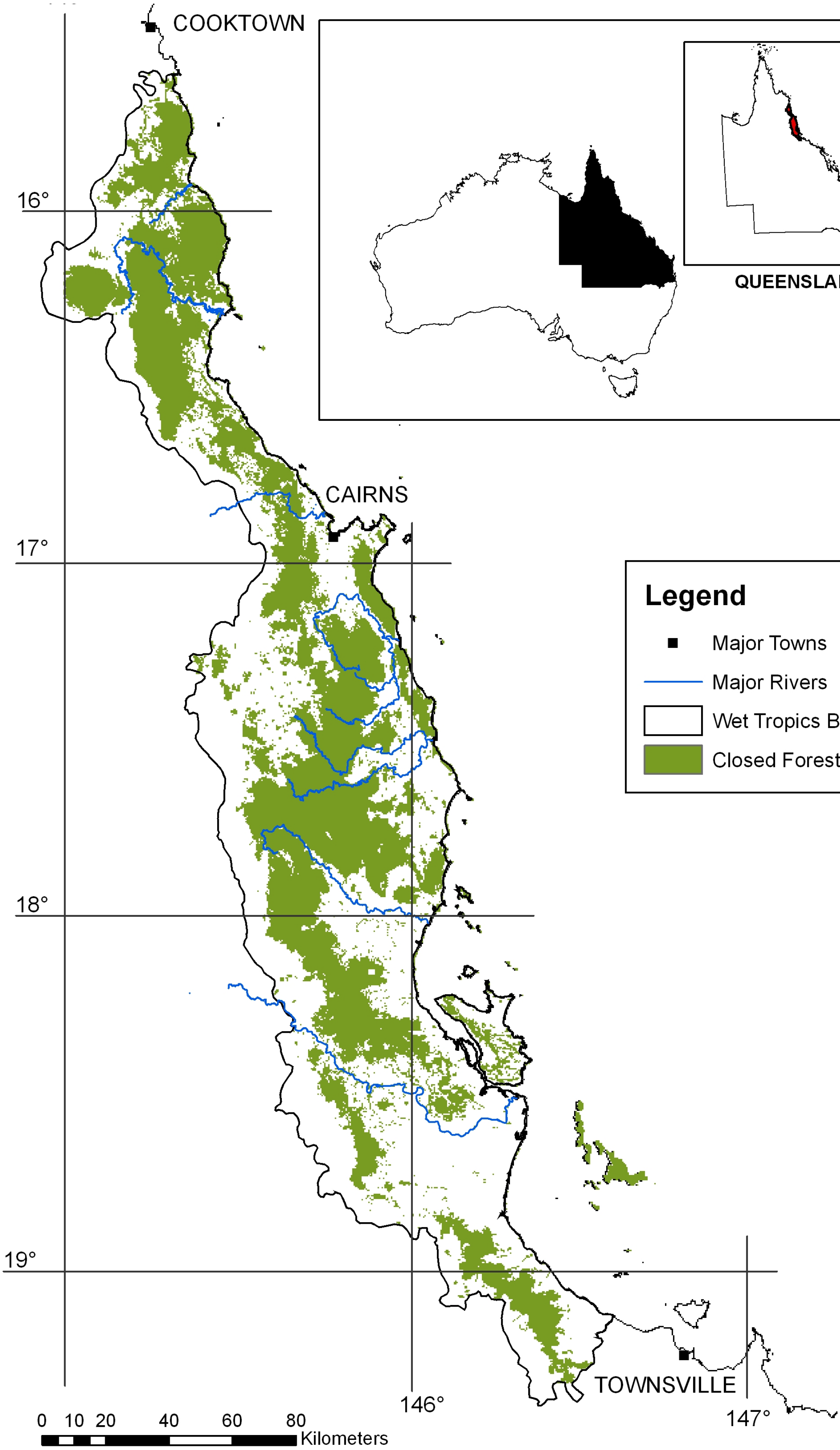

Figure 1: The distribution of rainforests within the Wet Tropics bioregion.

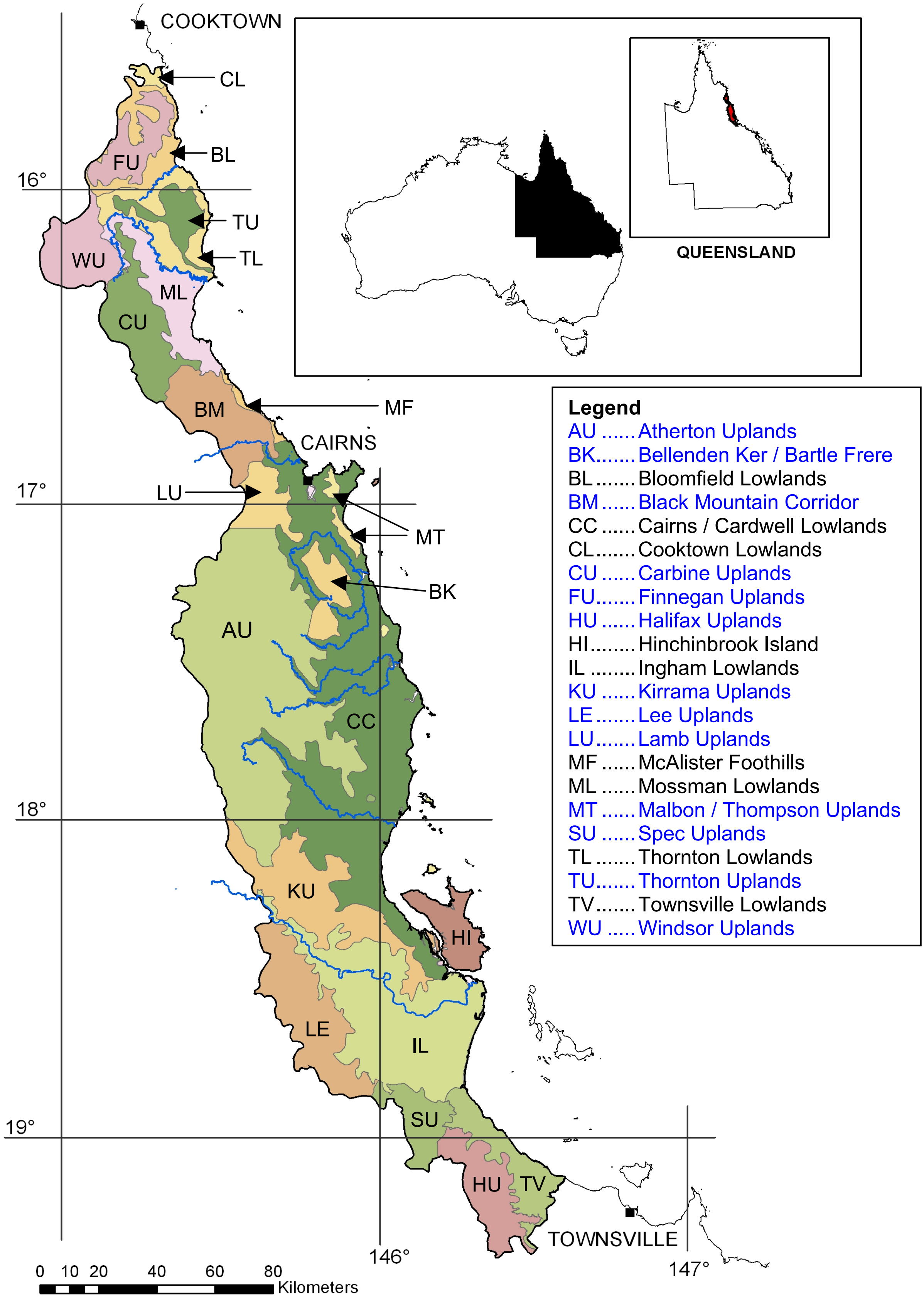

Figure 2: Subregions of the Wet Tropics bioregion. Upland subregions more than three hundred metres above sea level are indicated in blue in the legend.

Regionally endemic birds are known to exhibit complex variability in abundance within current elevation ranges (Shoo *et al*. 2005a) and the same has also been demonstrated for other vertebrate taxa in the region, including arboreal mammals (Trenerry and Werren 1993; Kanowski *et al*. 2001) and microhylid frogs (Shoo and Williams 2004). Species richness was previously considered to be highest in the lowlands (Kikkawa 1991), declining toward the uplands where a very different assemblage of species is apparent (Kikkawa 1982; Boles and Longmore 1989; Crome and Nix 1991). However, analyses based on subregional species richness suggested that species richness of rainforest birds in the upland and lowland forests were not significantly different and species richness and endemism were positively correlated with rainforest area and habitat diversity (Williams *et al*. 1996).

With the recent availability of systematic standardised surveys of vertebrates across the region, detailed altitudinal patterns of species richness are now available (Williams *et al*. in press) (Figure 3). Historical contraction of rainforest to small refugia, followed by non-random species extinctions, may explain the general paucity of specialised species and low endemism in the lowlands (Williams and Pearson 1997). Molecular data provides additional support for the hypothesis that there were local extinctions during periods of rainforest contraction and subsequent expansion (Joseph *et al*. 1995; Schneider and Williams 2005).

Protecting the biota and ecosystem functions of the Wet Tropics bioregion is only possible if we have some understanding of current patterns of biodiversity and the factors that maintain ecosystem processes and determine the distributions of species, assemblages and habitats. Therefore, it is imperative that we gain an understanding of the factors determining the distribution of species. The distribution and abundance of a species is determined by a number of complex and often interacting factors within four general categories (Brown and Lomolino 1998):

1. Biogeographic history (e.g. extinction episodes due to habitat contraction);
2. Physiological preferences and tolerances of species and habitats to the abiotic environment (e.g. temperature, rainfall and climatic stability);
3. Biotic interactions (e.g. competition and predation); and
4. Disturbance (e.g. fire and cyclones).

The maps included in this report are a step forward in the ongoing research to improve our knowledge of species distributions in the Wet Tropics region and the processes that determine these distributions. This knowledge is crucial if we are to maintain this unique ecosystem into the future, particularly in the face of global climate change. Until recently, the major threats to the biodiversity values of the Wet Tropics were habitat clearing, fragmentation, pests and diseases. It is now apparent that climate change and the interactions between a changing climate and other pressures are the key challenges we now face in protecting our tropical rainforests.

The bioclimatic models that provided significant input into these maps largely influenced my decision to redirect my research efforts. Initially, my research was focused on understanding spatial patterns of biodiversity. I smugly thought that we had one of the best systems in the world for this research because we had a high-biodiversity area that was accessible, well studied and well protected. The realisation that climate change induced by anthropogenic greenhouse gas emissions could cause catastrophic impacts on the Wet Tropics was a shock. Since the early analyses predicting these impacts, the impacts of climate change on biodiversity in the Wet Tropics has been the primary focus of my research.

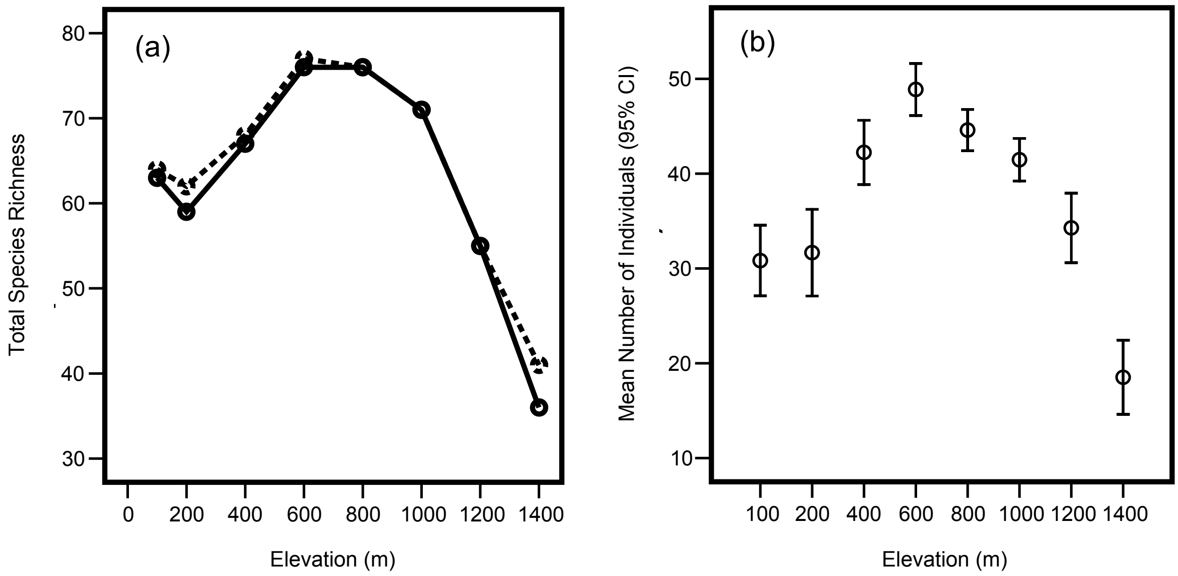

Figure 3: Changes across the elevational gradient in bird species richness and abundance, (a) observed (S_{obs} – solid line) and estimated total species richness (Michaelis-Menton Means, S_{mmm} – dashed line); and (b) bird density (mean number of individuals recorded in a survey) (after Williams *et al*. in review).

1.1 GLOBAL CLIMATE CHANGE IN THE WET TROPICS

There is no doubt that the global climate is changing due to anthropogenic greenhouse gas emissions. Average temperatures have already risen approximately 0.6°C and are continuing to increase (Houghton *et al*. 2001). The Australian Bureau of Meteorology has announced that 2005 was the hottest year on record. Regional climate modeling in Australia suggests that during the remainder of this century we will experience an increase in average temperatures of 1.4 to 5.8°C, combined with increases in atmospheric CO_2 concentrations.

Changes in rainfall patterns are also predicted with rainfall becoming more variable, longer dry spells and increased frequency of disturbance events such as flooding rains and cyclones (Easterling *et al.* 2000; Walsh and Ryan 2000; Milly *et al.* 2002; Palmer and Raianen 2002). Additionally, a rise in the average basal altitude of the orographic cloud layer is expected (Pounds *et al.* 1999), which will likely exacerbate the effects of longer and more variable dry seasons due to a reduction in cloud capture by the canopy in mountain rainforests (Still *et al.* 1999).

It is now widely accepted that climate change is probably the most significant threat to global biodiversity and human well-being (Hughes 2000; Parmesan and Yohe 2003; Root *et al*. 2003; Thomas *et al.* 2004a,b; Root *et al*. 2005; Pounds *et al.* 2006). There is a common, though incorrect, perception that the impacts of climate change will be worse in temperate regions than in the tropics although it is generally accepted that all mountain biota are extremely vulnerable. Global biodiversity is concentrated in the tropics, where there are also often high levels of vulnerable species and restricted endemics. Mountain systems represent hotspots of biodiversity and endemism due to the compression of climatic zones over the elevational gradient (Körner 2002). It is this dependence on elevational gradients that makes these systems vulnerable to climate change.

Many studies have demonstrated, or predicted, that climate change will result in shifts in the latitudinal and altitudinal range of affected species, with concomitant complex changes in assemblage structure and ecosystem function (Parmesan 1996; Hill *et al.* 2002; Peterson *et* *al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003). However, the rainforests of the Wet Tropics, Cape York and Eungella are each isolated habitats with no potential for rainforest endemics to move beyond their current bioregion. Furthermore, the biogeography of the region predisposes the fauna to being vulnerable to climate change for two reasons:

1. Endemic fauna are adapted to cool, wet and relatively aseasonal environments; and
2. The impacts of increasing temperatures should be most noticeable across altitudinal gradients and, in this region, the altitudinal gradient and the associated complex topography dominate the biogeography of the region (Nix and Switzer 1991; Williams *et al.* 1996).

Predictive modeling of impacts on species distributions and population size suggested the potential for catastrophic extinctions in the Wet Tropics (Williams *et al.* 2003; Shoo *et al*. 2005a,b; Williams and Hilbert 2006). Bioclimatic models of the spatial distribution for endemic rainforests vertebrates predict that many species will lose the majority of their core habitat under relatively small increases in temperature, resulting in an amplification of extinction rates and a significant reduction in overall biodiversity in the region (Williams *et al.* 2003).

In a recent study using population size and density rather than distributions (based on standardised abundance surveys) of Wet Tropics birds, Shoo *et al*. (2005a) predict that 74% of rainforest species will become threatened as a result of projected mid-range warming in the next one hundred years. However, extinction risk in rainforest birds varied according to where a species is currently most abundant along the altitudinal gradient. Upland birds are expected to be most affected and are likely to be immediately threatened by small increases in temperature. However, there is a capacity for the population size of lowland species to increase, at least in the short term. Many microhylid frog species are also predicted to suffer large declines in population size as climates that currently support high density populations of species on mountaintops are likely to disappear under moderate levels of climate warming (Williams *et al.* in review). It has also been predicted that for regionally endemic birds and frogs, as temperature increases, population size is likely to decline more rapidly than distribution area. This indicates that for these species, extinction risk associated with climate change will be more severe than expected from decline in distribution area alone (Shoo *et al.* 2005; Shoo 2005).

Finally, Williams *et al.* (in revision) found that species richness and density of Wet Tropics rainforest birds is highest at elevations of six to eight hundred metres (Figure 3) and is positively related to net primary productivity and energy input. The authors suggest that an increase in temperature due to global warming may result in an increase in net primary productivity that could ameliorate some of the predicted negative effects of climate change on upland rainforest birds (Williams *et al*. in revision).

It is not only the vertebrates that are expected to suffer from climate change. Studies on invertebrate fauna have found many species restricted to high altitudes, including low vagility arthropods (Monteith 1985,1995; Monteith and Davies 1991), schizophoran flies (Wilson *et al.* in review) and ants (Yek unpublished data). These results suggest that the impacts in the invertebrate assemblages will be similar to those previously predicted for regionally endemic vertebrates by Williams *et al.* (2003).

Ultimately, the impacts of global climate change will depend on two factors; firstly, the final, realised degree of change, and secondly, the resilience of the species and ecosystem in question. The relative resilience of a species will depend on its ability to adapt via ecological or evolutionary plasticity within biogeographic constraints such as habitat connectivity. The imperative now is to understand the patterns and processes of the rainforest ecosystem in order to allow effective conservation management. Knowing which species occur in any given area is a basic, but vitally important, piece of information for almost all aspects of ecology, conservation, natural resource management, impact assessment and general natural history. I hope these maps and summaries will be useful in all of these areas of interest.