Influences of past, present and future climate on the structure and diversity of rainforest bird assemblages in north-eastern Australia

Alexander Sibthorpe Anderson

Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University, Townsville, QLD, Australia.

Still though art blest, compar'd wi' me:
The present only toucheth thee:
But och! I backward cast me e'e,
On prospects drear,
An forward, tho I cannot see,
I guess an fear!

--Robert Burns, 1785

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Statement of other contributors

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due reference is made in the thesis itself. However, analyses in chapters 5, 6, and 7 of this thesis have been made possible in part by access to data collected previously in the study region by other researchers: Steven Williams, Rob Henriod, Emily Bolitho, Samantha Fox, Jeff Middleton, and Luke Shoo. Co-author contributions to data chapters are as follows:

Chapter 3: ***Alex Anderson***: concept, funding, data collection, analysis, writing, editing. ***Tiago Marques***: concept, editing. ***Luke Shoo***: concept, editing, ***Richard Pearson****:* concept, editing. ***Stephen Williams***: concept, funding, editing.

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Chapter 7: ***Alex Anderson***: concept, funding, data collection, analysis, writing, editing. ***April Reside*****:** analysis, editing ***Jeremy VanDerWal*****:** climate data. ***Luke Shoo***: concept, data collection, editing. ***Richard Pearson****:* editing. ***Stephen Williams***: concept, funding, data collection, editing.

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Dedicated to the memory of Gordon R.V. Anderson 1946 - 2009

Abstract

In this thesis I endeavour to advance our understanding of the influence of climate on patterns of diversity and assemblage structure of rainforest birds in north-eastern Australia. In chapter 3, I apply a distance sampling method to quantify the factors influencing detectability of rainforest birds. In doing so I aimed to extend basic measures of abundance of species at sites to estimates of absolute density. Recognising that distance sampling presents a significant logistical challenge, particularly for rare species, in chapter 4 I develop a compromise approach to estimating density that involves modeling the detectability of species as a function of their characteristics. In chapter 5, I use the improved density estimates to test predictions of Species-Energy Theory using the More-Individuals Hypothesis as a framework. This analysis shows a strong contribution of historical climate change in shaping contemporary patterns of energy flux, and hence density and diversity of birds, particularly among insectivores. These results highlight an ongoing influence of long-term environmental instability on patterns of energy uptake in this system, along with secondary effects of resource seasonality. In chapter 6, I apply the refined density estimates to a space-for-time substitution analysis of the influence of temperature on the elevational density profiles of rainforests birds. Temperature is shown to be a strong correlate of elevational patterns of density across the bird community, validating a key assumption of species distribution modelling, used to predict impacts of climate change on biodiversity. Based on this, in chapter 7 I extend previous species distribution modeling work undertaken in the Australian Wet Tropics with the addition of new data from lowland sites, and with data from neighbouring rainforest regions to the north and south, including both species whose ranges extend outside the AWT, and some endemic species restricted the Central Queensland Coast and Cape York Peninsula. The results of these analyses are consistent with previous predictions of biodiversity losses of upland endemic species, as their preferred cool, moist environments contract up-slope, and also indicate extensive reshuffling of assemblage composition across the elevation gradient as lowland species expand up-slope into previously unsuitable climates. Crucially, however, predicted impacts on patterns of species richness are strongly influenced by underlying assumptions about dispersal between regions. Under a scenario of free dispersal, lowland biotic attrition predicted in the Australian Wet Tropics is completely offset by an influx of warm-adapted species with New Guinean affinities expanding southwards from Cape York Pensinsula lowland rainforests. This result suggests that dispersal limitation as well as historical biogeography continue to play an important role in defining the realised distributions of many rainforest species, and that habitat changes will play a critical role in determining the composition of future assemblages. These key findings are discussed in terms of

their significance for broader ecological theory, and their relevance to the identification of suitable environment for future translocation of upland endemic species.

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Chapter 1. General introduction

"*In the midst of this chaos, I can take comfort by remembering another uniqueness of the coexistence problem: it is probably the only scientific endeavor which has a patron saint, Santa Rosalia"*

-- G.E Hutchinson 1959

Plate 1. *Massive canopy emergents flanked by fan palms (*Licuala ramsayi*) characterise the warm lowland forests of the northern Australian Wet Tropics. Despite the ample available energy in these forests, they appear to support the co-existence of fewer bird species than forests at higher elevations.*

1.1 Background

Tropical mountains support a large proportion of global biodiversity (Korner & Spehn 2002). Steep environmental gradients and high habitat diversity have driven complex evolutionary histories, making tropical montane systems important centres of endemism (Renjifo *et al.* 1997; Rahbek & Graves 2001; Herzog *et al.* 2011). Among birds, nearly 60% of all terrestrial species can be found above 1000m elevation, and 87% of these occur within the tropics (Jetz 2010a), making tropical mountains also globally important reservoirs of avian species diversity (Davies *et al.* 2007). More than half of all Australian terrestrial bird species can be found in the montane rainforests and adjacent wet-sclerophyll forests of the north-east: in Cape York Peninsula, the Australian Wet Tropics and the Central Queensland Coast bioregions, together comprising less than 0.3% of total continental land surface (Marshall 2001). These include 14 endemic species, 13 species found elsewhere only in new Guinea (Frith & Frith 1995), and several endemic subspecies. These three regions have recently been identified as Important Bird Areas (Birdlife International 2008), highlighting their disproportionate contribution to Australia's avifaunal diversity (Dutson *et al.* 2009). Previous studies have also predicted a high level of vulnerability to climate change in this fauna, particularly among upland endemics (Williams *et al.* 2003; Hilbert *et al.* 2004). Steep environmental gradients in the montane tropics (Corlett 2011), and the narrow distributions (Jankowski *et al.* 2009) and thermal tolerances of tropical species (Laurance *et al.* 2011), may make these ecosystems particularly vulnerable to global warming (Nogué *et al.* 2009; Young *et al.* 2011). Physiographic attributes of upland forests may also increase their vulnerability to indirect effects of climate change, such as the raising of the cloud-layer (Foster 2001). The few published observations of climate impacts on montane tropical ecosystems already include direct evidence of extinctions (Pounds *et al.* 1999), and up-slope shifts in species distributions (Raxworthy *et al.* 2008; Larsen *et al.* 2011). Climate change may thus represent the most significant threat to tropical montane bird biodiversity both globally (La Sorte & Jetz 2010), and within Australia (Williams *et al.* 2003).

The high species richness found in the montane tropics attracted the interest of early theorists (Wallace 1890; MacArthur 1969) and has seen a recent resurgence of importance in macroecology (Brown 2001). A main focus of this renewed interest has been on patterns of declining richness from lowlands to uplands, widely held to be both a general pattern (Huston 1994), and analogous to the pattern of declining richness from the equator towards the poles (Rosenzweig 1995; Gaston 2000; Rahbek & Graves 2001). Such broad-scale species richness trends are strikingly correlated with climate (Currie *et al.* 2004; Ruggiero & Hawkins 2008), but while temperature gradients

dominate, a direct effect of increased temperature *per se* on diversity (e.g. through increased speciation rates (Rohde 1992)) has usually been subordinated to the correlated influences of both increased geographic area and energy availability (Clarke & Gaston 2006). The importance of area as a driver of species richness was identified in the theory of island biogeography (MacArthur & Wilson 1963, but see Brown & Lomolino (1989) for reference to an earlier independent formulation). Here species richness was modelled as an equilibrium between extinction and recolonisation: larger "islands", having lower extinction rates and higher recolonisation rates than smaller ones, supporting higher diversity. Later, a role for increased energy availability in reducing extinction risk was incorporated, leading to a general "species-energy" theory (Wright 1983). Here, higher population densities in high energy areas also reduced extinction risk, and allow accumulation of higher species richness. These two processes are hypothesised to interact (Jetz 2010b), and also to fundamentally influence species richness in a similar way: through increasing population size, reducing extinction risk, and allowing diversity to accumulate.

Explicitly formulated as the More-Individuals Hypothesis (MIH) (Wright *et al.* 1993) this mechanism provides a testable prediction for species-energy relationships: high richness at high energies should be associated with high population density. However, while the MIH predicts a monotonic species-energy relationship, in practice, observed relationships between energy and species richness are heterogeneous (Mittelbach *et al.* 2001). A unimodal species-energy response (in which species richness increases linearly with available energy up to a peak, and then declines at higher energy availability) has been described in a wide variety of taxa and ecosystems (for reviews see; (Rohde 1992; Waide *et al.* 1999; Brown 2001)), to the extent that the pattern has been described as "ubiquitous" (Huston 1994). Two seminal studies of diversity across elevational gradients in tropical rainforest birds also illustrate a unimodal response (Kikkawa & Williams 1971; Terborgh 1977). The challenge presented by this anomalous species-energy relationship has led macroecologists to seek alternative mechanisms that might moderate the species-energy relationship at high productivities to produce a unimodal curve. Density-dependent interactions such as interspecific competition may be important in structuring tropical bird communities (MacArthur 1969; Diamond 1973), and may structure bird species distributions (Jankowski *et al.* 2010) and diversity across elevation in the montane neotropics (Terborgh 1977), depressing diversity at high productivities. Elsewhere, competition among seabirds has also been shown to be a greater influence in high productivity zones (Ballance *et al.* 1997). A non-biological explanation has also been offered, with the influence of bounded domains hypothesised as a constraint on species richness patterns so that a mid-domain peak may be expected independently of environmental gradients (Colwell & Lees 2000). The assumption that species richness patterns are

at equilibrium with current energy patterns has also been questioned; diversity in many biotas is strongly mediated by fluctuations of climate during the Quaternary (Rohde 1992; Hawkins *et al.* 2003a) and thus may not reflect current conditions.

Environmental instability over shorter timescales has also been hypothesised to play a role. Williams *et al.* (2010a) reported a unimodal species energy response in the pattern of diurnal rainforest bird species richness across elevation in the montane tropics of north-eastern Australia. Seasonality in the pattern of resource availability was proposed as a potential driver of the unexpectedly low species richness in lowlands, supported by evidence of a similar seasonality effect across latitude in the same system (Williams & Middleton 2008). Alternatively, historical environmental instability of lowland forests during the climate fluctuations of the Pleistocene were also proposed as a driver (Williams *et al.* 2010a), supported by numerous examples of the importance of extinction filtration in other groups in the Australian Wet Tropics (AWT) (Williams and Pearson 1997; Moritz 1999; Schneider *et al.* 2005). A number of data limitations in Williams *et al.* (2010a) however hindered the explicit testing of these alternative mechanisms. Estimates of absolute density were lacking, hindering direct testing of the predictions of the more individuals hypothesis, as were local estimates of species richness (α diversity). Other opportunities for improvement in data coverage included increasing sampling in the lowland forests, and sampling in regions at the extremes of the seasonality and temperature gradient, in north-eastern Australian rainforests -namely, the warm tropical forests of Cape York peninsula (CYP) and cooler temperate and subtropical forests of Central Queensland Coast (CQC). Since montane systems in the tropics both contribute to global diversity gradients (Davies *et al.* 2007) and also possibly reflect some of the same underlying drivers as those operating at global scales (Ruggiero & Hawkins 2008), the study of elevational patterns of richness in this system can also make an important contribution to our understanding of drivers of biodiversity pattern more generally (Lomolino 2001).

The framework provided by species-energy theory and the MIH provides an approach to disentangling the importance of some of the hypothetical drivers of species richness in this system, but depends on accurate estimates of density and species richness. For density, such data are often difficult to obtain in wildlife surveys (Buckland at al. 2008). This is particularly true in closed-forest bird surveys (Pitelka 1981; Karr 1981), and in mountainous terrain (Dawson 1981) and especially at the broad spatial scales relevant to macroecology (Brown 1995). Using indices of relative abundance may be appropriate in some cases (Rosenstock *et al.* 2002; Johnson 2008), but as detectability often varies between surveys, sites or species, indices can introduce a bias which may make underlying ecological processes difficult to infer (Burnham & Anderson 1984). Distance

sampling techniques (Buckland *et al.* 1993) are one widely used approach to address this problem. By describing the relationship between decay in detection probability and distance from the observer, application of distance sampling to strip transects yields estimates of absolute density, instead of the indices of relative abundance commonly substituted (Buckland *et al.* 2004).

Distance sampling however is not without its own limitations. The methods require relatively large sample sizes per site and species, and accurate estimates of distance to each individual record (Thomas *et al.* 2002). For rare species, and across large areas, the problem of sample size may be particularly acute (Mackenzie *et al.* 2005), and in diverse tropical assemblages, preclude the application of Distance analysis to the estimation of absolute density for many species of interest. One approach that may circumvent these obstacles for rare species is to "borrow" detectability information from similar and more common species (Alldredge *et al.* 2007a). Information is lacking, however, on the characteristics of species that should be used to judge this similarity (Mackenzie *et al.* 2005). In addition, variation between sites and surveys which can be expected across large environmental gradients will still play an unknown role (Thomas *et al.* 2010), and the increased training and logistics required may raise the cost of field data collection (Keppler & Scott 1981). The study of drivers of montane tropical bird diversity will therefore benefit from the development of techniques that identify variation in detectability between both sites and species, and that can be readily applied to diverse rainforest assemblages and across broad regional scales.

The task of improving our understanding of patterns of avian diversity and population density in tropical montane ecosystems is particularly urgent given the prospect of anthropogenic global warming. Over the last century increased CO_2 emissions have driven increases in global surface temperatures of a magnitude unseen in the previous 1000 years, (IPCC 2001). An increasing number of studies demonstrate shifts in species distributions (Thomas & Lennon 1999; Tingley *et al.* 2009) and behavioural phenology (Inouye *et al.* 2000, Chambers 2005) associated with these temperature changes. Global warming is also predicted to alter global patterns of biodiversity (Araujo & Rahbek 2006), driving a wave of extinctions of vulnerable species (Thomas *et al.* 2004). While measured temperature changes have been more severe in high latitudes (IPCC 2007), metabolic (Dillon *et al.* 2010) and geophysical processes (Janzen 1967; Colwell *et al.* 2008) may cause even greater impacts in the tropics (Parmesan 2006). Steep gradients and narrow thermal tolerances may make tropical montane ecosystems particularly vulnerable to the effects (Raxworthy *et al.* 2008; Sekercioglu *et al.* 2008; Nogué *et al.* 2009; Young *et al.* 2011). Given their importance as centres of diversity and endemism, the threat posed to avian diversity by climate change is thus a serious one (Jetz *et al.* 2007). An ability to mount an adequate conservation response will depend

on both an improved understanding of what drives this diversity in the first place, and how it is likely to change in the future.

Current predictions of the impact of climate change on montane species suggest we can expect a general trend of upslope shifts, mirroring that seen latitudinally towards the poles (Parmesan 1996). These predictions hinge on the assumption that the distributions of species will track spatial changes in the distribution of their preferred environmental conditions (their "Grinellian" niche (Grinnell 1917)). This assumption has given rise to a large number of studies using correlations between species occurrence data and environmental data firstly to define species preferred environmental envelopes, and then to predict spatial changes to these distributions in an altered future climate (Pearson & Dawson 2003). These predictions are supported by ample evidence from birds (Peterson & Martínez-Meyer 2009; Tingley *et al.* 2009), and other taxa in temperate climates (Konvicka *et al.* 2003; Wilson *et al.* 2007b), which suggest that these shifts are already occurring, but studies on montane tropical birds are relatively few (e.g. Pounds *et al.* 1999; Peh 2007). The assumption that correlative models of species environmental envelopes are transferable in time has also been widely challenged (Pearson *et al.* 2006; Dormann 2007). One criticism rests on the wealth of literature indicating that the current realised distributions used to predict future impacts are constrained by many factors in addition to those of climate (Soberon 2007; Jeschke & Strayer 2008). Other important constraints include historical processes (Martinez-Meyer 2005), barriers to dispersal (Svenning & Skov 2004), and biotic interactions (Araújo & Gusian 2006). This complexity suggests a need for careful validation of the assumptions of environmental niche models used to predict species future distributions (Jeschke & Strayer 2008).

Despite these limitations cases of up-slope shifts in response to global warming have been widely demonstrated by comparing current and historical distribution data (e.g. Konvicka *et al.* 2003; Lenoir *et al.* 2008; Chen *et al.* 2009). These shifts match predictions based on correlative models of current distribution (Parmesan & Yohe 2003). Historical data are often lacking however, particularly in the species-rich and data-poor tropics (Parmesan 2006). As a substitute, information on the distributions of species from locations representing contrasting parts of an environmental gradient can also be compared (Randin *et al.* 2006). Such space-for-time substitutions are a crucial tool for the evaluation of species distribution models in the context of climate change (Rastetter 1996). In either context however, it remains a challenge to accurately describe species' distributional limits in order to document a change with any statistical confidence (Shoo *et al.* 2006). One approach is to focus instead on mean elevations of species distribution, where species are most abundant (Shoo *et al.* 2006). A further refinement of this method, developed in analysis of

plant communities, first identifies species with a unique density optimum using a hierarchical modeling approach (Huisman *et al.* 1993), then uses simple logistic regression to locate density optima along environmental gradients (Oksanen *et al.* 2001). It is then possible to compare observed elevational differences in species distributions to expectations based on climatic gradients (Randin *et al.* 2006). This approach provides a test in space of a critical assumption of predictions from correlative distribution models- that of transferability of niches on time (Jeschke & Strayer 2008).

A further limitation of predictions from correlative species distribution models arises as a result of the future climate scenarios themselves. The predicted magnitude of global warming is such that in some areas of the globe climates may emerge that have no contemporary analogue (Williams & Jackson 2007). In this context, the up-slope shifts in distributions of cool-adapted species as they track their preferred cooler climates has an important corollary: the emergence of novel warm environmental space in lowlands to which few local species may be adapted (Martinez-Meyer 2005). In the absence of sources of warm-adapted species to fill these new niches, the result is predicted to be a decline in lowland species richness or "lowland biotic attrition" (Colwell *et al.* 2008). An essential condition for this process is thus isolation from assemblages of species adapted to novel warm environments due to unsuitable climate, or barriers to dispersal such as inhospitable habitat. In this context, upslope shifting taxa may not be replaced by warm-adapted species (Colwell *et al.* 2008). Assemblage changes due to climate constraints on species distribution may thus be strongly mediated by the influence of barriers to dispersal (Svenning & Skov 2004). In contrast, for some cool-adapted upland species, these changes may result in their isolation in diminishing refugia surrounded by a matrix of suitable habitat, but unsuitable environments (la Sort & Jetz 2010). For these species, identifying suitable environmental areas to receive climate "refugees" in a program of assisted migration may be a critical (Thomas 2011) if controversial (Ricciardi 2009; Schwartz *et al.* 2009) contribution to their continued survival.

1.2 Thesis aims

Understanding the drivers of avian assemblage structure and composition in Australia's montane tropical rainforests is a complex task, and one with ramifications for our understanding of both biodiversity patterns generally, and in predicting future impacts of climate change. Here I focus on two main aspects: identifying the relative influences of current versus historical climate on patterns of assemblage structure and diversity in birds of the rainforest in north-eastern Australia; and

secondly, predicting the potential for change to these patterns as a result of future climate change. Within these two main areas, I focus on several distinct but interrelated questions:

1. *What is the influence of detectability variation between species, sites and surveys on accurate estimation of diurnal bird species density across elevational gradients in rainforest in the study region?*

2. *Is it feasible to develop a method for estimating density, calibrated for detectability, that can be applied across broad regions?*

3. *Using density estimates based on these more accurate methods, and the More Individuals Hypothesis as a framework, what is the support for two key factors suspected to drive the observed unimodal relationship between bird species richness and available energy in the AWT: current climate and productivity versus historical environmental stability?*

4. *Given the known threats to montane tropical biodiversity, to what extent is the underlying assumption of transferability of environmental niche borne out by a space-for-time substitution in the AWT avifauna?*

5. *Using a correlative species distribution modeling approach, to what extent do I alter predictions of the vulnerability of this fauna by extending data coverage in lowlands, and what further changes do I identify for regionally restricted species in CYP and CQC not included in previous studies?*

6. *Based on the information from the cumulative analysis of species distribution models, what can I predict about climate effects on patterns of bird species richness across elevational gradients? Specifically, what is the likelihood of a process of lowland biotic attrition in the lowlands of the AWT? To what extent is this process mediated by dispersal from neighbouring regions?*

7. *Given the results of the mechanistic analysis of diversity pattern (question 3) and correlative analyses of distributions (questions 5 and 6), and their limitations, what are the next steps for advancing understanding of the drivers of biodiversity pattern, and the risks posed by climate change? What are the implications for biodiversity monitoring and assisted migration in a changing climate?*

1.3 A note on the structure of the thesis

This thesis consists of a collection of five core investigations, which have each been prepared as manuscripts for submission. These manuscripts have been reformatted as five data chapters, (chapters 3 to 7). For the purposes of this thesis, I use the first person singular “I” in all references to the investigator, but here I wish draw the readers attention to the fact that in publication this will be changed to “we”. These are preceded by a general methods chapter to reduce some of the repetition in the chapter methods sections. Tables and figures are numbered in two parts (e.g., “Table 2.1”) with the first number indicating the relevant chapter or appendix, and the second number the position within that section, for ease of tracing references between chapters and appendices. Appendix 1 includes an excerpt of a published journal article based in part on work completed by the author thesis during candidature. Subsequent appendices hold the sometimes repetitive additional tables and plots which are omitted from the chapters for succinctness, but which are necessary given the multi-regional and multi-species nature of the analyses.

Chapter 2. Description of the study region and sampling methods

Plate 2. *Cool montane rainforest shrouded in cloud overlooks warm tropical lowlands in the Daintree rainforest, in the northern part of the World Heritage-listed Australian Wet Tropics.*

2.1 Geography and climate of north-eastern Australian rainforests

Rainforests in north-eastern Australia are generally restricted to the mountains of the Great Dividing Range and adjacent coastal lowlands. In an otherwise low relief landscape, these mountains form a "mesotherm archipelago" (Nix & Switzer 1991) of cool uplands embedded in a matrix of lower elevation warmer climates (Figure 2.1). Orographic cloud formation along the coastal ranges also creates a strong moisture gradient in parallel to those of temperature (plate 2), with high rainfall areas in the uplands and drier climates in the lowlands (Figure 2.2). The three main montane regions that are sufficiently high and near to the influence of humid coastal air flows to support substantial rainforest are the McIlwraith and Iron Ranges in the Cape York Bioregion (CYP) between -14˚ 8'33.78"S 143˚22'36.65"E and -12˚37'24.44"S 143˚14'22.22"E, the Australian Wet Tropics Bioregion (AWT) between -15˚45'32.69"S 145˚ 1'53.87"E and 19˚18'0.65"S 146˚ 9'41.17"E; and the Clarke and Conway Ranges in the Central Queensland Coast Bioregion (CQC) between 20˚16'53.11"S 148˚18'8.45"E and 21˚23'25.87"S 148˚42'9.65"E (Figure 2.1). Within these regions rainforest is found across elevational ranges of between 100 and 1200 m asl in the CQC, between 50 and 1645 m asl in the AWT, and between 35 and 826 m asl in CYP.

From data based on modeled climate surfaces in BIOCLIM (part of the ANUCLIM 5.1 software (Houlder *et al.* 2000)) rainforest sites across these three regions occupy broad and over-lapping environmental spaces in terms of mean annual temperature and rainfall, dominated by the elevational gradient. The climate is characterised by warm average temperatures and high rainfall concentrated in the summer wet season (October to May). Upland forests experience higher rainfall and lower temperatures than lowland forests, and seasonality of rainfall decreases from north to south and from lowlands to uplands, while seasonality of temperature follows the reverse trend. Lowland mean annual temperatures reach 21.75 ˚C in CQC, 23.33 ˚C in the AWT and 24.71 ˚C in CYP, while mean temperatures in the uplands fall to 18.74 ˚C in CQC, 19.16 ˚C in the AWT and 22.52 ˚C in CYP. Temperature seasonality is lowest in the CYP and highest in CQC, and also increases from lowlands to uplands (map in Appendix 2.1). Mean annual rainfall in the lowlands reaches 1721 mm in CQC, 2510 mm in the AWT and 1488 mm in the CYP, and in the uplands reaches 2174 mm in CQC, 2757 mm in the AWT and 1536 mm in CYP. Rainfall seasonality is also highest in the CYP and lowest in CQC, and increases from lowlands to uplands (map in Appendix 2.2)

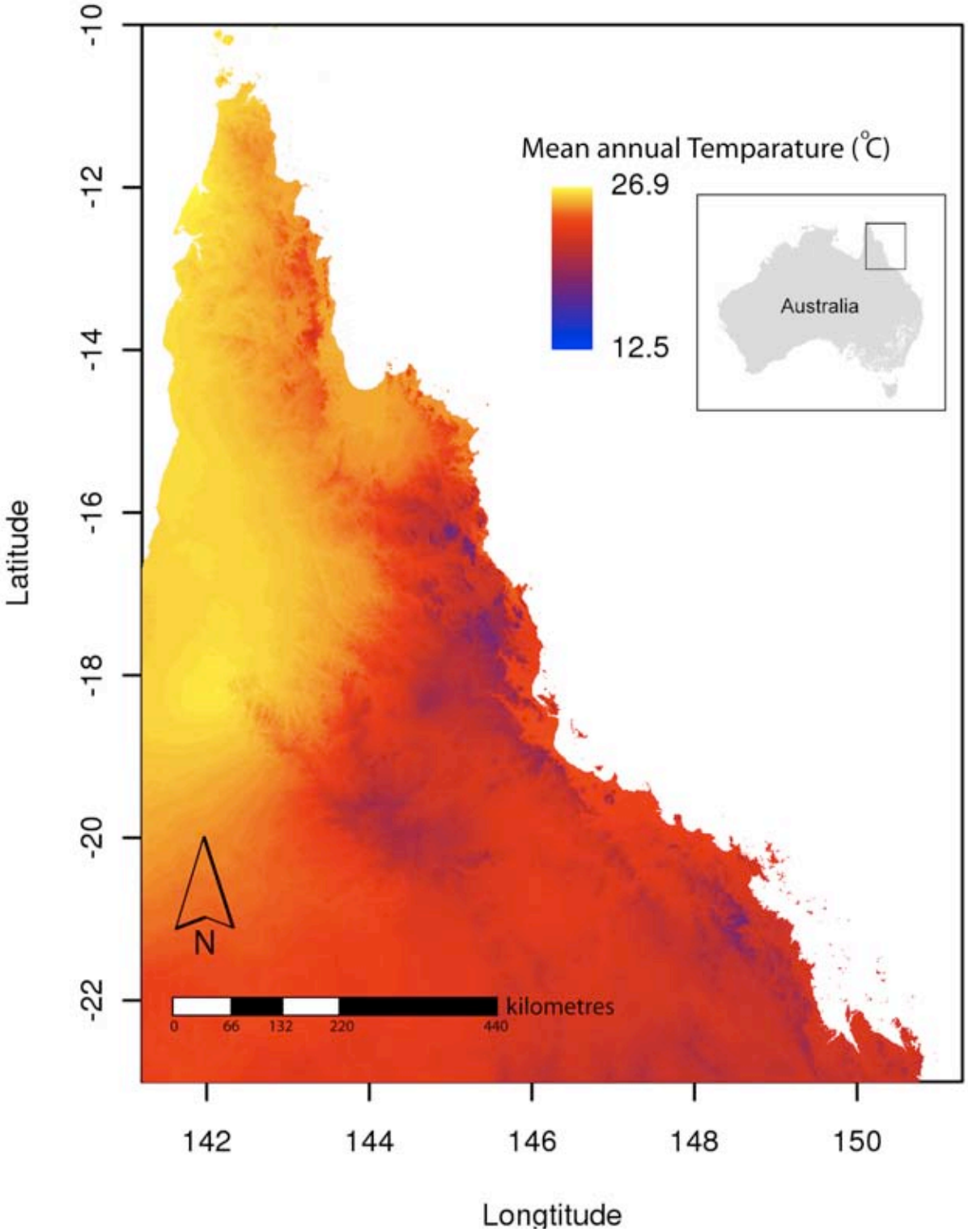

Figure 2.1. *Map of northern Queensland showing mean annual temperature gradients across the region, dominated by the north-south gradient, with highest temperatures on Cape York (yellow tones). Strong temperature variation also occurs across the elevational gradient, with highest temperatures in the lowlands of CYP, and lowest in the uplands of AWT (blue tones). Data are from BIOCLIM, see text for reference.*

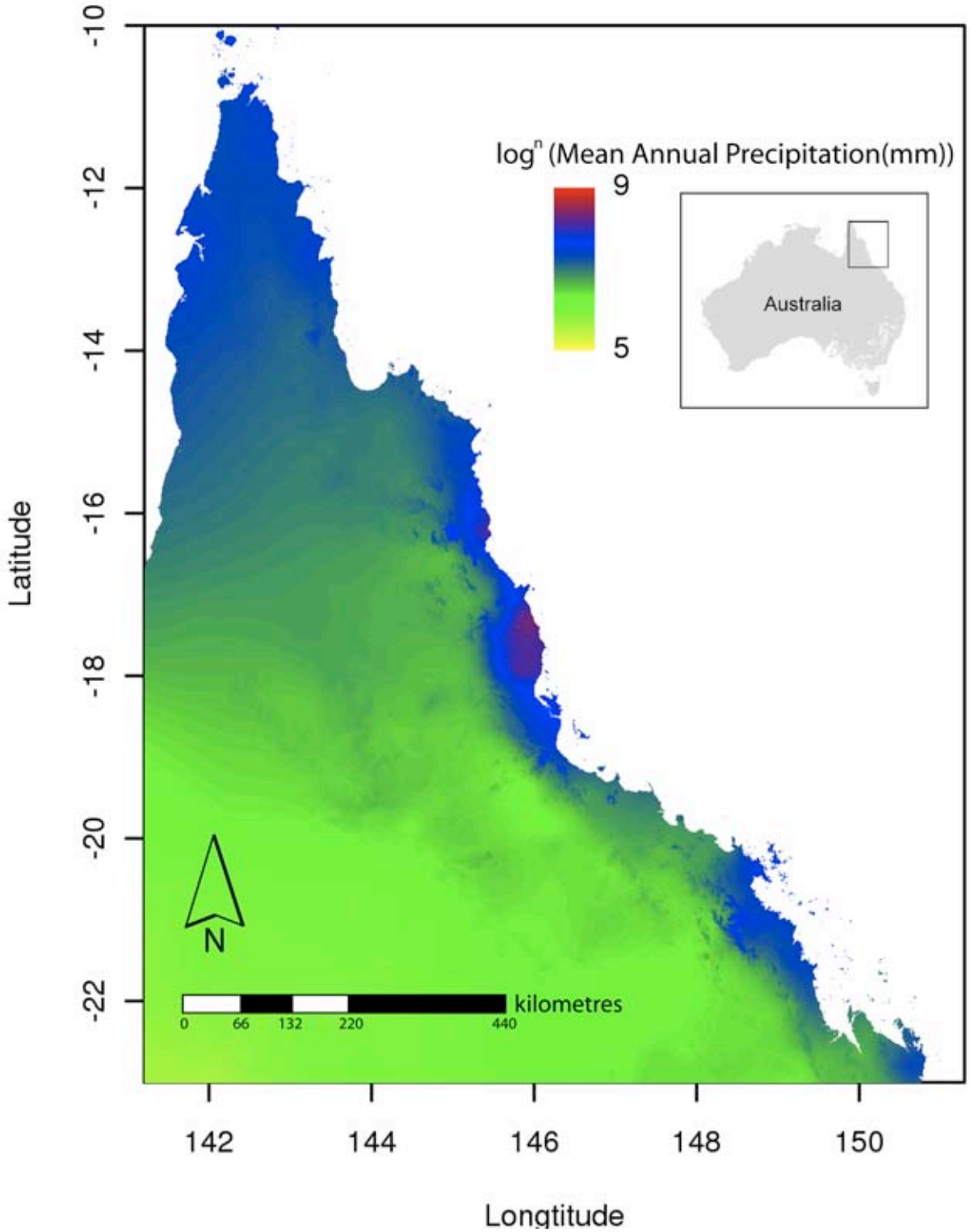

Figure 2.2. *Map of northern Queensland showing annual precipitation patterns. These are strongly influenced by orographic processes in the coastal ranges ad adjacent lowlands, and to a lesser extent by a latitudinal gradient of monsoonal influence. Rainfall in rainforest reaches a maximum in the central uplands of the AWT (red tones), and a minimum in the lowlands of the CQC (green tones). Values in this plot are logged due to the extreme variation in precipitation between the rainforest uplands and non-rainforest lowlands of the arid interior. Data are from BIOCLIM, see text for range of data values and reference.*

2.2 Vegetation, productivity and climate history

Driven by climate and lithology, the structure and floristics of forests varies substantially across the study region from complex mesophyll vine forests in the coastal lowlands to notophyll vine forest and microphyll fern thicket on high peaks and plateaus, though most surveys were conducted in simple to complex notophyll vine forests (Webb 1959; Queensland Herbarium 2011). Soils range from nutrient-poor granitics in the CYP, northern AWT and CQC to fertile volcanics in the central AWT (Webb 1958). Climate and soil differences are also likely to drive variation in Net Primary Productivity (NPP). NPP plays a key role in driving patterns of energy availability in natural systems, and hence in patterns of abundance and diversity (Gaston, 200, Hawkins *et al.* 2003b). In practice however, estimating available energy in a system can be challenging. Direct measures such as litter-fall may be difficult to relate to NPP (Shoo & VanDerWal 2008) so that climate surrogates are often used (Schuur 2003; Williams *et al.* 2010a). Advances in remote sensing technology however offer direct measures over broad scales that may overcome limitations in using climate surrogates (Huete *et al.* 2006). Here I used the remote-sensed Enhanced Vegetation Index (EVI) to estimate level of photosynthetic activity in the forest canopy as an index of NPP (details in the methods of chapter 5). Briefly, EVI patterns show rainforests to be highly productive relative to the surrounding habitats, and within rainforest, productivity decreases from lowlands to uplands (Figure 2.3). Seasonality of NPP is also apparent, with distinct variability especially in uplands (details in chapter 5). Gradients in vegetation structure in the study region are less marked than in systems that span greater elevational change (e.g. Terborgh 1977), but in general canopy height decreases with increasing elevation, while basal area increases (Hilbert 2010) so that lowland forests are characterised by fewer, larger emergents (see plate 1) while upland forests have more, smaller and more even-girthed canopy trees. The study area also experiences natural disturbance from cyclones (Turton 2008) such that forests have been described as a mosaic of different stages of recovery from storm damage, particularly in the coastal lowlands (Webb 1958). Lowland forests in the CQC and AWT in particular have also been extensively cleared for agriculture, restricting most remnants to a zone above ~250 asl (Hilbert 2010). In contrast mid-slope to upland forest remains relatively intact, apart from local clearing and selective logging (Stork & Turton 2008), as has lowland rainforest in the Iron Range on Cape York Peninsula. Sampling in this study was focussed in large patches and areas of contiguous forest to limit as much as possible the confounding influence of current habitat area on patterns of assemblage structure and diversity.

In north-eastern Australian rainforests, the cycles of global cooling and drying which characterised the Plio-Pleistocene have strongly shaped the distributions of a diverse fauna (Williams and Pearson

1997; Schneider *et al.* 1998; Moritz 1999; Kershaw & Bretherton 2007). Many species are now restricted to the cool and moist upland forests, with warm tropical and subtropical lowland forests in general supporting a less-diverse assemblage of widespread species (Williams *et al.* 1996; but see CYP below). The region is also bisected by a number of biogeographic barriers (Figure 2.4) formed by interactions of climate history, fire and vegetation (Moritz *et al.* 2005). The AWT captures the entire global distribution of 12 endemic bird species, and a range of endemic subspecies. To the south drier savanna habitats of the Burdekin-Lynd barrier (Keast 1961) separate temperate and subtropical montane forests in the Central Queensland Coast bioregion (CQC). These forests support a less diverse fauna at the northern limits of the ranges of a different suite of temperate rainforest species, including an endemic bird (the Eungella Honeyeater *Lichenostomus hindwoodi*). To the north, across another dry gap at the Coen-Cooktown barrier (Tate 1952), warm tropical and monsoon rainforests of the Cape York Peninsula bioregion support a contrastingly diverse lowland fauna with affinities to Papua New-Guinea, including an endemic bird species (Frilled Monarch, *Arses lorealis*) and a number of endemic species and subspecies in other groups (Kikkawa & Pearse 1969; Keast 1981; Flannery 1990).

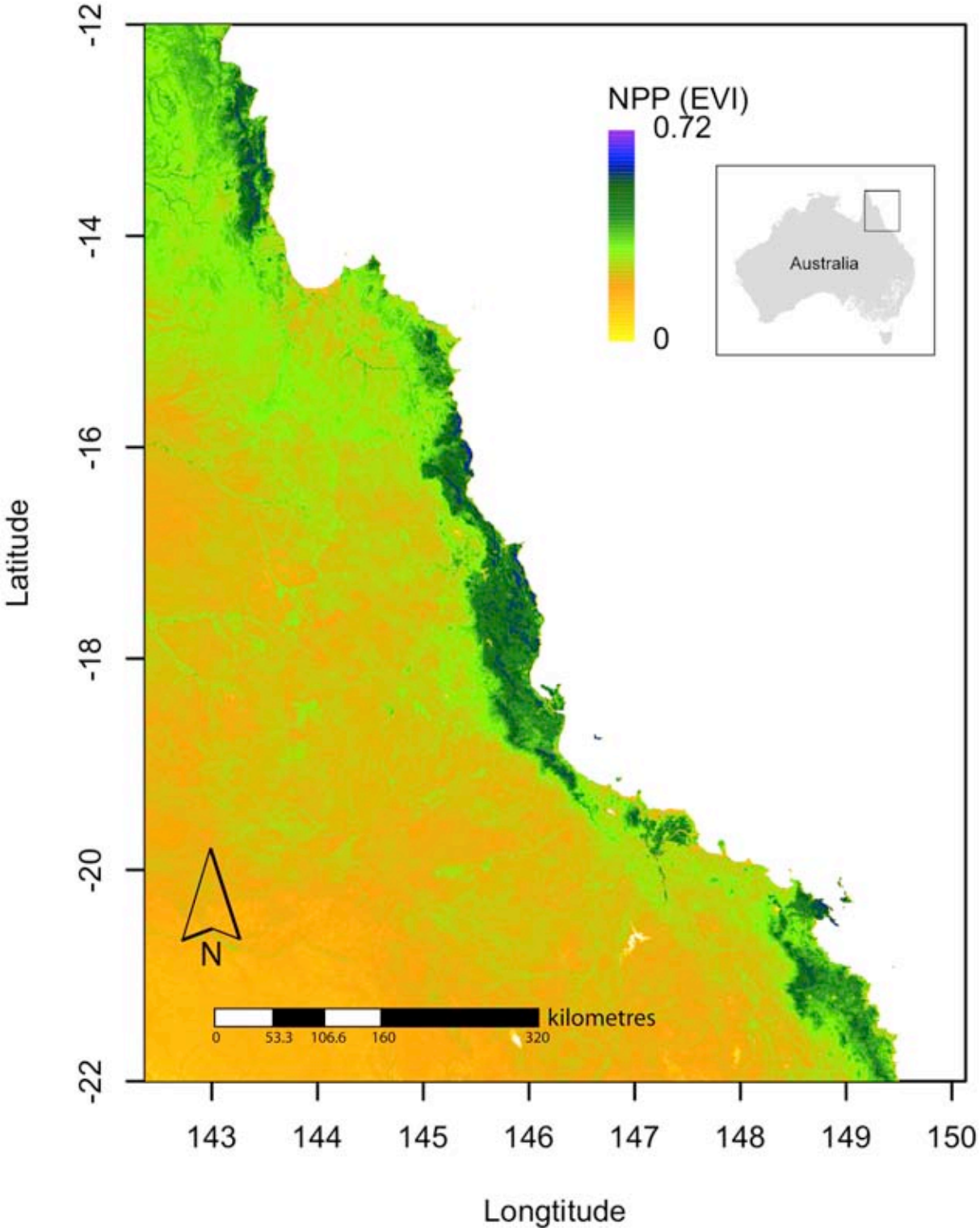

Figure 2.3. *A map of northern Queensland showing the distribution of NPP estimated with the remote-sensed Enhanced Vegetation Index (EVI). Productive rainforests are restricted to the high rainfall areas along the eastern slopes of the Great Dividing range, with maximum NPP reached in the lowlands and declining with increasing elevation. NOTE: As it is an index of NPP, EVI itself does not have any associated units.*

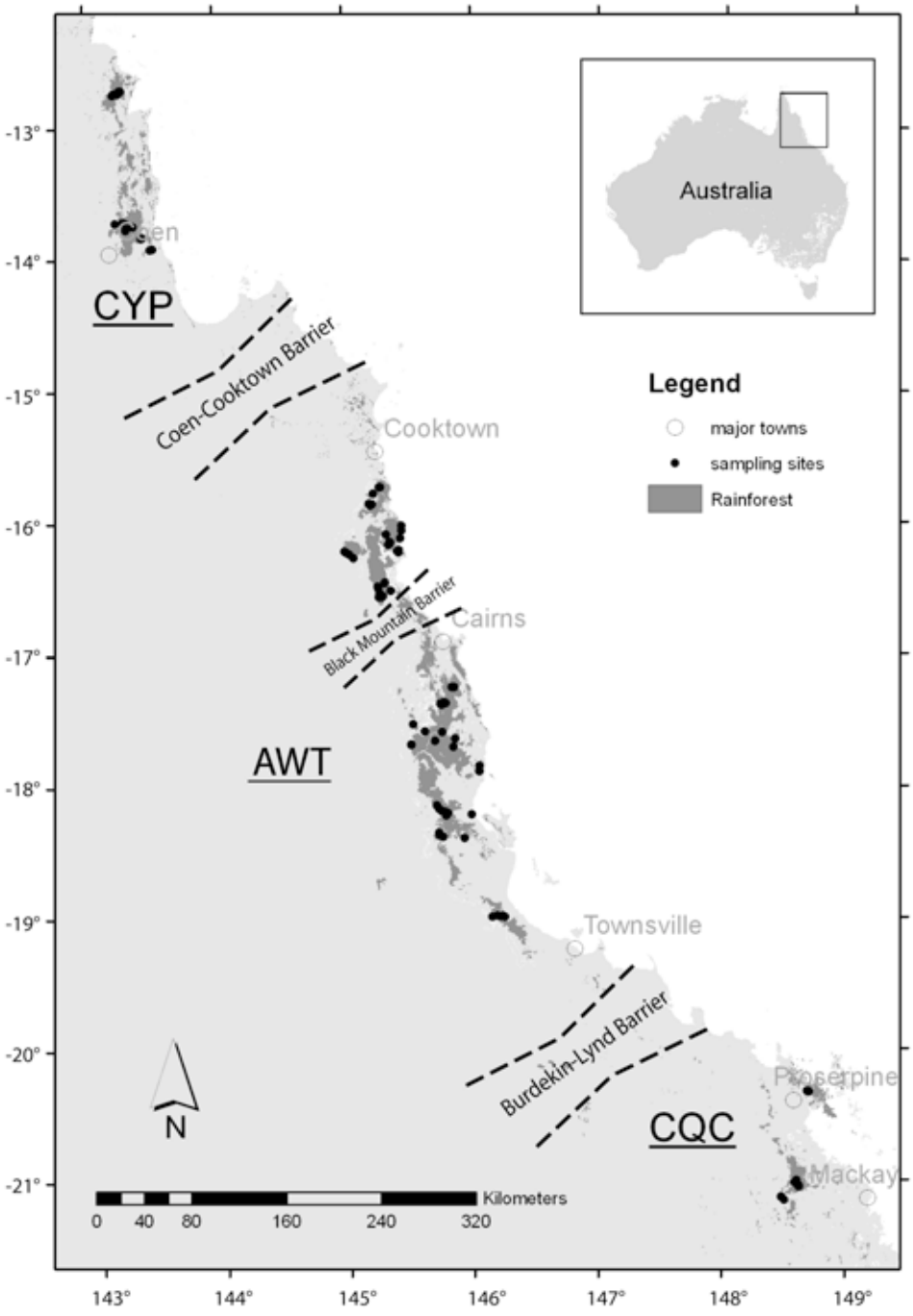

Figure 2.4. *A map of northern Queensland showing the geographic distribution of rainforests and sampling locations. Areas dominated by rainforest vegetation are shaded in dark grey. Sampling sites are indicated with filled circles and major towns with empty circles. The dotted lines indicate major biogeographic barriers (see text for details).*

2.3 Future climate predictions

Anthropogenic global warming is poised to influence the structure of a complex array of rainforest bird assemblages across this region. Mean annual temperature is projected to increase between 0.8 to 4.3°C between now and 2070 (Suppiah *et al.* 2007). Greater uncertainty surround predictions of rainfall patterns, but best estimates are that annual rainfall will increase in Cape York but become

less seasonal, while further south seasonality is expected increase, though rainfall overall decreases. Overall precipitation is expected to change by between -22 and +7% by 2070. Previous studies have predicted a high level of vulnerability, particularly to temperature changes, among upland endemic rainforest birds in the Australian Wet Tropics (Williams *et al.* 2003; Hilbert *et al.* 2004), but impacts on the avifauna of neighbouring rainforests is largely unknown. In addition, increased CO_2 concentrations and changed rainfall regimes may drive shifts in the distribution of rainforest habitats in northern Australia with global warming (Hilbert *et al.* 2001; Bowman & Murphy 2010).

2.4 Bird data collection

Here I adopted a standardised method for surveying diurnal rainforest birds that has been widely applied in the AWT by researchers at the Centre for Tropical Biodiversity and Climate Change CTBCC (Shoo *et al.* 2006; Williams & Middleton 2008; Williams *et al.* 2010a). Surveys were conducted in both the summer ("wet") season (October to May) and winter ("dry") season (June to September). Sampling sites have been established at representative sites across altitudinal and latitudinal gradients in the rainforests of the study region (Williams 2006), in addition to which I added new locations in under-sampled lowland forests, and in the neighbouring rainforests of CYP and CQC described above (locations of sites shown in Figure 2.4). These sites were arranged at 200-m intervals across the elevational gradient in rainforest (Figure 2.5). Survey transects began at points located 200m apart along 1 km sampling arrays ("sites")- and proceeded perpendicularly (where possible) away from the main line of the array through the forest for 150 m, timed for completion in 30 minutes. Briefly, the diurnal bird survey protocol used in previous investigations in this system consisted of audio-visual surveys through rainforest between 0600 and 0930h to coincide with peak calling activity, during which all birds seen or heard were identified to species and recorded, excluding those flying overhead or through the site. In addition I also applied a distance sampling method in order to account for variation in detectability between species, sites and surveys that may bias indices of relative abundance, described in detail in chapter 3. All fieldwork was conducted under Queensland Department of Environment and Resource Management research permit numbers WISP04061506 and WITK04061406.

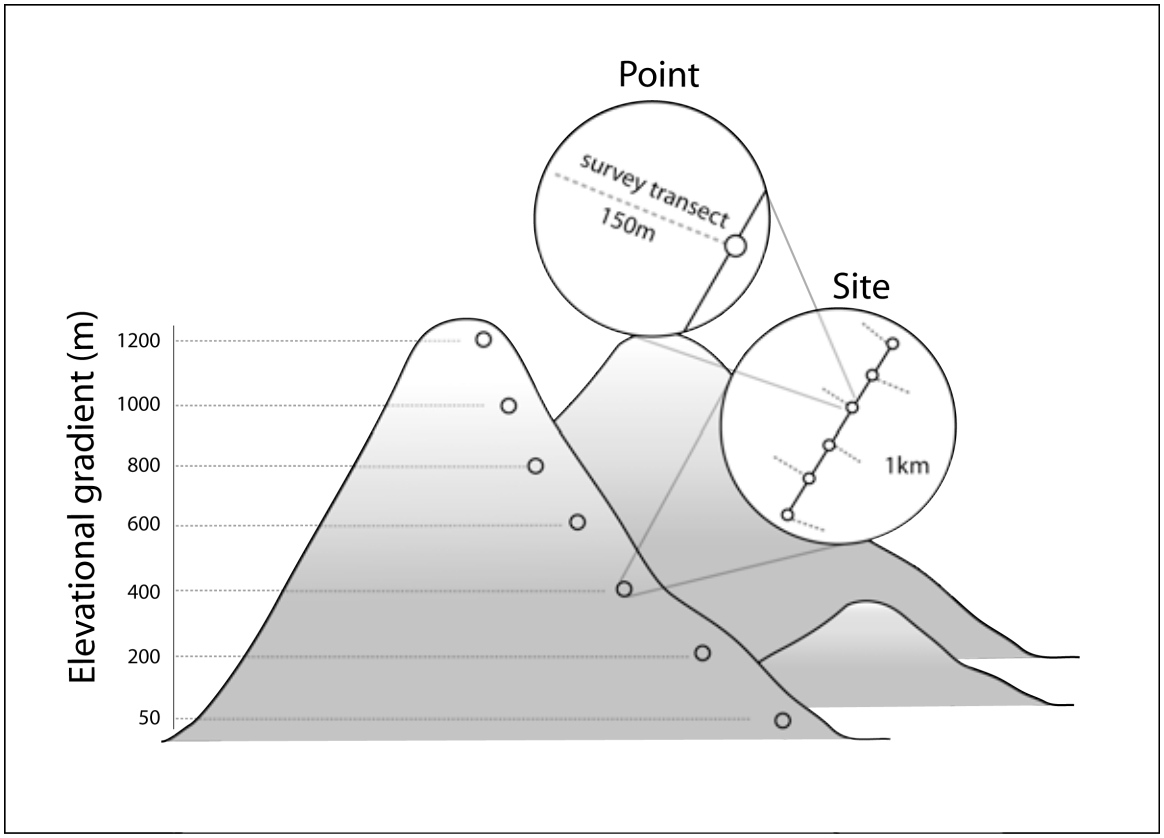

Figure 2.5. *Schematic diagram of the arrangement of sampling sites at 200 metre intervals across the elevational gradient in rainforest within the study regions. Within each site, survey points were located at 200 metre intervals along a 1km transect giving 6 points (excepting in a small number of locations where topography dictated a 500 metre array). At each point, 150m perpendicular bird survey transects were walked on each visit.*

Chapter 3. Species, weather and habitat: factors influencing detectability and density estimation of tropical rainforest birds

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Article type: Full Length Article:

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[1]Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia.
[2] Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, St Andrews KY16 9LZ United Kingdom and Centro de Estatística e Aplicações da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal.
[3] School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

"Using just the count of birds detected (per unit effort) as an index of abundance is neither scientifically sound nor reliable... It is necessary to adjust study counts by the detection probability"

--(Burnham *et al.* 1980)

Plate 3. *The Rufous fantail (*Rhipidura rufifrons*) is a species of small-bodied, understory insectivore often detected only by their call.*

3.1 Abstract

Deriving accurate estimates of density for animal communities in diverse tropical rainforest ecosystems is a difficult task. Widely applied indices of relative abundance do not control for variation in the probability of detection between species, locations, or times. These sources of variation are important because they can bias estimates of density such that underlying ecological processes are difficult to infer. Distance sampling can be used to correct for detectability, but requires some understanding of factors that can modify detection probability. This is particularly true in rainforest, where dense vegetation and diverse assemblages complicate sampling, and information is lacking about factors affecting application of distance sampling methods. Rare species also present a challenge, as data may be too scarce to fit detection functions. Here I present an analysis of distance sampling data collected for a diverse tropical rainforest bird assemblage across a broad elevational and latitudinal gradient in North Queensland, Australia. I assessed the influence of various factors on one useful parameter used in density correction, Effective Strip Width (ESW). Body size and species exerted the most important influence on ESW, with larger species detectable over greater distances than smaller species. Secondarily, wet weather and high shrub density decreased ESW for most species. ESW for several species also differed between summer and winter surveys, possibly as a result of seasonal differences in calling behaviour. Though adding distance sampling to a field protocol proved logistically intensive, large differences in ESW between species showed that correction for detection probability is necessary to obtain accurate density estimates for each species. Further work modeling detectability as a function of species characteristics including body size and call characteristics may be useful in developing a calibration for non-distance sampling data, reducing the logistical demands required by distance sampling. Such an approach will also be useful for estimating densities of rare species where detections are too scarce to fit detection functions.

3.2 Introduction

Worldwide many bird species are in decline (Thomas *et al.* 2004; Schwartz *et al.* 2006). This problem is particularly acute in the montane tropics, where high levels of diversity and endemism are coupled with increased vulnerability to changes in both climate and land use (Williams *et al.* 2003; Jetz *et al.* 2007; Sekercioglu *et al.* 2008). Detecting and understanding changes in population size and distribution associated with species decline is crucial to planning appropriate conservation strategies, and depends on accurate information on patterns of density in space and time (Bibby *et al.* 2000). High diversity and challenges of accessibility can make this essential information problematic to collect in the tropics (Karr 1981; Sodhi *et al.* 2004). There is thus a pressing need for efficient methods for collecting accurate information about the patterns of population density in diverse tropical rainforest bird assemblages. As a complete census of animal populations is typically unachievable in natural systems (Buckland *et al.* 2008), most monitoring programs and ecological studies use fixed area or effort counts that generate some "index of relative abundance" (White 2005; Johnson 2008). While such indices are popular (Rosenstock *et al.* 2002) and relatively simple to apply (Schwarz & Seber 1999) comparison between different places or times are only valid to the extent that the probability of detection does not vary between these (Rosenstock *et al.* 2002). In practice however detection probability may vary widely between individuals, survey locations or times (Burnham & Anderson 1984; Nichols 1992). Sources of variation in detectability in incomplete counts thus have the potential to bias estimates of density such that underlying ecological processes are difficult to infer (Norvell *et al.* 2003; White 2005; Buckland *et al.* 2008).

Since early efforts such as the limited-width strip transects of Emlen (1977), a variety of methods have been proposed to estimate the difference between the detected and total population in a survey area (for reviews see; Schwarz & Seber 1999; Buckland *et al.* 2008)). Distance sampling is a widely employed approach to the problem of estimating detection probabilities (Buckland *et al.* 2001) which uses the distribution of distances between the observer and detected individuals to model the decay in detection rate with increasing distance (Burnham *et al.* 1980), referred to as the detection function g(x). A well developed theoretical basis (Buckland *et al.* 2001), and freely available software (Thomas *et al.* 2010) including the capability to include covariates in the detection function model (Marques & Buckland 2003), has likely contributed to its widespread adoption. The detection function can be used to estimate the detection probability, or equivalently the effective strip (half-)width (ESW). This is defined as "the transect half-width at which the total count over the area L×(2×ESW) would be on average equal to the observed count (where L =

survey length)" (Thomas *et al.* 2010). Distance sampling relies, however, on a number of critical assumptions, including a 100% probability of detection along the transect midline; accurate measurement of distances; transects that are distributed randomly in the environment; and the detection of all individuals before they move relative to the observer (Buckland *et al.* 2001). Whereas surveys in open environments and of large taxa may satisfy these underlying assumptions (Thomas *et al.* 2002), in more complex environments and with more cryptic taxa, some care must be taken to ensure that this is the case (Rosenstock *et al.* 2002), and that the influence of additional factors is taken into account (Johnson 2008).

Four main classes of factor can influence detection probability: (1) the characteristics of the objects being detected (e.g., size of individuals and characteristics of detection cues); (2) the conditions of the survey (e.g., weather, time of year); (3) the characteristics of the location (e.g. habitat structure, density of trees); and, (4) the characteristics of the observer (e.g. experience, training). In audio-visual bird surveys for example, the visual detection function tends to decrease more steeply than the aural (Marques *et al.* 2007). This effect may be magnified in closed-forest bird surveys as visual cues rapidly attenuate in their characteristic low light conditions and dense foliage (Karr 1981; Waide & Narins 1988). Consequently, audio cues can make up more than 80% of total detections in some situations (Scott *et al.* 1981). This effect also necessitate some care in analysis, as differences between cues also influence the distribution of distances from the transect in the samples, for example, visual detections may cluster close to the observer (Marques *et al.* 2007). In this case, care must be taken to avoid the fitting of a "composite" detection function where data are combined across cues.

Detection probability can also vary markedly between species (Emlen 1971; Boulinier *et al.* 1998; Diefenbach *et al.* 2003) for example as a result of call structure, (Waide & Narins 1988; Schieck 1997), call volume and singing rate (Best 1981; Gibbs & Wenny 1993; Alldredge *et al.* 2007b), and body size (Waide & Narins 1988). Clusters of individuals may also be more detectable than single individuals (Thomas *et al.* 2002), so that differences in flocking behaviour can drive differences in detection probability. Cue production and hence detectability can also be influenced by survey weather (Robbins 1981; Buckland *et al.* 2001; Lindenmayer *et al.* 2009), and season (Wilson & Bart 1985; Gottlander 1987; Selmi & Boulinier 2003) and bird reproductive status (Gibbs & Wenny 1993). High bird diversity and abundance during counts can also reduce individual detection probability by "swamping" the observer (Bart & Schoultz 1984; Simons *et al.* 2007) and may also increase errors in distance estimation (Buckland *et al.* 2008). Detection probability may vary between habitats of different density due to the attenuation of visual and audio cues by intervening

vegetation (McShea & Rappole 1997; Alldredge *et al.* 2007c; Pacific *et al.* 2008), or by differences in topography (Dawson 1981). While I analysed data collected by a single observer in this study, differences in observer audio or visual acuity (Emlen and Dejong, 1992; Sauer *et al*. 1994) and experience (Diefenbach *et al.* 2003; Sauer *et al.* 1994) can also be a source of variation in detection probability.

A sustained program of field sampling over recent decades has established the Australian Wet Tropics among the better-studied topical rainforest systems. Extensive count data on birds in particular has facilitated a range of ecological analyses (Williams *et al.* 2010a, Williams & Middleton 2008). High levels of diversity and endemism in the avifauna of this region have contributed to the listing of the major rainforested mountain ranges and adjacent lowlands in the study region among Australia's Important Bird Areas (Dutson *et al.* 2009). Recent projections of climate change impacts on distributions (Williams at al. 2003) and populations (Shoo & Williams 2005) of upland endemic species in particular have highlighted the importance of understanding and monitoring patterns of density in these species in space and time (Shoo *et al.* 2005). However, studies to date have relied on estimates of relative abundance only, so that potential biases in detectability between species, sites and surveys remain unknown (Williams *et al.* 2010a). Here I identify the important covariates of detection probability and sources of error in this system. This will enable estimation of absolute density controlling for differences in detection probability between species, surveys or sites. In doing so, I also take the first steps towards developing a calibration of Akaikedetectability which could be applied to non-distance sampling data. Not only will such a calibration be valuable for ecological research and conservation management in this region, but it will have application in efficient monitoring of diverse rainforest bird communities elsewhere.

3.3 Methods

3.3.1 Study region

Data collection and analysis for this chapter was focussed in the rainforests of the Australian Wet Tropics bioregion (AWT) between 15˚45'32.69"S 145˚ 1'53.87"E and 19¬18'0.65"S 146˚ 9'41.17"E). A full description of the geography, climate and vegetation is given in chapter 2 above. Briefly, rainforests in the AWT occur on coastal ranges of the Great Divide and adjacent lowlands, giving a broad elevational range (200m to 1600m asl). The structure and floristics of forests varies across this gradient from complex mesophyll vine forests in the coastal lowlands to notophyll vine forest and microphyll fern thicket on high peaks and plateaus, though most surveys were conducted

in simple to complex notophyll vine forests (Webb 1959). Based on modeled climate surfaces from BIOCLIM (part of the ANUCLIM 5.1 software (Houlder *et al.* 2000)) climate of the study region is characterised by warm average temperatures (lowlands: 23.33 ˚C uplands: 19.16 ˚C) and high rainfall (lowlands: 2510 mm, uplands: 2757 mm) concentrated in the summer.

3.3.2 Survey locations

I adopted the standardised method for surveying rainforest birds (also described in chapter 2) that has been widely applied in the AWT (Shoo *et al.* 2006; Williams & Middleton 2008; Williams *et al.* 2010a) with the addition of distance sampling method described below. The locations of the sampling sites within the AWT are shown in detail Figure 3.1, and have been established at representative locations across elevational and latitudinal gradients in the rainforests of the study region (Williams 2006). As in many tropical bird surveys though, dense vegetation and steep terrain make strictly random placement of transects difficult (Dawson 1981; Karr 1981) necessitating the use of roads and tracks for access. While non-random, these locations were used for consistency with the existing data base, and are considered representative of forests and environmental space regionally (Williams *et al.* 2010a). Transect placement with respect to roads versus contiguous forests could however influence detection probability due to changes in species behaviour or vegetation structural features (Laurance *et al.* 2008; Marques *et al.* 2010). The small number of surveys along roads and tracks in this study precluded explicit analysis of the effects of transect placement, and it remains an issue in rainforest surveys to be explored further.

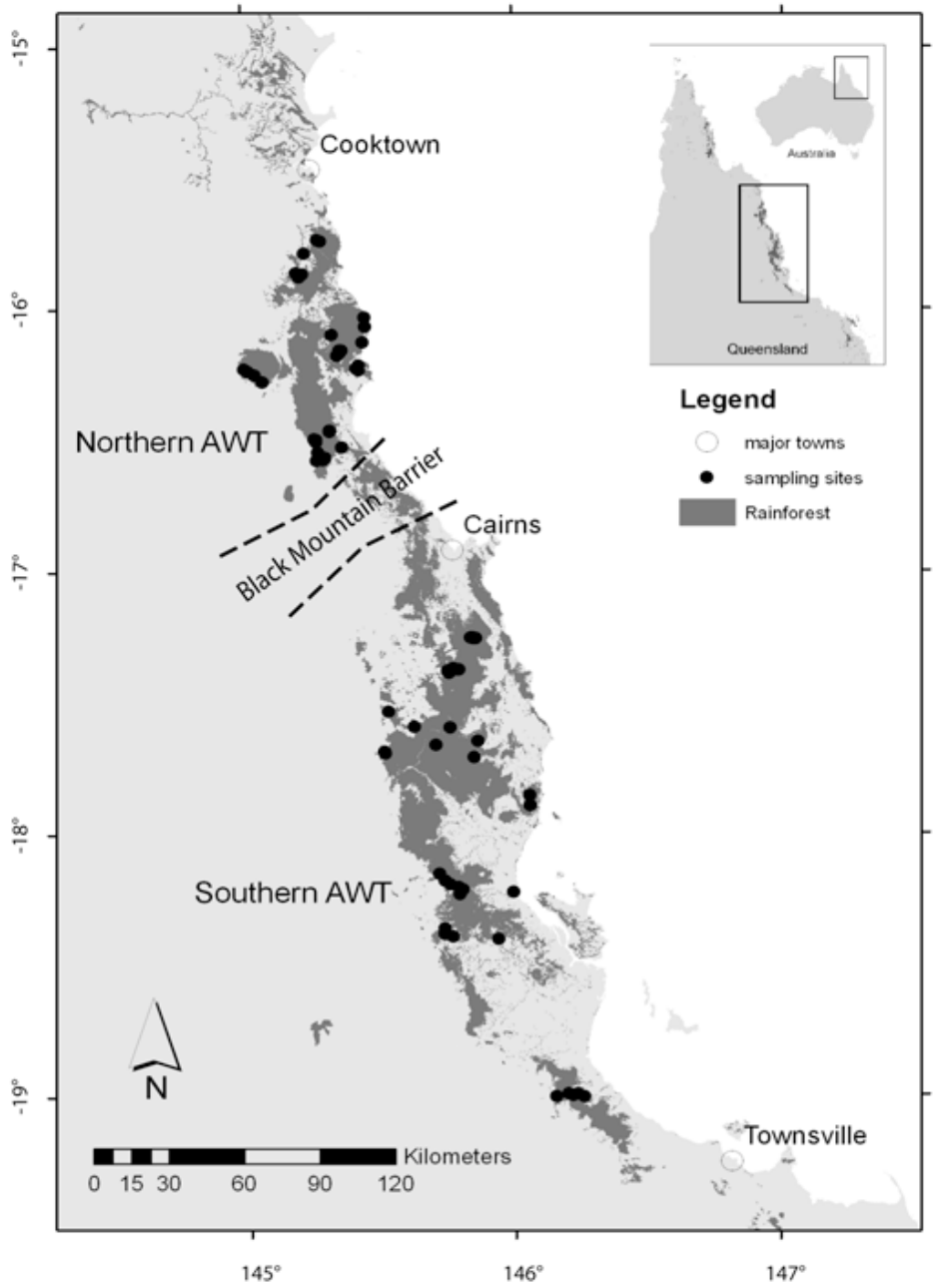

Figure 3.1. *Locations of the sampling sites in the AWT in relation to the major areas of montane rainforest. Sites are positioned at approximately 200m intervals across the elevational gradient, and each contains an array of either 3 or 6 sampling points arranged at 200m intervals along the main site axis. Full descriptions of the study area and the sampling design are given in chapter 2.*

3.3.3 Distance sampling

Perpendicular distance from the transect midline to each sighting was measured to the nearest metre using an Opti-logic (TM) LH400 Laser Range finder. Distances were also estimated to all individuals detected aurally from call to the best of the observers ability (see schematic in Figure 3.2). Distances to unseen calling individuals closer than 40 m were later binned into 10 m intervals, and those further away into 20 m intervals to reflect the tendency for error rates to increase at large

distances (Alldredge *et al.* 2007c). Detections greater than 100 metres from the transect where recorded during surveys, but later excluded from analysis (see below). Group size was also recorded where appropriate, though where membership of groups was difficult to assign individuals were treated as single objects. In the case of mixed-species flocks, conspecifics were treated as members of discrete sub-groups for simplicity.

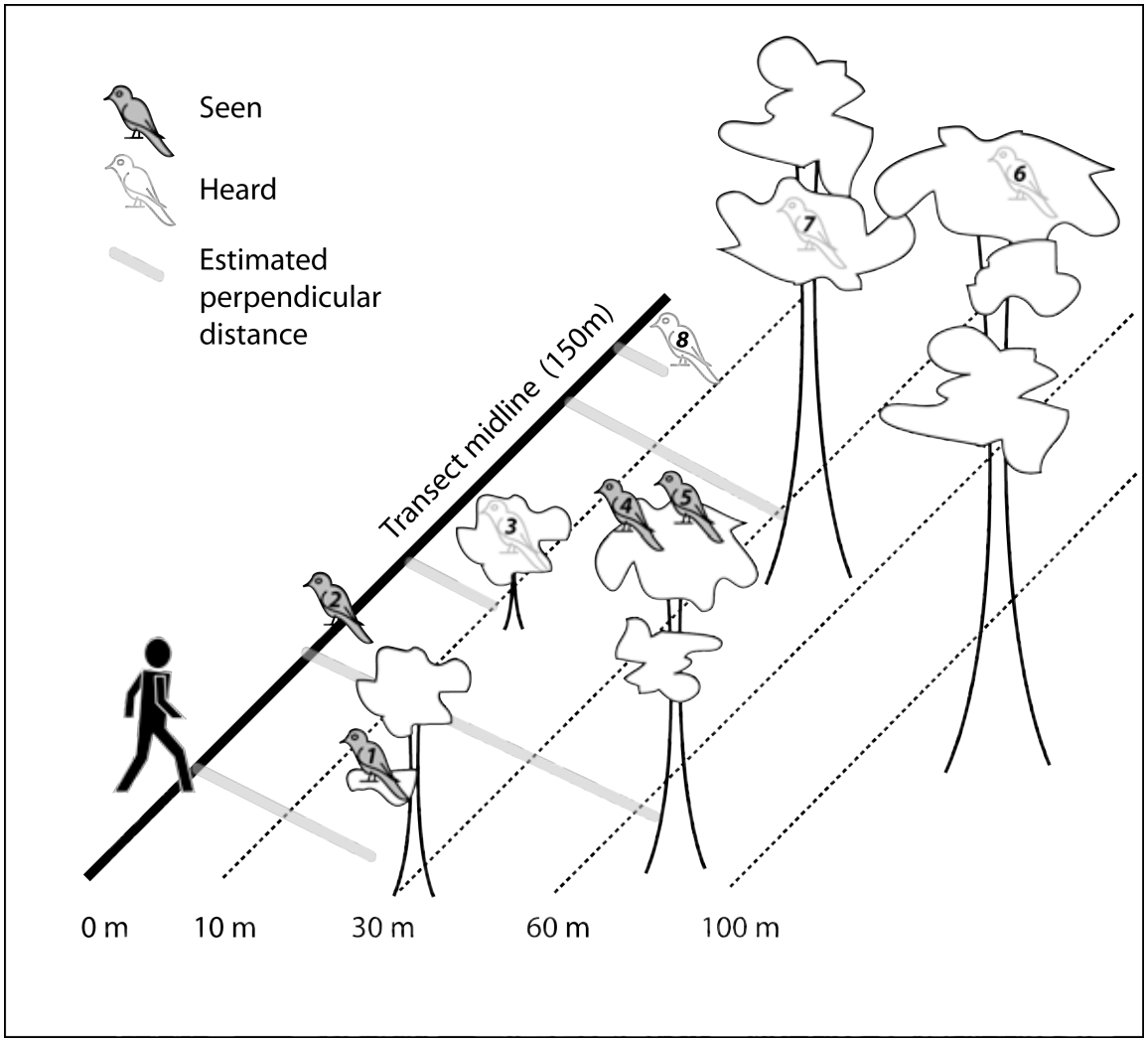

Figure 3.2. *Schematic of the audio-visual bird survey method with distance sampling. Transects were walked for 30 minutes, and the distances to all birds seen or heard were estimated or measured directly where possible. 1) Distances to birds seen close to the transect were measured with a laser rangefinder. 2) Birds on the transect midline were recorded at zero metres before they move to avoid the observer. 3) Distances to birds calling from concealment within 40m of the transect were estimated, later binned to 10m intervals. 4) and 5) A single distance to groups of birds was measured or estimated to the group centre, and number of individuals counted or estimated. 6) Birds heard calling at distances estimated to be greater than 100m were excluded from later analyses, as distance estimation becomes unreliable at larger distances. 7) Distances to birds estimated to be calling from between 50m and 100m were later binned in 20m categories. 8) Distances to birds heard calling from close to the transect well ahead of the observer were estimated accordingly, and later confirmed visually were possible. Estimated heights to seen individuals were also recorded.*

3.3.4 Weather, habitat and interference

Air temperature was recorded, and overall scores assigned for levels of wind, rain, wetness of the environment, and background noise for each transect. Wetness here refers to the amount of moisture in the soil, on leaf surfaces and dripping from the canopy, and is estimated independently of rain. Background noise came from wind, rain, canopy drip, running streams, as well as from calling birds and insects such as cicadas. The scoring system employed is shown in appendix table 3.2. The total number of individuals and total species count per transect were also calculated to give a survey score for bird species diversity and abundance. Data on the vegetation structure at each site was also collected using a modified Braun-Blanquet methodology (Williams *et al.* 2002) to quantify the percentage foliage cover in the shrub and canopy layers as an index of the density of vegetation in each layer. Briefly, habitat structure was described in three plots at each of three points on each 1km site array. At each plot foliage density within a 5 m radius was estimated in five vertical strata (ground cover 0-1 m; low shrubs 1-2 m; shrubs 2-5 m, sub-canopy, and, canopy) on an eight-point scale (0, absent; 1, present (~1% cover); 2, ≤ 5%; 3, 5-25%; 4, 25-50%; 5, 50-75%; 6, 75-95%; 7, 95- 100%). These measurements of vegetation density were used to derive estimates of foliage density for the canopy and shrub layer, and an estimate of vegetation complexity across all strata at each site.

3.3.5 Distance Analysis

I used the Distance software program version 6 (Thomas *et al.* 2010) to characterise the relative influence of the survey and habitat factors described above on the detection of rainforest birds, as a precursor to estimating densities for each species. While 60 or more observations are recommended for reliable inferences (e.g. Buckland *et al.* 2001)), there are numerous examples of published studies with lower sample sizes (e.g. Buckland 2006)) and here I used a lower threshold of 35 individuals for further analysis. This is a compromise between including sufficient distances to fit an accurate detection function, and including more species across which to compare factor effects. Distance frequency histograms for each species were inspected and raw data binned to minimise the effect of heaping (see distance Glossary, Appendix 3.2). Distances were also truncated at 100 metres (≈10% of the distances) to avoid problems in fitting the tail of the detection function (Buckland *et al.* 2001). Akaike's Information Criterion adjusted for small sample sizes (AICc) was used to select the most parsimonious model from all possible combinations of Uniform, Half Normal and Hazard Rate models with Cosine, Simple Polynomial and Hermite Polynomial adjustment keys, except in the case of the species models, where I constrained the models to a Half Normal function with Cosine adjustment to achieve consistent convergence (see glossary in Appendix 3.1. And Buckland *et al.* 2001 for explanation of Distance analysis terminology). Data

across all species, surveys and sites were then analysed with the Multiple Covariates Distance Sampling (MCDS) analysis engine (Marques & Buckland 2003) to compare the relative contribution of the factors (covariates).

Cue type, body size, species and cluster size were added as covariates in the MCDS analysis engine to examine the effect of object characteristics. Cue type compared audio detections against those from visual detections. The body size covariate compared small (<10g), medium (10-50g) and large (>50g) bodied species, based on mean weights from the Handbook of Australian, New Zealand and Antarctic Birds (Marchant & Higgins 1990; Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Higgins, Peter, & Steele 2001; Higgins & Peter 2002; Higgins *et al.* 2006). Species, based on the taxonomy in (Christidis & Boles 2008) was also included as a factor covariate. Cluster size was analysed as a continuous covariate based on the observed group sizes from survey data. Covariates for temperature, rain, wind, wetness, and noise were included as a binary factor of either a high or low score for each survey relative to the mean for that factor. Abundance (mean: 48.78 individuals, max: 93) and diversity (mean: 19.4 species, max: 31) can be high in the study region, warranting their inclusion as covariates to check for potential observer swamping. The effect of site habitat structure was examined by including elevation as a binary covariate (upland versus lowland), as well as shrub and canopy layer foliage density scores for each site (high and low density), and an overall complexity score as the sum of foliage densities across all strata. For all covariate comparisons an improvement in model fit was assessed relative to the distance-only ("no covariates") model using AICc.

As the MCDS analysis implemented in distance only allows for covariates to influence the scale of the detection function and not its shape (Marques & Buckland 2003; Buckland *et al.* 2004), I also divided the data into subsets for each factor level and fitted separate detection functions. These subsets were then analysed for each species separately to quantify the effect of interaction between species and factors on ESW (defined above). A significant factor effect on ESW for a species was defined as non-overlapping 95% confidence intervals between the estimates of ESW for each factor level. Non-overlap of 95% confidence intervals is a conservative test of difference (Payton *et al.* 2003), which I considered an appropriate gauge of factor influence in this context of multiple species comparisons. Model selection based on AICc was repeated for each factor level individually to account for any changes in the scale or shape of the detection function, and a combination of AICc and visual inspection of the fit of the detection function was used to select the best-fit models in each case. Overall factor effects were assessed using Mann-Whitney U-tests of the differences in ESW between treatments across all species. Together these approaches yield a

series of overall comparisons of each factor treatment effect on ESW, and a series of pairwise comparisons of the effect on each species. yields a series of overall comparisons of each factor treatment effect on ESW, and a series of pairwise comparisons of the effect on each species. All additional statistical tests not performed in the Distance software were carried out using the "R" framework for statistical analysis, version 2.13.1 (www.r-project.org).

3.4 Results

A total of 284 distance sampling surveys in the AWT yielded 10,341 bird records across 41 sampling sites. Of these, 8,698 were of individuals, while 1,220 records belonged to clusters. The most often detected species was the Yellow-spotted Honeyeater *(Meliphaga notata,* 608 records*)*, and the rarest was the Russet-tailed Thrush *(Zoothera lunulata*, 6 records), with a mean of 46.23 records per species. A total of 70 species were recorded, 52 of which had 35 or more records which was considered sufficient for further analyses. Model key function, adjustment terms, and estimates of the ESW, density and mean cluster size across all sites and surveys for each species are provided in Appendix Table 3.3.

3.4.1 Characteristics of detected objects

Pooling across all species, surveys and sites, the best performing model in terms of AICc was one incorporating species as a factor covariate (Table 3.1, model 1, AICc = 30995.5), substantially better than that for the basic model without covariates (Table 3.1, model 4, AICc = 33223.65). This is driven by pronounced variation between ESW seen when each species is analysed separately (Figure 3.3). ESWs for species ranged from 11.62m for the quiet 12 g Atherton Scrubwren *(Sericornis keri)*, through 33.64 m for the 10 g and vocal but cryptic Rufous fantail (plate 2) to 100m for the large (287 g) and vocal Pied Currawong *(Strepera graculina)*. For species commonly detected at distances greater than 100 metres (e.g. Black Butcher bird *Cracticus quoyi,* 156 g) ESW clustered at this 100 m truncation limit of the data, with no variation around the estimate, indicating a high probability of detecting all individuals available within this distance. A histogram of all ESWs (Figure 3.3, inset) showed however that ESWs for most species cluster within 30 to 60 metres (mean = 49.08m) and that variation around this mean was substantial (s.d. =20.24m).

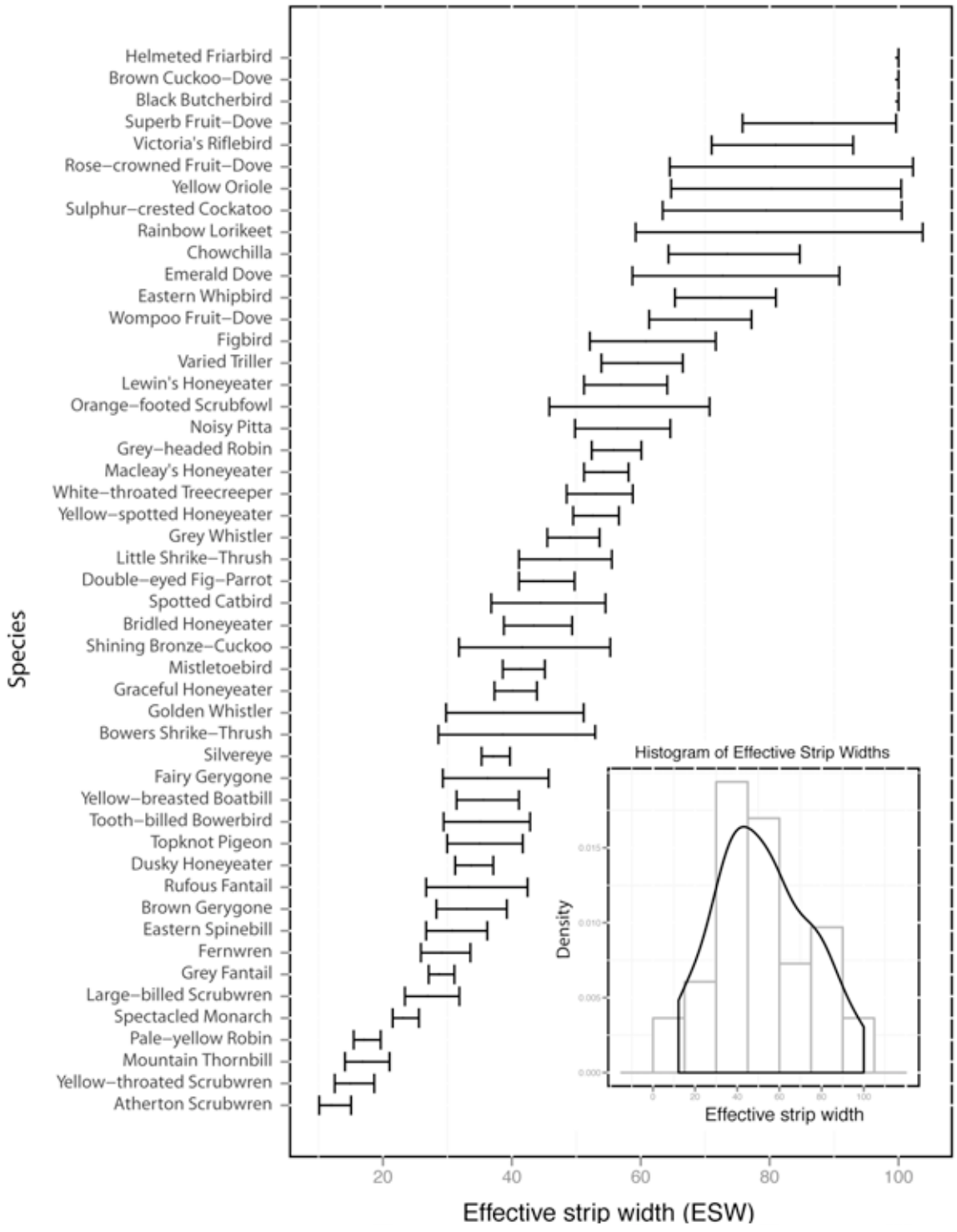

Figure 3.3. *The distribution of estimated Effective Strip Widths (ESW) across species of rainforest birds in the study region. Species are ranked in order of their estimated ESW from Distance analysis (Thomas, 2010). Error bars are upper and lower 95% confidence intervals around the estimate. The histogram (inset) illustrates the distribution of ESWs with respect to the mean value, showing the substantial variation between species which would not be captured by a traditional fixed-width transect.*

Body mass is indicated as an important driver of species' ESW differences (Table 3.1, model 3, AICc = 32148.7). In a comparison of the distance histograms and fitted detection functions produced by Distance analysis for each of three size classes examined (Figure 3.4, left column), smaller species (Figure 3.4a) show a uniform decay over shorter distances, and no detections at greater distances, while larger species (Figure 3.4c) show the pronounced "shoulder" and a long tail characteristic of distance sampling data, suggesting limited decay in detection probability over short distances. Medium-sized species show an intermediate response (Figure 3.4b). Cue type however is suggested as a more important covariate than body mass (Table 3.1, model 2, AICc = 31321.71) and comparing the distance histograms for audio and visual records, (Figure 3.4, right column) Effective Strip Widths tend to be much larger for audio records (mean ESW difference: 21.64m, s.d.:14.85m). Importantly there was also an apparent deficit of detections at small distances when comparing histograms for cue types (indicated by the arrow in Figure 3.4d), such that probability of detection at the transect midline was less than 1 for audio cues. There was also evidence of surplus of detections between 10 and 20 metres, a long flat shoulder over intermediate distances, and a long tail over larger distances. In contrast the visual cue data (Figure 3.4e) show no deficit of small distances, a steeper decline over shorter distances, few detections at intermediate distances, and none at large distances. As visual records are scarce in rainforest I prioritised visual confirmation of any calling bird within range, and audio detections of birds that were then sighted were included as visual records. As noted above this can create problems in distance analysis as the pooling of data from both cues could create a "composite" detection function (Marques *et al.* 2007). However, while density based on audio data may be biased low by this violation of the assumption of certain detection on the survey midline, the histogram of combined audio and visual data (Figure 3.4f) removes the apparent deficit of detections at small distances. I thus take this composite detection function to be an adequate representation of the true function across both cue types in this study, and use combined data in all subsequent analyses. Finally, perhaps because clusters represented a small proportion of records overall (<10%) they proved to have little influence on ESW in this study, both overall (Table 3.1, model 19, AICc = 33395.77), and on a per-species basis (Appendix 3.4c, 3.4d, mean difference = -2.34, s.d. =5.88, t = -1.1512, d.f. = 10.928, p-value = 0.8629), and was significant for only one species (Silvereye (*Zosterops lateralis*)).

***Table 3.1**. A comparison of models incorporating likely habitat, weather, temporal and species covariates of the detection function. Models are ranked in order of their Aikaike Information Criterion score, corrected for small sample size (AICc). Effective Strip Widths (ESW) for each model over all sites and species are shown, along with upper and lower 95% confidence intervals (in brackets). The model without covariates is shown in bold.*

model	model factors	AICc	ESW
1	Species	30995.5	35.14 (34.49, 35.81)
2	Detection cue	31321.71	38.80 (38.04, 39.58)
3	Body size	32148.7	38.85 (38.20, 39.51)
4	**No covariates**	**33223.65**	**44.13 (42.40, 45.92)**
5	Survey site	33259.37	41.60 (40.95, 42.26)
6	Site elevation	33340.83	42.05 (41.41, 42.71)
7	Survey temperature	33350.42	42.09 (41.44, 42.74)
8	Survey route	33372.28	42.14 (41.50, 42.80)
9	Survey wetness	33373.07	42.16 (41.51, 42.81)
10	Bird diversity	33378.77	42.17 (41.53, 42.83)
11	Bird abundance	33381.01	42.18 (41.53, 42.83)
12	Habitat complexity	33382.97	42.18 (41.54, 42.84)
13	Wind	33383.48	42.19 (41.54, 42.84)
14	Noise	33384.69	42.18 (41.54, 42.84)
15	Canopy density	33385.2	42.19 (41.54, 42.84)
16	Shrub density	33385.41	42.19 (41.55, 42.85)
17	Survey season	33385.43	42.19 (41.54, 42.85)
18	Survey rain	33395.04	42.22 (41.57, 42.87)
19	Cluster size	33395.77	42.22 (41.57, 42.87)

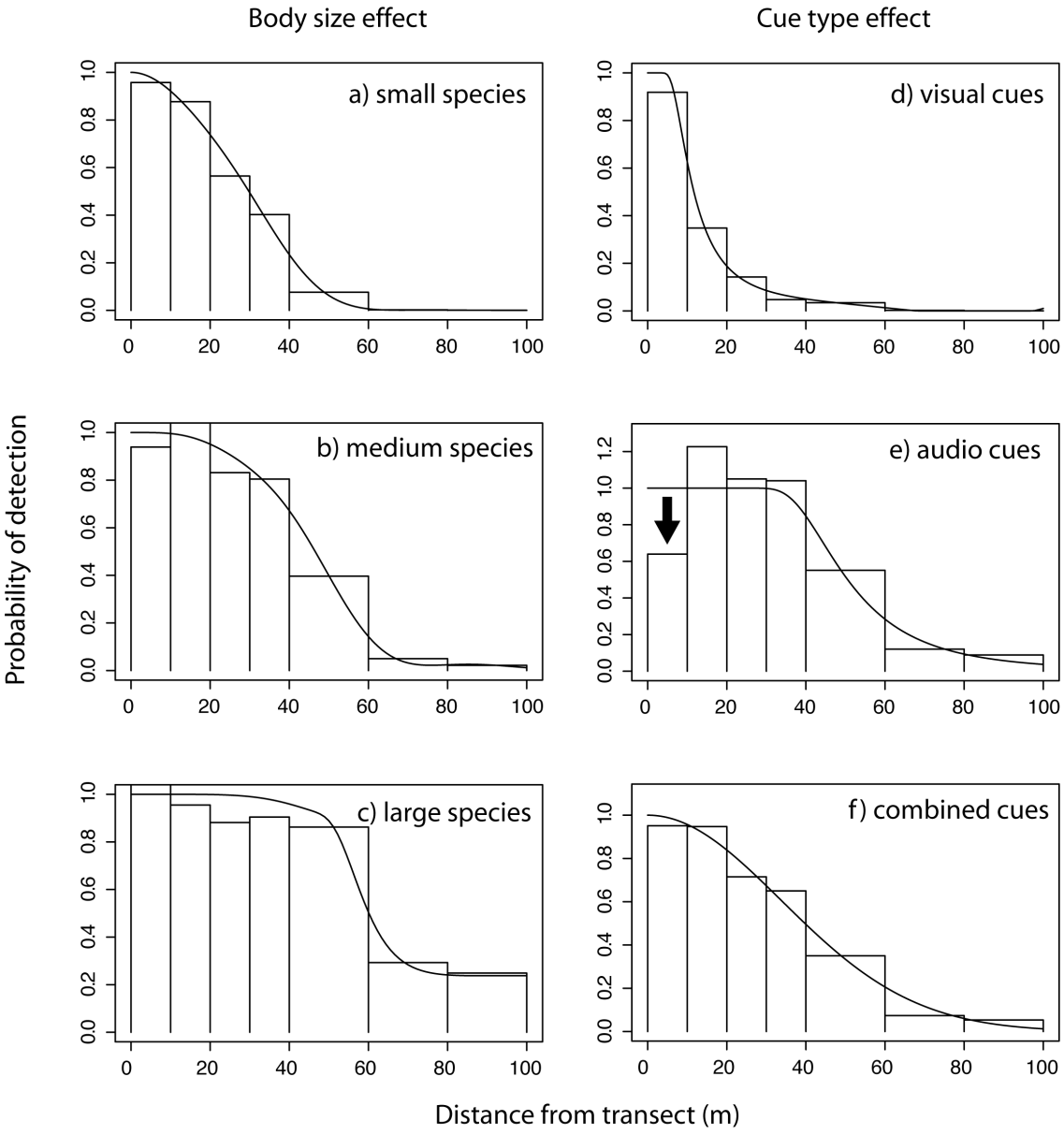

Figure 3.4. *A comparison of the distance histograms and fitted detection functions between small, medium and large bodied species (left), and between visual, audio and combined cues (right). Distance from the transect in meters is displayed on the x-axis, and the probability of detection across all species in each category is displayed on the y-axis. An arrow indicates the apparent deficit of short distances audio detections, possibly due to the way animals both seen and heard at short distances were classified as visual detections.*

3.4.2 Characteristics of surveys

On average ESWs in wet season surveys tended to be about 2 metres shorter than those during the dry season (Figure 3.3a). A Mann-Whitney U-test indicated this trend was significant (results of Mann-Whitney tests in Table 3.1). The importance of species and body size on both the scale and the shape of the detection function however highlights the necessity of analysing factor effects for each species separately. According to the 95% confidence intervals for species estimates, the effect of season on ESW was significant for only four of the 33 species examined (Figure 3.5b):

(Silvereye (*Zosterops frontalis):* 34% decrease, Wompoo fruit-dove *(Ptilinopus magnificus):* 25% decrease, Superb Fruit-dove, (*Ptilinopus superbus):* 40% decrease, and Victorias' Riflebird (*Ptiloris Victoriae):* 26% increase, mean decrease = 33%). Very wet surveys (excluding rain) overall had significantly shorter ESWs by about 4 metres, (Figure 3.5c, Mann Whitney U test results: Table 3.2), though the decrease was significant for only five of 25 species (Figure 3.3d: Large-billed Scrubwren (*Sericornis magnirostris):* 25% decrease, Rufous Fantail *(Rhipidura rufifrons):* 33% decrease, Brown Gerygone *(Gerygone mouki):* 28% decrease, Varied Triller *(Lalage leucomela):* 33% decrease, and Superb Fruit-dove (25% decrease), overall decrease 28.8%). Noise level (Appendix Figure 3.3c, 3.3d) had no overall significant influence on ESW, (Table 3.2), though significantly reduced ESW for two of 15 species. At the intensities allowed by our sampling protocol, wind during surveys (Appendix Figure 3.3a, 3.3b, table 3.2) and rain (Appendix Figure 3.3g, 3.3h, Table 3.2) had little systematic influence on Effective Strip Width. Similarly observer swamping effects due to high abundance (Appendix Figure 3.2.c,d, Table 3.2) or high diversity of birds encountered on the survey (Appendix Figure 3.2a,b, Table 3.2) had little influence on detection probability. The results of Mann Whitney U tests for these covariates are shown in table 3.2

***Table 3.2**: Results of overall and per-species analyses of the effects of each factor covariate on ESW. Mean difference in ESW are the estimated median values derived from Mann-Whitney U-test, for which the direction of the effect and p-value is also shown. Significant effects are indicated in bold. The proportion of tested species showing non-overlapping 95% confidence intervals is shown as a conservative estimate of significance considered appropriate for multiple comparisons.*

	model factor	Mean difference in ESW	Influence on ESW	Mann-Whitney p-value	Proportion of significant species differences
1	Elevation	-9.08	Negative	0.500	0.14
3	Temperature	1.23	Positive	0.193	0.17
4	Route	3.59	Positive	0.121	0.18
5	**Wetness**	**4.14**	**Higher on road**	**0.031**	**0.20**
6	Bird diversity	0.17	Positive	0.458	0.06
7	Bird abundance	0.97	Positive	0.257	0.14
8	Complexity	3.21	Positive	0.095	0.05
9	Wind	2.71	Positive	0.285	0.14
10	Noise	2.79	Positive	0.167	0.13
11	Canopy density	2.58	Positive	0.099	0.05
12	**Shrub density**	**4.48**	**Positive**	**0.011**	**0.17**
13	**Season**	**-2.13**	**Lower in Wet**	**0.045**	**0.12**
14	Rain	-1.16	Negative	0.247	0.03
15	Cluster size	8.19	Positive	0.250	0.09

3.4.3 Characteristics of habitat

High shrub layer density was also associated with reduced ESW (Figure 3.5e Mann-Whitney U-test, Table 3.2), with a significant negative effect for five of 30 species (Figure 3.5f: Large-billed Scrub-wren: 43% decrease, Mountain Thornbill *(Acanthiza katherina):* 48% decrease, Grey Fantail: 41% decrease, Silvereye 37% decrease, Eastern Spinebill (*Acanthorynchus tenuirostris*): 31% decrease, overall mean = 40% decrease). In contrast, neither canopy layer foliage density (Appendix Figure 3.3c,d, Table 3.1, significant for 1 of 22 species), nor overall habitat complexity (Appendix Figure 3.2c,d, significant for one of 20 species), showed a significant effect on ESW.

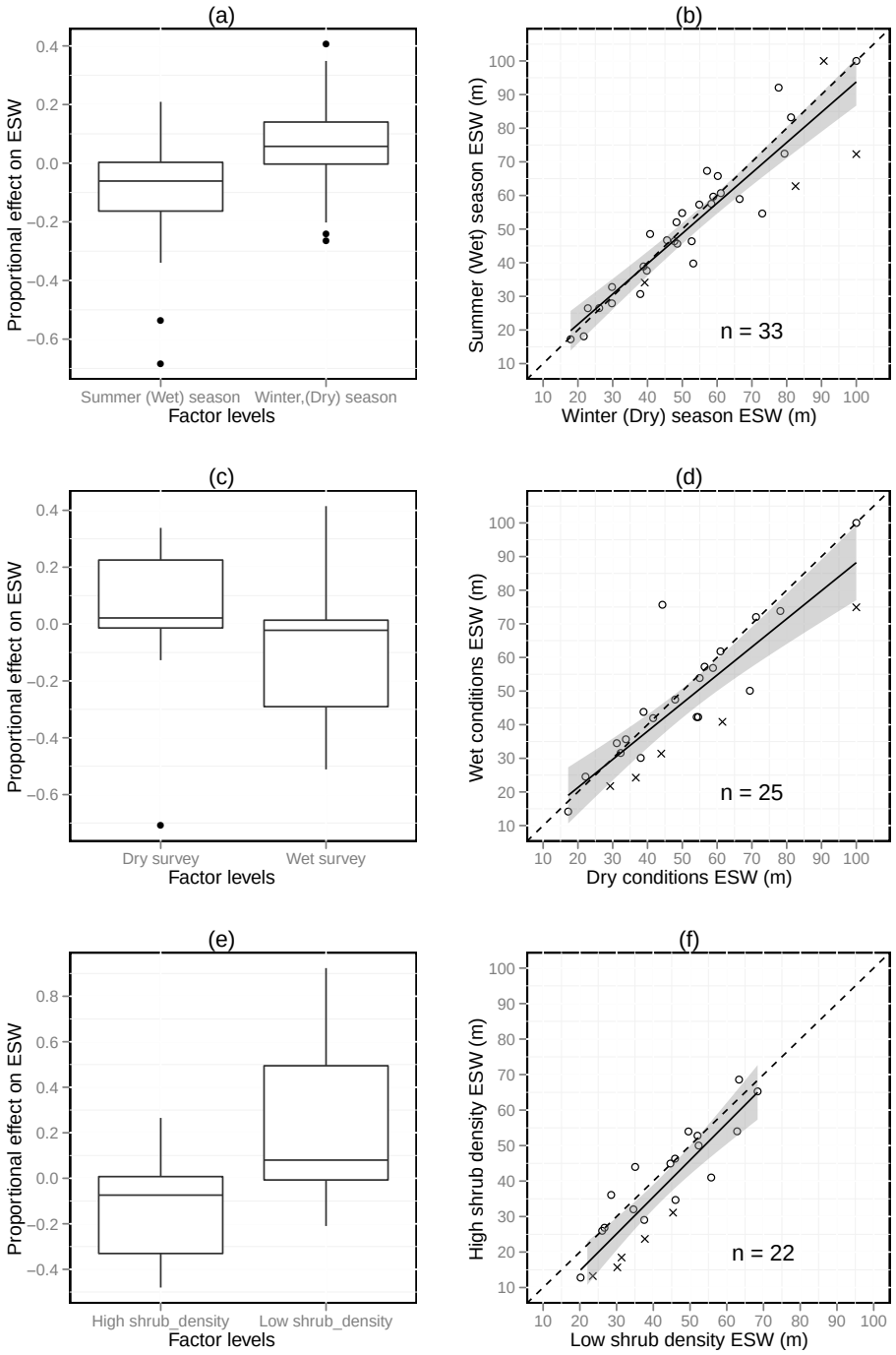

Figure 3.5*: Left column: A comparison of the relative effect of survey season, survey wetness and site shrub density on Effective Strip Width (ESW). Horizontal bars represent the median, boxes the 25th quantile, and whiskers the 75th quantile of the range of ESW relative differences between treatments, expressed as the proportion of each species' total ESW (for example, outlying points in a) represent a 50% and 65% relative increase in ESW for those species during the dry season). Right column: Biplots of covariate effects on each treatment, showing the distribution of shifts in ESW associated with each factor covariate treatment. Species with non-overlapping 95% confidence intervals are marked with an "x". N values refer to the number of species for which sufficient samples were available (see text). Dashed diagonal lines indicate zero difference, and the solid line is a simple linear regression of the relationship indicating the trend relative to the line of zero difference. Shaded areas delimit the upper and lower 95% confidence intervals for the regression.*

3.5 Discussion

Detection probability in forest bird surveys can vary appreciably between species, surveys and sites. Knowing which variables to account for is important in designing efficient monitoring programs and data collection for ecological studies in these systems. I show for a regional rainforest system that interspecific differences in detectability (mediated to some extent by body size) pose the most important concern for density correction. This suggests that the primary goal of sampling designs should be to achieve adequate replication of distance samples at the species level to satisfy minimum requirements for fitting individualistic detection functions. Secondarily, a relatively simple protocol of excluding surveys in excessively windy or rainy conditions is expected to minimise the influence of weather on detection probability. Similarly, exclusion of wet conditions without rain may be important as this factor, decreased Effective Strip Width by as much as 28% for some species. Detectability of most species did not vary markedly through the year, though some species had significant and idiosyncratic seasonal differences, both increases and decreases, likely related to calling and reproductive behaviour. Variation in habitat structure within the broad vegetation class of rainforest also had a negative effect on detectability, with species showing a reduction of as much as 40% in ESW in sites with high foliage density in the shrub layer, particularly over shorter distances. Overall factor effects however tended to be slight, and differences non-significant, though with some exceptions among species. I discuss some of the possible reasons for these findings and their implications for field survey and monitoring of rainforest birds below.

3.5.1 Characteristics of detected objects

As could be expected, audio and visual detections showed markedly different detection functions in this study. In such cases Buckland *et al.* (2008) recommend analysing data from calls and sightings separately, but in our field protocol we prioritised sightings for their increased distance estimation accuracy, leading us to seek visual confirmation of initially audio detected birds, resulting in composite detection function with an apparent deficit of aural detections at the transect midline. Combining audio and visual cues however gave both a plausible detection function with an adequate shoulder and a sufficient data set for ~70% of species, justifying in this case the pooling of data across cue types. We note, however, that this approach should be verified experimentally in before application elsewhere. Given the large variation in body size, call characteristics, plumage and behaviour among birds, it is unsurprising that species was the primary influence on detection probability. This suggests that species-specific data is necessary for correction of detectability effects, but poses significant problems for density estimation in the diverse bird communities of

tropical rainforest, where some species are rarely encountered on surveys. Additional surveys will ultimately increase sample sizes for fitting detection functions, but this may be a slow and labour-intensive process and the benefits must be weighed against the costs. As an alternative, Alldredge *et al.* (2007a) recommend borrowing information about detectability from species with similar maximum detection distances. For problematic rare species Mackenzie *et al.* (2005) also suggested sharing data between species with similar visibility, activity patterns, size and social behaviour. The results presented here indicate some promise in such approaches, as including body size as a covariate in the detection function yielded a high-performance model, suggesting size as a promising grouping covariate despite the fact that about 80% of detections were aural in this habitat. I suggest that this may be due to correlation between body size and call characteristics, since larger species may call more loudly (Brackenbury, 1979) and at lower frequencies than smaller species, resulting in calls which carry further, attenuate less rapidly (Waide & Narins 1988), and remain identifiable at greater distances from the observer (pers. obs. A. Anderson). In addition to body size however, sound attenuation in forest also differs with height above the forest floor for some frequencies (Marten *et al.* 1977) suggesting aspects of behaviour like preferred height stratum might also influence the detection function, and could be included in future analyses.

Cluster size had little influence on detection probability in this study, suggesting that group detectability in these audio-visual surveys differed little from single individual detectability. However, single-species clusters made up a relatively small proportion of total records in this study, and I did not attempt to analyse data on mixed flocks. Unlike those of new world obligate ant-following species and their attendants (e.g. Hutto 1987; Graves & Gotelli 1993), membership of mixed flocks in Australian rainforest can be dynamic and sometimes difficult to define (pers. obs. A. Anderson). Nonetheless, they form a focus for bird activity, and so are likely to operate as clusters from a detection perspective. Detectability for members of a mixed flock might then be more similar to the detectability of its most conspicuous member species than its least, and by extension, may bias density estimates where mixed flocking is common. While mixed flocking has been noted frequently in Australian woodland birds, particularly among insectivores (e.g. Bell 1980), there is little in the literature about its occurrence in rainforest species, and mixed species flocking remains a potential source of bias in rainforest bird detectability that warrants exploration in future. For simplicity however, here such “mixed species clusters” were analysed as unassociated individuals.

3.5.2 Characteristics of surveys

Time of season has been previously identified as a potential influence on density estimation in bird surveys (Wilson & Bart 1985; Selmi & Boulinier 2003) for example through an effect on singing

phenology. For this study region for example, Crome (1975) has argued that surveys using audio cues were of limited utility for estimating abundance of frugivorous pigeons in the AWT, as their calling frequency is low in the mid-wet and peaks in the mid-dry season. All the species that showed a significant effect of season on detectability in this study forage in the canopy, and are more often detected by their calls than visually (pers. obs. A. Anderson.). I concur with Crome (1975) that the influence of season on detectability in these species may thus be linked to seasonal differences in calling behaviour that reduce their rates of cue production in the wet season (or dry season in the case of Victorias' Riflebird, *Ptiloris victoriae* Appendix Table 3.3). Provided survey effort is approximately equal in both seasons as in the present study, seasonal bias in overall density estimates will be mitigated, but the inclusion of a season covariate would be recommended where temporal variation is of interest. This highlights the idiosyncratic effect of detection covariates with respect to species, reinforcing the importance of species-specific corrections for detectability in density estimation.

Conditions at the time of survey also have the potential to influence detection probability, through interference from foliage movement, from rain, wind, or foliage drip, and through influences on bird activity such as decreased calling rate and intensity of foraging behaviour (pers. obs. A. Anderson; Robbins 1981; Lindenmayer *et al.* 2009). Here as in Williams *et al.* (2010a) sampling was not conducted during moderate to heavy rain, periods of substantial background noise, or on excessively wet or windy days, and our results suggest that this protocol eliminates most of the effects of poor weather conditions on detectability. The apparent lack of observer swamping in this study, even at high diversity and abundance, would also suggest sufficient observer training and experience to overcome these effects. Wetness however remained a significant and systematic influence on ESW for some species. Canopy drip in rainforest can continue for long periods following rain and when moisture is condensing on leaves directly from clouds, particularly in high elevation forests, leading me to suggest that the effect of wetness on ESW here may be a combination of increased background noise from dripping foliage and a decrease in bird activity in wet conditions. Comparisons of density estimates between sites that are more often wet and those that tend to be drier, for example across elevations, may therefore be influenced by a downward bias in wetter sites if surveying is not conducted in optimal conditions, or if density estimates are not corrected for detectability. While only five of 25 species showed a negative influence of wetness on ESW, if uncorrected in these species I found that the bias could result in as much as a 20% underestimate of density. In studies where comparisons are made across a large climatic gradient, care should therefore be taken to ensure sampling is either a) conducted extensively in optimal conditions, or b) that relevant weather measures are included as covariates.

3.5.3 Characteristics of habitat

Dense habitats are expected to reduce detectability though the attenuation of visual cues, and hence in audio cue dominated surveys such as those in rainforest, could be expected to have a reduced role. Nonetheless shrub layer foliage density had a significant negative influence on ESW in this study overall, and a significant negative effect for five species. This effect was concentrated over shorter distances (and hence smaller species), and translates to a mean decrease of 40% in ESW for these species in sites with dense understory. This is likely to be a simple result of the difficulty of sighting birds in dense habitats, and the importance of sightings for smaller, quieter species, but may also include an increase of the attenuation of audio cues by reflection of sound signals from foliage. Shrub layer foliage density may therefore be a potential source of bias in the estimation of population density for some birds, particularly smaller species. Where site-specific density estimates are not made directly using distance analysis, this result indicates that a shrub layer covariate should be included to correct for detectability differences between sites where shrub foliage density differs.

3.5.4 Limitations and sources of error

Rainforests are complex environments, and detection of birds is at times difficult. Birds close to the transect line may be hidden from view, birds may not call when the observer is within range, and even if they do call they may not be heard amongst the myriad of other sounds in the forest. The field of view for an observer on the forest floor is often limited, and birds may be 40 metres above an observer or obscured in dense understory foliage. In one study truthed with canopy surveys, a ground observer underestimated population densities of canopy-singing species by 33-46% (Waide & Narins 1988). Combining audio and visual cues in dawn surveys maximises availability for detection, but the proportion of undetected individuals at the transect midline remains unknown. The assumption of 100% probability of detection along the transect midline ($g(0) = 1$) is critical to the distance sampling approach (Thomas *et al.* 2010), but may be rarely met (Bächler & Liechti 2007). As a result, density estimated using this and most other practicable methods is likely to underestimate true density, especially for cryptic species. Nonetheless distance-corrected transects surveys compare well to alternative methods (Norvell *et al.* 2003) when contrasted with full census approaches, and it has been shown that the use of experienced observers can minimize within-site detection differences relative to variation between sites (Lindenmayer *et al.* 2009). Thus, careful and systematic sampling by an experienced observer is expected to limit the problem for most species, yielding useful density estimates even in the challenging conditions presented by tropical forest bird surveys. I suggest that where deviations from this assumption are suspected to be large,

some more intensive method specifically targeted to species could be applied to estimate the proportion of missed individuals at the transect midline, such as double-observer sampling (Nichols *et al.* 2000). In addition, large, rare and shy species are unlikely to be well surveyed by the methods shown here, as they may be rarely seen. In the AWT, the Southern Cassowary (*Casuarius casuarius)* falls into this category.

Error in density estimation may also arise from inaccuracy in the estimation of distances to detected individuals (Scott *et al.* 1981; Alldredge *et al.* 2007c) and more seriously so in audio-dominated forest bird surveys (Emlen & Dejong 1992; Alldredge *et al.* 2007c). Location of a sound source involves cuing on binaural differences in both signal intensity and quality (Casseday & Neff 1973), so observers need sufficient experience to compare cues to baseline information about each species' call intensity and quality at the source. Error rates in this localisation process increase with distance (Alldredge *et al.* 2007b) and may increase with increasing frequency (Waide & Narins 1988), peaking between 1 and 4 KHz (Casseday & Neff 1973). Habitat structural differences may also influence the rates of signal decay through reverberation and attenuation, driving differences in error rates between sites (Simons *et al.* 2009). In this study I took advantage of the flexible binning possible in Distance analysis (Thomas *et al.* 2010) by increasing bin sizes with increasing distance to reduce the impact of estimation error. While calls will always remain a less accurate cue for density estimation than sightings, particularly for rare species, it has been shown that experienced observers can estimate distances to detected birds with reasonable precision and accuracy up to 65 metres (Schieck 1997; Alldredge *et al.* 2007c). In addition, the paucity of sightings in rainforest surveys limits the scope for practical alternatives: sufficient visual data will be difficult to accumulate for all but the most common species, and detectability decay too steep to accurately fit a detection function. Adequate training, experience, and careful surveying will thus likely remain the best tool for reducing error rates in surveys in general, and for sound cue localisation in particular (Scott *et al.* 1981; Alldredge *et al.* 2007c). In some settings, calibration experiments could be used to characterise the error structure as proposed by Borchers *et al.* (2010). On the other hand, newly developed techniques such as "acoustic spatially explicit capture/recapture" might prove useful in some settings (Dawson & Efford 2009).

Finally, transect placement can be problematic in tropical forests (Dawson 1981; Karr 1981). While Distance analysis assumes that transects are placed at random in the landscape, access in montane rainforests may not be random, but by necessity may employ existing tracks and trails. Transect placement with respect to roads can influence density estimation in cases where species density also varies with distance from roads (Marques *et al.* 2007). For example, some bird species may be

attracted to roads, while others may be repelled (Sutter *et al.* 2000; Laurance 2004). In such cases the assumption in Distance analysis that true density is uniform with respect to distance from the observer is violated, confounding variation in detection probability with variation in true density. A secondary effect of roads may arise from their influence on habitat structure (Harris 2007). In rainforests, increased light availability along roads may alter the structure of vegetation (Pohlman *et al.* 2007) and hence affect the attenuation of survey cues. While in this study surveys were conducted along roads too infrequently to assess the importance of either density or attenuation effects, there is some indication that density estimates in particular may be influenced by the presence of roads for some species. The most common effect appears to be attraction (Appendix Figure 3.1e), largely restricted to under-storey insectivores, with 11 of 17 species showing some effect though only 2 species significantly (Appendix Figure 3.1f), perhaps as a result of increased light penetration and hence prey availability. Other species appeared to be repelled by roads (Appendix Figure 3.1f). Where surveys in rainforest are commonly limited to roads, or where surveying is restricted to roads in a systematic manner with respect to the distribution of sampling sites overall, this effect could bias density estimates for the some species. I suggest that surveys on roads be avoided, but where necessary, a further exploration of the effect of roads on density estimation would be advised.

3.5.5 Conclusions: protocols for rainforest bird density estimation

Accurate density information is an increasingly important resource for biodiversity conservation (Trauger 1981; Caughley 1994; Link & Sauer 1998). Distance sampling provides an approach to convert raw counts of animals to meaningful estimates of density, but its utility requires the recognition and adequate treatment of covariates that may strongly affect detection probability. Several detailed studies have examined differences between observers, forest types, survey conditions, and different species of birds (e.g. Alldredge *et al.* 2007b). However, information has been lacking for diverse assemblages across broad regional systems. Here, species characteristics, particularly body size, were the primary covariates influencing detectability, though season, wetness, and high shrub layer foliage density also reduce the Effective Strip Widths of surveys. Combining these results with the standardised sampling methods established previously in this system, it is possible to outline a preliminary protocol for sampling and analysis that will maximize the utility of rainforest audio-visual survey data for birds. Firstly, idiosyncrasies of species characteristics, site habitat structure and survey conditions suggest that distance sampling is highly recommended in rainforest bird surveys, provided that 1: sampling is sufficient to estimate density for each species, 2: information about site habitat structure at least in the shrub layer is collected, 3: surveys are conducted under optimum conditions where possible (including seasonal sampling), but

that standardised information about environmental wetness is recorded as a minimum requirement.

The results presented here also indicate some alternative approaches that may be useful where formal distance sampling is not practicable, such as for rare species, or where scope for training or logistics may be limiting, e.g. in citizen-scientist or volunteer based surveys. Firstly, an Effective Strip Width could be estimated for sites, surveys and species based on their characteristics, and used as a multiplier to convert relative abundance to rough estimates of density. This approach will only be as accurate as the estimates of ESW, and will require at least some preliminary distance sampling to establish the appropriate values. Alternatively, in the absence of ESW estimates for important covariates, to be comparable surveys should at minimum: 1; pool data across sites with regard to averaging out variation due to habitat structure, especially in the shrub layer, 2: pool data across surveys with regard to averaging out variation due to survey wetness and season, and 3: share detectability information across species data based on shared characteristics of at least body size. The importance of species as a covariate suggests an avenue for developing a more refined approach to estimating density where direct distance estimation is difficult, such as for rare species. In particular our data suggests that a useful starting point will be a proper consideration of the acoustic properties of species' calls. Finally, it is important to note that application of these findings depends also on the question being asked. In an assemblage-wide study were species composition changes across the study region, species differences may be the more significant contributors to bias in density estimates. Studies concerned with differences between sites or time periods within a single species however, such as monitoring of population changes, will likely need to counter the bias introduced by site and survey differences instead.

Chapter 4. Body size, song and detection probability: estimating density of rare species

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Article type: Full Length Article:

A.S. Anderson[1], L.P. Shoo[1,3], R. G. Pearson[1], S.E. Williams[1] (in prep). Body size, song and detection probability: estimating density of rare species and correcting for bias in rainforest bird surveys.

[1]Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia.
[2] School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia.

How

out of its throat

smaller than a finger

can there fall the waters

of its song?

Luminous ease!

Invisible

power

torrent

of music

in the leaves...

(Pablo Neruda -1971)

Plate 4. *White-faced Robin (*Tregallasia leucops*), found within the study region only Cape York Peninsula, provided a test of the models developed in this chapter.*

4.1 Abstract

Distance sampling is widely advocated for use in wildlife surveys to correct for variation in detection probability between species, locations, or times. However, the methods may be logistically difficult to apply in field conditions, requiring specialised training and equipment, and in addition, data on rare species may be too scarce for models to be fitted accurately. In chapter 3, distance sampling data from rainforest in north-eastern Australia showed variation between species to be more important than habitat and survey conditions. In this chapter I specifically model the Effective Strip Width of surveys for each species as a function of a range of their ecological and physical characteristics. I show that considerable variation in Effective Strip Width for many species can be explained using information from the literature on body size and call characteristics, though explanatory power is increased by the inclusion of field measurements of maximum detection distance and foraging height. Further the models perform well in two independent testing regions with both shared species and species for which the models were not trained. This represents a method for improving estimates of density for rare species for which data are insufficient to accurately model detectability using formal distance analysis. I envisage its application in predicting the detection probability for rare species, and for calibrating data from non-distance sampling surveys, in which context this approach is a compromise that enhances the utility of survey data while being logistically simpler than full distance methods.

4.2 Introduction

Accurate density information is valuable to biodiversity conservationists as it provides a basis quantifying population size or evaluating the effectiveness of management interventions to sustain or recover viable populations (Caughley 1994; Link & Sauer 1998). Recently, bird declines in the tropics have been highlighted as an concerning trend (Sodhi *et al.* 2004). Identifying species with critically low population size is likely to be particularly important in montane tropical bird assemblages, where high biodiversity, endemicity and concentrations of rare species coincide with high vulnerability to changes in both climate and land use (Sekercioglu *et al.* 2008; La Sorte & Jetz 2010, Terborgh *et al.* 1990; Thiollay 1994). Accurate estimation of population sizes, distribution patterns and temporal trends of rare species is crucial in conservation biology, so developing ways to estimate density of rare species is therefore an important challenge for conservation biologists (Scott *et al.* 2008). This task is complicated by the fact that detection probability varies markedly between species (Emlen 1971; Boulinier *et al.* 1998; Diefenbach *et al.* 2003), for example, as a result of body size (chapter 3, this volume; Waide & Narins 1988), call structure, (Waide & Narins 1988; Schieck 1997), call volume or singing rate (Best 1981; Gibbs & Wenny 1993; Alldredge *et al.* 2007b). Distance sampling and analysis provides a tool for accounting for variation in detection probability (Thomas *et al.* 2010), enabling true density to be estimated. However, its application can be constrained where the number of detections is insufficient to fit detection functions. While opinion varies as to the minimum number required, detections of rare species may nonetheless be too scarce to fit detection functions (MacKenzie & Kendall 2002). In such circumstances, Alldredge *et al.* (2007a) recommended "borrowing" information about detectability from more common species with similar visibility, activity patterns, size and social behaviour. However, detailed information is lacking about which of these characteristics of species drive their probability of detection, and hence which common species may be appropriate surrogates from which to borrow detectability information.

The results of analysis in chapter 3 indicated that species differences were more important as covariates of the detection function than most characteristics of habitat and survey conditions. These results also suggested that a substantial amount of the variation between species can be captured using body size as a covariate of the detection function in Distance analysis. This effect may remain important even where aural detections dominate, as in rainforests, since larger species may also call more loudly (Brackenbury, 1979) and at lower frequencies than smaller species, resulting in calls which carry further, attenuate less rapidly (Waide & Narins 1988), and remain identifiable at greater distances from the observer (pers. obs. A. Anderson). Here I present a further

analysis of distance data from rainforest birds in north-eastern Australia, this time focussed on the influence of species-specific ecological characteristics on the detection function. I assess the contribution of species' physical characteristics, such as body mass, on the Effective Strip Width (ESW) of surveys for rainforest birds, an important parameter of the detection function that can be used to correct for detectability bias. I also assess the influence of behavioural characteristics such as the dominant frequency of calls, call intensity, and the mean foraging height on ESW. I derive models of increasing complexity which can be used to predict the ESW of many rainforest bird species with reasonable accuracy. I then test the power of each model to predict ESW for rainforest bird assemblages in adjacent regions with some shared and some new species for which our models have not been trained. I discuss the utility of these models for deriving density information from raw count data and for estimating density of rare species for which distance data are unavailable.

4.3 Methods

4.3.1 Study regions

In addition to the data from rainforests of the Australian Wet Tropics bioregion (AWT) analysed in chapter 3, here for comparison I also sampled rainforest bird assemblages across the Clarke and Conway Ranges in the Central Queensland Coast Bioregion (CQC) between 20˚16'53.11"S 148˚18'8.45"E and 21˚23'25.87"S 148˚42'9.65"E, (Figure 4.1) and in the McIlwraith and Iron Ranges in the Cape York Bioregion (CYP) between -14˚ 8'33.78"S 143˚22'36.65"E and -12˚37'24.44"S 143˚14'22.22"E (Figures 4.2). The relationship between these regions and the AWT is indicated in the inset maps, and in more detail in Figure 2.4. Bird assemblages in these neighbouring regions include both shared and unique species against which to contrast findings within the AWT.

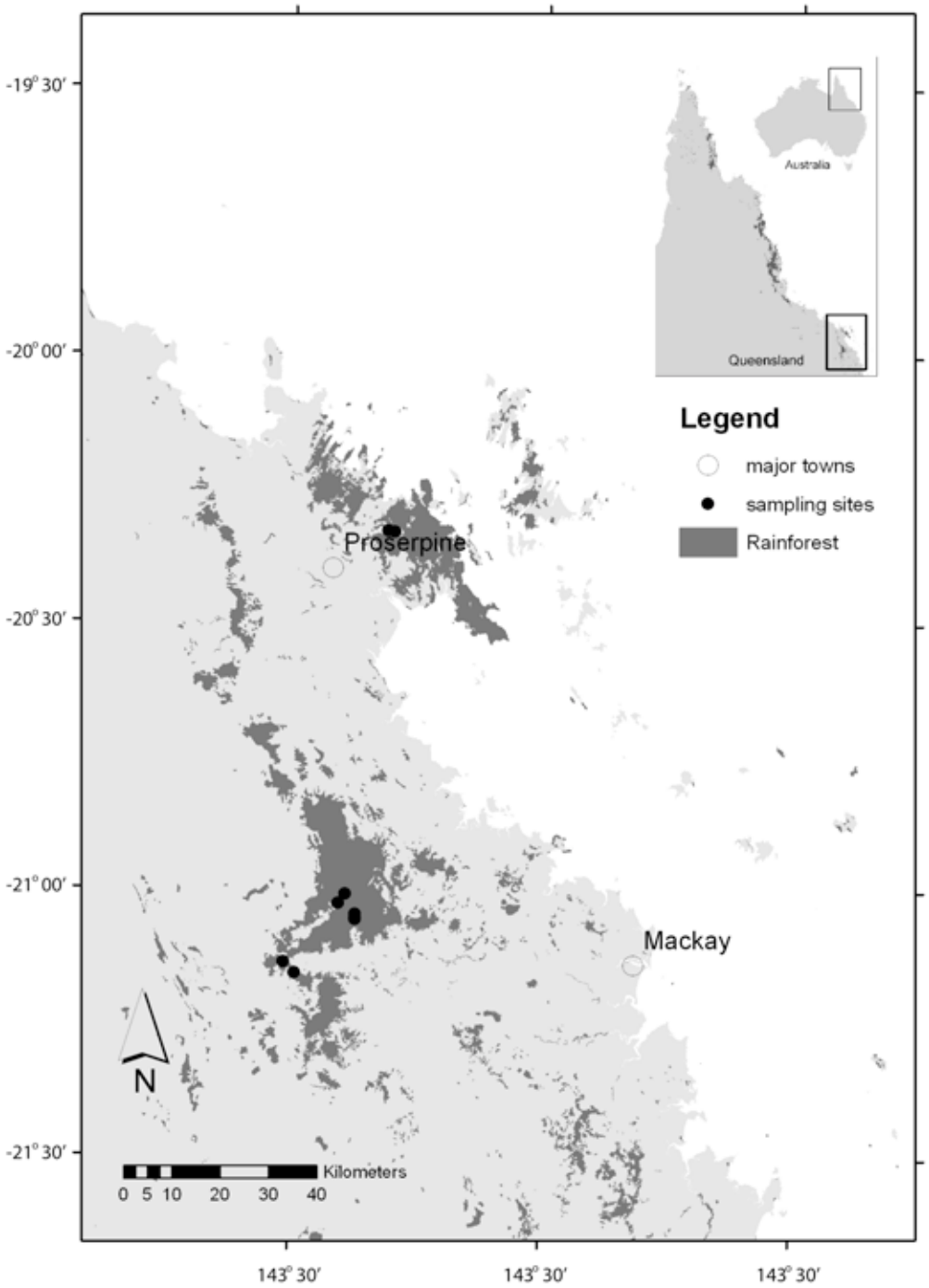

Figure 4.1. *Locations of the sampling sites in the CQC in relation to the major areas of montane rainforest. As in the AWT, sites are positioned at approximately 200m intervals across the elevational gradient, and each contain an array of either 3 or 6 sampling points arranged at 200m intervals along the main sampling site. Full descriptions of the study area and the sampling design are given in chapter 2.*

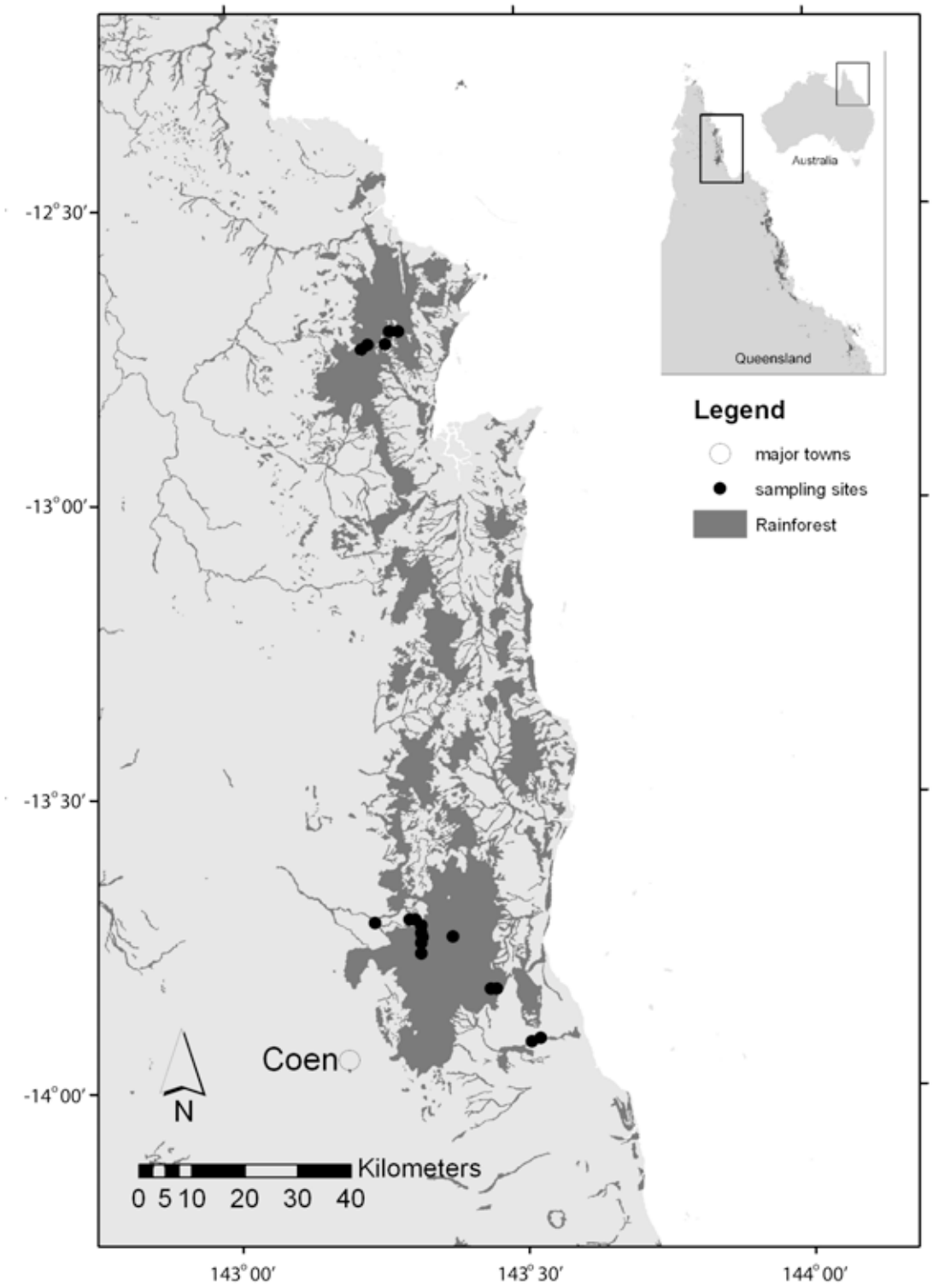

Figure 4.2. *Locations of the sampling sites in the CYP in relation to the major areas of montane rainforest. As in the AWT, sites are positioned at approximately 200m intervals across the elevational gradient, and each contain an array of either 3 or 6 sampling points arranged at 200m intervals along the main sampling array. Full descriptions of the study area and the sampling design are given in chapter 2.*

4.3.2 Distance data and analysis

The sampling design and locations used here follow those described in chapter 2, and the Distance sampling methods follow those described in chapter 3. As in chapter 3 I used the Program DISTANCE version 6 (Thomas *et al.* 2010) to estimate Effective Strip Widths for each species. Effective strip (half-)width (ESW) is defined as the transect half-width at which the total count over the area L×(2×ESW) would be on average equal to the observed count (where L = survey length) (Thomas *et al.* 2010). Raw distance frequency histograms (similar to those shown for aggregated data in Figure 3.4) produced for each species were inspected and the data binned in order to minimise the effect of heaping. Distances were also truncated at 100 m to eliminate the largest 10% of distances as recommended (Thomas *et al.* 2010) to facilitate the fitting of the detection function. Akaike's information criterion adjusted for small sample sizes (AICc) was used to select the most appropriate model from all possible combinations of Uniform, Half Normal and Hazard Rate models with Cosine, Simple Polynomial and Hermite Polynomial adjustment keys (for detailed explanation of Distance terminology and analyses see Thomas *et al.* 2010). These analyses were performed for all species with sufficient sample sizes in each of the three subregions surveyed (AWT, CYP and CQC). While 60 or more observations are recommended for reliable inferences (e.g. Buckland *et al.* 2001), there are numerous examples of published studies with lower sample sizes (e.g. Buckland 2006). Here I used a lower threshold of 35 individuals for further analysis as a compromise between sufficient distances to fit the detection function and allowing the inclusion of more species for the purposes of fitting and testing our models.

4.3.3 Ecological characteristics

Physical characteristics, behaviour, and calls of birds may all influence detectability, suggesting that modeling covariates of detection could be a complex process (Alldredge *et al.* 2007b). However, I aimed to develop a model that balanced accuracy and efficiency, and would be broadly applicable across assemblages in this region, and potentially in others. I therefore limited model factors to those that were either readily available from the literature, or could be easily measured in the field. For body mass I used values published in the Handbook of Australian, New Zealand and Antarctic Birds (Marchant & Higgins 1990; Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Higgins, Peter, & Steele 2001; Higgins & Peter 2002; Higgins *et al.* 2006). Species-specific estimates of dominant call frequency were derived from sonograms in HANZAB, with additional data for pigeons from Frith (1982) and for birds of paradise from Frith & Beehler (1998). I defined dominant frequency as the frequency at which the call reached its highest intensity for the longest period, based on a visual assessment of published sonograms. Where species had multiple call types, I selected the call I considered to be the most common in this context, based on field

experience. Measures of foraging height were infrequently reported in the literature, so I derived estimates of the mean foraging height for each species using data recorded during our surveys. Call intensity (volume) is likely to be a critical factor determining detectability (Alldredge *et al.* 2007b) especially in rainforest bird surveys where audio detections dominate (Scott *et al.* 1981), but is rarely measured in a natural setting. I therefore used the un-truncated maximum detection distance from our data as a substitute for call intensity, as recommended by Alldredge *et al.* (2007a).

4.3.4 Model training, evaluation and testing

I examined a range of models of increasing complexity, from the simplest model which used only data available from the literature (weight and dominant frequency of call), to a full model including field data on maximum detection distance and foraging height. All statistical analyses were conducted using the "R" framework for statistical analysis version 2.13.1 (www.r-project.org). I used distance data from the AWT alone to develop the models using a model averaging approach in the R package "MuMIn" (Barton 2010) to assess the relative importance of each factor, included as both a linear and quadratic (2^{nd} order polynomial) term, and all possible two-way interactions. I then constructed a linear model, beginning with all model terms with a greater than 0.50 importance score plus their interactions, and proceeding to the simplest model with no non-significant terms by stepwise removal. Model terms were selected for removal based on their p-values, stopping at the model maximising both the significance of terms and r^2 adjusted for small sample size. I also constructed a regression tree using the R package "mvpart" (Therneau & Atkinson 2009) to visualise the structure of the regression model including its interaction terms. I compared the performance of our range of models against a "best model" based on ESW calculated directly for each species in the Distance software (Thomas *et al.* 2010) and the "simplest model" assuming a fixed-width transect set at the mean ESW for all species. Differences between the directly estimated and model-predicted ESW values allow the assessment of the degree of improvement offered by this approach over fixed-width transects for common species. Finally I conducted an independent test of the models by comparing predicted Effective Strip Widths with direct field estimates for species in CQC and CYP. These subregions support assemblages with both shared and unique species, allowing us to evaluate the utility of our model in situations with the same species but at novel sites, and with novel species at novel sites.

4.4 Results

Data from the AWT analysed here are as for chapter 3, and details of model fitting, ESW and density estimation are given in Appendix Table 3.3. In addition, seventy-six field surveys in the

CYP yielded 3,487 records, from which 26 species had sufficient data for model fitting in Distance, including seven not occurring in the AWT (Tawny-breasted Honeyeater (*Xanthotis flaviventer)*, Trumpet Manucode (*Phonygammus keraudrenii)*, Tropical Scrubwren (*Sericornis becarii)*, White-faced Robin (*Tregellasia leucops)*, Red-cheeked Parrot (*Geoffroyus geoffroyi)*, Eclectus Parrot (*Eclectus roratus)* and Magnificent Riflebird (*Ptiloris magnificus*). Thirty-nine field surveys in CQC yielded 2,584 bird records, from which 22 species had sufficient data, including two not occurring in the AWT (Eungella Honeyeater (*Lichenostomus hindwoodi)* and Brown Thornbill (*Acanthiza pusilla)*). Details of model fitting, ESW and density estimation for CQC and CYP for all species with greater than 35 records are shown in Appendix Tables 4.1 and 4.2 respectively.

4.4.1 Ecological characteristics

Log of body mass was positively correlated with ESW (Figure 4.3a: $r^2 = 0.401$, F-statistic = 31.82 , d.f = 45, $P < 0.001$). Dominant frequency of song was negatively correlated to body mass (Figure 4.3b: $r^2 = 0.428$, F-statistic = 35.48, d.f. = 45, $P < 0.0001$), such that species with high-pitched songs tended to be smaller, and by extension have smaller ESWs. Maximum detection distance was negatively correlated with dominant frequency, so that species detected at greater distances also tended to call at lower pitches and have larger ESW's (Figure 4.3c: $r^2 = 0.243$, F-statistic = 15.82, d.f. = 45, $P = 0.0002$). There was substantial variation around this tendency, however, with some species (e.g. Topknot Pigeon (*Lopholaimus antarcticus)*, lower left corner of Figure 4.3c) displaying a much shorter maximum detection distance than the dominant frequency of their call would predict. There was also a weakly positive but non-significant relationship between foraging height and ESW, suggesting that, at least for some some species, foraging in the upper canopy may result in greater detection distances from the transect (Figure 4.3d: $r^2 = 0.02$, F-statistic = 1.71, d.f. = 45, $P = 0.154$).

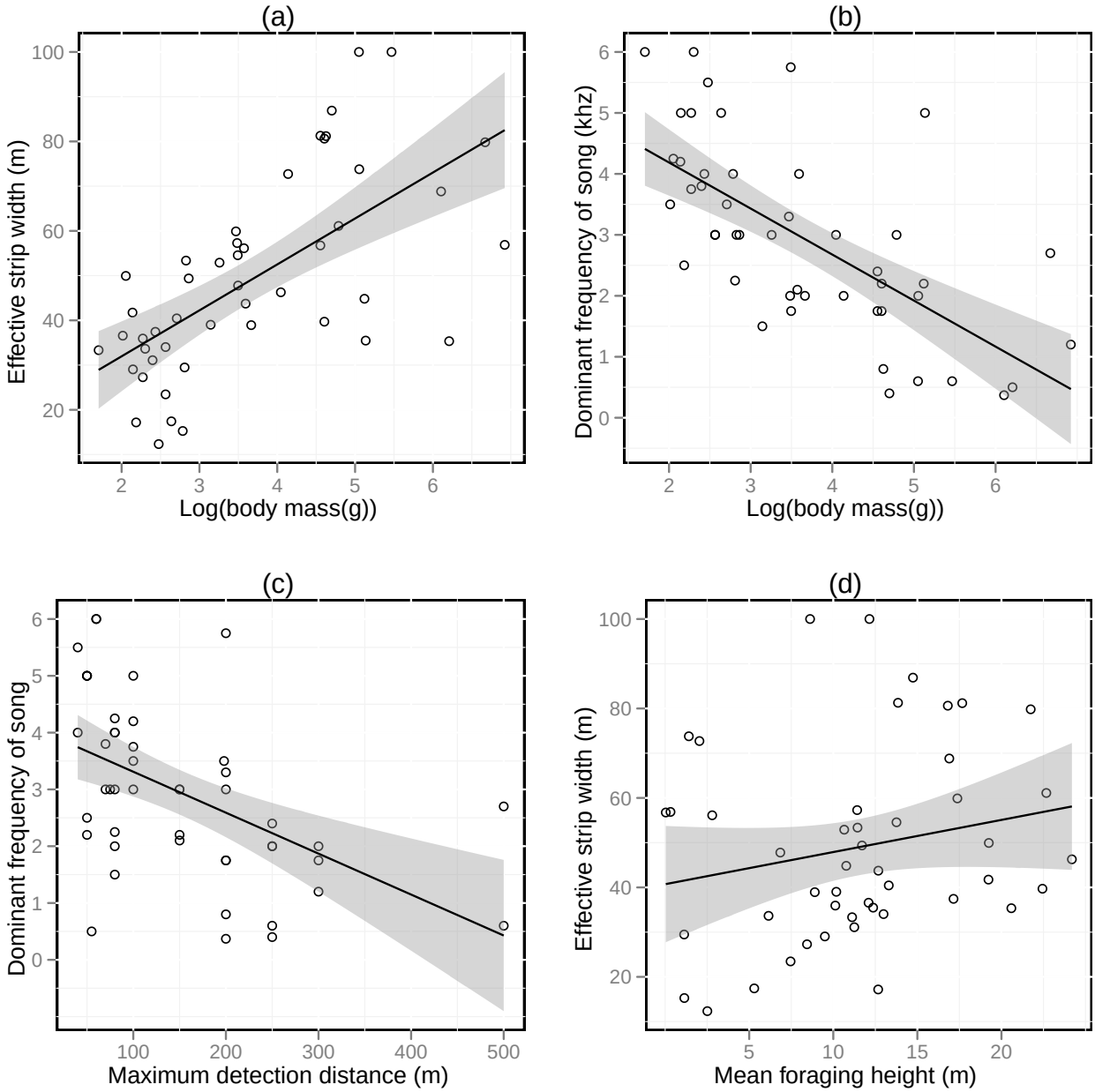

Figure 4.3*. Biplots showing relationships between ecological and physical characteristics and ESW estimated in Distance software for each species with sufficient data in the AWT. a) log(body mass(g)) versus ESW; b) dominant frequency of song (khz) versus log(body mass(g)); c) maximum detection distance (m) versus dominant frequency of song (khz), and d) maximum detection distance (m) versus foraging height (m).*

4.4.2 Model training and evaluation

Model averaging across the full range of factors followed by stepwise removal selected a linear term for square root of maximum detection distance and for untransformed body mass, and both a linear and quadratic term for dominant frequency of song. There were important interactions between dominant frequency of song and mean foraging height, and between body mass and maximum detection distance. The full model (model 1) was highly significant and explained more than 80% of the variation in estimated ESW for the species analysed (Table 4.1). Omitting the least

important factor by p-value, a model without dominant frequency of song (model 2) was the best overall (r^2 = 0.838), followed by a model without mean foraging height, which resulted in only minor reduction in explanatory power (i.e., r^2 = 0.802) when excluded. Maximum detection distance alone explained 71% of variation in ESW, out-performing the model derived from body mass alone (i.e, r^2 = 0.47).

Table 4.1. *Summary of model statistics for a hierarchical series of models of decreasing complexity describing ESW as a function of species' ecological characteristics. Model terms were selected using a model averaging approach to identify important terms, followed by stepwise removal to establish optimal models comprised only of significant explanatory variables. Regression values for the top performing model (model 2) are shown in bold.*

Model number	**1**	**2**	**3**	**4**	**5**
Terms	**Full model**	**body mass + height + maximum detection distance**	**body mass + maximum detection distance**	**Maximum detection distance only**	**body mass only**
√(maximum detection distance)	3.919	5.306	3.819	4.487	-
I(√(maximum detection distance)2	-	-0.216	-	-	-
body mass	-0.022	-0.06	-0.067	-	-0.084
I(log(body mass)2	-	-	1.35	-	2.455
Dominant frequency of song	-19.578	-	-	-	-
I(Dominant frequency of song)2	2.023	-	-	-	-
Mean foraging height	-	0.557	-	-	-
Dominant frequency of song : height	0.268	-	-	-	-
log(body mass) : √(maximum detection distance)	-	0.909	-	-	-
Degrees of freedom	41	**41**	43	45	44
F- statistic	45.97	**48.62**	63.1	115.17	21.03
r^2	0.84	**0.854**	0.802	0.713	0.465
P-value	<0.001	**<0.001**	<0.001	<0.001	<0.001

A multiple regression tree using only body mass, mean foraging height and the square root of maximum distance from the best model above shows the nature of the interactions indicated by this model (Figure 4.2). At shorter maximum detection distances, (< 14.11m), larger species (>16.5g) tend to have larger ESW (mean 44.6m), while among smaller species (<16.5g) species with shorter maximum detection distance have still smaller ESW (mean 17.9m). Amongst species with larger maximum detection distance (>14.11m), those with smaller body mass (<47.88g) showed a shorter ESW (mean 54.9m) while amongst larger species (>47.88g) mean foraging height was also important, with species foraging above 0.8 m having a substantially increased ESW (mean 80.6) than lower foraging species (mean = 56.8m).

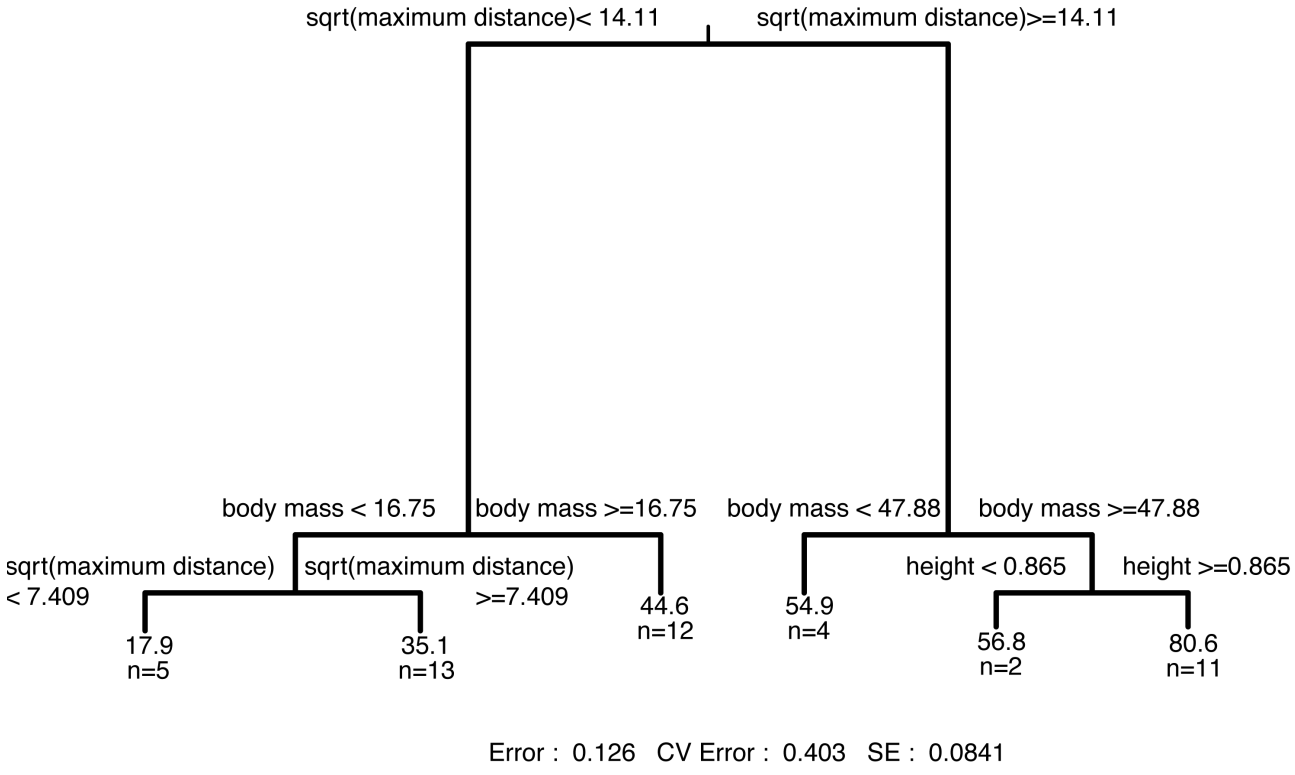

Figure 4.4. *Multiple regression tree for model 2 showing the principle splits in the ESW data for species in the AWT for which data are sufficient. Branch lengths are proportional to the variation explained, and values above the branches indicate the threshold values for factors defining each split. Values at nodes indicate mean values for that factor for the species in that node. N values are the number of species grouped within each node.*

Comparing models for each species in the AWT based on the difference between predicted ESW and corresponding estimates calculated directly in the Distance software (Thomas *et al.* 2010), fixed-width transects tended to substantially overestimate ESW for smaller species, and underestimate ESW for larger species (Figure 4.5). While there is variation among species in the error of ESW estimates relative to their corresponding Distance calculated estimates, even the simplest model represents an improvement over a fixed-width estimate for the majority of species. Nonetheless, ESW for some species appears to be poorly estimated across most models, including the best model identified above. Most models tend to overestimate ESW for the smallest species, including Atherton Scrubwren, Yellow-throated Scrub-wren, Mountain Thornbill, Pale Yellow Robin and Spectacled Monarch. In contrast most models tend to underestimate ESW for large species, including Victoria's Riflebird, Superb Fruit Dove, Pied Currawong, Black Butcherbird and Brown Pigeon. Five other species also tended to be underestimated by the models: Brown Gerygone, Rufous Fantail, Grey Whistler, Grey Headed Robin and Orange Footed Scrub Fowl. ESW for several larger species was also overestimated, including Spotted Catbird, Metallic Starling, Little Shrike-thrush, Australian Figbird and Sulphur-crested Cockatoo (Figure 4.5).

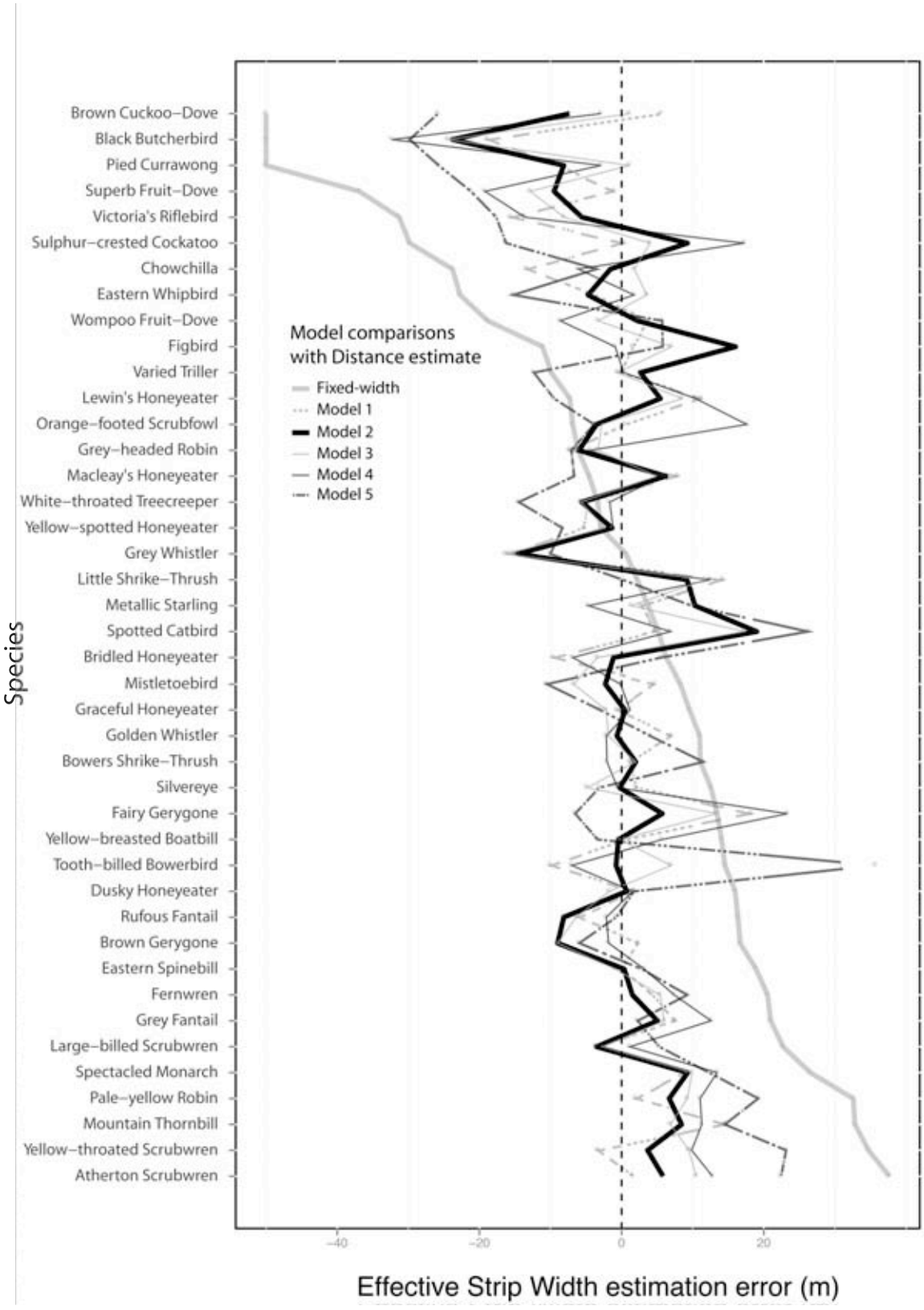

Figure 4.5. *Model performance for a hierarchical series of 5 models of decreasing complexity. Modeled ESWs are compared to estimates calculated in the Distance software as a "best estimate", and a fixed width model as a "worst estimate" (bold grey line). Model performance is assessed based on the departure from ESW estimated directly in the distance software, represented by the dotted line of "zero difference". Species are ranked from the origin in order of increasing ESW.*

4.3.4 Model testing

Finally, I tested the utility of this model in predicting ESW for birds in novel assemblages by comparing the measured and predicted values both in the AWT where the models were trained and for new data from surveys of birds assemblages in adjacent rainforests in CYP and CQC (Table 4.2). The partial model incorporating body weight, maximum detection distance and mean foraging height (model 2) outperformed the full model for data collected in the CYP rainforests (Table 4.2, r^2 = 0.812), though the full model (model 1) performed better in CQC (Table 4.2, r^2 = 0.82). The model trained in the AWT predicted ESW effectively within this region (Figure 4.6a) as well as in the CYP (Figure 4.6b) and CQC (Figure 4.6c) even for unique species in these regions for which the model had not been trained. Exceptions to this however include several species in CYP: Spotted Catbird *(Ailuroedus melanotis)*, Trumpet Manucode *(Phonygammus keraudrenii)*, Wompoo Fruit-dove *(Ptilinopus magnificus)* and Black Butcherbird *(Cracticus quoyi),* and two species in CQC: (Noisy Pitta *(Pitta versicolor)* and White-throated Tree-creeper *(Cormobates leucophaea)*. The simpler model with only body mass also predicted well for data in the adjacent regions, (CYP, Table 4.2, r^2 = 0.657, CQC, Table 4.2: r^2 = 0.715), as did the model using only maximum detection distance (CYP, Table 4.2: r^2 = 0.676, CQC, Table 4.2: r^2 = 0.640).

Table 4.2. *results of model testing in adjacent rainforest communities on Cape York Peninsula (CYP) and the Central Queensland Coast (CQC). Model names correspond to the models tested in the AWT. N Values refer to the number of species considered to have sufficient sampling (35 records, see text for a justification of this sample size) for a full Distance analysis estimate of ESW, with which to compare the model predictions.*

Region		Model	N	Intercept	Slope	D.f	F-statistic	r^2	P-value
CQC	**1**	**full model**	22	12.27	4.28	20	97.0	**0.820**	<0.001
CYP	**1**	**full model**	28	-7.80	6.08	26	111.2	0.803	<0.001
CQC	**2**	**Body mass + maximum detection distance + foraging height**	22	13.63	4.80	20	71.7	0.771	<0.001
CYP	**2**	**Body mass + maximum detection distance + foraging height**	28	-7.10	5.86	26	117.7	**0.812**	<0.001
CQC	**3**	**Body mass + maximum detection distance**	22	14.60	5.26	20	56.7	0.726	<0.001
CYP	**3**	**Body mass + maximum detection distance**	28	-3.23	6.46	26	85.2	0.757	<0.001
CQC	**4**	**Body mass**	22	5.70	6.53	20	53.6	0.715	<0.001
CYP	**4**	**Body mass**	28	-9.19	8.92	26	52.8	0.657	<0.001
CQC	***5***	**Maximum detection distance**	22	13.85	6.45	20	38.3	0.640	<0.001
CYP	***5***	**Maximum detection distance**	28	-5.91	8.17	26	57.2	0.676	<0.001

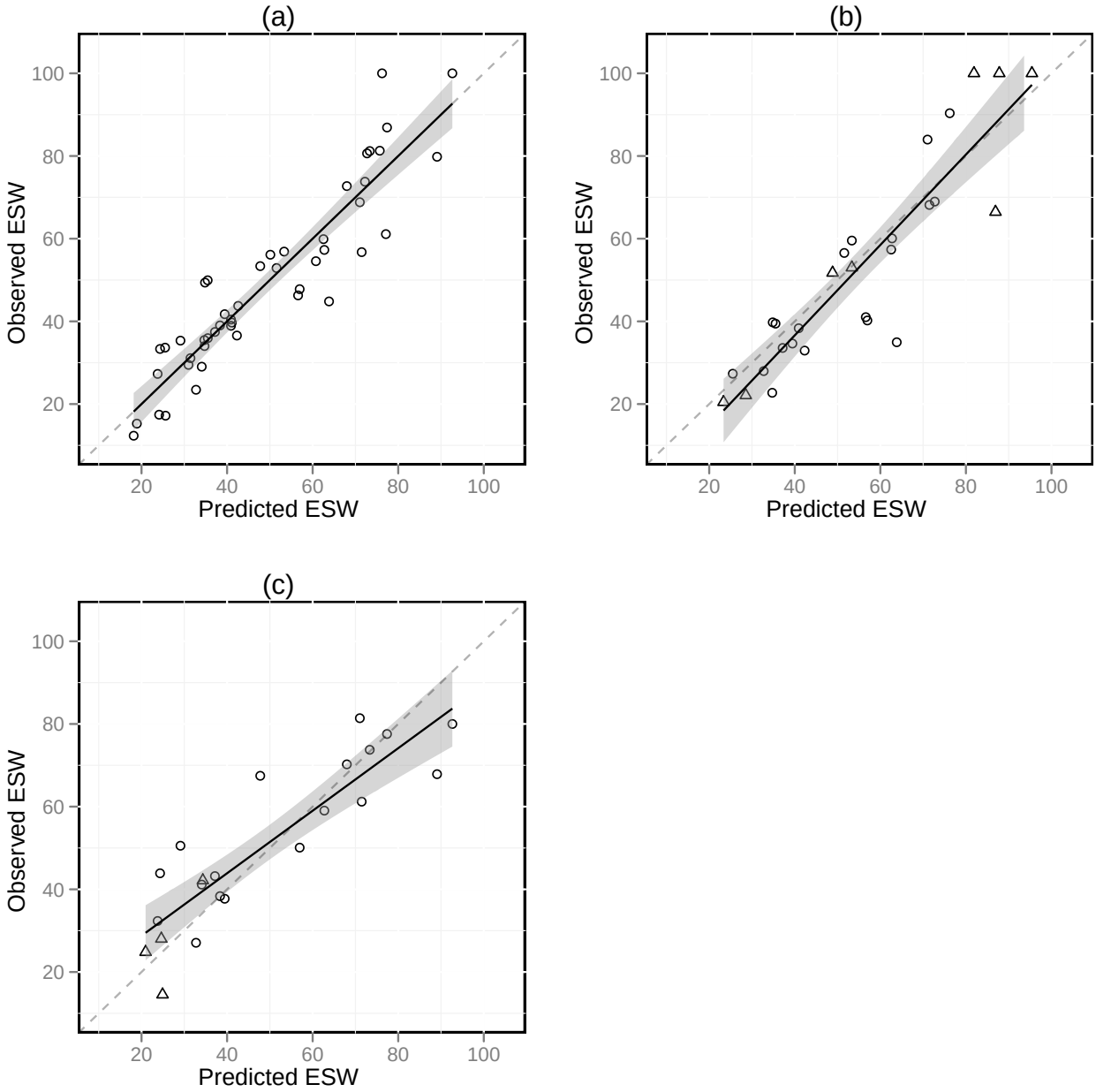

Figure 4.6. *Comparison of observed ESW (x axis) and predicted ESW (y axis) using model 2 (incorporating weight + maximum detection distance + foraging height) for species in the AWT (a), CYP (b) and CQC (c). Each point represents a species with sufficient data for model fitting in the program Distance (35 records). The regression lines represent the simple linear model regressing predicted against observed values, and the shaded area shows the 95% CI around the model. Species for which the AWT model was not trained are marked with a triangle.*

4.5 Discussion

I show that in our audio-visual surveys of rainforest birds, around 85% of variation in ESW among species can be explained as a simple function of body mass, mean foraging height and maximum detection distance (model 2). The importance of body mass is consistent with previous findings of the influence of body mass on call intensity or volume in birds (Brackenbury, 1979). However, maximum detection distance remained important, consistent with findings in the literature

(Alldredge *et al.* 2007b), suggesting a mass-independent effect of song volume is also present. The height of calling birds in forest strata has been found to influence transmission of bird calls (Mathevon *et al.* 2005) and so its inclusion in the top performing model (model 2) here also seems justified. Importantly, model 2 also performed well in predicting detectability across a broad range of species both in the AWT and independent test regions north and south, explaining 77% to 81% of the variation in ESW of birds in the CQC and CYP respectively. This is despite the presence in these assemblages of several species which do not occur in the AWT or are at insufficient abundance there for measuring ESW using Distance analysis. These novel species tended to be well accommodated by the AWT model, suggesting that this approach is broadly applicable rather than being region-specific. Model 2 also represents a reasonable compromise between explanatory power and data availability. Nonetheless, it does require ecological information derived from field data (foraging height), and some in formation about the detection process (maximum detection distance). I suggest however that the small investment of field effort to quantify foraging heights and maximum detection distances is justified by substantial improvement in the utility of the resulting bird survey data relative to fixed width transect, due to the marked differences in detectability between species. To this end, even models relying on body mass alone provided a substantial improvement over fixed-width models for estimating density of the majority of species.

4.5.1 Limitations and sources of error

The overall performance of the models demonstrates that knowledge of the ecological characteristics of species, combined with a minimum of field measurements, can be successfully used to convert count data to estimates of density using this approach. However, it is important to note some limitations of this method. Firstly, detectability for several species was either over- or under-estimated by the best performing models. It remains to be investigated in more detail, but I suggest that in a model designed to estimate ESW in combined audio-visual surveys, interspecific variation in the ratio of cue types could influence ESW. For example, species with soft or indistinct calls may be more often visually recorded (e.g. Atherton Scrub Wren (*Sericornis keri))* and hence underestimated by models incorporating call characteristics, while species with louder or more distinctive calls (e.g., Grey Whistler *(Pachycephala simplex))* may be overestimated by models incorporating physical characteristics. Factors influencing the relative importance of different cues (such as call distinctiveness) may thus play a role in driving ESW independently of maximum detection distance for problematic species.

Secondly, testing of the models outside the AWT also highlighted several cases in which the model performed less-well when applied to novel assemblages. These included both novel species for the

model, as well as some that had been involved in model training. This may indicate that differences between both species and populations are important in driving detectability variation among bird assemblages. This highlights the role of our methods as a compromise between full distance sampling and indices-based approaches. Lastly, in this study I did not attempt to quantify errors in identification or in distance estimation, though these undoubtedly play a role in contributing to observed variation (Alldredge *et al.* 2007c). As such, the models constructed here also retain an element of the subjectivity in estimations of distance to detected individuals during distance surveys. In rainforest bird surveys with a strong component of audio detections however, this subjectivity may be to some extent unavoidable. I suggest as an immediate solution only increasing investment in observer training, particularly in distance estimation and in gaining sufficient experience with the bird fauna of interest (Lindenmayer *et al.* 2009). While the approach I present is an improvement over fixed-width approach to estimating density from count data, the variation in ESW driven by species' idiosyncrasies would suggest a continued role for distance sampling.

4.5.2 Applications

This approach has several potential applications in ecological and population monitoring studies. Firstly, provided field methodologies are standardised, the models can be used to calibrate existing count data, converting indices of relative abundance to estimates of absolute density to facilitate the exploration of a range of macroecological questions (an example being investigation of the relationships between density and diversity, e.g. Ding *et al.* 2005). The same approach has potential application in analysis of historical trends. Calibration of count data using estimates of ESW could allow the analysis of temporal trends in absolute population size, a crucial tool in conservation management, and in understanding the impacts of processes such as climate change on bird populations (Shoo at al. 2005) and the threat of low populations size for rarely observed species. Importantly however, both of these applications depend critically on standardisation of field methods for the calibrations to be valid. While I show in the present study that our models can be used to predict ESW of species for which the models have not been trained, and the results of chapter 3 also demonstrated that variation in habitat structure was insignificant relative to the variation between species, the same will not be true in applications to novel habitats. In addition, some effect of habitat structural variation was shown in chapter 3, suggesting that where available, direct Distance analysis-derived estimates are desirable. This also highlights the necessity of Distance sampling as a component of the approach in transferring it to new habitats and assemblages

Even when distance sampling is used to overcome such habitat effect however, tropical avifaunas may present a particular challenge due to the presence of many rare species (Terborgh *et al.* 1990; Thiollay 1994). Pooling distance data across groups of similar species has been suggested previously (Marsden *et al.* 1997). It was noted, however, that such density estimates should be interpreted cautiously because detectability patterns may well differ between species. Alldredge *et al.* (2007a) proposed a more explicit formulation of this approach, grouping species according to measurements of maximum detection distance and song rate. Here this reasoning is extended by providing for the first time a data-driven framework for understanding the factors influencing variation in detectability between species. This framework includes a hierarchy of models of increasing complexity, providing a tool to approach the problem of modeling rare species that is flexible with respect to data requirements. Importantly however, our results also indicate idiosyncratic influences of some species' calls, physical characteristics and behaviour on their detectability characteristics. There is thus a continued role for Distance sampling in several capacities: in collecting basic information for the models (maximum detection distance), in applying this approach in different habitats and assemblages, and in estimating density of species with unusual detection characteristics that are difficult to model using this approach.

4.5.3 Conclusions

The approach promises to be useful in increasing the utility of unadjusted count data by correcting for variation in detectability between species. Within similar habitats this approach will be useful in macroecological studies at scales where distance sampling may not be practical, and in studies where information on absolute population size is needed, such as in analyses of population size. In addition, the approach will be useful in estimating the densities of rare species for which distance analysis is impeded by lack of data, providing an explicit framework for identifying the factors which influence their detectability and yielding vital density information for conservation managers. This approach thus provides a much-needed tool in cost effective survey and monitoring of rainforest bird populations. In chapter five I apply this ESW modelling approach in combination with direct distance sampling to estimate density of rainforest birds across the elevational gradients in the CYP AWT and CQC, in order to disentangle drivers of density and diversity. In chapter 6 I then apply the same approach in analyses of species' elevational density profiles, the results of which will be useful in detecting population trends in a changing climate.

Chapter 5. Climate instability at multiple temporal scales drives a unimodal species-energy relationship in a montane tropical avifauna

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[1]Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia.
[2] School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia.

"The primary challenge in the future will not be simply to accept or reject individual hypotheses, but rather to determine the circumstances under which the various causal factors are most important, how they interact, and how they can be combined into a more comprehensive and multi-factorial model"

(Heaney 2001)

Plate 5. *Grey-headed Robin (*Heteromyias albispecularis*), an endemic to the Australian Wet Tropics, reaches its highest density in cooler rainforests of mid and upper elevations.*

5.1 Abstract.

The More Individuals Hypothesis (MIH) proposes that productive environments support more species, as they support higher population density and hence reduced rates of extinction. However, this does not predict the declines of species richness often observed at high productivities in natural systems. Here I test the assumptions of the MIH hypothesis in a diverse avian assemblage in rainforest of the Australian Wet Tropics. A unimodal species-energy response has previously been shown for birds across the elevational gradient in this system. I estimated the rate of energy flux (energy consumption), population density and species richness of rainforest birds from 44 field sites across the region and generated spatially matched indices of Net Primary Productivity from remotely sensed data. The combined data enabled a comprehensive analysis of the flow of energy from forest primary productivity to density of birds and ultimately species richness. Evidence is found for a decoupling of Net Primary Productivity and species richness in this system, attributed to a combination of resource seasonality and unexploited resources in high productivity forests. This corresponds directly to a paucity of regionally-endemic birds in highly productive rainforests of the lowlands, probably as a result of non-random extinctions during historical fluctuations in rainforest distribution due to climatic changes throughout the Quaternary. These results suggest that historical environmental instability, coupled with contemporary resource seasonality, are important moderators of the More-Individuals Hypothesis, leading to lower than expected density and species richness in high productivity forests.

5.2 Introduction

Montane tropical rainforests, and particularly their avifaunas, have played an important role in the development of theory about drivers of biodiversity pattern (Terborgh 1977). Widely accepted to consist of a monotonic decline from lowlands to uplands (Rohde 1992) elevational patterns of species richness have been assumed to mirror those across latitude (Stevens 1992) driven by analogous environmental gradients of decreasing temperature and productivity (Ruggiero and Hawkins 2008). Rainfall and temperature variation across elevation also drive strong gradients in productivity, which have previously been noted as potentially important drivers of patterns of species richness in montane systems (Terborgh 1977). Species-energy theory (Wright 1983) has provided a useful conceptual framework for understanding these patterns, building on the theory of island biogeography (MacArthur & Wilson 1963) by incorporating energy availability as a modifier of the effect of area in determining population sizes, and hence equilibrium species richness. In a more explicit formulation, the More-Individuals Hypothesis (MIH) (Wright *et al.* 1993) proposes that increased energy availability results in higher population densities and reduced extinction risk, thereby facilitating a greater accumulation of species in high productivity areas. Thus in its simplest form the MIH predicts a monotonic positive species-energy relationship (Srivastava & Lawton 1998), which has found empirical support in numerous studies (for reviews see; Evans at al. 2005b; Hillebrand & Cardinale 2010). However, a unimodal species-energy response (in which species richness increases linearly with available energy up to a peak, and then declines at higher energy availability), has been described in a wide variety of taxa and ecosystems, from montane plant communities (Whittaker & Niering 1975) to marine benthos (Rex 1981) (for reviews see e.g. Rohde 1992; Waide *et al.* 1999). The unimodal species-energy response has even been described as "ubiquitous" (Huston 1994), and it is proving a challenge to explain the decoupling of richness and energy at high productivities from within the MIH framework (Rosenzweig & Abramsky 1993; Mittelbach *et al.* 2001).

Energy availability may be an important driver of diversity (Currie 1991; Clarke & Gaston 2006), but important roles for historical climate instability and seasonality have also been hypothesised (Williams *et al.* 2010a). Climate history has been found to be an important influence on patterns of bird species richness at continental scales (Hawkins *et al.* 2003b), similarities that suggest the analysis of montane systems may shed light on drivers of diversity pattern more generally (Brown 2001; Lomolino 2001). Moreover as with latitudinal patterns of species richness, it seems unlikely that observed elevational patterns of species-energy relationships are the result of a single driver,

but of interactions between a variety of factors (Terborgh 1977), leaving the task of disentangling their relative contributions (Heaney 2001).

Mid-elevational peaks in species richness previously reported have rarely measured energy availability (Kikkawa & Williams 1971; Terborgh 1977; Blake & Loiselle 2000; Brown 2001), or have employed climate surrogates (Williams *et al.* 2010a), making species-energy hypotheses difficult to test explicitly in terms of the MIH. The species-energy relationship may also vary between trophic or phylogeographic groups (Terborgh 1977; Waide *et al.* 1999; Kattan & Franco 2004), and depend on the level of equilibrium with current conditions, such that climate influences can range from the long-term historical (Hawkins *et al.* 2003a) to the seasonal (Carrara & Vazquez 2010). Along with disturbance (McCoy 1990) and area (Rahbek 1997) such factors may be collinear with environmental variables, confounding analysis of specific drivers. In rainforest bird communities, habitat structural effects (Terborgh 1977), interspecific competition (Jankowski *et al.* 2010) and individual energy consumption (Ding *et al.* 2005) may also interact across elevational gradients to influence assemblage structure and diversity. Scaling up from microcosm studies (e.g. Srivastava & Lawton 1998) to regional scales is also hampered by a lack of high-resolution data on species density over the necessary large spatial areas. Meso-scale studies that examine the intermediate links along the "pathway" between energy and species richness using direct measures of energy, density and local diversity are therefore needed in order to test predictions of the MIH (Srivastava & Lawton 1998; Yee & Juliano 2007).

This "energy-richness pathway", consisting of links between Net Primary Productivity (NPP), the energy consumption of the community (energy flux (E)), population density (N) and local species richness (S_α) provides a useful conceptual framework for examining departures from the monotonic species-energy relationship predicted by the MIH (Figure 5.1). Within this framework alternative hypotheses for drivers of a unimodal species-energy relationships can be localised to a decoupling at a particular step in the pathway, facilitating the separation of hypothesised contributions from different drivers with reference to explicit mechanisms. At step 1 a decoupling occurs in the transfer of energy from primary producers to the community (measured by energy flux). At step 2 energy flux is not translated into increased density. At step 3, increased NPP at high productivity sites is translated into correspondingly increased bird energy flux, but this is not translated into increased density. At step 4 increased density does not result in higher species richness.

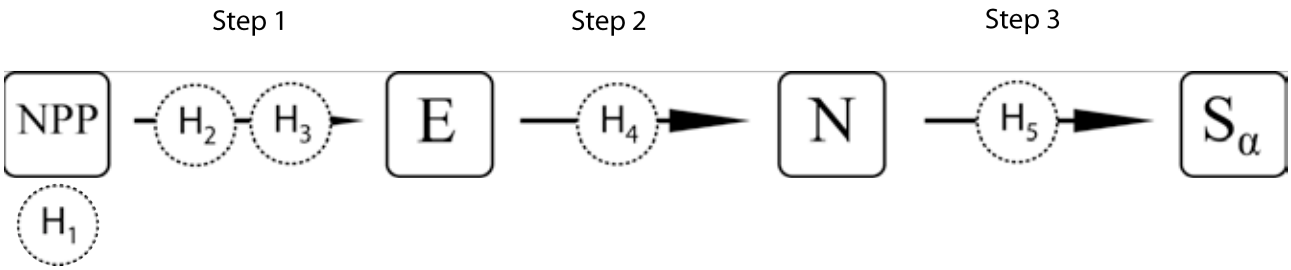

Figure 5.1. *Pathway diagram describing the mechanistic relationships between Primary Productivity (NPP), Energy Flux (E), Population density (N) and Species richness (S_α). The steps in the pathway are numbered, and the locations to which each of the alternative hypotheses applies (H) are indicated by the dashed circles (see text for an explanation of the hypotheses).*

Here I examine support for localisation for the decoupling between energy and species richness in a tropical montane bird community, for which a unimodal species-energy response has been documented. In the Australian Wet Tropics (AWT), bird species richness is observed to be lowest in low productivity forests, and increases with additional productivity, but declines again in high productivity environments (Williams *et al.* 2010a). My analysis of these patterns within the framework of the MIH is made possible by major improvements in regional data as recommended by Williams *et al.* (2010). I use remotely-sensed estimates of forest productivity in place of climate surrogates, and substitute estimates of relative abundance with actual density, allowing the explicit testing of energy-based mechanisms along the species-energy pathway. I also generate site estimates of species richness (α diversity) to examine the species-energy response independent of area. Two main mechanisms were proposed by Williams *et al.* (2010) to explain the decoupling of species richness and available energy in this system. Firstly, it was suggested that bird richness responded to seasonal resource bottlenecks in energy availability, rather than primary productivity averaged across the year, suggesting no decoupling in the species-energy pathway, but an inappropriate measure of energy availability (H_1). I use seasonal estimates of NPP to test this hypothesis. Alternatively, non-random extinction due to historical processes may have eliminated specialists from particular resource niches, compromising the uptake of energy in productive environments, localising decoupling at step 1 (H_2). Here I analyse differences in energy-richness response between endemic and widespread species, likely to reflect equilibrium with both historical and annual temporal scales of climate variability respectively, and I compare patterns between regions with contrasting biogeographic history to explore the generality of these differences.

Based on evidence from the literature additional hypotheses are also testable within the MIH framework. Elevational patterns of species richness in montane tropical rainforest birds have

previously been shown to vary importantly between trophic groups, attributed in part to energy availability (Terborgh 1977), suggesting a further plausible explanation that also localises the decoupling at step 1, but with the difference being that the assemblage-wide pattern may be influenced by particular guilds (H_3). Here I explore the patterns of different guilds, and interactions with patterns of endemicity to test this mechanism. Ding *et al.* (2005) also identified a decoupling between montane tropical bird energy consumption and density as the primary cause of a unimodal species-energy relationship. Here I index individual energy consumption (step 2) to test the hypothesis that increases in consumption at higher productivity sites could constrain population density and species diversity (H_4). Finally, competition acting at step 3 may also be important in structuring diversity in montane rainforest avifaunas (Terborgh & Weske 1975), and may act preferentially in high productivity areas (Ballance *et al.* 1997). I index energetic dominance to test the hypothesis of a few dominant species in productive sites reducing local species richness despite high available energy (H_5). The results of this step-by-step multifactorial approach have bearing on our understanding of drivers of diversity pattern both within this system, and in tropical montane faunas elsewhere, as well as informing our understanding of biodiversity patterns more generally.

5.3 Methods

5.3.1 Study area and sampling locations

The location of study sites follows the description presented in the preceding chapters, and sampling here was focused within the Australian Wet Tropics Bioregion (AWT) between -15˚45'32.69"S 145˚ 1'53.87"E and 19˚18'0.65"S 146˚ 9'41.17"E) (map shown in Figure 3.1). In addition I used data collected in the Clarke and Conway Ranges in the Central Queensland Coast Bioregion (CQC) between 20˚16'53.11"S 148˚18'8.45"E and 21˚23'25.87"S 148˚42'9.65"E (see map in Figure 4.1), and in the McIlwraith and Iron Ranges in the Cape York Bioregion (CYP) between -14˚ 8'33.78"S 143˚22'36.65"E and -12˚37'24.44"S 143˚14'22.22"E (map in Figure 4.2). Full descriptions of study region and sampling design are provided in chapters 2, 3 and 4. Bird survey methods followed Williams *et al.* (2010) (described in more detain here in chapter 2), and build on the data analysed therein, supplemented with targeted data collection from poorly sampled locations and environments in the AWT, as well as the new data from neighbouring regions.

5.3.2 Climate

The climate of the study regions is described in detail in chapter 2. Briefly however, rainforest sites across three study regions cover broad and over-lapping environmental space in terms of mean annual temperature and rainfall (Figure 5.2). Variation within regions is dominated by the

elevational gradient, with lowland mean annual temperatures reaching 21.75 ˚C in CQC, 24.33 ˚C in the AWT and 26.41 ˚C in CYP, while temperatures in the uplands fall to 17.74 ˚C in CQC, 17.16 ˚C in the AWT and 21.82 ˚C in CYP. Mean annual rainfall in the lowlands reaches 1721 mm in CQC, 2510 mm in the AWT and 1488 mm in the CYP, and in the uplands reaches 2674 mm in CQC, 6572 mm in the AWT and 1736 mm in CYP. This range of climate variation is well sampled by the standard sites visited in this study (Figure 5.2). These patterns of temperature and rainfall also combine to produce important variation in the spatial pattern of NPP within rainforest across the elevational gradient, described below.

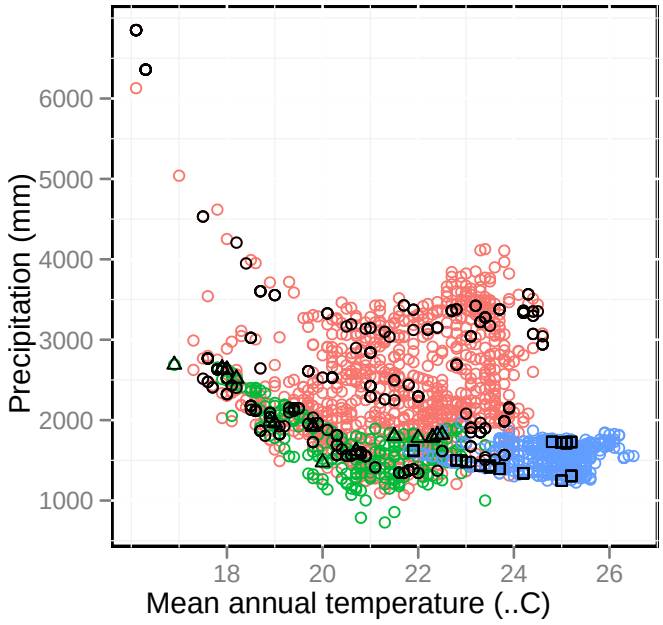

Figure 5.2. *Environmental space of the three study areas as defined by modelled surfaces from BIOCLIM for mean annual temperature and mean annual rainfall. Samples from a regular grid of 2000 points across rainforest are shown in red for the AWT, green for the CQC and blue for CYP. Overlaid in black are the positions in this climate space of the sampling points visited in the current study, with symbols identifying the three bioregions: CQC (squares); AWT (circles); and, CYP (triangles), corresponding to those used in subsequent plots. Bird survey data for sampling points shown here in black are summarised into their respective site averages in all subsequent analyses.*

5.3.3 Vegetation

Vegetation in the study region is described in detail in chapter 2. Briefly, however, rainforests in north-eastern Australia range from complex mesophyll vine forests in the coastal lowlands to notophyll vine forest and microphyll fern thicket on high peaks and plateaus, although the majority of sampling in this study was conducted in simple to complex notophyll vine forests (Queensland Herbarium 2011). The elevational gradient in vegetation structure here is much less marked than in systems that span greater elevational change (e.g. Terborgh 1977), thus in this analysis I focus on

energetic rather than structural differences related to the vegetation. That said, the study area experiences natural disturbance from cyclones (Turton 2008) such that forests have been described as a mosaic of different stages of recovery from storm damage, particularly in the coastal lowlands (Webb 1958). While fragmentation from logging and agricultural land uses has had a strong influence on rainforest extent in the AWT in particular (Stork & Turton 2008; Hilbert 2010), sampling in this study was focussed in large patches and areas of contiguous forest to limit as much as possible the confounding influence of current habitat area on patterns of diversity.

5.3.4 Distance sampling methods

Bird surveys consisted of 30-min, 150-m audio-visual surveys through rainforest between 0600 and 0930 h to coincide with peak calling activity of birds, as used in previous studies in this system (e.g. Williams & Middleton 2008), and described in detail in chapters two and three. Data used here included information from surveys conducted by other observers since January 2000. In addition to these I conducted distance sampling surveys across all regions in which the perpendicular distance of all individuals was recorded, as described in chapter 3, and analysed in the program Distance (Thomas *et al.* 2002). This enabled a detection function to be derived for each species that characterised the decay of detectability with distance from the transect. Each sampling site was surveyed an average of nine times to allow the accurate estimation of mean density of each species present at the site across all surveys at that site. For species and site combinations yielding more than 35 records, Effective Strip Width of surveys was estimated directly, while for less common species, data were pooled across sites until sample sizes were sufficient to estimate ESW. For very uncommon species density was estimated using the ESW modelling methods described in chapter 4. This collection of directly estimated and modelled Effective Strip Widths was then used to convert count data, including those collected previously without distance sampling (Williams *et al.* 2010a) into accurate estimates of density for analysis in the MIH framework. Cassowaries are encountered in my surveys, and their density is thus difficult to estimate by this method, but the may make an important contribution to energy in lowland forests. For this reason densities for this species used were calibrated here against published density data in Moore (2007).

5.3.5 Bird species richness

All statistical analyses were carried out within the R framework for statistical analysis version 2.13.1 (R Core Development Team 2011). To estimate species richness at the local scale (α diversity) I aggregated data from sampling points within each site (see chapter 2 for description of the sampling arrays). Bird species richness at each site was estimated using the Chao statistic (Chao *et al.* 2000) calculated using the “fossil” package (Vavrek & Larsson 2011) in R, which uses

an approach derived from the software "EstimateS" (Colwell 2004). Ten repeated random resamples without replacement of two survey's data from each site were used to calculate Chao's statistic using an MCMC randomization process to remove the effects of uneven sampling effort on richness estimation. While these estimates do not plateau towards an estimate of true regional (γ) richness, they provide the "snapshot" of local α diversity of interest in this study.

5.3.6 Bird energy flux

I used published equations characterising the relationship between metabolic rate and body mass for birds (Nagy at al. 1999) and determined the daily flux of energy represented by each species per hectare by multiplying species-specific estimates of body-mass-corrected metabolic rates by the estimated density for that species at each site. I generated estimates for the assemblage as a whole and for subgroups by summing those values across relevant species subsets. Body masses for each species used in the energy flux calculations where mean values compiled from a review of the literature summarized in the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB) (Marchant & Higgins 1990; Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Higgins, Peter, & Steele 2001; Higgins & Peter 2002; Higgins *et al*. 2006).

5.3.7 Guild definitions and endemicity

I classified species into broad trophic groups or guilds in the sense of Simberloff & Dayan (1991) based on published dietary information summarised in the HANZAB (see above for references), combined with expert knowledge used in previous studies of assemblage structure in this system (e.g. Williams & Middleton 2008). As in many tropical forest systems (Terborgh 1977), the dominant guilds in the study region were insectivores, frugivores, and nectarivores, with smaller numbers of species also representing omnivores, granivores and carnivores. Insectivores and frugivores were assigned to a trophic guild if that resource was considered to comprise more than ~50% of their diet. Nectarivore diets in Australia often include pollen, invertebrates and fruit (Barker & Vestjens 1990; Gartrell 2000) so here I included as nectarivores both specialists (e.g. lorikeets, some honeyeaters), and generalists (most other honeyeaters) which also take some fruit and invertebrate prey. Granivores included those species taking the majority of their energy from non-fleshy fruits. The carnivores were species including some vertebrate prey in their diet, though most in this assemblage also take some invertebrates, and omnivores were defined as those species taking a range of plant and animal materials. Following the taxonomy of Christidis and Boles (2008) and distributional data summarised in HANZAB I delineated two groups to quantify the effects of historical processes on the species-energy relationship. The first ("non-endemics") consisted of species widespread in Australia and/or New Guinea (PNG), the second ("endemics")

consisted of species restricted to the AWT (12 species), CYP (one species) or CQC bioregion (one species). In addition to this, I added to the list for CYP 13 species which also occur extralimitally in PNG but nowhere else in Australia, as for the purposes of this analysis these species reflect the unique biogeographic history of the CYP.

5.3.8 Net Primary Productivity

I used the Enhanced Vegetation Index (EVI) as an index of Net Primary Productivity. EVI is part of the MOD13A2 high resolution satellite product (1 km grid) from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS), available for download from: https://lpdaac.usgs.gov/lpdaac/products/modis_products_table. EVI is designed to enhance the vegetation signal in high-biomass regions and has been shown to have a strong linear relationship with on-ground measures of NPP in tropical forest systems (Huete *et al.* 2002) where, unlike NDVI, it does not saturate (Huete *et al.* 2006). As a result EVI can detect even subtle variation in NPP in tropical evergreen forests (Xiao 2005). Downloaded tiles were cropped and reprojected using the MODIS Reprojection Tool (https://lpdaac.usgs.gov/lpdaac/tools), and summarised using the SDMTools package in R (VanDerWal *et al.* 2010). Estimates of EVI available at 16-day intervals were averaged for each month over the ten-year period from February 2000 to February 2010 to coincide with the period of data collection for birds. I then calculated three summary parameters of EVI: mean monthly NPP = the average of monthly EVI estimates across the ten-year sampling period; minimum NPP = the moving-window average of the three consecutive months with the lowest combined EVI values; seasonality of NPP = the co-efficient of variation of EVI within years over the ten-year sampling period.

5.3.9 Historical rainforest instability

Historical rainforest instability for the Australian Wet Tropics has been modeled previously using a combined BIOCLIM envelope and logistic regression approach to estimate the variation over recent geological time in the suitability of climate for rainforest in the region (Graham *et al.* 2010). This analysis yielded coefficients of variation of the cumulative environmental suitability scores for rainforest, projected onto models of historical climate at 500 years intervals over the last 18,000 years. Here I used these data to index environmental instability as a potential driver of patterns of species richness, choosing values from a dynamic model allowing 20m per year dispersal of rainforest in response to climate fluctuations (see Graham *et al.* 2010 for an explanation of the models and assumptions). These data were taken as an indication of the extent to which extinction filtration due to contraction or disappearance of rainforest (“rainforest instability”) may have played a role in shaping rainforest bird assemblages at each sampling site.

5.3.10 Statistical analysis

The relationships between each step in the species-energy pathway (see Figure 5.1) were described using simple linear regression. The inclusion of a significant polynomial (2nd order quadratic) term was taken to indicate significant curvature. I also examined the evidence for significant segmented relationship by testing for the presence and location of breakpoints in the distribution using the regression approach implemented in the package "segmented" in R (Muggeo 2010). Segments where constrained to 0.3 of the data extent and breakpoints where determined iteratively using plausible starting values chosen visually based on the data (see Muggeo 2003 for a detailed explanation of the segmented regression approach).

I examined the relative contribution of different trophic guilds to the total energy flux and species richness of the assemblage using moving-window averages of values in binned productivity categories, limiting further analysis to the most energetically important guilds. I assessed the relative influence of NPP, variability in NPP and historical rainforest stability on patterns of total bird energy flux using a hierarchical multiple regression approach, using model fit (adjusted r^2), significance (p-values) and information content (AICc) in increasingly complex models. I repeated this approach for insectivores, frugivores, nectarivores and omnivores, endemic and non-endemic species, and in endemic and non-endemic insectivores, frugivores and nectarivores separately (there being no endemic omnivores in the study region). I applied segmented regression in cases showing significant curvature, estimating the location of breakpoints empirically. This approach allowed the isolation of the key drivers of patterns in energy flux and diversity in terms of both trophic groups and groups with contrasting biogeographic histories, and to contrast the relative importance of each factor for these subsets. Importantly, this approach also allowed the attribution of separate drivers to the increase and decrease phases of curved or segmented relationships, consistent with a multifactorial approach to understanding diversity pattern (Heaney 2001).

5.4 Results

5.4.1 Net Primary Productivity

Variation in NPP indexed by EVI showed a distinctive elevational pattern similar to indices derived from the climate surrogates of Schuur (2003) used in Williams *et al.* (2010a). Across the sampling sites surveyed in this study, lowland forests are highly productive, with mean monthly NPP declining steadily towards upland sites (Figure 5.3a: adjusted $r^2 = 0.399$, d.f. = 52 , F-statistic = 533.1 $p < 0.001$). Mean minimum NPP was ~0.05 units lower than annual averages, but was highly

correlated with mean monthly NPP ((Figure 5.3b: adjusted $r^2 = 0.952$, F-statistic = 533.1, d.f. = 52, $p < 0.0001$). In contrast the index of NPP seasonality indicated greater variability in low productivity areas than in high productivity areas (Figure 5.3c: adjusted $r^2 = 0.292$, F-statistic = 12.17, d.f. = 52, $p < 0.001$). Importantly mean monthly NPP and rainforest instability covary such that sites most unstable during the Pleistocene-Holocene tend to also be the most productive in the present-day (Figure 5.3d: adjusted $r^2 = 0.255$, F-statistic = 7.339, d.f. = 35, $p = 0.0021$).

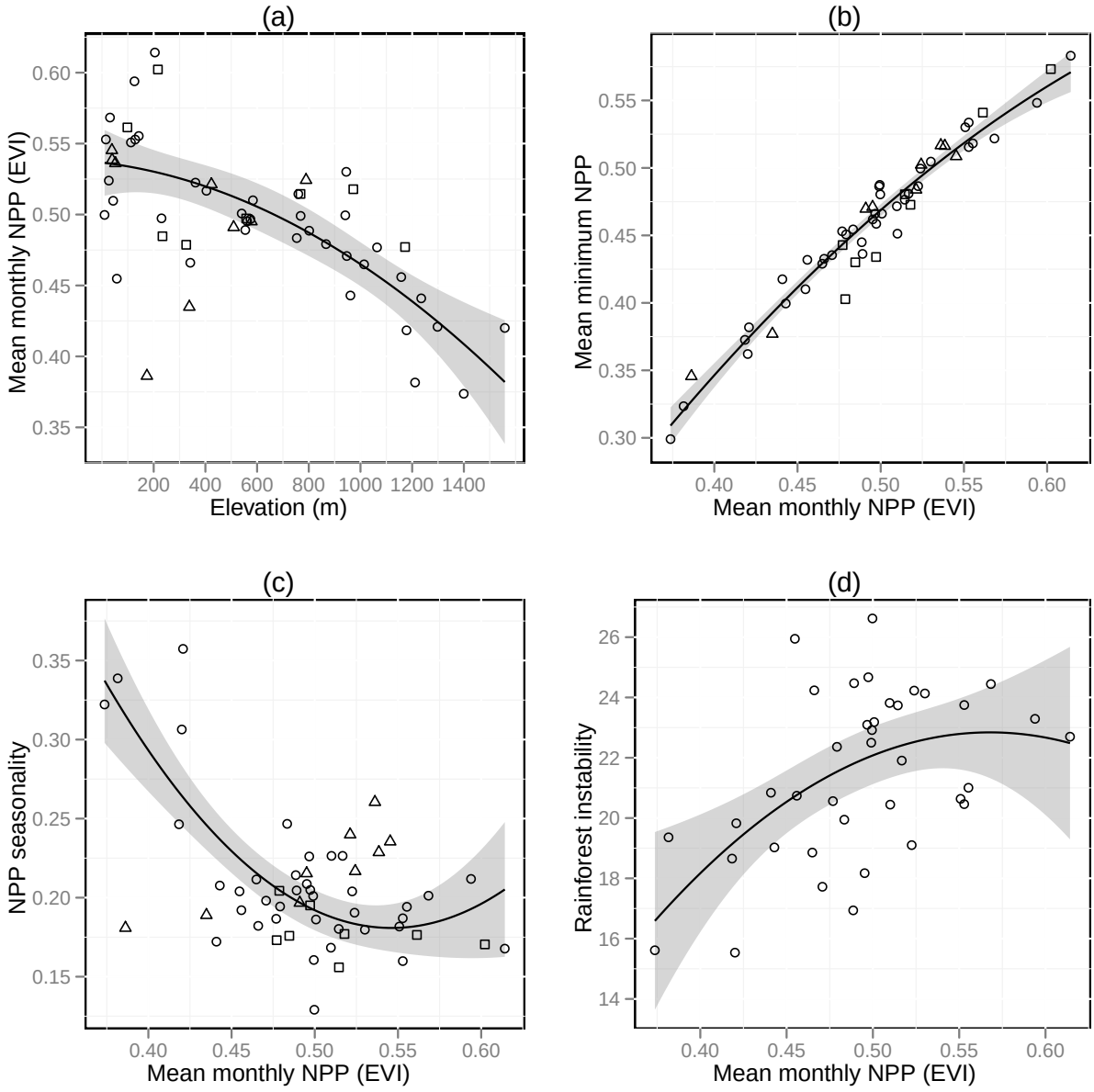

Figure 5.3. *Relationships between predictor variables across three bioregions. a) mean monthly Net Primary Productivity indexed with EVI declines with increasing elevation. b) mean minimum NPP is closely correlated with the mean annual NPP. C) seasonality of NPP decreases with increasing mean annual NPP. d) rainforest instability increases with increasing mean monthly NPP (note: rainforest instability data available for AWT only). Values for sites in the AWT are denoted with circles, for CQC with squares and for CYP with triangles. Regression lines are fitted using a linear model with a second order quadratic term, and the shaded area corresponds to the 95% confidence interval around the predicted values.*

5.4.2 Bird assemblage data

I collated data for a total of 40 sites (CQC = 7, AWT = 26, CYP = 7) comprising 39,077 individual bird records from 1037 surveys. Data included records of 107 species overall in 79 genera and 34 families (CQC = 51 species, 44 genera, 25 families; AWT = 88 species, 70 genera , 34 families; CYP = 66 species , 56 genera, 27 families). Despite these efforts, data for some sites in the CQC and CYP are limited relative to the decade of data available for the AWT, and I focus here on re-examining in finer detail the relationships in the AWT, and draw on the patterns shown by data in the CYP and CQC to indicate the generality of the trends. Based on our expanded data set, rainforest bird species richness in the AWT showed a clear unimodal or hump-shaped relationship with NPP. Lowest richness is found in low-productivity environments, highest richness in the moderate productivity environments, and lower richness again in the highest productivity environments (Figure 5.4a: dotted line for a 2nd polynomial regression model, adjusted $r^2 = 0.477$, F-statistic = 14.24, d.f. = 27, p-value < 0.0001). This pattern is better modeled as a segmented relationship with an increase and decrease phase separated at an estimated breakpoint mean monthly NPP value of 0.51 (Figure 5.4a solid lines, overall: F-statistic = 17.34, $r^2 = 0.524$, d.f. = 25, overall p-value < 0.001, increase phase F-statistic = 11.13, p = 0.002, decrease phase F-statistic = 23.73, p-value <0.0001).

At step two in the species-energy pathway, a qualitatively similar relationship was found between bird energy flux and NPP across all sites for the AWT (Figure 5.4b, 2nd order polynomial regression model, F-statistic = 2.34, $r^2 = 0.149$, d.f. = 25, p-value = 0.043). Again this relationship is better characterized by a segmented model, with a breakpoint estimated at a mean monthly EVI value of 0.48 (Figure 5.4b dotted line, $r^2 = 0.30$, d.f. = 25, p-value = 0.004, increase phase (dashed line) F-statistic = 1.48, p-value = 0.235, decrease phase (solid line) F-statistic = 11.44, p <0.0001). In contrast, bird density showed a positive monotonic relationship with bird energy flux (Figure 5.4c, F-statistic = 64.78, $r^2 = 0.815$, d.f. = 27, p-value < 0.0001). Similarly the relationship between species richness and density in the AWT was also positively monotonic (Figure 5.4d, F-statistic = 20.59, $r^2 = 0.575$, d.f. = 27, p-value < 0.001). These results indicate that decoupling between available energy and diversity in the AWT bioregion can be isolated at the step between energy flux and species richness, suggesting little role for either increased individual energy consumption or competition in depressing bird energy flux or species richness at high productivity sites.

Importantly, evidence from the energy-richness pathway in the rainforest bird assemblages of neighbouring regions suggest that the pattern observed in the AWT is not universal. In CYP energy

flux increased linearly with increasing NPP (Figure 5.5b, circles, F-statistic = 10.018, adjusted r^2 = 0.623, d.f. = 5, p-value = 0.025), as did energy flux with density (Figure 5.5c, circles, adjusted r^2 = 0.944, F-statistic = 102.790, d.f. = 5, p-value = < 0.001) and richness with density, (Figure 5.5d, circles, r^2 = 0.652, F-statistic = 12.240, d.f. = 5, p-value = 0.017). While a lack of data hindered the resolution of relationships in CQC, the relationship between bird density and energy flux there was significant and curved, with bird density peaking at intermediate levels of energy flux (Figure 5.5b, triangles, r^2 = 0.466, F-statistic = 7.102, d.f. = 6, p-value = 0.037) Full details of the pathway relationship in CYP and CQC are shown in Appendix 5.1.

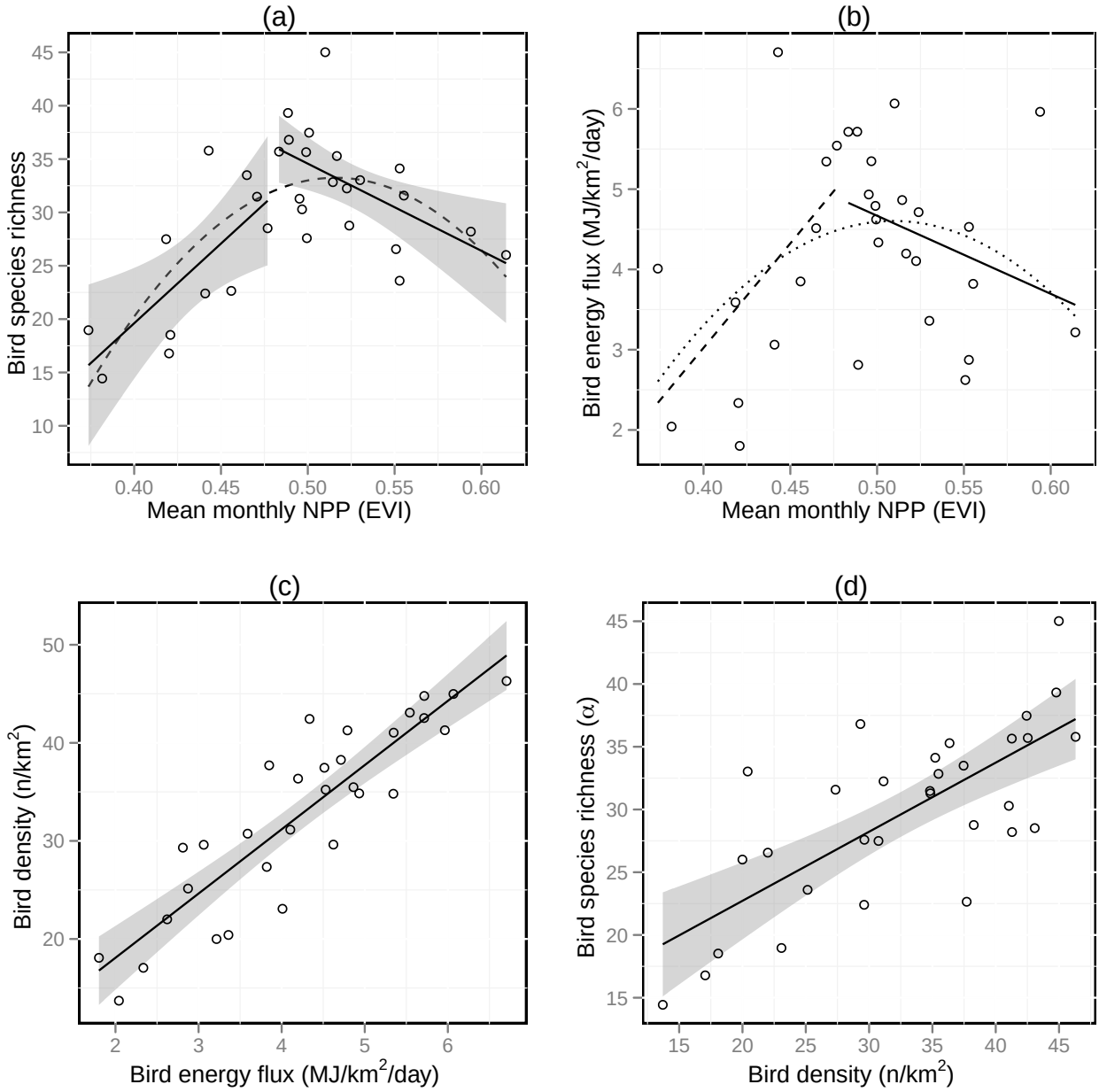

Figure 5.4. *Breakdown of the species-energy pathway in the AWT showing the relationship between: (a) species richness and NPP (mean annual EVI), (b) bird energy flux and NPP, (c), bird density and energy flux, and (d) bird species richness and density. Regression lines are fitted using a linear model with a second order quadratic term where curvature is indicated, and the shaded area corresponds to the 95% confidence interval around the predicted values. Breakpoints in the segmented regression are estimated empirically (see methods).*

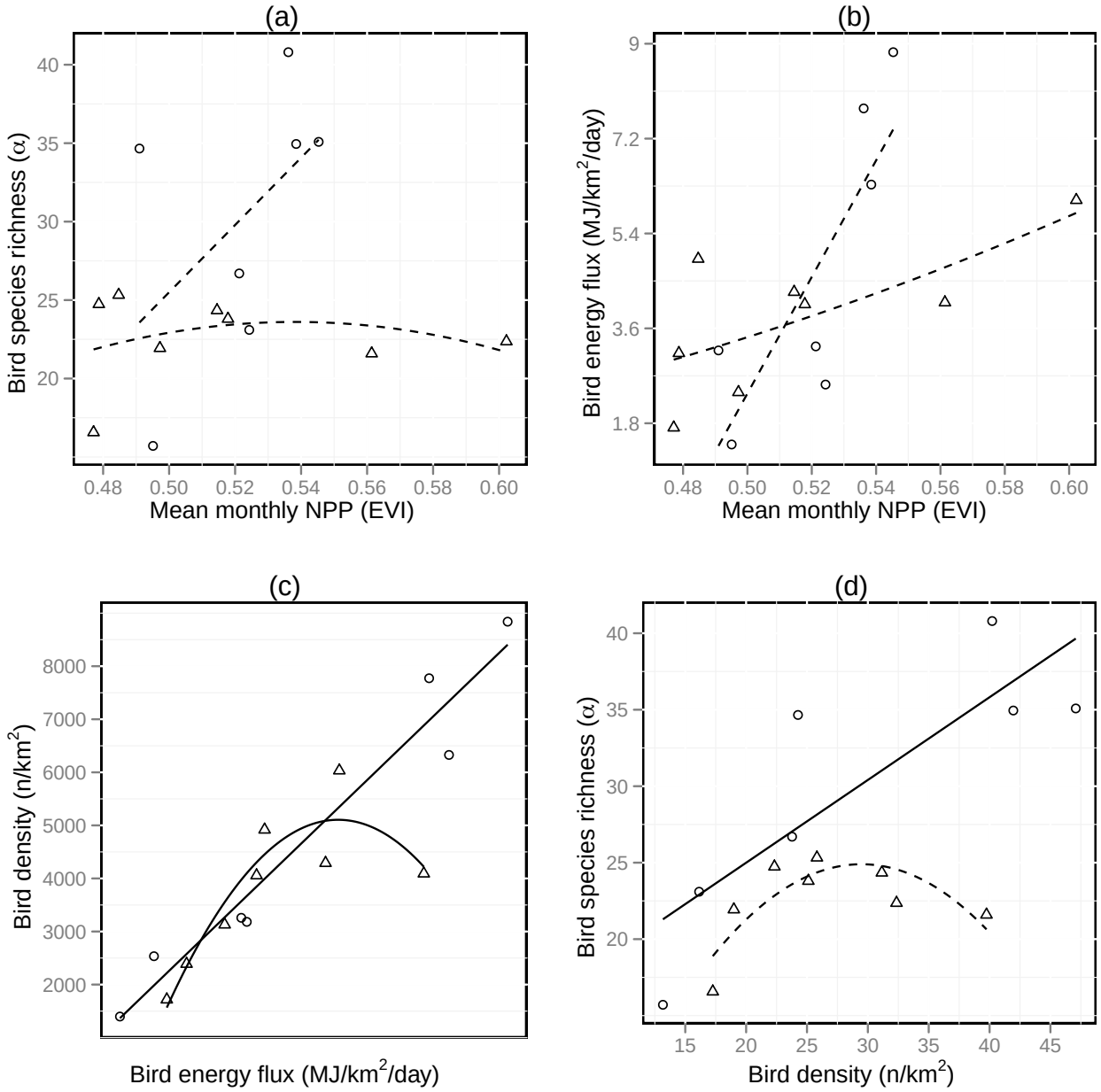

Figure 5.5. *Breakdown of the species-energy pathway in CYP and CQC showing the relationship between: (a) local species richness (α) and NPP (Mean Monthly EVI), (b) bird energy flux (Mj/km/day) and NPP, (c), bird density (individuals/km) and energy flux, and (d) bird species richness and density. Regression lines are fitted using a linear model, solid lines indicate a significant relationship, dashed lines were non-significant regression models.*

5.4.3 Alternative hypotheses

Seasonal bottlenecks in resources (H_1): The strong linear relationship between mean monthly and minimum NPP suggests that this index of a seasonal resource bottleneck cannot explain the unimodal species-energy relationship. Substituting NPP seasonality for mean monthly NPP improved explanation of energy flux (Figure 5.6a), but this relationship remained curved, peaking at moderate levels of NPP seasonality (2nd order polynomial regression, F-statistic = 10.8 , $r^2 = 0.403$,

d.f. = 25 , p-value = 0.0003,). There is a marginal improvement fitting this relationship with segmented regression (r^2 = 0.407, p < 0.001, d.f. = 25), but only the increase phase is significant (p = 0.011).

Non-random extinction (H_2): No relationship was observed between total bird energy flux and modeled estimates of historical rainforest instability across the AWT, shown in Figure 5.6b (F-statistic = 0.085, r^2 = -0.067, d.f. = 25, p < 0.918). This is despite a positive correlation between NPP and habitat instability (see Figure 5.3d above, F-statistic = 6.675, r^2 = 0.3281, d.f. = 28 p = 0.004).

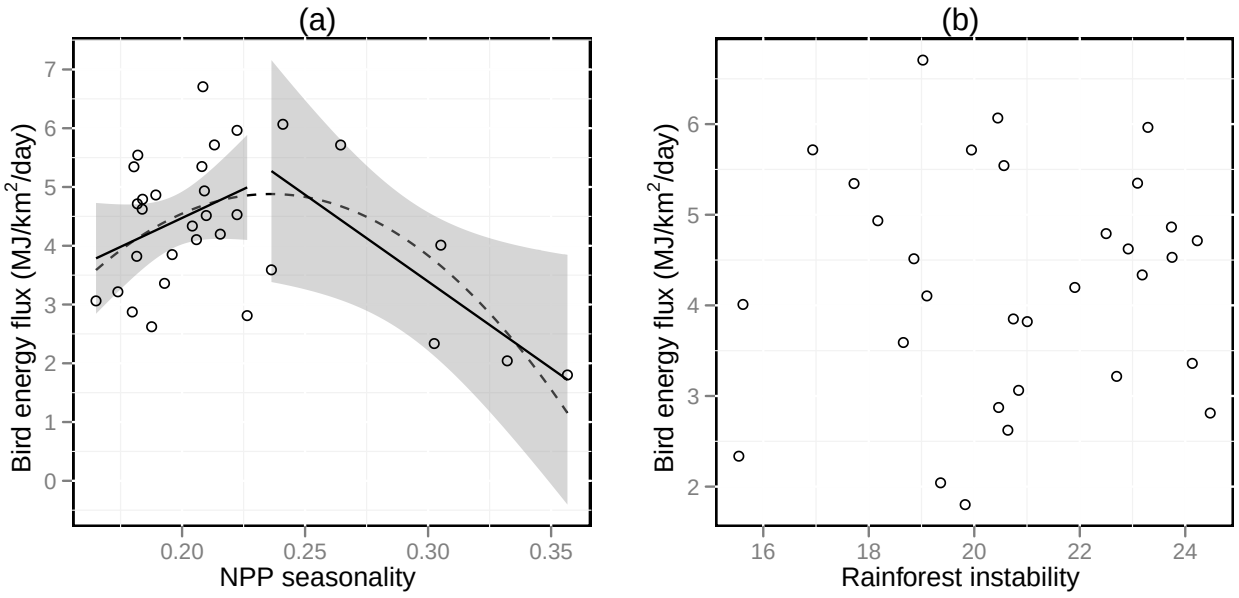

Figure 5.6. *Relationships between bird energy flux (MJ/km²/day) in the AWT and NPP seasonality (a) and historical rainforest instability (b). Regression lines are fitted using a linear model with a second order quadratic term, and the shaded area corresponds to the 95% confidence interval around the predicted values. The breakpoint in the segmented regression was estimated empirically (see methods).*

Trophic guilds track resources differently (H_3): The pattern of variation in total energy flux with NPP varied strongly between guilds across the NPP gradient (Figure 5.7). The majority of energy flux could be attributed to just three guilds, the insectivores, frugivores and omnivores, which between them accounted for 77% of the total energy flux across all sites (33.4%, 25.13% and 18.67% respectively), while the contribution from the remaining 4 guilds was relatively insignificant (nectarivores, 7.9%, granivores, 13.35% and carnivores 1.48%). Species richness followed a similar pattern, with the insectivores and frugivores accounting for 71.59% of the total

richness across all sites (45.45%, 26.13%). In terms of species richness however nectarivores (13.63%) replaced omnivores (3.4%) as the third most important group (Figure 5.8). Patterns across the gradient amongst the three dominant guilds also differed, with omnivores and frugivores both showing a trend of monotonically increasing energy flux (Figure 5.7, regression values for un-binned data in table 1.) and richness (Figure 5.8) from low to high productivity, while insectivores showed a significantly unimodal energy flux (regression values in Table 5.1) and richness response across the productivity gradient.

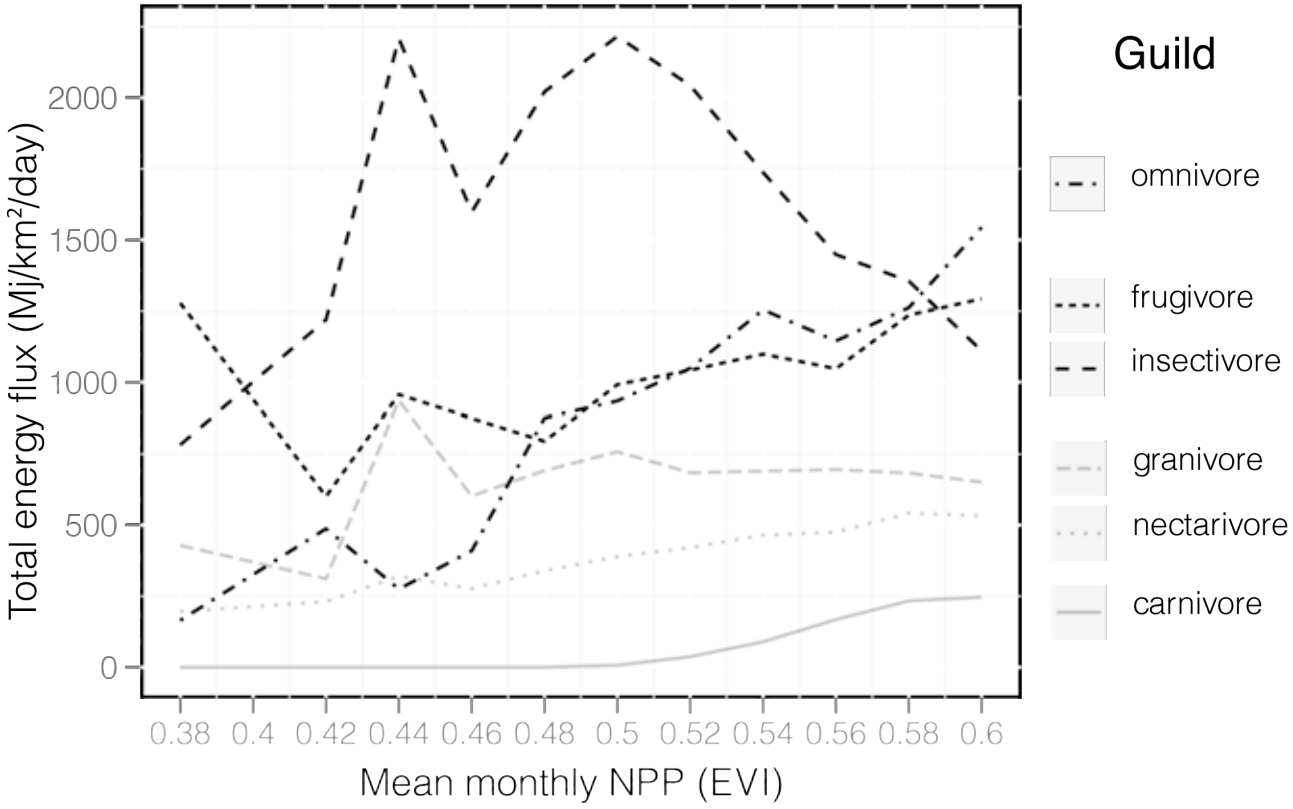

Figure 5.7. *The contribution of different trophic groups to total bird energy flux (Mj/km/day) across the NPP gradient in the AWT, expressed as a moving window average (window = 3) of total flux in each guild at each site within mean monthly NPP bins. Binned values for NPP where calculated by grouping sites in intervals of 0.02 EVI units for clarity. (see table one for regression results for un-binned data.*

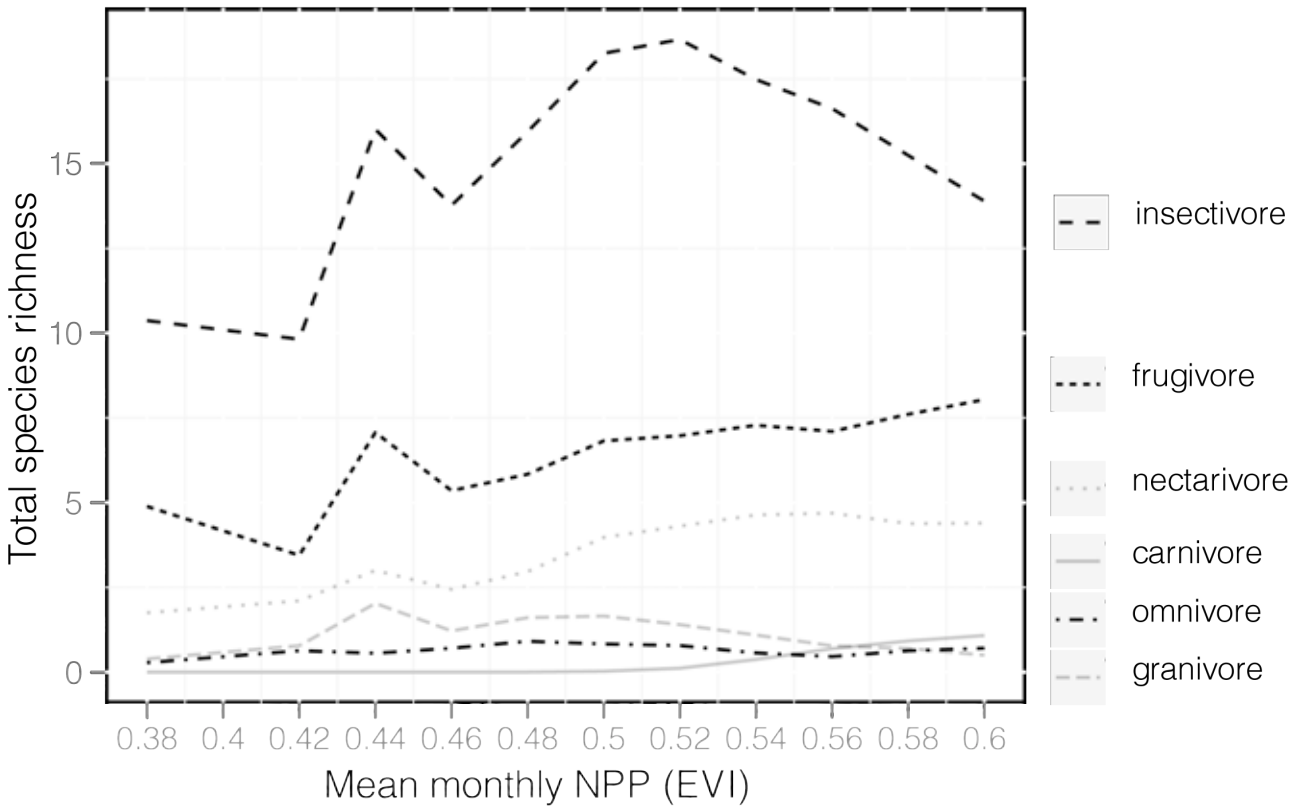

Figure 5.8. *The contribution of different trophic groups to estimated total bird species richness across the gradient in the NPP AWT, expressed as a moving window average (window = 3) of the species richness in each guild at each site within NPP bins. Binned values for NPP where calculated by grouping sites in intervals of 0.02 EVI units for clarity. Regression results for species richness in the three dominant guilds are as follows: Nectarivores: adjusted $r^2 = 0.315$, F-statistic = 7.677, p-value = 0.002, d.f. = 27), Frugivores : adjusted $r^2 = 0.208$, F-statistic = 4.812, p-value = 0.016, d.f. = 27), Insectivores: adjusted $r^2 = 0.399$, F-statistic = 10.61, p-value = 0.0003, d.f. = 27).*

Non-random extinction revisited for guilds using endemicity patterns (H_2/H_3): Total energy flux of non-endemic species was positively correlated with mean monthly NPP (EVI), but best modelled with a segmented regression (Figure 5.9a, $r^2 = 0.283$, d.f. = 25, $p < 0.0001$, estimated EVI breakpoint = 0.467), while the total endemic species energy flux-mean monthly NPP relationship was best modeled with a segmented regression (Figure 5.9b, F-statistic, $r^2 = 0.59$, d.f. = 25, p = 0.04, estimated EVI breakpoint = 0.462). Patterns of endemic and non-endemic insectivore energy flux across the NPP gradient were also best approximated using a segmented regression: Non-endemic insectivore energy flux increases with increasing NPP to a breakpoint at an EVI value of 0.499 (Figure 5.9c, $r^2 = 0.49$, d.f. = 26), and then tends to decrease again at higher NPP, though only the increase phase is significant (p = 0.001). Endemic insectivore energy flux also increases with increasing NPP to an estimated breakpoint at an EVI value of 0.449 (Figure 5.9d, $r^2 = 0.622$, increase-phase p = 0.007, d.f. = 26) and decreases at higher NPP sites. Non-endemic frugivores in contrast exhibit a monotonic positive relationship to NPP across the gradient (Figure 5.9e, F-

statistic 9.15, r^2 0.219, d.f. = 26, p < 0.005), while endemic frugivores exhibit the reverse pattern, declining across the gradient to high NPP sites with zero endemic frugivore energy flux (Figure 5.9f, F-statistic 14.21, r^2 = 0.31, d.f. = 28, p = 0.0007). Omnivores are not represented among endemic species in the study region, but non-endemics also show a slight but significant trend of increasing energy flux with increasing NPP (Table 5.1). The energetically less important, but more speciose nectarivore guild showed the same pattern as the frugivores, with non-endemic energy flux increasing monotonically and endemic energy flux decreasing monotonically with increasing NPP (Table 5.1) .

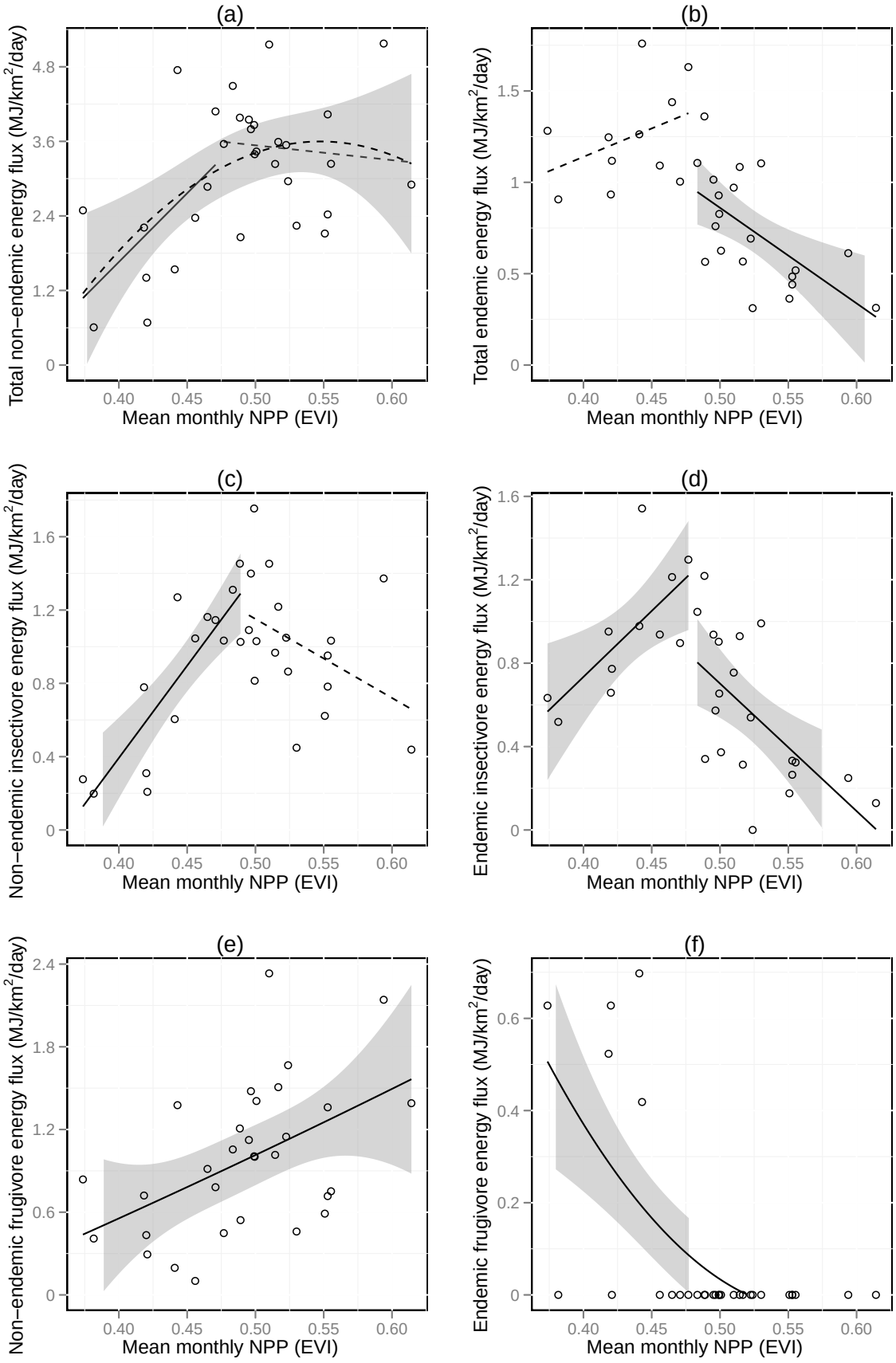

Figure 5.9. *Relationships in the AWT between bird energy flux (Mj/km/day) and mean monthly NPP for endemic (a,c,e) and non-endemic (b,d,f) birds and frugivores (a,b) nectarivores (c,d) and insectivores (e,f). Regression lines are fitted using a linear model and the shaded area corresponds to the 95% confidence interval around the predicted values.*

5.4.4 Multifactorial hypothesis testing

Energy flux for the entire assemblage was best described by a unimodal regression function with a 2nd order polynomial term for NPP seasonality (r^2 = 0.4 p-value < 0.001), all model regression statistics shown in Table 5.1). This model outperformed monotonic alternatives and all other combinations of factors including the full model. Separating the relationship into segments around an empirically estimated breakpoint yielded higher r^2 values however, such that increasing mean monthly NPP best explained the increase phase, and increasing NPP seasonality the decrease phase. This pattern was echoed in the relationship between energy flux attributable to insectivores, consistent with the dominant contribution of this guild to total energy flux, with the exception that the decrease phase also included negative terms for mean monthly NPP and rainforest instability. In contrast, the distribution of energy flux attributable to frugivores was best modeled as a monotonic and positive response to mean monthly NPP alone, and similarly for omnivores and nectarivores, with the addition of a negative term for NPP seasonality. Separating the data into endemic versus non-endemic energy flux across all species, mean monthly NPP, NPP seasonality and rainforest instability contributed to the pattern for endemics, but only NPP was significant for non-endemics. Some curvature remained however, such that modelling non-endemics with a segmented regression implicated decreasing NPP seasonality as an important influence in the increase phase, while increasing seasonality was (though less strongly) an influence in the decrease phase. Total endemic energy flux in the increase phase was also significantly related to decreasing NPP seasonality, but not to increasing mean monthly NPP, while the decrease phase was significantly related to decreasing mean monthly NPP, increasing seasonality, and increasing instability. Among insectivores the pattern of both endemic and non endemic energy flux is also best approximated by a segmented model. Non-endemic insectivore energy flux in the increase phase was significantly related to increasing mean monthly NPP, decreasing NPP seasonality, and decreasing rainforest instability, while the decrease phase was non-significantly related to increasing NPP seasonality. Endemic insectivore flux in the increase phase was related to increasing mean monthly NPP and NPP seasonality, while the decrease phase was significantly related to decreasing mean monthly NPP, increasing NPP seasonality, and decreasing rainforest instability.

Table 5.1. *Highest-scoring models from multiple regressions of whole community and guild energy flux patterns and mean monthly NPP, seasonality of NPP and historical rainforest instability. Key results are shown for unimodal, monotonic and increase and decrease phases of unimodal relationships where applicable. Factors included in each model are indicated by estimated coefficient values, except in cases fitted with a unimodal curve. r^2 values greater than 0.35 and p-values greater than 0.05 are indicated in bold. Cumulative rankings based on F-statistic, r^2, p-values and AIC were used to choose between competing models in each subset.*

Model	**data**			**Factors**			**Fit**			
endemic or non endemic	**trophic guild**	**model or phase of curve**	**break point**	**Mean monthly NPP**	**NPP seasonality**	**Rainforest instability**	**F-statistic**	**Adjusted r^2**	**P-value**	**AICc**
all	all	decrease	> 0.484	-	39082	-	17.286	**0.489**	**0.001**	293.595
all	all	increase	< 0.484	27548	-	-	5.617	**0.334**	**0.039**	212.546
all	all	monotonic	none	-	-8172	-	3.111	0.068	0.089	515.586
all	all	unimodal	none	-	+++	-	10.796	**0.403**	**<0.0001**	503.794
all	frugivore	monotonic	none	-	66	-	2.252	-0.036	0.145	466.270
all	insectivore	decrease	> 0.465	-10638	6039	-49	23.257	**0.563**	**0.000**	322.393
all	insectivore	increase	< 0.465	19114	-	-	8.654	**0.565**	**0.022**	145.853
all	insectivore	monotonic	none	-	-5671	-85	3.252	0.087	0.054	478.252
all	insectivore	unimodal	none	+++	+++	+++	9.932	**0.473**	**0.001**	470.219
all	nectarivore	monotonic	none	866	-55	29	13.198	**0.292**	**0.001**	396.186
all	omnivore	monotonic	none	9915	6365	-	4.800	**0.147**	**0.037**	500.364
endemic	all	decrease	> 0.462	-6363	736	-26	23.482	**0.489**	**<0.001**	317.438
endemic	all	increase	< 0.462	-	-1896	-	1.984	0.123	0.209	120.783
endemic	all	monotonic	none	-5305	-2924	-25	14.538	**0.479**	**<0.001**	430.511
endemic	frugivore	monotonic	none	-2170	-985	-22	14.214	**0.323**	**0.001**	406.129
endemic	insectivore	decrease	> 0.448	-6395	816	-37	26.818	**0.534**	**<0.001**	331.313
endemic	insectivore	increase	< 0.448	6610	-1757	-	6.599	**0.465**	**0.050**	121.275
endemic	insectivore	monotonic	none	-3468	-	-	9.081	**0.240**	**0.001**	438.939
endemic	nectarivore	monotonic	none	411	-	6	5.708	**0.129**	**0.024**	349.947
non endemic	all	decrease	> 0.462	-	23338	-	15.180	**0.403**	**0.001**	350.751
non endemic	all	increase	< 0.462	-	-10314	-	2.598	0.186	0.158	145.729
non endemic	insectivore	decrease	> 0.4998	-	9088	-	4.293	0.190	0.059	222.123
non endemic	insectivore	monotonic	none	-	-3796	-	7.166	**0.175**	**0.012**	444.554
non endemic	nectarivore	monotonic	none	-	-1312	-	6.985	**0.171**	**0.013**	381.564
non endemic	all	monotonic	none	9422	-	-	5.416	**0.184**	**0.027**	507.832
non endemic	insectivore	increase	< 0.4998	8261	-1978	-11	41.773	**0.745**	**<0.001**	217.530

5.5 Discussion

Contrary to expectations of the MIH, our data reveal a decline in species richness within high productivity forest, echoing patterns seen elsewhere in montane tropical avifaunas (Kikkawa & Williams 1971; Terborgh 1977; Blake & Loiselle 2000; Kattan & Franco 2004). This simple unimodal response belies a complex underlying pattern, but one that is largely driven by the unimodal energy flux response of insectivorous birds across the productivity gradient, in striking similarity to the results of Terborgh's (1977) seminal analysis in the neotropics. Representing more than 30% of total energy flux and more than 45% of species, insectivores are the dominant trophic group in these forests, and their energy flux response is largely driven by a decline in endemic species and an increase in non-endemic species across the NPP gradient. This supports the hypothesis made by Williams *et al.* (2010) that extinction filtration during historical climate fluctuations may play a role in limiting energy uptake in high productivity environments in this system, and surprisingly resembles phylogeographic differences recorded in the neotropics across much more diverse avifaunas and larger elevational gradients (Kattan & Franco 2004). Importantly however, the responses of endemic and non-endemic insectivores within this pattern are themselves not wholly monotonic. Among endemic insectivores a decline towards high productivity sites is consistent with historical effects and seasonality, but a decline towards low productivity sites is instead explained by high NPP seasonality in the uplands, supporting the notion of limitation of energy transfer by seasonal resource bottlenecks. In contrast non-endemic insectivores increase with increasing productivity as expected, but at high productivity sites the relationship tends toward a negative response and becomes increasingly noisy, suggesting an influence of another factor not well captured by the NPP indices used here.

5.5.1 Resource seasonality

The importance of intra-annual seasonality in NPP alongside monthly means as drivers of species richness pattern has been demonstrated at a continental scale (Carrara & Vazquez 2010), and in regulating diversity in birds in particular (Hurlbert & Haskell 2003; Evans *et al.* 2005a). Seasonality in NPP as a driver of bird diversity has been related to precipitation limitation in temperate climates (Hawkins 2004), but in very high rainfall zones in tropical forests, NPP may also decline due to excessive precipitation (Schuur 2003). Very high precipitation in the AWT uplands (Figure 2.2) indicate the conditions for such an effect, and the low productivity indexed by EVI at high elevations in this system is consistent with the hypothesis of Williams *et al.* (2010a) that NPP limitation in extremely wet conditions drives the decrease in bird species richness observed in upland forests. Williams *et al.* (2010a) also hypothesised however that seasonality may

drive decreases in the lowlands. Here I show an influence of NPP seasonality on bird energy flux in lowland forests that confirms this role.

Resources such as insects have been shown to vary seasonally in neotropical forests, driving peaks in abundance and diversity at mid-elevations (Janzen 1973), that may contribute to unimodality in elevational patterns of neotropical insectivore diversity (Terborgh 1977). Frith & Frith (1985) have also shown declines in insect availability in uplands during the dry season in the AWT, and mid-elevation peaks in both diversity and abundance of some insects groups have been shown in this system (Wilson, Trueman, *et al.* 2007a). The patterns of energy flux and density of insectivores shown here indicate that such a process of specific seasonal resource limitation may indeed be an important driver, and contributes substantially to patterns in the assemblage as a whole, but that resource availability for this guild may not always be well-indexed by EVI. Among other guilds there is also indication that EVI may not always index relevant resource variability. Frugivores and nectarivores are also found in relatively high densities at low productivity sites, indicating that the pronounced seasonality of NPP indexed by EVI may be of less relevance to the productivity of fruit resources than it is to insect prey abundance. This highlights the fact that while remotely-sensed indices of NPP may be useful for understanding broad-scale assemblage patterns, they may have limited application in understanding energy responses of trophic groups that track specific resources (e.g. fruit, nectar) whose variability is not well captured by canopy reflectance.

5.5.2 Non-random extinction

In contrast, endemic species contributed little to total energy flux in high productivity sites, and tended to be influenced more by indices of historical habitat instability than non-endemic species, consistent with the effects of climate history on patterns of extinction in this system (Williams *et al.* 2010a). In the AWT, reconstruction of palaeoclimates and vegetation communities from pollen cores (Kershaw 1994; Kershaw & Bretherton 2007) and evidence from soil charcoal (Hopkins *et al.* 1993) indicate repeated contraction and isolation of rainforest to restricted refugia during Pleistocene glacial maxima. Patterns in the phylogenetic structure of rainforest specialised species in the AWT (Moritz *et al.* 2000; Hugall *et al.* 2002), and patterns of vertebrate assemblage structure (Williams & Pearson 1997; Winter 1997; Graham *et al.* 2006) suggest that these rainforest contractions imposed an extinction filter on the resident fauna, such that cool-adapted species persisted in upland refugia while warm-climate species became locally extinct. Subsequent expansion of lowland rainforest during the Holocene has resulted in a lowland fauna derived largely from widespread generalist species. The results presented here also show this effect to be particularly pronounced among insectivores and frugivores, consistent with fragmentation studies

that suggest these groups are particularly vulnerable to local extinction (Stratford & Stouffer 1999; Ṣekercioğlu *et al.* 2002, Sodhi *et al.* 2004; Lees & Peres 2008).

These results indicate that as a result of this long-term history of climate and rainforest habitat instability, endemic species are lacking from high productivity lowland environments but remain an important component of energy flux and diversity from uplands down to mid-slopes, in partial disequilibrium with current patterns of energy availability. In contrast, energy flux and diversity of non-endemic birds is largely at equilibrium with current patterns of NPP, increasing with increasing energy availability, and decreasing with seasonality. A secondary role of seasonality is then seen in driving declines in endemic species at the extremes of the elevational gradient. While fewer samples are available for the CYP and CQC, the importance of unique regional biogeographic history in shaping current patterns of diversity despite prevailing energy availability is also found in the contrasting patterns outside the AWT. Bird energy flux of both endemic and non-endemic species on CYP is highest in high productivity sites in the lowlands, despite evidence that lowland rainforest there underwent contraction during Quaternary climate fluctuations at least as severe as the AWT, if not more so (Crisp *et al.* 2001; Luly *et al.* 2006; J. VanDerWal, unpublished data). As among rainforest mammals of CYP (Flannery 1990; Winter 1997), the presence of a diverse lowland endemic fauna in CYP is likely owed to connectivity with Papua New Guinea over land-bridges that has allowed the recolonisation during periods of low sea level (Kikkawa & Pearse 1969; Frith & Frith 1995). Thus it could be said that habitat connectivity has replaced stability in the role of maintaining specialist species in these productive, but relatively young rainforests.

A even more strongly curved relationship between diversity and NPP was observed for the isolated uplands of the CQC, but less so for energy flux, suggesting a different combination of processes. Here rainforest contractions have left only a single endemic rainforest bird species (Longmore & Boles 1983), despite refugia remaining for other small vertebrates (Stuart-Fox *et al.* 2001). Subsequent expansion of lowland rainforest has been limited to smaller isolates, with apparently little opportunity for recolonisation from more diverse assemblages hundreds of kilometres to the south and north across dry barriers (Keast 1981). I postulate that as a result, bird energy flux increases in higher productivity sites but is not matched by an increase in diversity due to a lack of available species. Further data collection in these regions would allow a more detailed analysis of the repercussions of these contrasting histories for assemblage structure. Taken together I suggest that the role of differential biogeographic histories shown here to be important in shaping species-energy relationships is analogous to the influences of “mass-effects” on mid-elevational diversity peaks, shown elsewhere in neotropical birds (Kattan & Franco 2004). Interpreted in these terms,

the pool of endemics adapted to exploit resources in uplands and mid-slopes in the AWT exerts a mass effect by contributing species to the observed mid-elevation diversity peak. The same effect however can drive a markedly different elevational diversity pattern given a different biogeographic history, so that in CYP, extinction of upland species and historical connectivity to the PNG create instead a dominant mass-effect from a lowland fauna, resulting in a monotonic positive species energy relationship.

5.5.3 Trophic guilds

I find strong concordance across guilds in the energy-flux and richness ramifications of historical habitat instability, reflecting the intensity of Pleistocene climate fluctuations, yet I document substantial differences between guilds in responses to current productivity conditions. This suggests that there may be considerable variation in the spatial and temporal scale of vulnerability to environmental fluctuations between trophic groups, with consequences for patterns of extinction vulnerability, and hence local diversity. Evidence from fragmentation studies suggest that insectivores may be particularly vulnerable to local extinction (Ṣekercioḡlu *et al.* 2002; Sodhi *et al.* 2004; Lees & Peres 2008), suggesting a plausible reason for the strong impact of seasonality in this group. Similar studies however also suggest frugivores may be vulnerable to local extinction (Kattan 1992; Stratford & Stouffer 1999; Sodhi *et al.* 2004). Further understanding of underlying mechanisms would be gained by examining correlations between guild energy flux and direct measures of the availability of relevant resources such as insects and fruit. Patterns of difference in the spatial scale of resource variability between trophic groups may therefore be revealed that help to understand spatial pattern of bird energy-flux and richness responses. Other important correlates that could be readily included are body size and dispersal ability (Sodhi *et al.* 2004). This system may therefore provide further insights into some of the drivers of heterogeneity in species-energy relationships through a more detailed analysis of the interactions between ecological traits and environmental variability, including those that influence extinction risk, with important ramifications for biodiversity conservation in the future.

5.5.4 Other potential drivers

Besides the NPP, seasonality and historical factors identified here, other drivers may also influence species-energy relationships. Increases in individual energy consumption have been implicated as drivers of unimodal species-energy responses in montane rainforest birds elsewhere (Ding *et al.* 2005). Here I also found a decline in energy consumption in frugivores and nectarivores with increasing NPP, while that of insectivores and omnivores increased. The net effect of each of these somewhat cancelled the other, so there was little overall relationship between energy consumption

and productivity. Nonetheless a deceleration of the accumulation of insectivore and omnivore species with added energy may add noise to the species-energy relationship at high productivity sites, and warrants further exploration. Competition may also play an important role in structuring bird species distributions and diversity in the montane tropics (Terborgh & Weske 1975; Jankowski *et al.* 2010). In the AWT, I postulate that mixed foragers among frugivores and nectarivores classified here here could compete for insect prey in high energy sites, contributing to a decline in density of specialist insectivores in the lowlands. A more detailed examination of energy availability and resource exploitation by birds in lowland forests may help to clarify the role of such competition in driving declines in density at high NPP sites.

Competition may also not be avian: bats are potential resource competitors of forest birds (Bell 1982; Heaney 2001), that may influence patterns of diversity (Terborgh 1977). For two reasons however I suspect this is not an important process here. Firstly, bird and bat pollination syndromes in plants differ such that demonstrations of competition are few (Shields & Bildstein 1979; Gorchov *et al.* 1995). Secondly, there is no reason to expect that the effect would be less severe in forests in CYP, where rainforest bat diversity is also high (Churchill, 2009). Interactions also need not be trophic in order to influence patterns of diversity. Infection rates of the avian malaria-causing *Plasmodium relictum* in the AWT are highest in lowland forests, and decline at higher elevations (Hilbert 2010) suggesting that disease could influence patterns of population density in rainforest birds. The importance of disease in a mediating role between climate and extinction risk, hence patterns of energy flux and diversity are poorly known, and warrant further exploration, especially in light of predicted climate changes.

Abiotic and non-climatic factors may also be important. The “Mid-Domain Effect” (MDE) is a geometric constraint on species distributions that may also contribute to a unimodal species-energy response across elevational gradients (Colwell *et al.* 2004). However, the extent to which the MDE is a “null” model, in that it invokes the action of past climate fluctuations to filter species at the margins of the domain, has been the subject of some debate (Hawkins 2002). A recent review of 53 studies also found little evidence for unequivocal support of its main predictions (Currie & Kerr 2008). Evidence for the MDE is also based primarily on the overlap of species distributions, and hence the size of species pools across larger scales (Zapata *et al.* 2003) and does not consider density variation. Here I contrast patterns of local species richness and density in a mechanistic framework which includes both history and current energy as factors. In this context the mid-domain effect may be seen as not constituting a “null” model, but as one formulation of the influence of long-term environmental stability on species distributions and diversity. The

contrasting patterns I found in adjacent regions also indicate a need for caution when describing "bounded" domains. In cases where climate fluctuations have influenced levels of historical connectivity and recolonisation potential as well as filtering species near domain margins, the concept of a static bounded domain may be of limited utility in understanding assemblage structure, even at broad scales.

Current habitat area is an often-overlooked factor which may be an important influence on both regional (MacArthur 1969; Jetz 2010b) and local patterns of species richness (Kattan *et al.* 1994; Laurance *et al.* 1997). Habitat area has also been found to be an important predictor of regional species richness in birds in this system (Graham & Grimm 1990). Current area though is often correlated with historical area in regional studies, so that area effects on diversity pattern may be confounded with historical ones (Williams & Pearson 1997). For two reasons I suggest that the effect of current habitat area is of limited importance to the unimodal pattern presented here. Firstly I restricted sampling to the larger areas of contiguous forest to limit the impact of current fragmentation on local diversity. Secondly, by using local estimates of species richness (α diversity) I avoid the area effect due to sampling when estimating diversity as the sum of species present in elevational bands, critical in studies lacking standard survey data from point localities (Kattan & Franco 2004).

Related to area, habitat structural effects, both vertical and horizontal (MacArthur 1964; Terborgh 1977; Jetz 2010b) may also be important influences on elevational and energetic species richness gradients. Rainforest structural variation across elevation in north-eastern Australia however is not pronounced (Webb 1959), much less than in regions with greater elevational range (e.g. Terborgh 1977; Pounds *et al.* 1999), suggesting a more limited role for forest structural and landscape heterogeneity in this system. Disturbance may also play an important role in driving patterns of vegetation structure and hence bird species diversity (Brawn *et al.* 2001). In the tropics, cyclones are an important source of disturbance and are drivers of structural change in rainforests (Lugo 2008; Metcalfe & Bradford 2008), and this may be particularly true in north-eastern Australian lowland forests (Webb 1958), where the impact of repeated cyclone disturbance on birds may be substantial (Freeman *et al.* 2008). In light of expected increases in the intensity of tropical cyclones in this region (Knutson & Tuleya 2004; Mitchell *et al.* 2006), the influences of habitat structure and disturbance on patterns of rainforest bird diversity warrant further study.

5.5.5 Conclusions

By disentangling the relative contributions of underlying drivers to the increase and decrease phases of the dominant trophic groups, I arrive at more nuanced model of the drivers for the observed energy-richness pattern than that hypothesised by Williams *et al.* (2010). By isolating intermediate steps in the species-energy pathway of rainforest bird assemblages in north-eastern Australia, I was able to localise the decoupling between energy and species richness proposed by the "More-Individuals Hypothesis " (Wright *et al.* 1993) at the stage of transfer between available energy to bird energy flux. These results provide valuable new insights into the mechanistic underpinnings of energy transfer in rainforest bird assemblages that have eluded previous efforts both here and in other tropical systems (Terborgh 1977; Blake & Loiselle 2000; Kattan & Franco 2004) due to data limitation. Examination of trophic and biogeographic subsets highlighted a role of historical habitat instability, and a secondary role for seasonality, but mediated by guild ecological characteristics.

These results also highlight the importance of a multivariate approach in understanding the relationship between species richness and available energy. While others have stressed that "direct" measures of energy are necessary to understand these patterns (Groner & Novoplansky 2003), these results suggest that investigations which combine not only indirect measures (e.g. NPP) and direct measures (e.g. energy flux, density) but also trophic distinctions, are necessary to disentangle the complexities of the species-energy pathway in tropical forest birds. The importance of these findings are twofold. Firstly the results here add to evidence for a role of historical climate processes in driving unimodal species energy patterns at a regional level, where previously its emphasis has been placed at broader scales (MacArthur 1969; Terborgh 1977; Hawkins *et al.* 2003a). Secondly, the importance of both historical extinctions and current seasonality in driving patterns of energy and species diversity highlight the potential for important impacts from climate change.

Anthropogenic global warming is predicted to rapidly alter future patterns of climate in terms of both monthly averages and seasonality (IPCC 2001). These changes have already begun to drive widespread shifts in species distributions (Parmesan & Yohe 2003; Thomas, Franco, & Hill 2006), and tropical montane birds may be particularly vulnerable (Sekercioglu *et al.* 2008; La Sorte & Jetz 2010). If the continuing repercussions of Pleistocene and earlier historical process seen in the north-eastern Australian rainforest avifauna are a reliable guide, we can also expect that global warming will induce changes in the trophic structure of communities, altering patterns of resource uptake. Furthermore, similarities with mass effects seen elsewhere (Kattan & Franco 2004) suggest

that the potential for other taxa to compensate for these changes by expanding into newly created environmental space is likely to be limited by the availability of species in regional pools (Colwell *et al.* 2008; Laurance *et al.* 2011). Thus an understanding of the role of historical climate and seasonality in driving current patterns of diversity is likely to improve our ability to understand and predict impacts of future climate change.

Chapter 6. A space-for-time substitution provides evidence that temperature constrains the distribution of montane birds in a tropical rainforest system

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Article type: Full Length Article:

A.S. Anderson[1], C.J.Storlie[1], L.P. Shoo[1,3], R. G. Pearson[1], S.E. Williams[1] (in review). Exploring current analogues of future climatic conditions to evaluate the likely response of a sensitive montane tropical avifauna to a warming world. PloSone.

[1]Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia.
[2] School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia.

Plate 6. *Lewin's Honeyeater (*Meliphaga lewinii*) demonstrate a clear density optimum across the elevational gradient in rainforest in north-eastern Australia, indicating temperature constraint of distribution.*

6.1 Abstract

Correlative models of species environmental niche have been widely used to predict changes in distribution with climate change, but direct tests of the relationship between key variables, such as temperature, and species distributions are few. In the absence of historical data with which to compare observations and detect shifts, space-for time substitutions offer an opportunity to test for species responses to climate variables. Data on limits of species' environmental tolerance can provide information on such constraints to distribution, but are difficult to measure as occupancy and density are low at distribution limits. Environmental optima offer a more accessible gauge of climate constraints on species distributions as they use more of the available data. I collected density data for rainforest birds across the elevational gradient in northern and southern subregions within the Australian Wet Tropics. Using environmental optima calculated from elevational density profiles, I detected a significant elevational difference in 4 of 18 species between the two regions. More species showed a positive (15 spp.) than negative (3 spp.) displacement, with a median difference of ~83 m across the species analysed that is concordant with that expected due to latitudinal temperature differences (61 m). These findings strongly suggest that temperature is a critical factor governing elevational distributions of a substantial proportion of the rainforest bird fauna in the AWT, a key assumption of modelling used to predict the impact of future climate change on patterns of biodiversity.

6.2 Introduction

Anthropogenic global warming over the last century has resulted in increases of global surface temperatures of a magnitude unseen in the previous 1000 years (McCarthy 2001). Extinctions due to the rapid rate of current change (Thomas *et al.* 2004) may profoundly impact global patterns of biodiversity (Araujo & Rahbek 2006). While the magnitude of measured temperature changes has been greater in high latitudes (McCarthy 2001), steep gradients and narrow thermal tolerances may make tropical montane ecosystems particularly vulnerable (Janzen 1967; Colwell *et al.* 2008; Laurance *et al.* 2011). As a result, climate change represents perhaps the most significant threat to tropical montane biodiversity (Raxworthy *et al.* 2008; La Sorte & Jetz 2010), with substantial losses to extinction expected in coming centuries if warming remains unchecked (Williams *et al.* 2003; Thomas *et al.* 2004). Research efforts to date have often focussed on temperate montane systems, (Konvicka *et al.* 2003; Lenoir *et al.* 2008; Tingley *et al.* 2009) leaving a knowledge gap in both predicted and documented impacts in their tropical equivalents (Chen *et al.* 2011). There is thus an urgent need to validate projected impacts of climate change on montane tropical bird species (Sekercioglu *et al.* 2008).

Species distribution modelling is widely used to predict potential impacts of climate change on flora and fauna. However, such models rely on correlations that implicitly assume causal relationships between species distributions and environmental variables. Thus independent tests of the assumption that climate factors drive the distributions of species are urgently needed (Hughes 2003). Historical analysis and a substitution of space for time are two approaches that can be used for this purpose (Araujo & Rahbek 2006). Where data are available, historical analysis has already identified numerous cases of range shifts in response to rapid temperature increases in the latter part of last century (Konvicka *et al.* 2003; Wilson, Gutierrez, *et al.* 2007b; Lenoir *et al.* 2008; Tingley *et al.* 2009; Chen *et al.* 2011). The majority of these have been up-slope shifts, in line with expectations from climate data, though some 20% of shifts have been downslope, suggesting more complex explanations may also apply (Lenoir *et al.* 2010). However, historical data are lacking for many ecosystems, and this can be particularly problematic for species-rich but data-poor tropical systems. In such situations, space-for-time substitutions may serve as a crucial tool for evaluating assumptions of species distribution models in the context of climate change (Rastetter 1996). A second challenge lies in how to measure distribution differences (Shoo *et al.* 2006). Efforts to quantify distribution differences in both space and time have often emphasised detecting change at the margins of species distributions (Brommer 2004; Thomas 2010; Chen *et al.* 2010). However, the low occupancy and abundance often observed at distribution margins can present important

obstacles for defining limits, which are highly sensitive to sampling effort (Shoo *et al.* 2006). Consequently, analytical approaches are increasingly being directed toward measures of central tendency (or optima) that utilise more of the available data and are less affected by sampling bias (e.g. Lenoir *et al.* 2008).

Defining species distributions by their environmental optima is not without its own complications however, as species' responses to environmental gradients can take a variety of forms (Oksanen & Minchin 2002). As a result it may not be accurate to assume that the response of a particular species to an environmental gradient (e.g. temperature or elevation) will have a single clearly defined optimum. For the purposes of detecting range-shifts, however, the problem will be simplified by concentrating on those species for which a response model with a clearly defined optimum is the most appropriate. The Gaussian response is one such model, often applied to species distributions across environmental gradients, for which it is possible to identify the optimum with confidence intervals (Oksanen *et al.* 2001). This approach allows statistical comparison of the location of density optima, and has been used to discern elevational range shifts over time (Wilson *et al.* 2005; Lenoir *et al.* 2008). There is considerable scope to extend this same analytical approach to evaluate contemporary constraints of environment on distribution by examining elevational differences between density optima along secondary spatial environmental gradients such as latitude. By using such a "space-for-time" substitution, it is possible to directly examine the evidence for a causative relationship between species environmental tolerances and their spatial distribution. Given two populations of the same species in different thermal environments, it is possible to infer the tendency for species' distributions to track environmental change without the need for historical data (Araujo & Rahbek 2006). The selection of an appropriate environmental gradient against which to measure shifts is also an important consideration. Climate predictions suggest that maximum and minimum temperatures are increasing more rapidly than mean values in some regions (Easterling *et al.* 2000). Some species may also be particularly vulnerable to extremes of heat and cold (Parmesan & Willig 2000) and hence may track maxima or minima more closely than average values. Changes in mean annual temperatures may therefore be a poor predictor of species distribution changes in some cases, necessitating the inclusion of other parameters of thermal gradients, such as extreme weather events (eg. Reside *et al.* 2010).

Here I use an extensive data set on the density of rainforest birds across elevational gradients in north-eastern Australia to test the hypothesis that temperature is a major driver of species distributions across space – and, by extension, over time under changing environmental conditions.

The region has previously been identified as an Important Bird Area (Birdlife International 2008), highlighting its contribution to Australia's avifaunal diversity (Dutson *et al.* 2009). Previous studies have also predicted a high level of vulnerability to climate change among upland endemic rainforest species in the area (Williams *et al.* 2003; Hilbert *et al.* 2004). Here I examine evidence for upslope displacement of elevational optima of species at lower latitudes consistent with expectations based on the gradient of temperature across elevation, an important assumption of the above climate change predictions. First, I use a hierarchical modeling approach (Huisman *et al.* 1993) to select species whose density response along elevational gradients can be well approximated by a unimodal curve. For the selected subset of species, I then apply simple logistic regression to estimate the location of peak density, with confidence intervals, characterising species by their environmental optima across the elevational gradient (Oksanen *et al.* 2001). Finally, I quantify directional differences in the elevations of density optima between latitudes and discuss the implications of our findings for predicting impacts of anthropogenic global warming on biological communities, and for monitoring the resulting temporal range shifts.

6.3 Methods

6.3.1 Study area

Data analysed in this chapter focusses on the Australian Wet Tropics (AWT) Bioregion between -15˚45'32.69"S 145˚ 1'53.87"E and -19˚18'0.65"S 146˚ 9'41.17"E). The geography and vegetation of this region are described in more detail in chapter 2. Sampling here is focussed on two discrete sections of the AWT, separated by the Black Mountain barrier (Keast 1981; Moritz *et al.* 2000). These are: the northern AWT between Cairns (~ -17˚S) and Cooktown (~ -15.5˚S) and the southern AWT south of Cairns to about -19.5˚S near Townsville (Figure 6.1). Across this biogeographic barrier there is little difference in the avifauna, though several species are split into distinct lineages (Joseph & Moritz 1994, Schodde and Mason 1999). The climate variation in rainforest of this region is also described in more detail in chapters two and four, but importantly is dominated firstly by the substantial elevational gradient, from 50 to 1622 m asl, with upland forests experiencing higher rainfall and lower temperatures than lowland forests, and secondly by latitude, with northern AWT forests warmer than those in the southern AWT. Thus the northern and southern AWT represent two contrasting thermal gradients in which to compare the elevational responses of populations of rainforest bird, the northern AWT being shifted upslope by the effect of latitude and the adiabatic lapse rate on temperature.

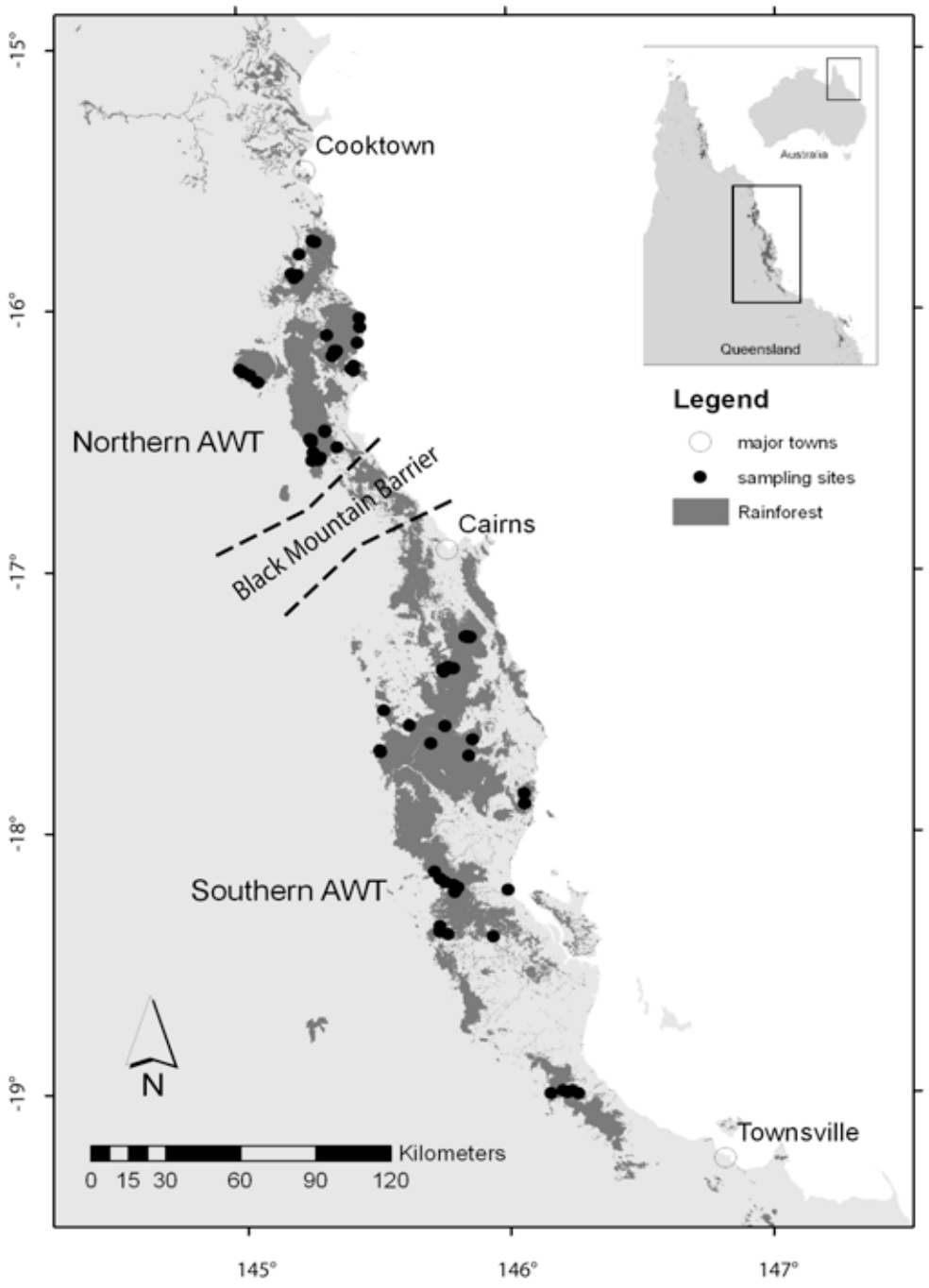

Figure 6.1. *A map of the rainforests sampling areas within the AWT study region. Areas dominated by rainforest vegetation are shaded in dark grey. Sampling sites are indicated with filled circles and major towns with empty circles. The dotted line indicates a major biogeographic barrier (the Black Mountain barrier) which separates the northern AWT and southern AWT regions compared in this study.*

6.3.2 Bird density estimation

The sampling design and survey methodology used in this analysis follow those used previously by (Williams & Middleton 2008) and described in detail in chapter 2. Surveys were conducted

between dawn and 9:30 am, and consisting of 30-minute, 150-m fixed-width transects. Distance sampling methodology was used to derive calibrated estimates of density, as described in chapters three and four. From these analyses accurate estimates of density could be derived for the majority of species (see chapter 4 for details). To provide the maximum spatial resolution possible for the fitting of density profiles, bird density data are analysed here at the level of sampling points within a site, rather than at the site level employed in chapter 5. To minimise confounding influence of decadal changes in temperature, I only include data from surveys between January 2000 and June 2010. These consisted of a total of 944 surveys across 340 points and 87 sites, giving a range of point density estimates across elevation that formed a picture of each species elevational density profile.

6.3.3 Expected elevational shifts

I characterised the thermal gradient across elevation in each subregion in terms of mean annual, minimum and maximum temperatures. I used temperature data from modeled climate surfaces with BIOCLIM in the ANUCLIM 5.1 software (Houlder *et al.* 2000) which uses a splined model of the relationship between temperature, measured at standard meteorological weather stations, combined with an 80 m resolution DEM (resampled from GEODATA 9 Second DEM Version2; Geosciences Australia, http://www.go.gov.au/). Elevational temperature profiles where then generated for the northern AWT and southern AWT subregions by querying the interpolated mean annual, maximum and minimum temperature layers from the above data sources at a random subset of 150 points each in the southern AWT and northern AWT (to give equal sample sizes). Subsequent statistical anlyses were all conducted in the "R" framework for statistical analysis version 2.13.1 (R Core Development Team 2011). I tested for parallel slope of the regressions of temperature and elevation (indicating no significant interaction term) for mean, maximum and minimum values between the southern and northern AWT using the "lm" function in R. Where slopes were parallel, I then tested for a significant difference of intercept using an ANCOVA approach, and estimated the elevational change represented by temperature differences based on the slope and intercept.

6.3.4 Density profile modeling

Calibrated density information was available for 115 species. I removed any species that did not have sufficient data across the elevational gradient to model a density response in both the southern and northern AWT. As a minimum, 10 survey points across the gradient were considered adequate for this purpose. I further limited analysis to those species for which the temperature response for all data combined approximated a unimodal curve, showing a clear optimum at which estimated

density reaches a maximum. I used the Huisman-Olff-Fresco (HOF) hierarchical modeling approach (Huisman *et al.* 1993) implemented in the R package "BiodiversityR" (Kindt 2011) to select only those species whose density profiles are best characterised by a symmetrical unimodal (Gaussian) distribution. Species' density profiles were compared to a flat, monotonic, plateau, Gaussian, and skewed distribution. The most appropriate model was selected using Akaike's Information Criterion (AIC). Only species displaying a unimodal (Gaussian or skewed) response were included in further analyses. While skewed abundance distributions may be relatively common across natural gradients (Austin 1976; Huisman *et al.* 1993), symmetrical distributions are widely used to approximate abundance responses in community ecology, and simplify the process of identification of optima and confidence intervals.

6.3.5 Observed elevational differences

Elevation of optimal density in the southern and northern AWT was identified for each species that showed unimodal or skewed responses to temperature across the gradient using the approach of Oksanen (2001). This approach fits a Gaussian curve to the patterns of species' mean density across an environmental gradient using simple logistic regression. As densities were generally low, and data often included zeros (absences), I expressed density as a proportion of maximum density for each species, and assumed a binomial error distribution, though selection of the available alternative error distributions (poisson and quasi-poisson) did not substantially alter the resulting model assignments. This approach defines the maximum density value as the peak of the unimodal curve, after which I calculated confidence intervals around the optimum using a Fieller likelihood method implemented by Oksanen (2001). I then compared the elevational optima of each species between its northern and southern AWT populations. Species with greater than 30% of deviance explained by the fitted Gaussian response curve and for which the Gaussian optimum in the northern AWT was located at a higher elevation than that for the southern AWT were considered to show strong support for a positive elevational difference between regions. I assessed the significance of the observed elevational differences based on the overlap or non-overlap of upper and lower 95% confidence intervals. These confidence intervals represent a conservative estimate of significant difference, in that non-overlapping 95% intervals do not necessarily indicate non-significance (Payton *et al.* 2003), but I retain them here rather than using a lower threshold, as the analyses involve multiple comparisons and hence a higher likelihood of type 1 error. Lastly, I pooled estimates of displacement across all species in the analysis to examine evidence for coherent community wide shift in elevation using a Wilcoxon rank sum test.

6.4 Results

6.4.1 Expected elevational differences

There was no subregion interaction in the relationship between mean annual temperature and elevation, indicating that regression slopes were not significantly different (multiple r^2 = 0.96, subregion term: t = 1.923, p-value = 0.055). Mean annual temperatures decreased by ~5.1˚ per 1000 m elevation in both regions, but were 0.32˚ warmer (SE $\pm$ 0.04˚) in the north based on the difference in intercepts of regressions between temperature and elevation (Figure 6.2a). This increase in temperature translated to a 61.6 m upward displacement in the thermal gradient between the two regions. In contrast there was a significant subregion interaction in the regressions of minimum temperature and elevation (multiple r^2 = 0.84, subregion term: t = 9.507, p-value = <0.001), and similarly for maximum temperature and elevation (multiple r^2 = 0.79, subregion term: t = -3.24, p-value = <0.013), indicating a difference in the slope of the elevational gradients for these parameters.

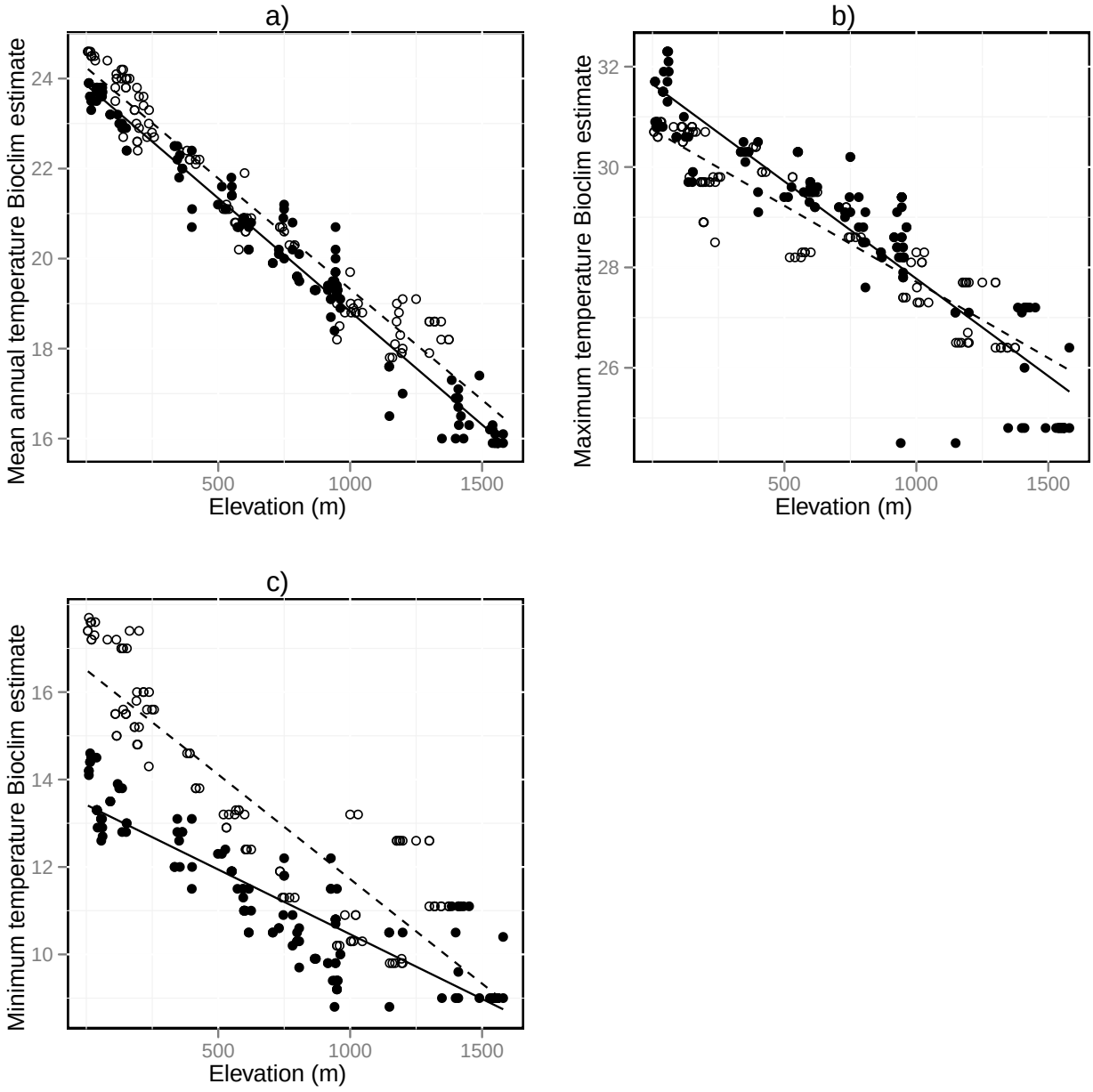

Figure 6.2. *Relationships between elevation and temperature parameters for the AWT estimated using interpolated climate from BIOCLIM. Data from the northern AWT (open circles) and southern AWT (filled circles) are indicated. The solid lines are simple linear models of the effect of elevation on temperature for each parameter, with the trend for southern sites shown by a solid line, that for northern sites with a dashed line (see text for model parameters).*

6.4.2 Density profile modeling

Hierarchical model testing in the HOF (Huisman *et al.* 1993) approach (Appendix Figures 6.1.1 - 6.1.80) identified 45 of 80 bird species as exhibiting a unimodal temperature response (Gaussian (type IV, 14 spp), skewed (type V, 31 spp)), and a further 23 with a monotonic (type III) and 10 a plateau (type II) response (summarised in table 6.1). Importantly in most taxa for which a skewed model returned a higher AIC score, the skewed model tended to generate similar estimates of the location of the optimum to the simple Gaussian response (e.g. Brown Gerygone (*Gerygone mouki*) Appendix 6.1.11 and Bridled Honeyeater (*Lichenostomus frenatus* Appendix 6.1.12). As subsequent model testing methods apply only to unimodal distributions, species with a plateau (type II) response (e.g. Grey-headed Robin (*Heteromyias albispecularis)* Appendix 6.1.32) or monotonic positive (type III) response (e.g. Double-eyed -Fig-parrot (*Cyclopsitta diopthalma*) Appendix 6.1.21) were excluded. It is important to note however that these species may also have a unimodal temperature response, but one that is truncated by the limits of the available temperature gradient in the study region.

Table 6.1. *Number of flat, plateau, monotonic positive, negative, Gaussian and skewed response detected using the HOF approach used in Oksanen (2000).*

#	Model	Count of species	% of total
I.	Flat	2	0.025
II.	Plateau	10	12.5
III.	Monotonic	23	28.75
IV.	Gaussian	14	17.5
V.	Skewed	31	38.75

6.4.3 Observed elevational differences

Of the 45 species demonstrating a Gaussian or skewed temperature response, 18 (40%) were also amenable to the approach used in Oksanen *et al.* (2001) for calculating the location and confidence intervals of the density optimum, having both sufficient sampling coverage (occupancy at 3 or more sites) and an optimum below the lower of the two gradient limits, (northern AWT at 1374 m). Inclusion of species with optima closer to the upper and lower limits of the gradient creates problems for model fitting with this approach (Oksanen *et al.* 2001; Lenoir *et al.* 2008). Table 6.1 shows the results of the Gaussian optimum calculations for these species. Across the taxa identified using the above criteria, a further 15 (83%) of these species showed a positive elevational difference. Of these species showing an up-slope displacement, a Gaussian model explained greater than 30% deviance in both northern and southern populations for 6 species (42.8% of the positively-differing species), and a significant elevational difference in density optima was indicated in 4 species by non-overlapping 95% confidence intervals between their southern and northern optima. Superimposing southern and northern elevational density profiles for these species (Figure 6.3) indicates the nature of these differences, relative to the remaining taxa (Appendix Figures 6.3.11 - 6.3.6).

Table 6.2. *Estimated elevation of density optima for southern and northern AWT populations of rainforest birds identified as having a unimodal (Gaussian or skewed) temperature response, with optima at least 100m from the gradient limits, and which could be estimated using the approach in (Oksanen et al. 2001). Species are shown in alphabetical order, with their optimum elevations and upper and lower 95% confidence intervals, as well as the estimated difference in elevation of density optima (positive or negative). Species with non-overlapping confidence intervals are marked in bold, as are values for deviance explained greater than 30%.*

		Southern AWT					Northern AWT					
	Common name	Optimum elevation (m)	lower 95% CI (Fieller)	upper 95% CI (Fieller)	% deviance explained	# Sites	Optimum elevation (m)	lower 95% CI (Fieller)	upper 95% CI (Fieller)	% deviance explained	# Sites	Estimated altitudinal shift (m)
1	Brown Gerygone *(Gerygone mouki)*	638.08	587.24	705.04	**41.48**	83	597.68	504.46	682.89	**34.16**	47	-40.40
2	Bridled Honeyeater *(Lichenostomus frenatus)*	876.64	758.42	1284.07	**32.55**	45	1032.44	888.56	1630.43	**32.31**	68	155.80
3	Brown Cuckoo-Dove *(Macropygia amboinensis)*	557.66	472.54	680.11	4.35	71	729.54	677.85	791.30	12.42	65	171.88
4	Bowers Shrike-Thrush *(Colluricincla boweri)*	890.27	745.71	1560.37	27.96	45	898.03	866.55	931.79	**54.46**	53	7.75
5	Spotted Catbird *(Ailuroedus melanotis)*	556.93	498.77	629.68	16.60	82	602.19	542.52	653.22	18.73	84	45.26
6	**Chowchilla *(Orthonyx spaldingii)***	696.07	640.65	777.77	26.68	74	923.72	879.52	982.63	**43.91**	73	227.65
7	**Eastern Whipbird *(Psophodes olivaceus)***	572.98	464.53	775.81	3.42	91	908.48	869.42	957.40	**43.72**	63	335.50
8	Grey Fantail *(Rhipidura albiscapa)*	698.33	572.41	1224.31	15.03	69	807.63	738.39	916.03	24.79	84	109.29
9	Golden Whistler *(Pachycephala pectoralis)*	782.59	733.43	851.90	**49.59**	64	894.21	849.92	949.23	**54.21**	67	111.62
10	**Lewin's Honeyeater *(Meliphaga lewinii)***	723.76	707.27	740.65	**67.25**	62	832.83	817.83	847.54	**68.94**	53	109.07
11	Rainbow Bee-eater *(Merops ornatus)*	348.72	288.61	409.73	27.92	16	468.37	366.44	540.85	24.72	28	119.65
12	Shining Bronze-Cuckoo *(Chalcites lucidus)*	723.93	639.35	850.23	20.67	17	785.47	763.45	805.54	**52.24**	22	61.54
13	Sulphur-crested Cockatoo *(Cacatua galerita)*	534.24	459.18	625.22	6.30	70	566.30	490.85	622.27	10.53	70	32.06
14	Tooth-billed Bowerbird *(Scenopoeetes dentirostris)*	800.74	746.03	894.36	**35.27**	27	889.13	835.97	951.64	**38.01**	39	88.38
15	Topknot Pigeon *(Lopholaimus antarcticus)*	755.82	641.51	865.85	28.08	14	620.44	-4.04	1123.01	23.51	13	-135.37
16	**Victoria's Riflebird *(Ptiloris victoriae)***	487.36	431.87	540.78	8.74	75	584.09	548.72	615.85	21.89	72	96.73
17	White-eared Monarch *(Carternornis leucotis)*	403.93	314.07	478.14	15.09	20	306.95	-778.95	459.44	13.49	17	-96.99
18	Yellow-throated Scrubwren *(Sericornis citreogularis)*	766.26	684.49	891.84	**42.98**	36	862.12	772.26	1005.61	**41.76**	60	95.86

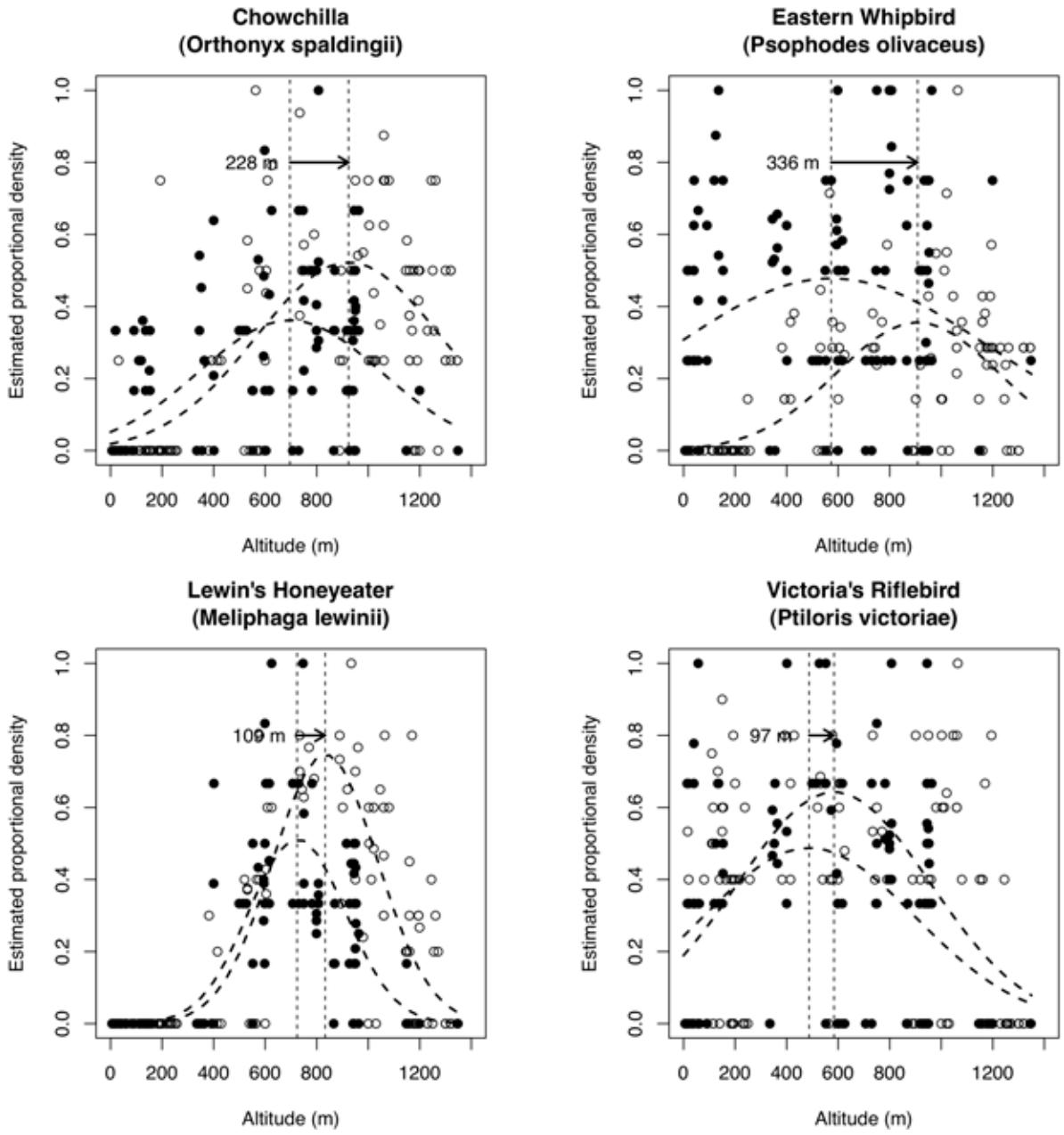

Figure 6.3 *Elevational density profiles for the species showing a significant difference in elevation of density optima between southern (filled circles) and northern (unfilled circles) AWT populations according to 95% confidence intervals. Data are proportional estimated densities corrected for detectability for each sampling point. The vertical lines mark the estimated elevations of density optima in the two regions. The value of the elevational difference in metres in each case is indicated in text within the plot, and direction of the difference indicated with an arrow.*

6.4.4 Comparison with predicted differences

Examining the unimodaly distributed species as a group, the positive elevational differences in density optima between the southern and northern AWT drive a consistent trend upslope relative to a line of no difference, and the slope of the line was constant across elevation (Figure 6.4a). A histogram of the observed differences (Figure 6.4b) also shows the positive bias in the median value

of upslope shifts across these 18 species. A Wilcoxon rank sum test indicated a significant positive median difference across these species of 88.83 (p-value 0.007), which was not significantly different from the BIOCLIM estimated temperature displacement of 61.6m (p-value = 0.324).

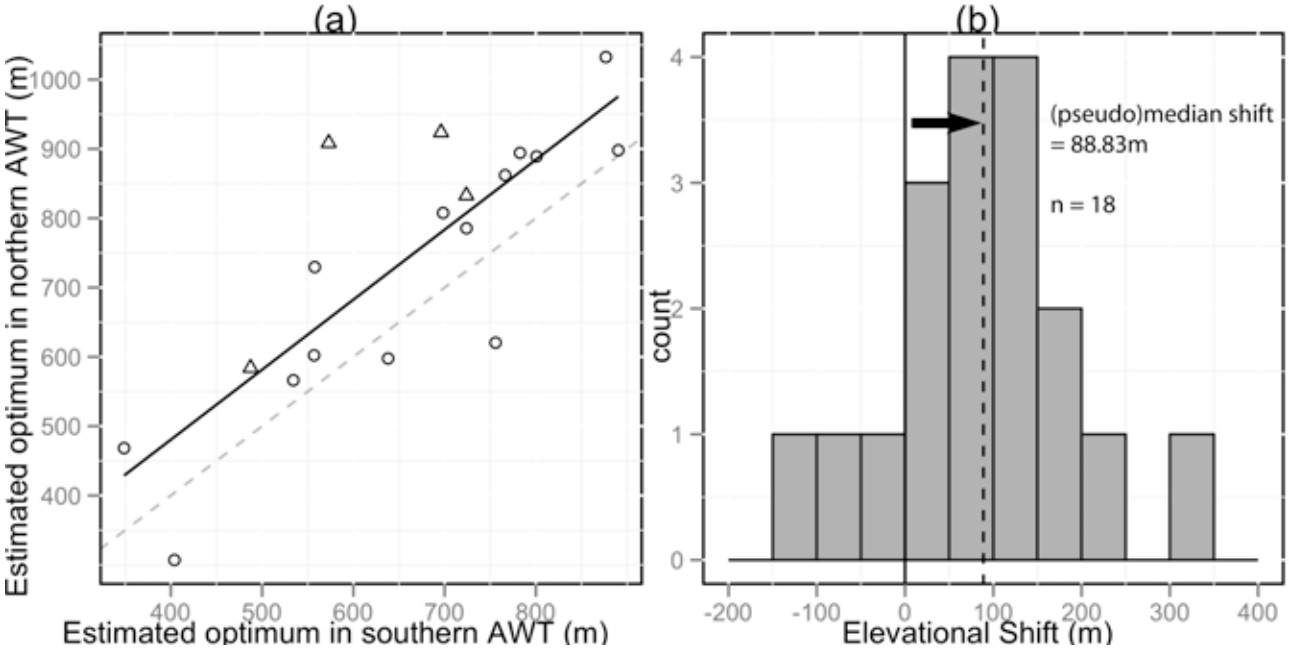

Figure 6.4. *a) Differences in the elevation of density optima between southern and northern Wet Tropics bird populations. Data are elevations of density optima estimated for species for which Gaussian response curves were identified as the best fit using AIC in the HOF approach, recalculated with confidence intervals using the approach of Oksanen et al (2001). The diagonal dashed line shows the line of no shift between subregions, while the solid line is a simple linear model fit to the density optimum data (r^2 = 0.644, f = 31.74, d.f. = 16 , p = <0.001). Species with non-overlapping 95% upper and lower confidence intervals are indicated with triangles. b) Histogram of the distribution of differences between the elevation of density optima fitted to Gaussian response species between the southern and northern Wet Tropics regions. The vertical lines separated by an arrow indicate the difference between zero (no shift) and the Wilcoxon test psuedomedian difference between southern and northern AWT optima values across the 18 taxa examined (+ 88.83 m).*

6.5 Discussion

Of the 80 rainforest birds species examined in this study, 45 (56.25%) exhibited a unimodal (gaussian or skewed) density response across the temperature gradient, and 18 were amenable to analysis using the Oksanen (2001) method for calculating the location and confidence intervals of density optima. Of the subset of tractable species, 15 (83%) exhibited a positive displacement in peak density between southern and northern AWT, driving a significant trend across this subset of the avifauna which matches expectations based on elevational temperature gradients. These results provide support for the hypothesis that temperature is an important factor constraining the elevational distributions of a substantial proportion of the rainforest bird assemblage in this system.

In addition it shows that these temperature sensitivities are conserved between populations, such that density profiles in southern and northern AWT subsets responded in a predictable fashion to the effect of latitude on elevational temperature gradients, rather than idiosyncratically. These differences were consistent across the elevational gradient, indicating also that temperature sensitivity is not limited to the upland species previously considered most vulnerable to climate change (Williams *et al.* 2003).

Narrow thermal tolerances have been recognised as a common feature of the tropical ectotherm biota (Tewksbury *et al.* 2008; Laurance *et al.* 2011), but there is little empirical data to support temperature as a critical determinant of distributions in tropical endotherms such as birds (Corlett 2011). The metabolic and water costs of endothermy however may expose birds to risks from elevated temperature similar to those predicted for ectotherms (McKechnie & Wolf 2010). The assumption that species' distributions are strongly influenced by climate, and in particular temperature, is critical to analyses that model those distributions as a function of climate variables, commonly used in projections of the future impact of global warming (Guisan & Thuiller 2007; Jeschke & Strayer 2008). Despite the widespread use of such models, including to predict impacts in rainforest birds in this system (Williams *et al.* 2003; Hilbert *et al.* 2004), historical data with which to test these assumptions are often lacking, and empirical studies of temperature sensitivity are costly and rare in the literature (Laurance *et al.* 2011). The space-for-time substitution approach taken in this study thus constitutes an important evaluation of the assumption of widespread temperature limitation and niche transferability in a tropical rainforest avifauna. This is in contrast to studies that have found little limitation of distribution by climate in some avifaunas (e.g. Beale *et al.* 2008), and supports arguments for continued careful use of correlative distribution models in predicting climate change impacts (Araujo and Thuiller 2009).

6.5.1 Monitoring of range shifts

The data and analytical approach presented here for quantifying elevational density profiles of species addresses important gaps in our understanding of climate related impacts in this diverse tropical system. First, I have used distance sampling to provide baseline estimates of density corrected for differences in detectability between sites and species. Absolute density provides a more robust measure of species' abundance responses to environmental gradients by controlling for the effects of extraneous factors such as differences in habitat structure, which may be influential across large environmental gradients. It is also expected to be critical for quantifying important changes in population size resulting from range shifts. Second, I have improved on previous efforts to quantify elevational abundance responses (Williams *et al.* 2003; Shoo *et al.* 2005) or elevational

position of bird distributions using basic measures of central tendency (Shoo *et al.* 2006). I have shown that elevational optima can be derived for a large portion of species using simple Gaussian response curves and can be employed to document modest upslope shifts involving temperature differences of as little as 0.32 ^{o}C. This would suggest a high capacity of this analytical approach to document early change in this avifaunal community. This magnitude of change is also within the range predicted for the AWT within 20 years under current warming trends (Suppiah *et al.* 2007).

6.5.2 Other drivers of elevational differences

Variation in magnitude of up-slope shifts between species shown here echoes findings in temporal studies of range-shift (e.g. Lenoir *et al.* 2008; Tingley *et al.* 2009). Variation in species' characteristics may be an important driver of such differences in temperature response (Lenoir *et al.* 2010). The sensitivity of species to environmental gradients may vary between species depending on their behaviour or physiology; for example migration phenology and diel rhythms may influencing the actual temperatures experienced by individuals, or alter their capacity for buffering against temperature variation (Humphries *et al.* 2004). Depending on their physiologies, species may also be more sensitive to temperature maxima or minima rather than means (Zimmermann *et al.* 2009; McKechnie & Wolf 2010). I document idiosyncratic relationships between elevation and temperature extremes across the regions examined here, which may underpin some of the observed variation in species' responses. Elevational gradients are also complex, and include interactions between temperature, habitat, rainfall and seasonality (Korner 2007), so species' responses may differ in cases of sensitivity to gradients other than temperature. Rainfall seasonality in particular varies across the elevational gradient in this study and is also likely to play an important role in determining species' distributions. Extreme rainfall events at high elevations have been shown to drive some species down-slope for example (Boyle *et al.* 2010), and sensitivity may vary between species, so that future work should also consider the impacts of such extreme weather events (eg. Reside *et al.* 2010).

Downslope shifts in species' distributions have also been documented as a result of climate change elsewhere (Lenoir *et al.* 2008; Tingley *et al.* 2009). Habitat modification, competitive interactions and the influence of climate variables other than mean temperature have all been identified as possible drivers of unexpected reversals of the overall up-slope trend in shifts (Lenoir *et al.* 2010). Habitat modification is unlikely to be important in the system studied here, as there is minimal impact over much of the elevational gradient (Stork & Turton 2008), and no systematic variation between the two regions compared. The interactions with competitors which may also influence species' distributions (Walther *et al.* 2002) are also unlikely to be responsible in this case, as there is

little assemblage change over the sub-regional scale examined here (Williams *et al.* 1996). As in the case of variation between species' up-slope shifts, influence of environmental factors besides broad scale estimates of mean annual temperature may however be important in driving down-slope shifts. Downslope shifts could result when the processes determining upper and lower range boundaries differ (Purves 2009), for example through trade-offs between life-history traits and metabolic costs (Loehle 1998). While the crude measures of other parameters of the thermal environment used here did not conclusively indicate an alternative to mean annual temperature as a driver of either the interspecific variation or the greater-than-expected differences, these results suggest that further exploration of these alternatives is warranted. The use of under-canopy temperature data may provide a more detailed picture of the thermal conditions actually experienced by species, helping to clarify these aspects (Dobrowski 2011). Finally, changes in patterns of Net Primary Productivity may also influence the distributions of species across elevation (eg. Williams *et al*. 2010a), further complicating the prediction of future range shifts with climate change.

6.5.3 Limitations of the approach

An important limitation of the approaches used in this analysis is the reduced capacity of the HOF (Huisman *et al.* 1993) approach to characterise the responses of species whose optima approach the limits of the environmental gradient. This reduces the scope of the analysis by limiting species amenable to testing, excluding both cool-adapted extreme upland-specialised species, and warm-adapted taxa close to the thermal maximum in the study region. Temperature responses in these species tended to be identified as having monotonic or plateau responses, but may equally consist of some fraction of a unimodal curve whose optimum is truncated by the gradient limits. The characterisation of such distributions from a monitoring perspective may thus need to rely on alternative approaches, such as comparisons of absolute density changes (e.g. differences between intercepts of monotonic responses). Further limitation may be encountered when fitting the Gaussian curve with confidence intervals using the approach of Oksanen *et al.* (2001). Problems in parameterising the Gaussian response in such cases may be resolved only by having sufficient data to accurately describe both the increase and decrease phases, suggesting increased sampling intensity at distribution limits may be a desirable component of programs for monitoring of climate-induced range shifts.

Skewed responses were also relatively common in the results presented here. A Gaussian curve is often assumed to be the underlying distribution in species' responses to environmental gradients, but there are physiological and ecological reasons to expect skewed distributions (Austin 1976).

The parameterisation of such non-symmetrical responses is a recurring issue in community ecology (Oksanen & Minchin 2002). Inter-specific interactions and metabolic constraints may drive asymmetry in gradient responses (Soberón & Peterson 2005). A systematic examination of the profiles of species with and without the presence of potential competitors may allow the assessment of the extent to which competition contributes to skewed responses in this system. The fact that many of the optima identified by skewed-distributions deviated little from the corresponding symmetrical Gaussian distribution for that species (see e.g. Appendix Figure 6.1.30, Grey Fantail (*Rhipidura albiscapa)* Bowers Shrike-thrush (*Colluricincla bowerii)* 6.1.12, and Bridled Honeyeater (*Lichenostomus frenatus)* 6.1.14) suggests however that this analytical limitation does not alter the overall conclusions of this analysis.

6.5.4 Conclusions and further work

Despite these complexities I nonetheless document a coherent signature of positive difference in elevation of density optima among rainforest birds in this system, which is consistent with expectations from a simple hypothesis based on temperature. These differences are distributed evenly across the entire elevational gradient, suggesting that an important influence of temperature on species' distributions is not limited to a specialised upland fauna, but extends into megatherm environments and widespread species. This tendency for lowland species to respond similarly to increases in temperature to their upland counterparts may reflect a general tendency toward narrow thermal tolerance in tropical species (Tewksbury *et al.* 2008), and has important repercussions for lowland biodiversity in a changing climate (Laurance *et al.* 2011). In some situations (Colwell *et al.* 2008), predicted upslope shifts of lowland species driven by thermal tolerances could result in a process of lowland biotic attrition in the montane tropics. The data I present here suggest that the assumption of temperature dependency underlying this prediction may be accurate for a substantial proportion of both the lowland and upland avifauna in the Wet Tropics.

Globally, montane rainforest birds are at high risk from the warming associated with climate change (Jetz *et al.* 2007; Sekercioglu *et al.* 2008). Unfortunately, in most cases elevational range information for tropical montane birds is limited to coarse estimates based on presence records. Such data may be useful in larger scale studies (Peterson & Martínez-Meyer 2009), but a lack of fine-scale information may have contributed to a failure to detect recent impacts despite documented climate change elsewhere (Thomas, 2006). The early detection of shifts necessary for effective conservation management in the face of global warming requires information over short spatial or temporal scales (Shoo *et al.* 2006). I demonstrate here an approach to collecting such data to derive region-wide estimates of optima for a diverse tropical community. My results also

demonstrate that these data can be used to predict and detect elevational range-shifts at fine spatial and temporal scale, and suggest a method for collection and analysis of baseline data in this system to build on existing information. As evidence validating the assumption of a temperature limitation on some species' distributions, results such as these also lend support to predictions from correlative distribution modeling (Williams *et al.* 2003) that global warming will have profound impacts on the biodiversity of the montane rainforest bird fauna in northeastern Australia. I therefore encourage development of other similar data sets to address the deficit of global change studies in vulnerable montane avifaunas of the tropics.

Chapter 7. Species distribution modelling predicts dispersal mediation of lowland biotic attrition due to climate change in Australia's north-eastern rainforest birds.

Article type: Full Length Article:

A.S. Anderson[1], A. E. Reside[2], J. VanDerWal[1], L.P. Shoo[1,3], R. G. Pearson[1], S.E. Williams[1]
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[1]Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia.
[2] School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia.

Plate 7. *Frilled Monarch (*Arses temporalis*) is a warm-adapted insectivorous species endemic to rainforests on Cape York Peninsula.*

7.1 Abstract

Montane tropical rainforests are critically important areas for global bird diversity, but are projected to be highly vulnerable to contemporary climate change. In the Australian Wet Tropics, species distribution modelling has forecast critical declines in suitable environmental area for upland endemic birds, but information is lacking for important neighbouring rainforest regions. Upslope shifts of lowland species may partially offset declines in upland species, but also result in a process of lowland biotic attrition. This latter process is contingent on the absence of species adapted to novel warm climates, and isolation from pools of potential colonisers. Here I use expanded data coverage to model the realised distributions of 120 bird species found in north-eastern Australian rainforest, including species from potential source locations in the north and recipient locations in the south. I reaffirm previous conclusions as to the high vulnerability of this fauna to global warming, and extend the list of species whose suitable environmental area is projected to decrease. Importantly, however, I find that expansion of suitable area for some species currently restricted to northern rainforests has the potential to offset biotic attrition in lowlands forests of the Australian Wet Tropics. By examining contrasting dispersal scenarios, I show that responses to climate change in this region may critically depend on dispersal limitation, as climate change shifts the suitable environmental envelopes of many species south into currently unsuitable habitats. For lowland and northern species, future changes to spatial pattern of rainforest is likely to be important mediator of climate change impacts in this system. In contrast, upland species are projected to become increasingly isolated and restricted. Here survival is likely to be more dependent on the viability of assisted migration, and the emergence and persistence of suitable environments in recipient locations, rather than dynamic change in habitats.

7.2 Introduction

Anthropogenic global warming over the last century has resulted in increases of global surface temperatures of a magnitude unseen in the previous 1000 years (IPCC 2001). Measured temperature increases in recent decades have been associated with a growing number of observed effects in plant and animal distributions (e.g. Wilson, Gutierrez, *et al.* 2007b; Peterson & Martínez-Meyer 2009, Chen *et al.* 2011) and phenology (e.g. Cotton 2003; Crick 2004; Chen *et al.* 2011). Temperature increases have been most pronounced at higher latitudes (IPCC 2007), and impacts in temperate systems are predicted to be more severe as a result (Parmesan 2006). Direct observations of changes in species' distributions in high latitudes also outnumber those in the tropics, although this may in part be driven by sampling bias (Parmesan & Yohe 2003). Conversely, steep environmental gradients in the montane tropics (Corlett 2011) and the narrow thermal tolerances of tropical species (Laurance *et al.* 2011) may make these ecosystems particularly vulnerable (Nogué *et al.* 2009; Young *et al.* 2011). Physiographic attributes of upland forests may also increase their vulnerability to indirect influences of temperature increase, such as raised cloud-layer (Foster 2001). The few published observations of climate impacts on montane tropical ecosystems already include evidence of extinctions (Pounds *et al.* 1999) and up-slope shifts in species distributions (Raxworthy *et al.* 2008; Chen *et al.* 2009). Climate change may thus represent the most significant threat to tropical montane biodiversity (La Sorte & Jetz 2010).

One approach to evaluating assemblage vulnerability to climate change is to model species' environmental suitability (Elith *et al.* 2011) based on correlations between species occurrence and key environmental variables, yielding a "bioclimatic envelope" (Berry *et al.* 2002). Such correlative models capture aspects of species' abiotic, "Hutchinsonian" niche (Hutchinson 1957), as distinct from niche models using biotic interactions such as habitat and resource availability (Soberon 2007). It is widely accepted however that Hutchinson's concept defines a species' "fundamental niche", while correlations between species presence and abiotic environmental factors used in species distribution modeling define a "realised niche", which is constrained by other factors such as barriers to dispersal (Phillips & Dudík 2004; Jeschke & Strayer 2008). Species' future distributions are often predicted by projecting bioclimatic envelopes onto future climate space (Pearson & Dawson 2003), but this application is criticised due to the potential discrepancy between a current realised niche and future predictions based on abiotic factors alone (Araújo & Gusian 2006; Duncan *et al.* 2009). Despite these complexities, elevational and latitudinal shifts predicted to result from global warming have been widely supported by historical studies (e.g. Wilson *et al.* 2005; Chen *et al.* 2009; Tingley *et al.* 2009; for review see; Parmesan & Yohe 2003).

In the absence of historical data there is also evidence from from space for time-substitutions in chapter 6 here that species distributions track critical environmental variables. Correlative bioclimatic models thus constitute perhaps our best tool for the urgent task of forecasting both species' responses to global warming (Silver 1998; Martinez-Meyer 2005; McPherson & Jetz 2007), and their assemblage-wide implications (Berry *et al.* 2002).

Distributional changes due to climate change are not a new phenomenon (Davis & Shaw 2001). In north-eastern Australia rainforests, cycles of global cooling and drying which characterised the Plio-Pleistocene have strongly shaped distributions of a diverse fauna (Williams and Pearson 1997; Schneider *et al.* 1998; Moritz 1999; Kershaw & Bretherton 2007). Many species are now restricted to cool and moist upland forests in a "mesotherm archipelago" (Nix & Switzer 1991) along the major cordillera of the eastern seaboard, and centred in the Australian Wet Tropics bioregion (see chapter 2, Figure 2.4). The region is also bisected by a number of biogeographic barriers formed by influences of climate history and fire on vegetation (Moritz *et al.* 2005). The Burdekin-Lynd barrier to the south (Keast 1961) isolate the temperate and subtropical montane forests of the Central Queensland Coast bioregion (CQC), and a suite of temperate rainforest species, including an endemic bird (the Eungella Honeyeater *Lichenostomus hindwoodi*), and other widespread species at their northern range limits. To the North, across the savanna of the Coen-Cooktown barrier (Tate 1952), warm tropical and monsoon rainforests of the Cape York Peninsula bioregion (CYP) support a diverse lowland fauna with affinities to Papua New-Guinea (PNG), including a range of endemic species (e.g. Frilled Monarch, *Arses lorealis*) and subspecies (Kikkawa & Pearse 1969; Keast 1981; Flannery 1990).

Anthropogenic global warming is poised to influence the structure of a complex array of rainforest bird assemblages across this region. Mean annual temperature is projected to increase between 0.8 to 4.3°C between now and 2070 (Suppiah *et al.* 2007). Greater uncertainty surround predictions of rainfall patterns, but best estimates indicate that annual rainfall will increase in Cape York but become less seasonal, while further south seasonality is expected increase, though rainfall overall decreases. Overall precipitation is projected to change by between -22 and +7% by 2070. Previous studies have predicted a high level of vulnerability, particularly to temperature changes, among upland endemic rainforest birds in the Australian Wet Tropics (Williams *et al.* 2003; Hilbert *et al.* 2004), but impacts on the avifauna of neighbouring rainforests is largely unknown. In addition, increased CO_2 concentrations and changed rainfall regimes may drive shifts in the distribution of rainforest habitats in northern Australia with global warming (Hilbert *et al.* 2001; Bowman & Murphy 2010).

Species' responses to climatic change are predicted to take two main forms: Firstly, species adapted to cooler upland environments are likely to face increased extinction risk as suitable environments contract towards isolated mountain tops (Chen *et al.* 2009; La Sorte & Jetz 2010). For these species, assisted migration may be the only means to ensure their continued survival, though it remains a controversial option. Secondly, lowland species may expand their distributions elevationally and latitudinally into previously unsuitable environments, driving changes in assemblage composition at low and mid elevations (Laurance *et al.* 2011; Corlett 2011). Where species adapted to novel warm environments are lacking due to isolation and barriers to dispersal, a process of lowland biotic attrition may result (Colwell *et al.* 2008) where upslope shifting taxa are not replaced by warm adapted species. Assemblage changes predicted on the basis of the constraints imposed on species distribution by climatic factors may thus be strongly mediated by the influence of barriers to dispersal (Svenning & Skov 2004). In assemblages with both climatic and habitat specialist species such as the montane tropical avifauna of the AWT (Williams *et al.* 2010b) this interaction is likely to be particularly important.

Responding to the conservation challenges of predicting climate change impacts on biodiversity thus depends on an understanding of both climatic and dispersal limitations on current patterns (Jetz 2010a). The montane tropical avifauna of north-eastern Australia is a well understood system (Williams *et al.* 2008) which facilitates interrogation of two key processes: shifting bioclimatic envelopes, and dynamic barriers to dispersal. Here I use a species distribution modelling approach to examine the relative importance of these processes. Modelling distributions using a multi-regional data set at fine spatial resolution, I improve on the accuracy of previous models (Williams *et al.* 2003) for species which occur both inside and outside the AWT and expand coverage of previously under-sampled lowland forests. This analysis includes a suite of species in the AWT and CQC whose environmental tolerances are likely to drive up-slope contractions and extinctions (Williams *et al.* 2003) with a downslope corollary being lowland biotic attrition, as warm environments emerge to which few local species are adapted (Colwell et al 2008). To the north however, currently CYP-restricted taxa represent a plausible source of species whose climate envelopes could extend southwards under future climate change, potentially offsetting the attrition process. To test this I project modelled species distributions onto future climates under two contrasting dispersal scenarios, one confining species to their current distributions, and the other allowing free dispersal across current subregional boundaries that correspond to described biogeographic barriers. In doing so I aim to address four key questions: 1) To what extent do predictions of potential distributions suggest contemporary barriers to dispersal as the key factor

defining realised niches, as opposed to climatic limitation? 2) Assuming no dispersal, what is the extent of upland contraction of AWT endemics and lowland biotic attrition in response to climate change 3) Under a free dispersal scenario, to what extent does expansion of warm adapted species have the potential to offset the process of lowland biotic attrition under future climate change scenarios? 4) What are the implications of these findings for planning of assisted migration an managing dynamic habitat barriers? Answers to these questions promise to further our understanding of climate change impacts in montane rainforest avifaunas both here and in other vulnerable regions globally.

7.3 Methods

7.3.1 Study region and avifauna

The analyses presented here encompass 120 species that commonly occur in rainforests in three discrete biogeographic regions: Australian Wet Tropics (AWT), The Central Queensland Coast (CQC) and Cape York Peninsula (CYP), described in detail in chapter 2 (for map see Figure 2.5). Their combined area captures the entire global distribution for 12 species endemic to the AWT, 1 species endemic to the CQC, and a further three regionally restricted species in CYP and AWT. A total of 240,501 bird occurrence records from 1990 to 2011 were sourced, providing a snapshot of current climate response. I sourced bird records from the Birds Australia Atlas (Barrett *et al.* 2003) and the WildNet database (Environmental Protection Agency 2004) (101,823 records combined) and the Centre For Tropical Biodiversity and Climate Change (CTBCC) standard survey data (109,753 records) and incidental data (53,473 records) (Williams *et al.* 2010b). I also used 7665 records collected in rainforests of the Cape York Peninsula and Central Queensland Coast during the present study, including from collaborative expeditions with traditional owners into remote and poorly-known areas of both lowland and upland rainforest in the McIlwrath ranges on Cape York Peninsula. The addition of data from these sources enabled the inclusion of several nocturnal species not surveyed during the data collection for previous chapters. I classified species based on their degree of habitat specialisation following the system used by Williams *et al. (*2010b), including as “rainforest specialists” all obligate rainforest species and those occasionally found in adjacent non-rainforest habitats, and as “rainforest generalist species” those found commonly in non-rainforest habitats as well as rainforest, to those for which rainforest is non-core habitat. I divided species into groups based on their subregional distributions, yielding eight groups: 1:"*Wide-spread (PNG and Australia)*" (62 species), 2: "*PNG and CYP only*" (13 species), 3:"*PNG and Northeast QLD*" (Including CYP, AWT and CQC, 8 species), 4:"*Australian endemic*" (21 species), 5:"*CYP endemic*" (1 species), 6:"*CYP and Northeast Queensland endemic*" (2 species), 7:

"*AWT endemic*" (12 species), and 8:"*CQC endemic*" (1 species). For the purposes of summaries below, I refer to groups 1 and 4 as: “Wide-spread species”, and the remaining groups as “Endemic and restricted” referring to their distributions within Australia.

7.3.2 Species distribution modelling

I used gridded spatial layers for climate parameters designed to be equivalent to those from BIOCLIM (Houlder *et al.* 2000) and a 250 m resolution digital elevation model (GEODATA 9 Second DEM Version 2; Geoscience Australia, http://www.ga.gov.au) for the year 1990 as a climate baseline. Variables included annual mean temperature, temperature seasonality (the annual mean coefficient of variation of temperature), maximum temperature of the warmest period, annual precipitation, precipitation seasonality and precipitation of the driest period. These variables have been previously identified as useful predictors of species distributions in AWT rainforest vertebrates (VanDerWal *et al.* 2009; Williams *et al.* 2010b). Spatial layers of current climate were combined with collated species occurrence data to create correlative models of species climatic distributions using Maxent (Phillips & Dudík 2004). Maxent has been shown to outperform competing methods for species distribution modelling (Elith *et al.* 2006), can incoporate interactions between variables, and is relatively insensitive to small sample sizes. I estimated environmental suitability for each species as a function of climate variables in a gridded domain at 250m resolution. Modelled performance was assessed by the area under the receiver operator characteristic curve (AUC) (Bradley 1997; Elith *et al.* 2006). AUC values ≥ 0.7 indicate a useful threshold above which to retain models for further analysis, while values ≥ 0.9 indicate “high” performance models (Swets 1988), and < 0.5 is no better than random (Phillips *et al.* 2006).

MAXENT returns a gridded environmental suitability surface with cell values between 1 (highly suitable) and zero (unsuitable), which is refined by applying a threshold above which species occupancy is considered likely based on predicted suitability. Inspection of the raw models suggested better approximations of “rainforest specialist” species’ realised distributions with a more conservative threshold (equating the entropy of the thresholded and original distributions), and “rainforest generalist” species with a less conservative threshold (balancing the training omission predicted area and threshold value). To convert the MAXENT-computed potential climatic distribution into realised species distributions I further restricted suitable area based on vegetation type using the Australian Herbarium NVIS broad vegetation subgroups (Australian Government Department of the Environment and Water Resources 2004) at a resolution of 250m. Rainforest specialists where limited to rainforests, vine thickets and wet sclerophyll forest with a rainforest understory, while generalists species’ habitat masks were expanded to include tropical mixed forests

and open *Eucalyptus* and *Melaleuca* forests and woodlands. The potential for dispersal to mediate the effects of climate change can be examined by comparing species distributions under contrasting scenarios (Peterson *et al.* 2001). I considered two such scenarios: under a "no dispersal" scenario (see below) I excluding suitable climate area outside species' current known regional distribution based on records in the database. Under a "free dispersal" scenario I allowed suitable climate grid-cells to remain even if they were in regions outside the current known distribution, simulating full occupation of the potential climatic distribution.

7.3.3 Future distribution and richness prediction

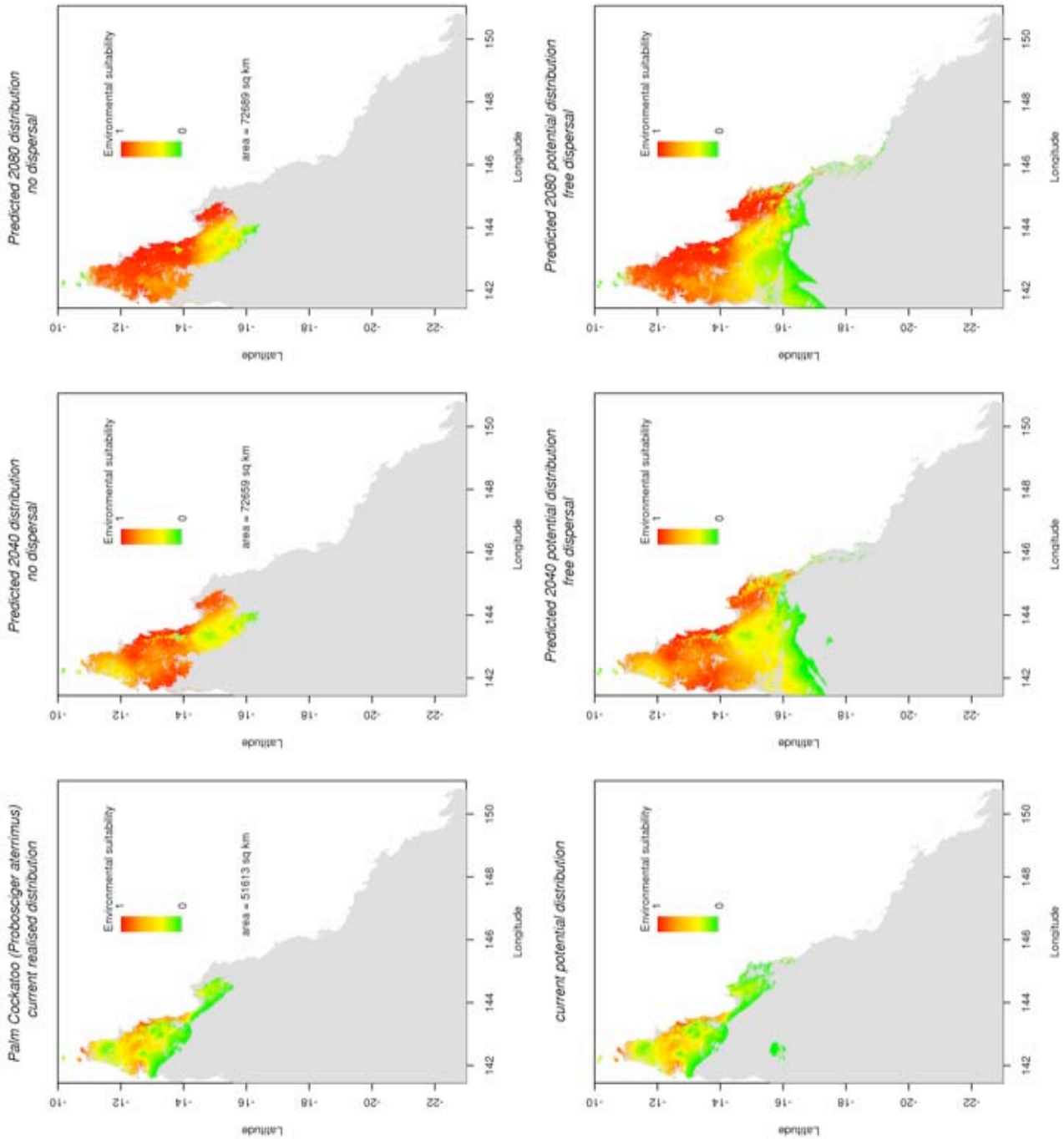
Spatial predictions of future climate were based on the IPCC Special Report Emission Scenario (SRES) A1B, which describes an "intermediate" severity of projected carbon emissions (Nakicenovic *et al.* , 2000). The A1B scenario is likely to be conservative given recent evidence that global temperature trends are tracking a "worst case" scenario (Canadell *et al.* 2007; Anderson & Bows 2008). I capture the uncertainty in broad-scale future climate modelling with eight different global circulation models (GCMs) (Cubasch *et al.* 2001), some with multiple realisations, realizations. Summaries were computed first across realizations within each GCM (to avoid disproportionate influence of GCMs with many realizations) and secondarily across GCMs to produce a mean projection for each interval. I projected the species models onto the 300 raw outputs of future climate/time-step combinations, including each variation of SRES, GCM and year. I then summarised outputs for each species into minimum, mean, and maximum projections, and clipped the resulting potential climatic distribution using the relevant threshold (see current model methods above). Here I report only the results for the current, 2040 and 2080 time-steps, and I restrict future distribution models by vegetation type as for the current models. I characterised trends for expansion and contraction in each species group (defined above) by summarising responses in terms of change in proportional area of suitable habitat (relative to current) in the year 2080 for each species, using projections from the "no dispersal" scenario. I then sub-sampled each projected distribution in each time-step at 2000 random locations currently within rainforest to examine the evidence of lowland biotic attrition. I modelled variation in predicted maximum species richness across elevation with smoothing splines incorporating third-order quadratic terms, and tested for significant effects of time-step in these models using ANOVA in the "R" framework for statistical analysis version 2.13.1 (R Core Development team 2011).

7.4 Results

7.4.1 Species distribution trends

Model performance was high across all the species examined, with an average AUC score of 0.97. AUC scores for eight of 122 species fell below 0.90, and none below 0.81 (Appendix Table 7.1). All species were thus retained for further analysis, though the outputs for 9 species with less than 30 records (indicated in bold in Appendix Table 7.1) are interpreted with caution. Patterns of change predicted for species under the A1B climate change scenario vary markedly between species and regions; some species are predicted to expand their distributions (e.g. Palm Cockatoo (*Probosciger aterrimus*) map in Figure 7.2), while others are predicted to decline (e.g. Golden Bowerbird (*Amblyornis newtonianus*), Appendix Figure 7.3). Assuming no dispersal, some species are predicted to contract to extremely limited upland refugia (e.g. Atherton Scrubwreb (*Sericornis keri*) Appendix Figure 7.4) while others are predicted to undergo little change relative to their current distributional area (e.g. Mistletoebird (*Dicaeum hirundinaceum)* Appendix Figure 7.5*)*. The mean proportional change in suitable environmental area by 2080 (relative to current) over all 120 species analysed was +1.026 (SE = 0.61, max = +3.94, min = -0.89), though of these 73 species contracted their distribution, and 47 species expanded. There were distinct differences in proportional area change between groups based on endemicity (Appendix Figure 7.1). Among 84 widespread species, suitable area for most Australian endemics contracted (median = -0.3064, max = 0.4175 , min = -0.8912), while there was broad variation in the response of those also found extralimitally in PNG (median = -0.05951, max = +1.05502, min = -0.49609). A Kruskal-Wallis rank sum test confirmed that change in area differed significantly between these groups (Kruskal-Wallis Chi-squared = 10.2217, df = 1, p-value = 0.0013).

Figure 7.1. *Example of current and predicted future species distributions: Palm Cockatoo (*Probosciger aterimus*), showing the impact of biogeographic barriers to dispersal, restricting suitable environmental space to a realised geographic distribution.*



Patterns also differed among the more restricted species, including regional endemics and those found in Australia only on CYP Figure 7.2). Suitable area declined by 2080 for the single Cape York endemic (Frilled Monarch, Appendix Figure 7.6), (unless dispersal towards the south was assumed, see below). Suitable area also declines for all 12 AWT endemics (e.g. Golden bowerbird, Appendix Figure 7.3), and the single CQC endemic (Eungella Honeyeater (*Lichenostomus hindwoodi)*, Appendix Figure 7.7). In contrast, suitable area expanded for all species found in both PNG and CYP (e.g. Palm Cockatoo, map in Figure 7.1), or in PNG and North Queensland (e.g. Metallic Starling (*Aplornis metallica)* Appendix Figure 7.8), while the predicted responses were mixed among the two CYP/AWT species, with Lovely Fairy-wren (*Malurus amabilis,* Appendix Figure 7.?) expanding slightly and Yellow-spotted Honeyeater (*Meliphaga notata,* Appendix Figure 7.?) contracting slightly. Median and quantile values for the suitable area changes in these subsets indicate a significant difference between the expanding CYP/PNG group and generally contracting southern (AWT/CQC) groups (Figure 7.2 inset boxplot), confirmed by a Kruskal-Wallis rank sum test (combining the CYP, CYP/AWT and CQC endemics into a single sample of north-eastern Queensland endemics): Kruskal-Wallis chi-squared = 30.1666, df = 3, p-value = <0.001). A summary of all species showing their Maxent AUC scores, distributional change and regions of endemicity is shown in Appendix Table 7.1, along with the mean scores for each subset analysed above.

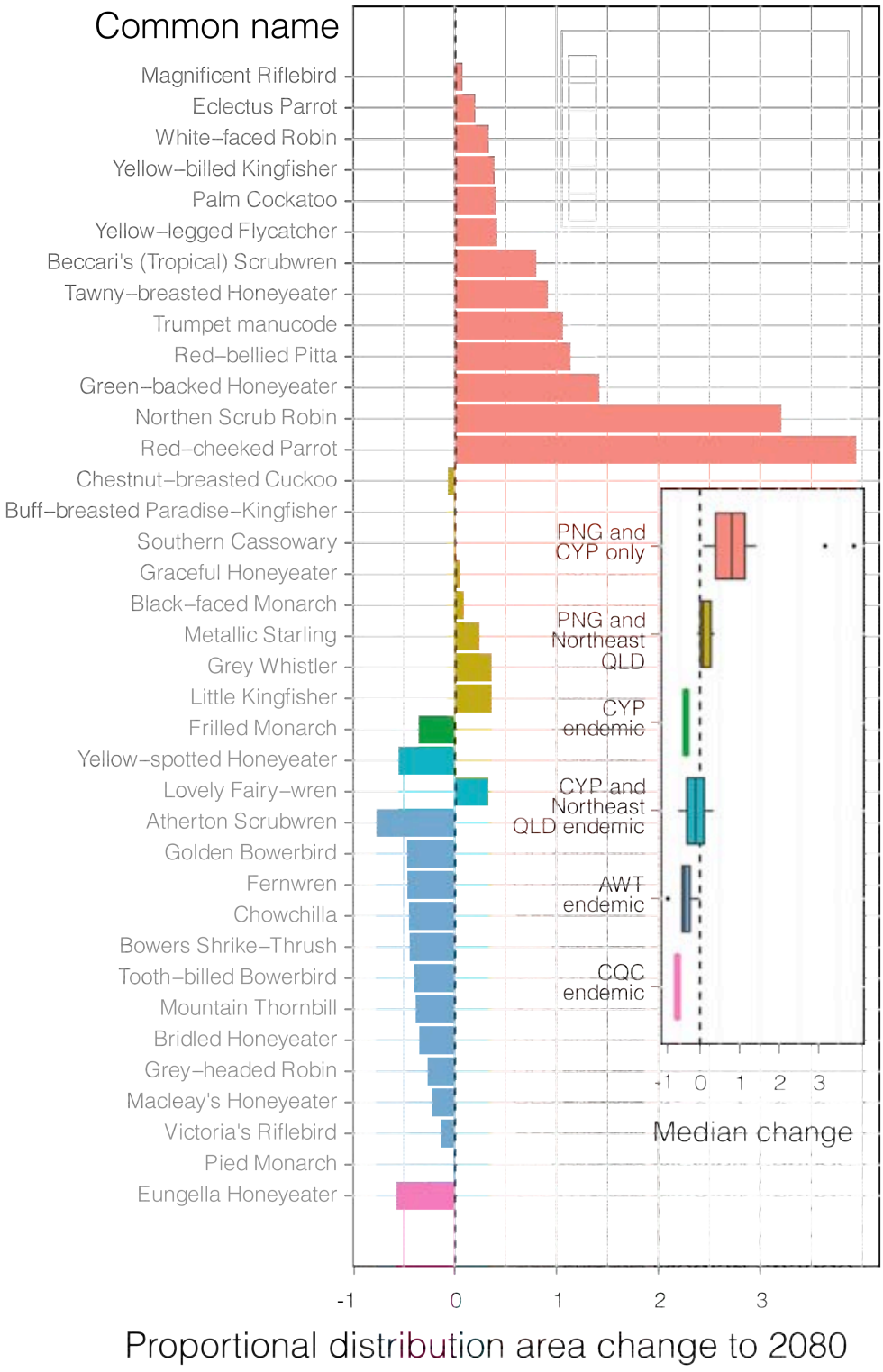


Figure 7.2. *Proportional change in predicted potential distributional area between the present and the year 2080 (assuming global warming scenario A1B and no dispersal) for endemic species. The difference is expressed as a proportion of current distribution, and both positive and negative values are shown, right and left of zero on the x axis respectively. The region to which species are endemic is indicated by colour, corresponding to the labels in the inset boxplot. The boxplot shows the distribution of outliers and upper and lower quartiles around the median of the distribution of proportional suitable area change for each regional subgroup. A significant general trend for increase in CYP and PNG species and declines in NEQ, AWT and CQC species is indicated by their positions relative to zero change on the inset x axis.*

7.4.2 Species richness patterns and predictions of lowland biotic attrition

The cumulative effect of contraction in Australian regional endemic birds from CQC, AWT and CYP, and expansion of species with affinities to PNG is evident in the elevational profiles of modelled endemic species richness (Figure 7.3). This contrasted with the relatively slight variation among widespread species (Appendix Figure 7.1). Modelled species richness of endemics and restricted species restricted varies markedly between time-steps, and the direction of variation differed between regions (Figure 7.3 a). Quadratic smoothing splines fitted to these distributions under a "no dispersal" scenario (statistics in table 7.1) show current modelled species richness in CYP declining from lowlands to uplands, while the reverse is true in the AWT (Figure 7.3b). Under the "no dispersal" scenario I predict richness of regionally restricted species in the CYP will remain stable in the lowlands in future (indicated by little influence of time-step in the regression model, Table 7.1). Over the same period in the AWT, however, I predict an increase in endemic species richness in the uplands, but a decline in richness in the lowlands (Table 7.1). Values across elevation between time-steps vary little CQC where few endemic or restricted species occur indicated by little influence of time-step in the regression model (Table 7.1).

7.4.3 Influences of climate versus dispersal constraints

Under a "free dispersal" scenario, allowing the expansion of species across current distributional boundaries, several important differences are apparent. Firstly, the current richness baseline is slightly increased in the CYP and AWT, and substantially so in CQC, as some species predict into areas where they do not currently occur (Figure 7.3 a,b and c respectively. Apart from this increased baseline, there is little qualitative difference in the elevational pattern of change in richness with time in the CYP (Figure 7.3 a). In the AWT in contrast, declines in lowland species richness are reversed by an influx of warm adapted species from CYP, though there is minimal change in the uplands (Figure 7.3 b), indicated by a significant effect of time-step in the model (Table 7.1). In CQC there is similar increase, but here the effect is greater in the mid slopes and uplands, reflecting the contribution of cool adapted species from the AWT (regression statistics in Table 7.1).

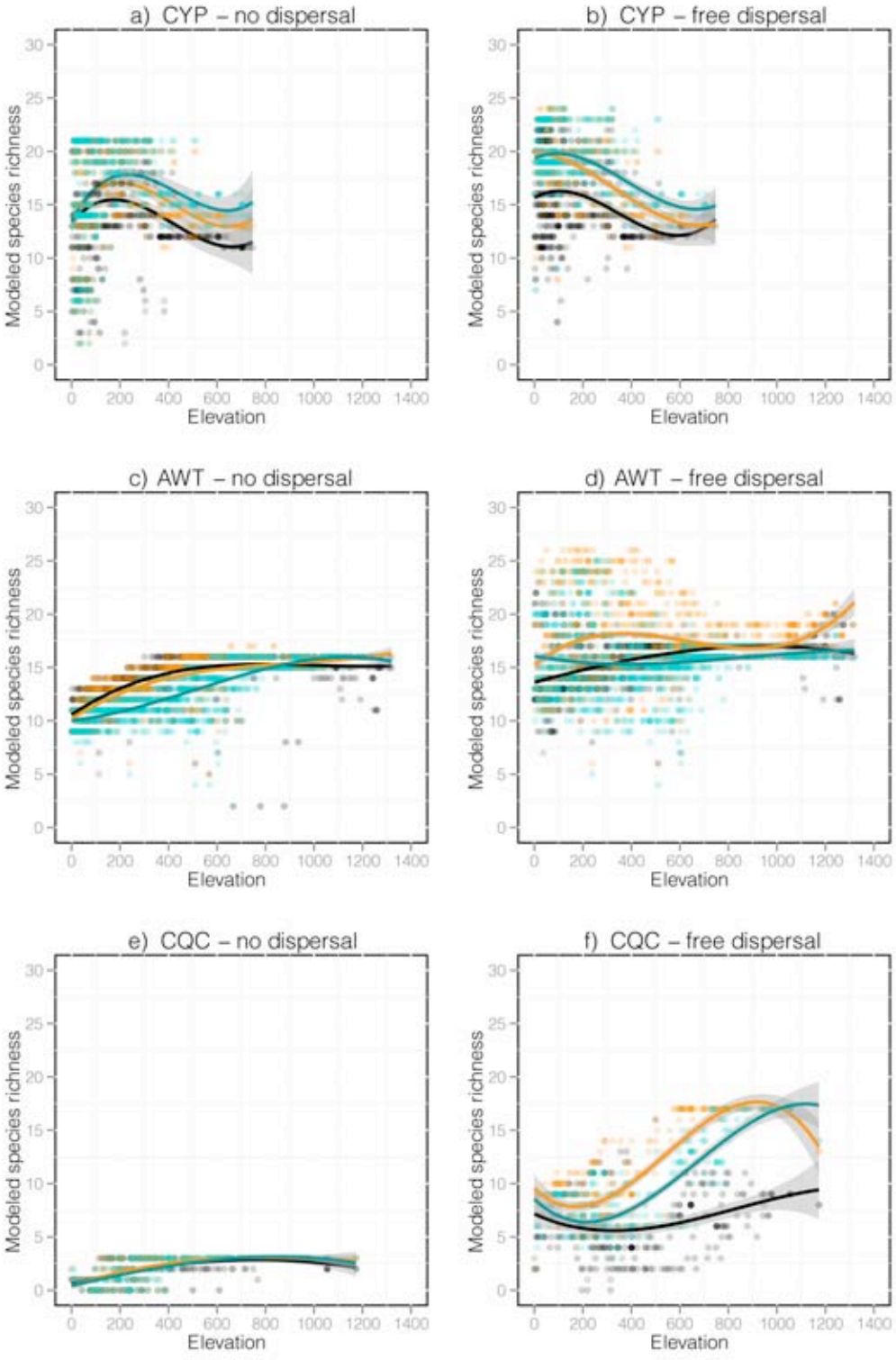


Figure 7.3. *Patterns of change in endemic species richness across elevation in CYP, AWT and CQC under climate change, showing the effect of both dispersal limitation on realised niches, and the effect of hypothetical unconstrained dispersal on predicted lowland biotic attrition in the AWT and CQC. Species richness layers were summed from binary species distribution models for all endemic species in each region, randomly sub-sampled from a regular grid of points in rainforest. Black points are estimated from current species distributions, orange points are estimated from 2040 predictions and blue points from 2080. Smoothing splines are fitted using 3rd order quadratic polynomials, (regression statistics in Table 7.1).*

Table 7.1. *Results of polynomial (3rd order quadratic) regressions of the distribution of endemic and restricted species richness across elevation in each subregion. Two models are compared for each region and under each dispersal scenario: one with a time-step term (a), and one without (b), in order to explore the influence of projected future climate change on elevational richness patterns. The results of an Analysis of Variance (c) indicates the effect of the inclusion of a time-step term, indicating the significance of projected temporal change in species richness.*

			a) Without timestep				b) With timestep				c) Difference	
	region	Dispersal scenario	R	F-statistic	DF	p-value	R	F-statistic	DF	p-value	ANOVA F-statistic	ANOVA p-value
1	CYP	No dispersal	0.100	56.38	1520	<**0.001**	0.101	33.94	1518	<**0.001**	0.344	0.708
2	AWT	No dispersal	0.453	1057	3833	<**0.001**	0.475	694.2	3831	<**0.001**	82.429	<**0.001**
3	CQC	No dispersal	0.329	394.9	802	<**0.001**	0.331	132	800	<**0.001**	0.707	0.493
4	CYP	Free dispersal	0.100	56.83	1520	<**0.001**	0.256	105.7	518	<**0.001**	47.192	<**0.001**
5	AWT	Free dispersal	0.148	223.2	3833	<**0.001**	0.149	137.7	3831	<**0.001**	2.920	**0.050**
6	CQC	Free dispersal	0.289	326.1	802	<**0.001**	0.368	155.4	800	<**0.001**	49.579	<**0.001**

7.5 Discussion

I predict dramatic changes to patterns of assemblage composition and species richness in rainforest birds of north-eastern Australia as a result of global warming, particularly among endemic, regionally endemic and restricted species. Species currently restricted to the CYP or with affinities to PNG tend to expand their ranges southward, while AWT and CQC restricted species tend to contract up-slope. These results join previous work in highlighting the threat of climate change to the Australian avifauna (Brereton *et al.* 1995; Chambers *et al.* 2005; Garnett *et al.* 2011). My data coverage expands on previous work limited to the AWT, incorporating critical rainforest habitat in the AWT lowlands, and in neighbouring regions of CQC and CYP. With an expanded geographic coverage of the area I reaffirm projected declines of 12 endemic species in the AWT predicted previously (Williams *et al.* 2003). I also predict that pervasive upslope shifts in the AWT may result in a process of lowland biotic attrition, and that habitat rather than climate may be currently limiting influx of candidate species that could otherwise offset this process. I also suggest that

temperature increases will further reduce climate limitations on expanding species, placing emphasis on habitat barriers and species dispersal characteristics in mediating climate change effects on avian assemblage structure in rainforests of the AWT.

7.5.1 Influence of climate versus dispersal barriers

Under a moderate warming scenario, the decline and possible extinction of a number of upland endemic species in the AWT may paradoxically have little net impact on species richness in the uplands, being offset by up-slope shifts of lowland taxa. An important corollary of these shifts may be a process of lowland biotic attrition, consistent with predictions for lowland tropical faunas generally (Colwell *et al.* 2008). The main conditions for lowland biotic attrition are twofold. Firstly, narrow thermal tolerances in lowland tropical species (Janzen 1967; Laurance *et al.* 2011) may predispose them to vulnerability to temperature change under global warming (Corlett 2011), driving upslope shifts similar to those expected for cool-adapted species. Secondly, species adapted to novel warm climates that might replace local lowland species may be unavailable due to historical vicariance or barriers to dispersal (Colwell *et al.* 2008). Here I predict declines in several restricted lowland species (e.g. Macleay's Honeyeater (*Xanthotis macleayana*)) and Yellow-spotted Honeyeater (*Meliphaga notata))* supporting the assumption of narrow thermal tolerances among lowland species. Widespread sensitivity to temperature gradients across elevation among rainforest birds shown in chapter 6 further corroborate this assumption. Testing the second condition, my results further suggest that current climatic limitations on the occurrence of CYP species in the AWT may be less important than habitat barriers, as relaxation of the assumption of constrained dispersal under current conditions already results in the prediction of several species into the northern AWT. Under a warmed climate scenario, climate constraints on this influx are further relaxed, with an important result being a predicted influx of CYP lowland taxa into the AWT that completely offsets incipient lowland biotic attrition.

Based on the comparison between dispersal scenarios, habitat barriers to dispersal may thus rank above climate as the dominant constraint on the current distributions of important elements of the CYP and AWT lowland rainforest avifauna. I also show that climate change is likely to further reduce the role of climate constraints, placing an increased emphasis on habitat and species' dispersal characteristics as mediators of assemblage change in the AWT. In the absence of future vegetation modeling, indirect evidence from a number of sources also suggests that habitat barrier components of the system may be changing. Rainforest expansion into savanna and woodland has already been documented in lowlands of Cape York (Stanton, & Fell 2005b) and in the Wet Tropics (Harrington & Sanderson 1994; Tng *et al.* 2010). Changes to fire regimes during the last century

may be an important driver, with observed rates of rainforest expansion in CYP much faster than those in upland forests further south (Russell-Smith *et al.* 2004). Wetter climates and increased CO_2 levels have also be implicated in this process, and suggest it may be an increasing trend across northern Australia (Banfai & Bowman 2006; Bowman & Murphy 2010) and globally in tropical forests (Gwynne & Torres 1982). Conversely however, rainfall seasonality is likely to increase in parts of the region (Suppiah *et al.* 2007) with repercussions for fire risk that are not well understood (Hilbert 2010). These habitat dynamics will also interact with species' preferences and dispersal capabilities to constrain realised distributions under climate change (Svenning & Skov 2004). As in other bird assemblages in monsoon tropical Australia (e.g. Woinarski *et al.* 1988), some rainforest species in CYP are observed to use riparian and mixed-forest communities (A. Anderson, unpublished data), though rainforest specialisation will likely remain a constraint for others. There is also little known about dispersal capabilities in this fauna, though several rainforest species currently migrate across ocean barriers between New Guinea and Cape York, and across dry forest barriers further south (e.g. Buff-breasted Paradise-kingfisher (*Tanysiptera sylvia*; Higgins 1999) while others are highly restricted (e.g. Green-backed Honeyeater, (*Glycicharea fallax*)), suggesting significant variation between species.

7.5.2 Species trends and conservation significance

Under the mid-range emission scenario examine here, I predict the total disappearance by 2080 of suitable environmental area on Cape York for two regionally endemic subspecies (Cape York Lewin's Honeyeater *(Meliphaga lewinii amphochlora)* and Cape York Pied Currawong (*Strepera graculina magnirostris*). Suitable area also declines for a further CYP endemic species (Frilled Monarch). In Central Queensland Coast rainforest I predict a greater than 50% reduction in area for the endemic Eungella Honeyeater, and a greater than 90% reduction in suitable area the CQC population of Regent Bowerbird (*Sericulus chrysocephalus)*, though occurrence records for the latter species are few. Though isolated, Regent Bowerbirds in CQC are not described as distinct, despite southern populations being divided into two subspecies (Mayr & Jennings 1952), and their taxonomic status may warrant further investigation in light of this threat. In the AWT, I predict a greater than 40% reduction in the distributions of 4 endemic species (Golden Bowerbird (*Amblyornis newtonianus)*, Atherton Scrubwren (S*ericornis keri)*, Chowchilla (*Orthonyx spaldingii)*, and Bowers Shrike-thrush (*Coluricincla bowerii*)). Proportional changes for all species are summarised in Appendix 7.2, including a further 6 restricted species and subspecies that I predict to experience greater than 30% reductions in suitable area.

Despite these predicted changes, of the species analysed here only the Southern Cassowary (*Casuarius casuarius*) is currently listed as at least Vulnerable under either Australian Government (2011) or IUCN (2011) threat categorisations. While it is beyond the scope of the current study to reassess their status in detail, I suggest that many of these species may thus no longer qualify under the category "Least Concern" of the IUCN scheme. It is also important to note that while these figures represent predicted changes in *total* distributional area, there is strong variation in density across gradients of environmental suitability within the distributions of many species (VanDerWal *et al.* 2009). This variation may decouple population trends from distributional area, so that population size may decrease sharply with a relatively small loss in area, increasing vulnerability to extinction from global warming (Shoo & Williams 2005). These findings thus support previous suggestions of a need to reassess the status of the Australian avifauna in light of climate change threats (Chambers *et al.* 2005; Garnett *et al.* 2011). These results also suggest a general increase in the Australo-Papuan elements of this rainforest fauna with global warming, and a concomitant decrease in Australian endemics. The implications of changes to patterns of interspecific competition that may accompany this assemblage reshuffle are poorly understood. Coupled with habitat degradation already problematic in some regions (Mac Nally *et al.* 2009), ecological implications for these declines warrant further investigation on a continental scale.

7.5.3 Upland refugia and assisted migration

In contrast to the expanding CYP lowland species discussed above, I predict an increase in the importance of climate constraints on realised distributions for upland and southern species. Global warming is projected to increase isolation for 12 endemic species in the AWT, and one in CQC, as suitable environmental space contracts towards mountain tops, stranding cool-adapted species in a matrix of unsuitable warm environments. Habitat considerations are therefore less important than the spatial distribution of suitable climate for these species, and my results highlight instead the potential importance of climate refugia in the relatively depauperate montane rainforest of CQC for at least some AWT endemics. Modelled bioclimatic envelopes for several vulnerable species already extend to this region, and may become suitable in the future for several additional species. Climatically at least, upland rainforests in the CQC are therefore suggested by this analysis as potential recipient locations for assisted migration. As a response to the risks to biodiversity posed by climate change, assisted migration remains controversial (Ricciardi 2009; Schwartz *et al.* 2009). However, advocates maintain that it may represent the only chance of survival for some species such as those restricted to mountain tops (Thomas 2011) and will be a key component of future integrated conservation management (Hoegh-Guldberg *et al.* 2008; Vitt *et al.* 2009). Assisted migration has also been suggested as a priority area for conservation research in Australia

(Chambers *et al.* 2005), including the tasks of predicting when potential refugia become suitable, and how long they last (McLachlan *et al.* 2007; Mcdonald-Madden *et al.* 2011). While it is beyond the scope of the present study to address in detail, these results suggest suitable environmental area in CQC may already be present for AWT endemics. Importantly however, for some species the suitable areas are small and short-lived (see e.g. maps for Golden Bowerbird Appendix Figure 7.3, Atherton Scrubwren Appendix Figure 7.4,).

7.5.4 Limitations and further work

I add new data which expands the coverage of the distributions of many rainforest species relative to previous efforts, an important step in improving model accuracy (Araujo & Thuiller 2009). Nonetheless these data do not cover the warmer end of the environmental niche of 24 species that occur extralimitally in New Guinea (e.g. Trumpet Manucode (*Phonygammus keraudrenii)*, Eclectus Parrot (*Eclectus roratus)*). Models for these species may thus underestimate their thermal tolerances, and hence responses to future climate change, and further work should include additional data from their entire distribution. By the same token I also underestimate the potential for assemblage change by omitting species currently not found in Australia. Some candidates are already regular visitors to the Torres Strait (Draffan *et al.* 1983), and their inclusion may add substantially to the projected changes to species composition in rainforests presented here. A further limitation common to all predictions from correlative species distribution models is reliance on the assumption of transferability of realised bioclimatic niches (Vaughan 2005; Dormann 2007). Two pieces of indirect evidence suggest however that this assumption may be appropriate in the present study, at least for some taxa. Firstly, models based on data from within the AWT for an example species (Lewins' Honeyeater (*Meliphaga lewinii*)) accurately predicted the distribution of the northern subspecies in Cape York Peninsula (Shoo *et al.* 2009, excerpt in Appendix 1), suggesting spatial transferability. Secondly, evidence from space-for-time substitutions in chapter 6 indicates simple models based on mean annual temperature accurately predict up-slope shifts in a range of both upland and lowland species within the AWT.

Lastly, biotic interactions may also be important in structuring assemblages across elevational gradients (Diamond 1973; Brown & Lomolino 1998). While some studies suggest that competition plays an important role in structuring montane rainforest avifaunas (Terborgh & Weske 1975) and indicate a strong influence in some neotropical species (Remsen & Graves 1995; Jankowski *et al.* 2010) its prevalence remains controversial (Weins 1989). A study in the Australian avifauna concluded little influence at broad scales (Gotelli *et al.* 1997), and there is some evidence from the elevational density profiles of congeneric honeyeaters in this system that competitive exclusion may

operate to skew the location of density optima in some species (A. Anderson unpublished data), but the generality of competition in influencing species' realised distributions in this system remains unknown. It is important to note however that competition may be prevalent without necessarily presenting a strong confounding influence on species realised distributions under climate change. Where up-slope or southward shifts are a prevailing response across the assemblage, zones of competitive interaction at the margins of species distributions may also track future climate shifts (Shoo *et al.* 2005). Nonetheless, there is experimental evidence that biotic interactions may exert an unpredictable influence on the impact of climate change for species realised niches (Davis *et al.* 1998), and variation in the environmental tolerances of competitors and hence the magnitude of their responses could complicate distributional responses, and warrant further study. Such competitive constraints on species distributions may also have impacts on the success of assisted migration, so that climatic assessments of recipient areas may need to be supplemented with additional ecological knowledge in order to plan effective translocation programs.

7.5.5 Conclusions

Here I demonstrate an important role for dispersal limitation in mediating the impacts of climate change on patterns of diversity and assemblage structure in a montane tropical avifauna. Species distribution models suggest widespread vulnerability to future temperature increases across the elevational gradient, including restricted and endemic upland species. These results also predict the offsetting of diversity attrition in lowlands when assumptions of dispersal barriers are relaxed. Future rainforest vegetation dynamics in north-eastern Australia may therefore play an important role in determining the composition of lowland avifaunas in the region. The potential influences of biotic interactions such as competition further suggests that future work in modelling the impacts of climate change on patterns of biodiversity will benefit from an integration of correlative models with ecological information (Guisan & Thuiller 2007), for which the present study will provide an important first step for north-eastern Australian rainforest birds.

Chapter 8: General discussion

Plate 8. *The Golden Bowerbird (*Amblyornis newtonianus*) is a cool-adapted species endemic to the upland rainforest of the Australian Wet Tropics, and threatened with dramatic contraction of its suitable environmental area with global warming.*

8.1 Significant findings of the main research questions

It is apparent from the results presented here that climate exerts a complex set of influences on the patterns of assemblage structure and diversity in montane rainforest avifauna of north-eastern Australia. Both current and historical climate plays a role in driving patterns of density and diversity, and future climate promises to further perturb these, with significant consequences for biodiversity conservation. I began the process of overcoming some of the challenges faced in understanding these patterns and processes by first seeking in chapter 3 to improve data quality, addressing the first key question: *What are the influences of detectability variation between species, sites and surveys on accurate estimation of bird density?*. I addressed the problem of detectability variation in surveys by applying a distance sampling approach. The key finding was a dominant effect of variation between species on the Effective Strip Widths of transects. Given the need for efficient survey methods in logistically challenging and diverse montane ecosystems, in chapter 4 I posed the second key question: *Based on this understanding of the detection process in audio-visual surveys of forest birds, can I develop a method for estimating density, calibrated for detectability, that can be applied across broad regional systems?* This was addressed by the development of a viable method for modeling Effective Strip Width for species relatively using field data and ecological characteristics. This was demonstrably useful in estimating density in both rare species and novel assemblages, and to derive a calibration for detectability that could be applied retrospectively to standardised count data.

Combining the distance sampling approach developed in chapter 3 with the modeling approach developed in chapter 4 for less common species, in chapter 5 I was able to ask*: Using density estimates and the More-Individuals Hypothesis as a framework, what is the relative support for two key factors suspected to drive an observed unimodal relationship between bird species richness and available energy in the AWT: current versus historical environmental stability?* I showed an important influence of historical climate stability on energy flux and hence diversity in the bird assemblage, and a secondary influence of resource seasonality for insectivores. Pattern in endemic species energy use across the dominant guilds further suggested that historical extinction filtration may explain the relatively depauperate, generalist lowland fauna and diverse upland fauna, whose overlap in mid-slopes drives the unimodal species-energy response. Given this historical influence of climate change, in chapter 6 I again applied the improved density estimates developed in chapters 3 and 4 to address the question *...to what extent are the underlying assumptions of transferability of environmental niche borne out by a space-for-time substitution in the AWT*

avifauna? A comparison of the elevational density profiles between regions showed a trend of upslope differences consistent with a strong influence of temperature on distribution for 18 species, a key assumption of correlative species distribution modelling.

Based on these conclusions, in chapter 7 I moved to using a bioclimatic envelope approach to model species distributions, addressing the question *… to what extent do I alter predictions of the vulnerability this fauna by extending data coverage in lowlands, and what further changes do I identify for regionally restricted species in CYP and CQC not included in previous studies?* I showed that future climate change is likely to exert a pervasive influence on patterns of rainforest bird assemblage composition in the region. Suitable environmental area for a number of restricted endemic subspecies in CYP was predicted to decline or disappear entirely. Declines in suitable area for many endemic species in the AWT was predicted to decline also, along with the sole endemic bird in the CQC. Reassessment of the conservation status of these taxa was recommended in light of the threat posed by climate change to their extinction vulnerability. In the same chapter I addressed some assembly-level questions: *what can I predict about changes to patterns of bird species richness across the elevational gradient of north-eastern Australian rainforest with climate change? Specifically, what is the likelihood of a process of lowland biotic attrition in the lowlands of the AWT? To what extent is this process mediated by dispersal from neighbouring regions?* I predicted that upslope migration of lowland species has potential to offset diversity loss in the uplands of the Australian Wet Tropics, but may drive a process of lowland biotic attrition in the lowlands. Importantly however, it was also likely that suitable climate for warm-adapted northern species will expand such that dispersal and habitat barriers become more critical than climate barriers in separating currently distinct faunas, potentially offsetting the effects of lowland biotic attrition.

These results identify specific sources of uncertainty in our ability to predict impacts of future climate change with a correlative bioclimatic envelope approach alone, due to the influences of habitat and species' dispersal capabilities. For cool-adapted upland taxa it was shown that suitable climate may contract so that isolation increases, raising the prospect that assisted migration to southern upland refugia may be required to ensure the continued survival of some species. The importance of montane rainforest avifaunas for biodiversity conservation both within Australia and globally make monitoring and responding to climate induced changes in assemblage structure an urgent task. The results presented here set out projected impact scenarios and key uncertainties that might inform the planning of an adaptation decision making process. Below I address the last key

questions: ...*what are the next steps for advancing understanding of the drivers of biodiversity pattern, and the risks posed by climate change? What might be the implications of these steps for biodiversity monitoring and conservation in a changing climate in this system?*

8.2 Density, detectability and monitoring for climate change impacts.

Accurate field estimates of density are an important component of monitoring population changes, such as those predicted under climate change, and are a key component of the National Biodiversity and Climate Change Action Plan (Australian Government Department of the Environment and Heritage (2007). Tropical rainforests avifaunas are critical for biodiversity conservation as they are often high in both diversity and endemism (La Sorte & Jetz 2010), and include some of the most threatened species worldwide (Sodhi *et al.* 2004). Climate change also represents a significant threat to this diversity, increasing the need for accurate estimates of density of rainforest bird populations (Sekercioglu *et al.* 2008). This is particularly true in Australia, where rainforest avifaunas comprise a significant proportion of total diversity, and are seriously threatened by climate change (Williams *et al.* 2003). However, field costs may be an important limitation in the collection of quality data over the broad spatial scales critical to effective regional management of climate change impacts on biodiversity (Jones 2011) and monitoring bird populations in the dense vegetation and rugged terrain of montane tropical forest can be costly and challenging (Dawson 1981; Karr 1981). In chapter 3 I sought to address some of this challenge by applying distance sampling methods to identify the factors influencing density estimation for rainforest birds in this system.

The key finding was that species' characteristics were the dominant factor influencing detectability, more important than habitat and survey conditions in determining Effective Strip Width (ESW) in most cases. This enabled the development in chapter 4 of a set of models for survey data that allowed the estimation of absolute density in uncommon species where small samples sizes prohibited conventional distance analysis. Though still requiring some distance information from field surveys, this approach has the advantage of lower sampling intensity, and hence potential for reducing costs and logistic requirements of field survey in closed forest density estimation. Importantly however, the significance of these results differ depending on the intended application of density estimates. In an assemblage wide study, such as that in chapter 5, species differences will be the more significant contributors to bias in estimates, particularly were assemblage changes occur across elevation in the study region (as in the AWT, (Williams *et al.* 2010a)). In contrast, studies concerned with differences between sites or time periods within a single species will need to

counter instead the bias introduced at the site level (e.g. by habitat structural differences) and survey (e.g. by weather conditions). For this reason, monitoring for changes in density of particular species across time and space will likely require the application of more than a species-specific calibration to yield useful estimates of density.

By combining the two approaches so that accurate Distance-analysis estimates are made for species where sampling is sufficient, but modelled detectability is used to calibrate estimates for rare species or where sampling is less intensive, a flexible compromise approach is also possible. The results presented here in chapters 5 and 6 are a field test of this approach in a diverse rainforest assemblage. I envision that the methods in chapter 6 in particular will be a useful component of efficient diversity and population monitoring in rainforest bird assemblages both here and elsewhere. Important areas for future monitoring protocol development will include using distance bins to reduce critical sources of error from distance estimation (Alldredge *et al.* 2007b) and developing methods for observer training to reduce ID and distance estimation error, important in rigorous monitoring (Lindenmayer *et al.* 2009). Further improvements would be made by some explicit testing of key assumptions of distance sampling such as the true error rates due to birds missed on the transect midline (Alldredge *et al.* 2007b). Finally, while roads and tracks facilitate access to sites in otherwise remote and difficult terrain, they may influence density estimates for some species (Laurance *et al.* 2009; Marques *et al.* 2010), so that an explicit examination of the influence of surveys close to roads may be useful in improving sampling designs for monitoring.

Another key attribute of adaptive monitoring, important in response to the threats posed by climate change (Lindenmayer & Likens 2009) will be sensitivity to density changes at high spatial and temporal resolution (Shoo *et al.* 2005). I suggest that an approach integrating Distance sampling field protocols used in chapters 2 and 3 with the analytical focus on detecting shifts in density optima demonstrated in chapter 5 will be an important component of monitoring programs for montane rainforest birds. Shoo *et al.* (2006), previously identified the statistical advantage of locating the mean of species distributions as opposed to range margins when predicting and monitoring range shifts. In chapter 6 I developed this approach further by combining it with detectability-calibrated density estimates and a method for identifying those species with unimodal temperature responses, for which it is therefore appropriate to model a single abundance optimum. The result is a method for collecting baseline data against which future counts can be compared for detecting range-shifts. The effectiveness of the method is further demonstrated by the detection of significant up-slope differences in a space-for-time substitution for 18 species, and over the small

spatial scales (~71 m elevation) relevant to detecting climate induced shifts in the near future (Shoo *et al.* 2006).

Importantly, however, in the current study I was limited in my ability to detect change in species whose range limits lay close to the margins of the elevation domain in this system (Oksanen *et al.* 2001), or had poorly defined density optima. This included both extreme upland (e.g. Golden Bowerbird *Amblyornis newtonianus*, plate 6) and lowland species in the AWT, and cases of comparison with species and populations in the CQC and CYP where the broader latitudinal scope pushed density optima close to these limits. Several strategies may be useful in addressing this limitation: firstly, sampling at a finer elevational resolution than the 200-m intervals used here may allow better characterisation of density optima. This could be coupled with increased sampling focus at the critical upper and lower margins of the elevational range. Similarly, the expansion of sampling in CYP and CQC forests would allow a more accurate characterisation of elevational density profiles there, including populations showing even more marked relative shifts than those examined within the AWT. Additional advantages may also be gained by the use of climate data from under-canopy logger stations. Measuring microclimates experienced by species directly may allow a better understanding of how distributions are influenced by temperature than that gained from regional modelled climate surfaces (Dobrowski 2011). Finally, identifying elevational shifts in density optima by this method will not be possible in cases where a species' optimum already lies outside the bounds of the existing gradient (e.g. Rose-crowned Fruit-dove, *Ptilinopus regina*, Appendix Figure 6.1.53, Rufous Fantail (*Rhipidura rufifrons*) Appendix Figure 6.1.54). In such cases, variation in the absolute density values themselves may constitute the only reliable gauge of change. For this purpose, the methods developed above may also prove invaluable, as calibration for detectability allows the accurate estimation of temporal variation in density. I suggest that applying and refining these methods in a program of regular, focussed monitoring expeditions across elevation in tropical forests will improve not only our understanding of the drivers of diversity in these precious ecosystems, but also improve our ability to understand, predict and respond to emerging threats.

8.3 Integrating biotic and abiotic constraints in models of realised niche

The results of the space-for time substitution analysis in chapter 5 also provided a crucial test of one of the underlying assumptions in the application of bioclimatic envelopes to predictions of species shifts: that of niche transferability (Soberón & Nakamura 2009). Correlative models are widely

used to predict climate change impacts on species distributions, but are limited by the omission of potentially important biotic influences such as niche plasticity, dispersal limitation and competition (Pearson *et al.* 2006; Guisan & Thuiller 2007). Since changes in biotic influences with climate change are not explicitly modeled by this approach, their predictive power may be reduced (Dormann 2007). The consistent spatial differences in elevation of density optima shown for 16 species in chapter 6 (coupled with the widespread monotonic responses among other species not analysed by this approach) would indicate validity of relatively simplistic temperature-only models of species' elevational distributions. This lends support to predictions of the widespread impact of climate change on patterns of assemblage structure in this system (Williams *et al.* 2003). Nonetheless, species' responses in future may vary due to biotic influences not captured by these models, and it will be important to systematically address other limitations of the correlative approach to ensure that we can make reliable predictions of climate impacts.

In addition to shifting spatially, species may be capable of in-situ acclimation or adaptation in response to climate change (Holt 1990), capacity for which may be mediated by the influences of past climate history on genetic capacity and environmental tolerances (Tewksbury *et al.* 2008). Such "niche plasticity" will have a fundamental role in the ability of species to adapt to climate change (reviewed in; Parmesan 2006), but correlative models assume that species' environmental niches remain constant, constraining them to track their current preferred environments or go extinct (Bell & Collins 2008). Indirect methods comparing environmental tolerances between closely related species, populations within species, and between source and colonist populations of invasive species may offer tests of adaptive capacity (Soberón & Nakamura 2009). Due to historical vicariance, there may be several such opportunities for indirect estimates of environmental niche conservatism in the avifauna examined here. Quaternary climate change has left a suite of species in north-eastern Australian rainforests with subpopulations distributed across a broad environmental gradient, separated to varying degrees; into discrete lineages (e.g. Chowchillas *Orthonyx spaldingii* across the Black Mountain barrier); subspecies (e.g. Satin bowerbirds between NE and SE QLD); and sister-species pairs (e.g. Bridled Honeyeater (*Lichenostomus frenatus* and Eungella Honeyeater *Lichenostomus hindwoodi* in AWT and CQC respectively). In chapter 6 the extent to which a simple temperature predicts elevational difference in density optima was demonstrated across the Black Mountain barrier, but scope therefore exists to perform the same tests in a spatially explicit context by comparing the power of models trained in one species, subspecies or lineage to accurately predict the distributions of their counterparts in other parts of the region. Such an approach could allow the characterisation of the extent and variation in

environmental niche plasticity across a wide range of species. A single species example using data on populations of the Lewin's Honeyeater in the AWT and CYP shows a high level of model transferability Shoo *et al.* (2009, see Appendix 1). I suggest that the same approach will be useful when applied more extensively in the AWT and in other such extra-regional comparisons.

Dispersal is also important in defining realised niches (Pulliam 2000). Current correlative models can be refined to accurately represent realised niches when good distribution data are available (Williams *et al.* 2010b), but the influence of dispersal in future scenarios is difficult to quantify (Guisan & Thuiller 2007). Incorporating mechanistic models of dispersal ability may be one avenue for addressing this issue (Jetz 2010a). Alternatively, population genetic studies may give insight into the level of connectivity between subpopulations, and allow dispersal capacity to be inferred (e.g. Galbusera 2000). Dispersal in forest birds is also likely to be strongly mediated by habitat, a critical limiting factor in defining current realised niches, and as habitat barriers and conduits to dispersal themselves may be dynamic (Thomas *et al.* 2001), this adds uncertainty to correlative model predictions. In the absence of future vegetation projections in chapter 7, I speculated on the impact that shifts in species bioclimatic envelopes may have on diversity pattern, but better inference will be made possible with advances in dynamic vegetation modeling that integrate ecosystem-functional, disturbance and climatic elements to predicting future habitat patterns (Woodward & Beerling 1997). As land-use change is also a critical determinant of extinction risk (Lee & Jetz 2011), such models will also improve broad-scale assessments of assemblage vulnerability and highlight target regions for conservation action (Jetz *et al.* 2007).

Biotic interactions such as mutualism, competition or predation may also constrain species' realised climatic niches (Soberón & Nakamura 2009). For example, in some temperate owl species, mutualism with hollow-making woodpeckers has recently been shown to influence realised distributions (Heikkinen *et al.* 2007). Mutualistic interactions may also play a role in shaping assemblage structure of neotropical ant-following birds and their attendants (Hutto 1987; Graves & Gotelli 1993), but their role in defining the realised distributions of Australian rainforest birds is unknown. Mixed-flocking behaviour is relatively common among Australian rainforest insectivores (pers obs A. Anderson), though its significance for species' survival and reproduction and the potential for climate change to perturb these interactions is also unknown. Interspecific competition has also been proposed as an important influence on the structure of montane rainforest avifaunas across elevational gradients (Diamond 1973; Terborgh & Weske 1975), and some studies indicate a strong influence among certain neotropical species (Remsen & Graves 1995; Jankowski *et al.*

2010). However, competition may be difficult to demonstrate directly, and the extent of its role in defining distributions is debated (Weins 1989). Importantly though, climate change has been demonstrated to drive mismatches of trophically interacting species (Schweiger *et al.* 2008). As with tests for niche conservatism, the mosaic of distributions in the rainforest avifauna of the study region may also present opportunities to investigate competition effects indirectly using comparative analysis among potential competitors. Examples of systems in which it will possible to examine broad-scale differences in species' climatic distributions with and without the presence of potential competitors include *Meliphaga* Honeyeaters *(M. lewinii, M. notata and M. gracilis)* which overlap in the AWT where they may undergo altitudinal replacement (unpublished data). Other examples include insectivorous species among the monarchs (genera *Monarcha* and *Arses*), robins (*Eopsaltria* and *Heteromyias)* and scrubwrens (genus *Sericornis*).

The role of biotic interactions in constraining species' realised distributions may also be scale dependent (Pearson & Dawson 2003; Morin & Lechowicz 2008). Occurrence may be well predicted at broad spatial scales by climate variables alone, but at finer scales, spatial patterns of habitat or the presence of resource or competitor taxa may prevail (Soberon 2007). Interactions between species have therefore been fitted into schemes of niche determinants as "Eltonian noise" operating at much smaller spatial scales than those relevant to predicting broad-scale patterns in species distributions with correlative models (Soberón & Nakamura 2009). Documenting the interaction between biotic "Eltonian" and abiotic niches may be a serious methodological challenge (Soberón & Nakamura 2009), but the availability of detailed density data in the present system may allow some advances in integrating broad-scale distributional and local-scale density patterns. Specifically, environmental suitability has been shown to consistently predict an upper bound for realised density (VanDerWal *et al.* 2009). By modeling species' density as a function of both environmental suitability and co-occurrence with potential competitors, this relationship could form a framework within which to test for competition effects in local-scale density variation.

Biotic interactions such as resource competition may thus constrain the future realised niche of species in ways unpredictable from their current pattern. By extension, we may also ask to what extent will future patterns of species richness in reshuffled assemblages be mediated by energy availability? There is a wealth of theory and evidence to suggest that energy limitation at broad scales is an important driver of species richness (Wright 1983; Currie 1991; Rosenzweig 1995; Hawkins *et al.* 2003b). Data presented in chapter 5 also indicated a secondary influence of variability in energy availability (alongside historical factors), on bird density and hence diversity at a local scale in this system, particularly in seasonal upland and to a lesser extent lowland sites.

Shifts in assemblage-wide patterns of species richness in lowland forests may therefore also be mediated by ecosystem-wide energetic constraints that are not incorporated into individual species models. It is beyond the scope of the current study to address these questions in detail, but it is possible to speculate on two key areas in which the answers to these questions will be critical determinants of the outcomes of climate-change-induced shifts predicted here.

At the assemblage-wide scale, I observed that the deficit of lowland endemic species in the AWT appears to leave unexploited resources in productive low-elevation forests (chapter 5, and Williams *et al.* (2010a). This suggests an historical precedent for secondary changes in patterns of energy use and trophic structure (such as lowland biotic attrition) as a result of climate change. Secondly, it hints that there may be resources to support an influx of lowland species into the AWT from CYP forests, should the species dispersal abilities and future landscape attributes allow it. However, this relatively simplistic model of energy-diversity relationships in a changing climate may be misleading, as it assumes a constancy of future NPP, species density and energy consumption about which little is known. I suggest important areas for future investigation will be in energy constraints on current species distributions, models of future productivity in tropical forests, and a synthesis of these fields with our understanding of competitive interactions in rainforest birds discussed above. Competitive and energetic constraints may also have significance for assisted migration. For example, the results in chapter 5 suggest a virtually flat species-energy relationship in the CQC where a depauperate rainforest avifauna persists in relictual montane rainforest. By extension, introductions of upland species into this system may not meet strong constraint from competition or energy availability. The energetic capacity for more diverse southern montane rainforests to support viable populations of introduced “climate refugees” is unknown. While assisted migration is a controversial option among conservation responses to climate change (Ricciardi 2009; Schwartz *et al.* 2009), it may be the only chance of survival for some upland restricted species (Thomas 2011) and may therefore be a key component of future integrated conservation management (Hoegh-Guldberg *et al.* 2008; Vitt *et al.* 2009). Answers to the above questions will help to assess viability of management options, including assisted migration, from an ecological and mechanistic perspective.

8.4 Conclusions

Our understanding of the drivers of species distributions and biodiversity pattern has many gaps, which may limit our ability to predict the effects of climate changes (Algar *et al.* 2009). However, data presented here show an interaction between both historical and contemporary patterns of

climate stability in driving patterns of montane rainforest bird diversity. Extinction filtration and seasonality have previously been shown to be important in driving continental gradients of bird diversity (Acevedo & Currie 2003; Hawkins *et al.* 2003a), suggesting that in addition to important differences (Korner 2007), drivers of elevational diversity patterns may echo some of those at larger spatial scales (Stevens 1992; Ruggiero & Hawkins 2008). Despite the limitations of bioclimatic modelling, data presented here and elsewhere also indicate sufficient knowledge on which to base robust inference about these impacts in the montane rainforests of north-eastern Australia (Parmesan & Yohe 2003; Williams *et al.* 2003; Hilbert *et al.* 2004; Chambers *et al.* 2005). These forests represent a significant proportion of Australian bird diversity, reflected in their identification among the continent's Important Bird Areas (Dutson *et al.* 2009). Understanding and monitoring climate change impacts on them is thus likely to be critical in the conservation of this biodiversity into the future (Jetz 2010a). Here I present baseline information and demonstrate methods for monitoring species and assemblage responses to climate change, including proof of their application to detecting shifts, likely to be critical to adaptive management approaches to conservation (Lindenmayer & Likens 2009). These methods may further be a useful component of future integrations of correlative models with ecological information such as dispersal, interspecific competition and energy limitation. Such an integration of abiotic and biotic constraints on the realised niche also promises to be important in advancing our understanding of biodiversity pattern in general.

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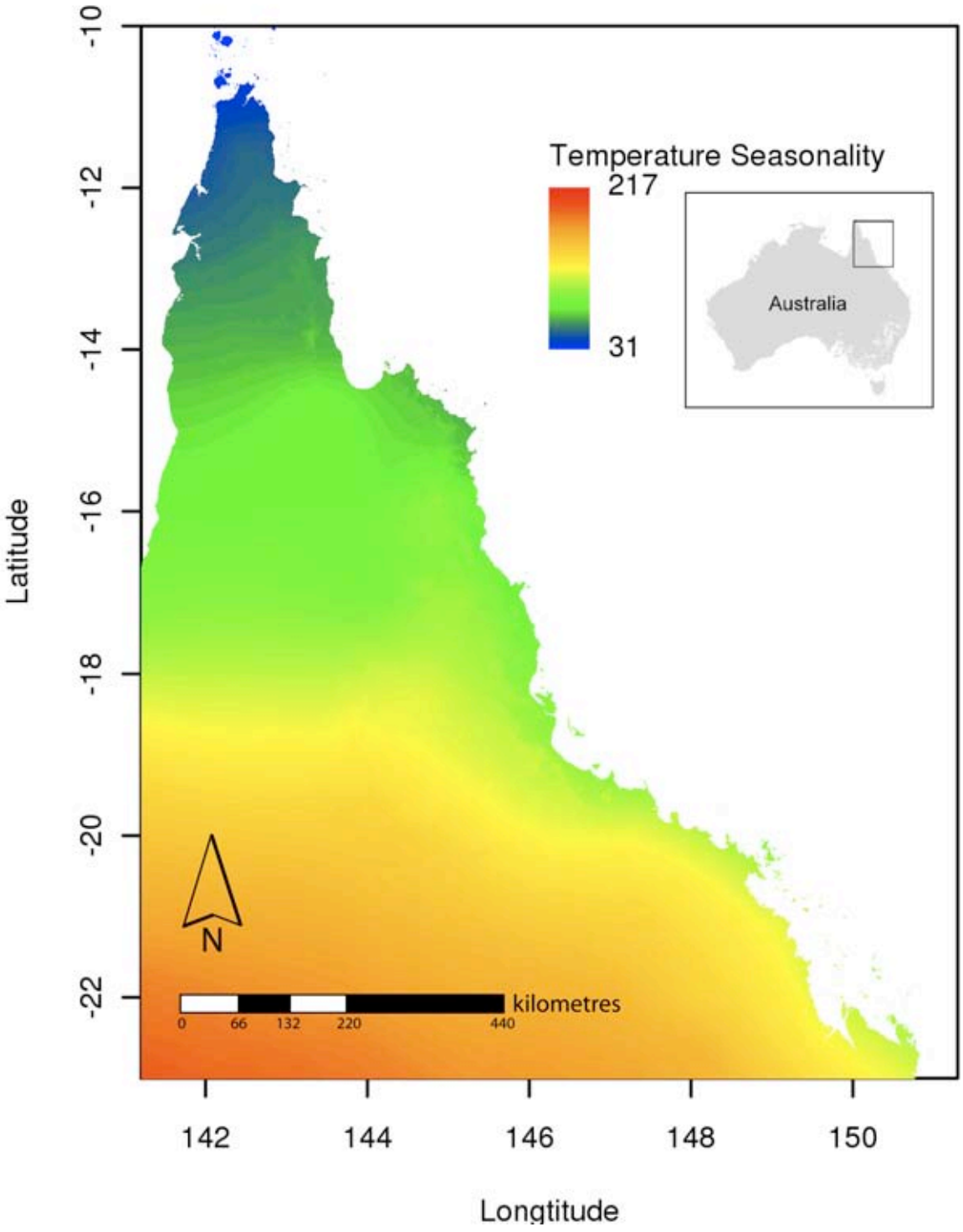
Appendices

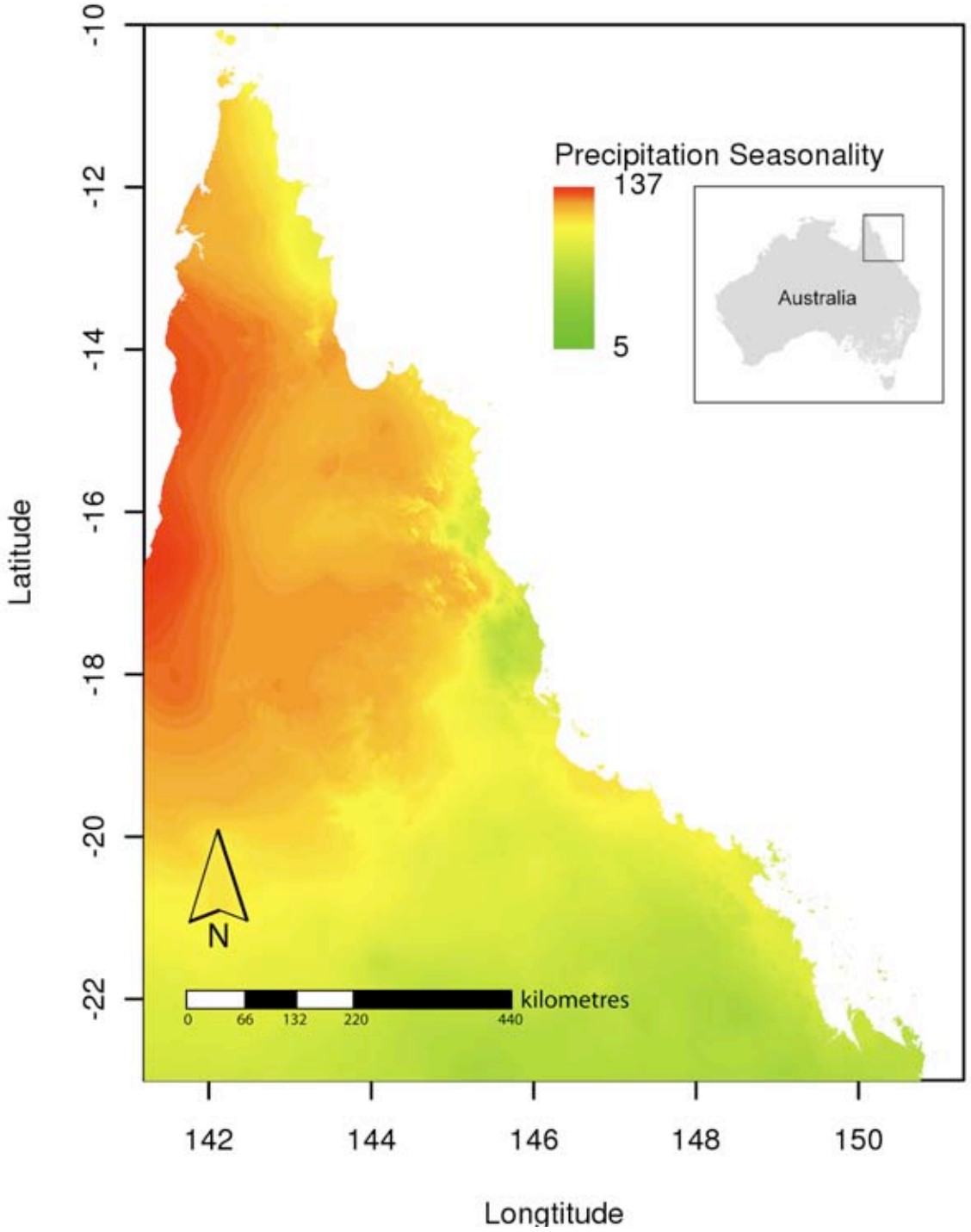
Appendix 1

Abstract of publication arising from work completed during the period of candidature, demonstrating the distance sampling methodology and niche transferability in a rainforest bird species.

Appendix 2



Appendix Figure 2.1. *Temperature seasonality also increases from the coast towards the interior, and from the north towards the south. In general upland are also more seasonal than lowlands. Data are from BIOCLIM, see text in chapter 2 for reference.*



Appendix Figure 2.2. *Precipitation seasonality increases from South to North, and from lowlands to uplands. Data are from BIOCLIM, see text in chapter 2 for reference.*

Appendix 3

Appendix Table 3.1. *Coding system used for collecting survey condition information during data collection:*

BIRD DATA CODES

RAIN : 0 no rain
1 periodic drizzle
2 drizzle or periodic light rain
3 light rain or periodic rain
4 rain or periodic heavy rain
5 continuous heavy rain

MIST
0 no mist
1 mist or periodic fog
2 fog

CLOUD: 0 0% Cloud cover
1 10%
.....
10 100%
important note: for reptiles, estimate % of *survey* overcast

WIND
0 still, leaves not moving
1 light breeze; leaves rustle
2 gentle breeze; small twigs moving
3 moderate breeze; sml branches moving
4 fresh breeze; sml trees in motion
5 strong breeze; large branches moving
6 near gale; whole trees moving

WET
0 litter & soil dry
1 Litter & soil damp
2 litter & soil wet
3 litter, soil and leaves wet
4 all surfaces dripping wet

BIRDS
H heard cal
G Ground
V Ground
S Shrub
B Sub-canopy
C Canopy
A Above Can
F Flying

FLOWERS (note genus &/or species if known)
0 none noted
1 present (1-3 plants/spp bearing)
2 common (3-5 plants/spp bearing)
3 abundant (more than 5 bearing)

FRUIT (note genus &/or species if known)
0 none noted
1 some fallen fruit noticed, <2 species, <10 fruits
2 2-5 species, or >10 fruits noted
3 5-10 plus species or <50 of fruits of one species

NOISE
0 **none**: no interfering noise besides normal dawn chorus
1 **mild**: slight noise over < 50% or medium over <25% of transect
2 **moderate**: loud noise on < 25% of transect, or medium noise over 50% or slight noise over 100%
3 **severe**: medium noise over whole transect, or loud over 50%

Appendix Table 3.2. *A glossary of important Distance Analysis terms (See Buckland et al. 2001. For additional explanations)*

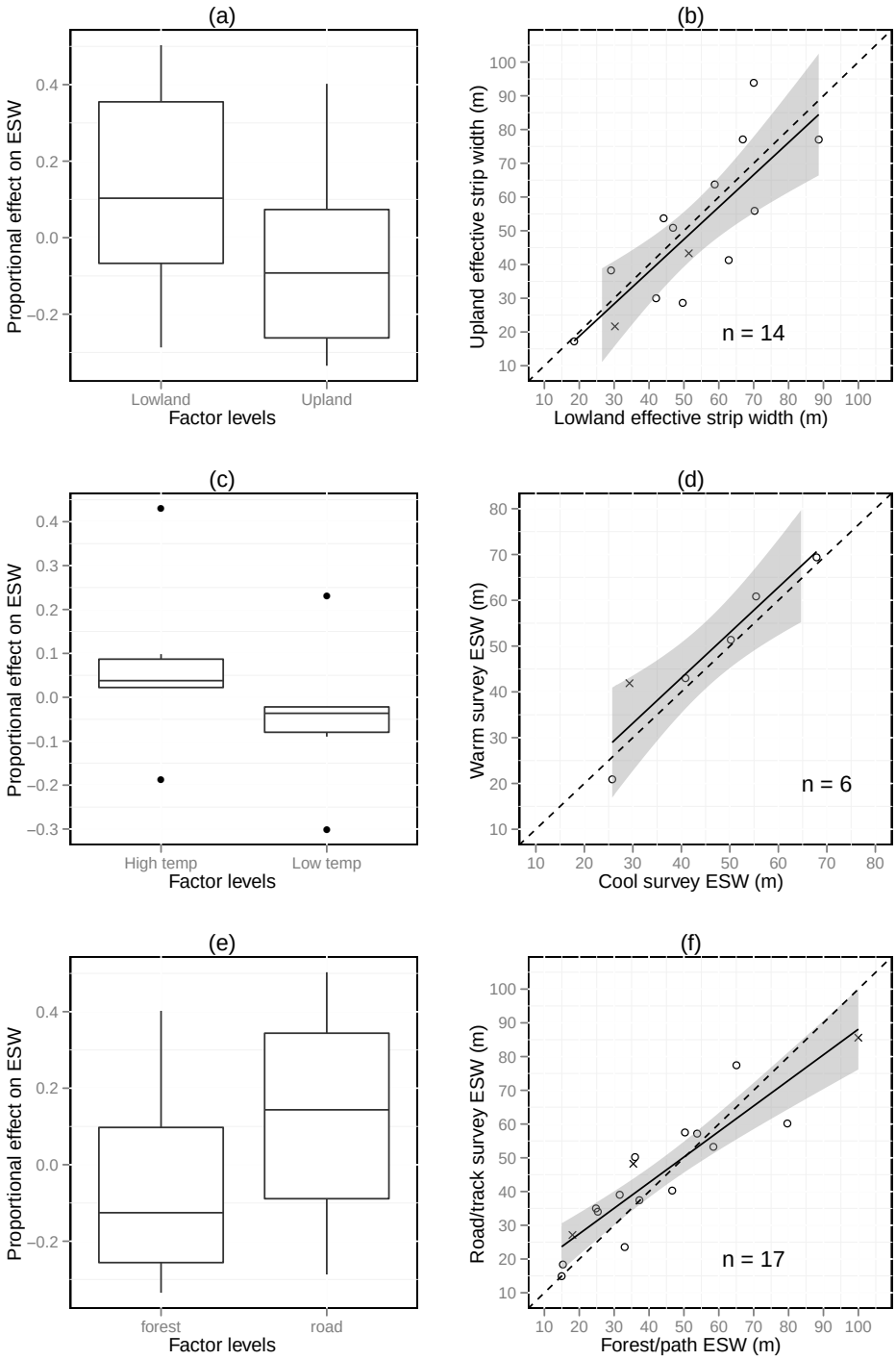
Term	Definition
Cluster	A group of individuals treated as a distinct unit for the purposes of analysis
Cosine adjustment	Adjustment added to Detection function using Cosine transformation
Half Normal model	Model of the detection function assuming a half-normal decay in detectability
Hazard Rate model	Model of the detection function assuming a hazard-rate decay in detectability
Heaping	The tendency for distance estimates to congregate at logical intervals due to observer habit, such as eg. 15m, 75m
Hermite Polynomial adjustment	Adjustment added to Detection function using Hermite Polynomial transformation
Polynomial adjustment	Adjustment added to Detection function using Polynomial transformation
Simple adjustment	Adjustment added to Detection function using simple transformation
Transect half-width	The width of one side of the transect, measured from the centre line to an arbitrary or in this case, experimentally verified limit.
Uniform model	Model of the detection function assuming a uniform decay in detectability

Appendix Table 3.3. *Estimates of ESW (Effective Strip Width) by species from Distance sampling and analysis in Australian Wet Tropics (AWT). AICc refers to AIC values corrected for small sample size. Density values refer to an estimate per hectare based on the mean counts across all surveys. Model abbreviations are as follows: hn = Half-normal, hr = Hazard rate, uni = Uniform, (see methods, and Thomas et al. (2010) for a detailed description).*

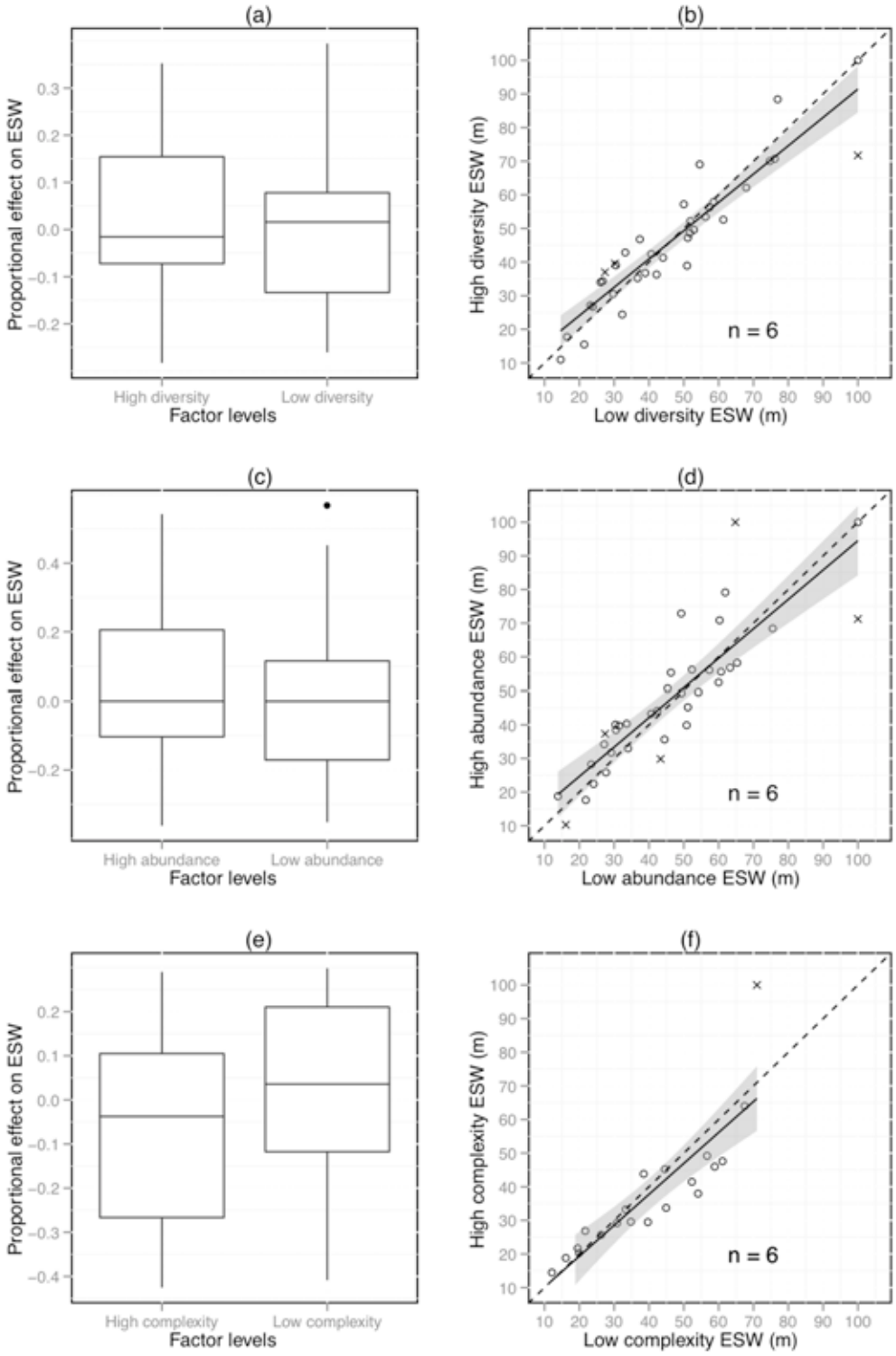
Species	Model	n	AICc	ESW	Density(per km^2)
Atherton Scrubwren *(Sericornis keri)*	hr	65	83	12.34 (10.1, 15.04)	109.48 (66.89, 179)
Barred Cuckoo-Shrike *(Coracina lineata)*	uni	42	39	39.7 (0.09, 18315.84)	26.64 (0.06, 12300)
Black Butcherbird *(Cracticus quoyi)*	uni	160	515	100 (100, 100)	31.52 (25.98, 38.2)
Bowers Shrike-Thrush *(Colluricincla boweri)*	uni	106	232	38.93 (28.6, 52.94)	57.12 (36.81, 88.6)
Bridled Honeyeater *(Lichenostomus frenatus)*	hr	137	376	43.74 (38.76, 49.36)	70.25 (49.77, 99.16)
Brown Cuckoo-Dove *(Macropygia amboinensis)*	uni	108	396	100 (100, 100)	21.79 (16.93, 28)
Brown Gerygone *(Gerygone mouki)*	uni	248	438	33.33 (28.3, 39.23)	158.6 (123.64, 203)
Chowchilla *(Orthonyx spaldingii)*	uni	143	437	73.78 (64.3, 84.68)	41.44 (30.79, 55.8)
Double-eyed Fig-Parrot *(Cyclopsitta diophthalma)*	uni	81	187	45.22 (41.1, 49.74)	42.89 (29.74, 61.9)
Dusky Honeyeater *(Myzomela obscura)*	hr	198	571	34.03 (31.2, 37.1)	121.04 (94.81, 155)
Eastern Spinebill *(Acanthorhynchus tenuirostris)*	hn	95	256	31.1 (26.7, 36.18)	65.08 (47.62, 88.9)
Eastern Whipbird *(Psophodes olivaceus)*	hr	236	888	72.72 (65.3, 80.98)	68.53 (55.73, 84.3)
Emerald Dove *(Chalcophaps indica)*	uni	39	123	73.02 (58.71, 90.82)	10.39 (6.46, 16.71)
Fairy Gerygone *(Gerygone palpebrosa)*	hn	119	375	36.57 (29.3, 45.71)	70.7 (50.8, 98.4)
Fernwren *(Oreoscopus gutturalis)*	hn	130	240	29.47 (25.88, 33.57)	91.27 (69.11, 120.53)
Figbird *(Sphecotheres vieilloti)*	hr	106	204	61.11 (52.1, 71.64)	45.53 (30.91, 67.1)
Golden Whistler *(Pachycephala pectoralis)*	hn	157	327	39.01 (29.8, 51.14)	82.39 (57.33, 118)
Graceful Honeyeater *(Meliphaga gracilis)*	uni	514	1346	40.44 (37.3, 43.88)	259.15 (223.58, 300)
Grey Fantail *(Rhipidura albiscapa)*	uni	194	561	29.04 (27.1, 31.07)	137.26 (111.44, 169)
Grey Whistler *(Pachycephala simplex)*	hr	228	524	49.37 (45.5, 53.6)	94.37 (77.96, 114)
Grey-headed Robin *(Heteromyias cinereifrons)*	hr	320	954	56.12 (52.4, 60.1)	115.52 (97.8, 136)

Species	Model	n	AICc	ESW	Density(per km^2)
Helmeted Friarbird *(Philemon buceroides)*	uni	45	121	100 (100, 100)	8.75 (5.92, 12.94)
Large-billed Scrubwren *(Sericornis magnirostra)*	hn	434	1180	27.28 (23.4, 31.86)	352.57 (284.42, 437)
Lewin's Honeyeater *(Meliphaga lewinii)*	hr	126	319	57.28 (51.2, 64.11)	43.56 (32.04, 59.2)
Little Shrike-Thrush *(Colluricincla megarhyncha)*	uni	580	1340	47.79 (41.1, 55.5)	242.98 (201.67, 293)
Macleay's Honeyeater *(Xanthotis macleayanus)*	hr	270	474	54.56 (51.2, 58.1)	97.89 (83.75, 114)
Metallic Starling *(Aplornis metallica)*	hn	295	835	46.28 (42.3, 50.66)	178.05 (122.11, 260)
Mistletoebird *(Dicaeum hirundinaceum)*	hr	304	571	41.74 (38.6, 45.12)	144.37 (123, 169)
Mountain Thornbill *(Acanthiza katherina)*	hr	153	359	17.18 (14.1, 21.01)	202.87 (140.64, 293)
Noisy Pitta *(Pitta versicolor)*	uni	86	255	56.75 (49.8, 64.6)	30.12 (21.61, 42)
Orange-footed Scrubfowl *(Megapodius reinwardt)*	hn	178	635	56.87 (45.8, 70.68)	63.62 (47.5, 85.2)
Pale-yellow Robin *(Tregellasia capito)*	hr	207	399	17.43 (15.46, 19.65)	249.54 (203.46, 306.07)
Rainbow Lorikeet *(Trichoglossus haematodus)*	hr	49	80	78.4 (59.2, 103.75)	14.76 (8.77, 24.8)
Rose-crowned Fruit-Dove *(Ptilinopus regina)*	hr	62	198	81.19 (64.5, 102.25)	15.02 (10.09, 22.4)
Rufous Fantail *(Rhipidura rufifrons)*	hn	110	265	33.64 (26.7, 42.44)	63.84 (46.47, 87.7)
Scarlet Honeyeater *(Myzomela sanguinolenta)*	uni	41	56	49.94 (28.88, 86.34)	15.97 (8.01, 31.86)
Shining Bronze-Cuckoo *(Chalcites lucidus)*	hn	37	37	41.93 (31.8, 55.26)	20.6 (12, 35.4)
Silvereye *(Zosterops lateralis)*	hr	367	1110	37.44 (35.3, 39.7)	245.4 (206.93, 291)
Spectacled Monarch *(Symposiarchus trivirgatus)*	hn	278	495	23.45 (21.5, 25.58)	235.31 (199.96, 277)
Spotted Catbird *(Ailuroedus melanotis)*	uni	252	658	44.83 (36.8, 54.53)	114.55 (89.15, 147)
Sulphur-crested Cockatoo *(Cacatua galerita)*	hn	87	187	79.81 (63.4, 100.49)	23.54 (15.56, 35.6)
Superb Fruit-Dove *(Ptilinopus superbus)*	hr	191	718	86.89 (75.8, 99.62)	44.81 (35.07, 57.3)
Tooth-billed Bowerbird *(Scenopoeetes dentirostris)*	uni	36	68	35.48 (29.4, 42.83)	20.43 (12.51, 33.4)
Topknot Pigeon *(Lopholaimus antarcticus)*	uni	45	83	35.34 (29.96, 41.69)	56.86 (28.5, 113.44)
Varied Triller *(Lalage leucomela)*	hr	155	268	59.89 (53.9, 66.51)	51.73 (42.12, 63.5)

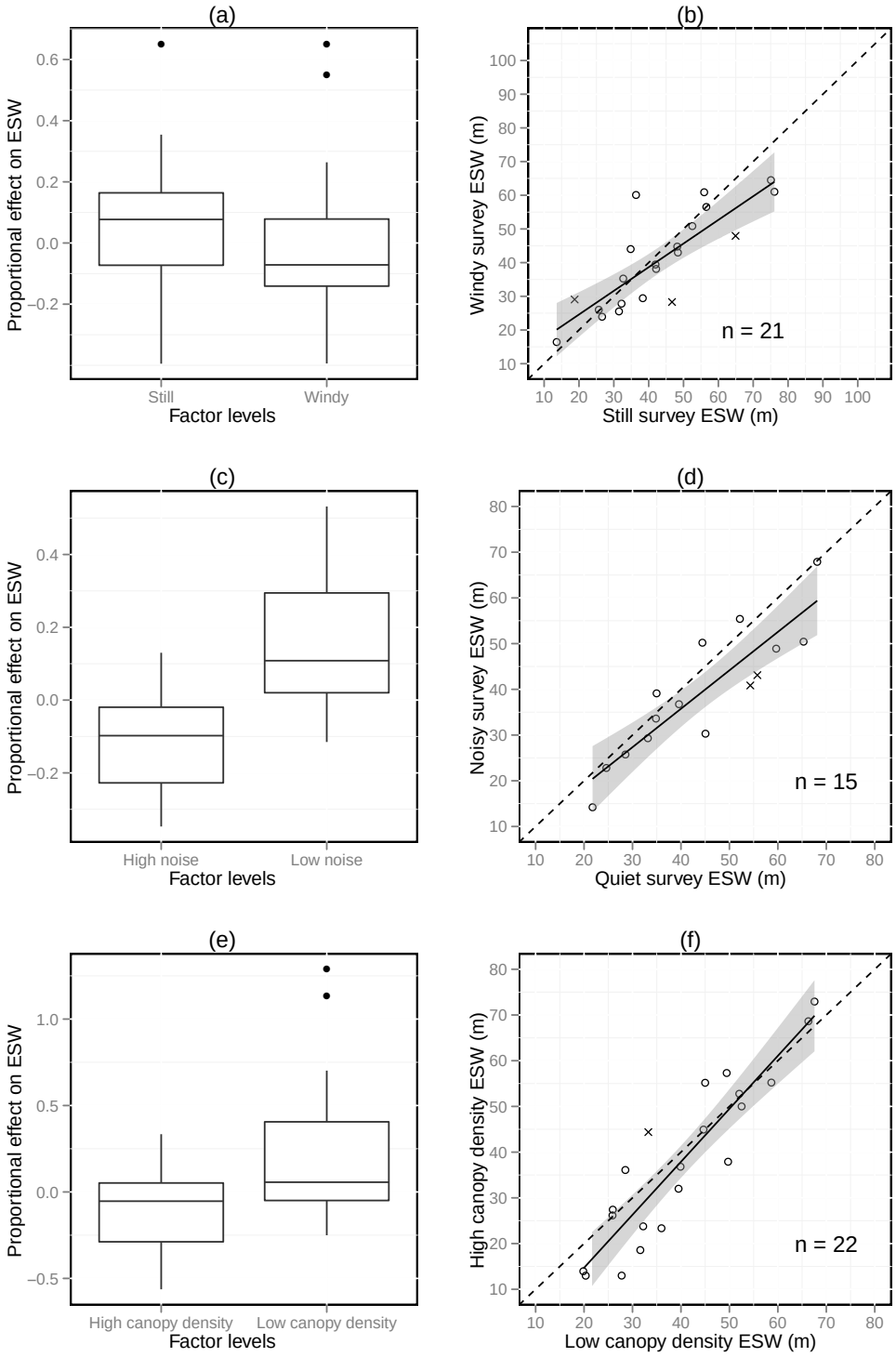
Species	Model	n	AICc	ESW	Density(per km^2)
Victoria's Riflebird *(Ptiloris victoriae)*	hr	133	419	81.27 (71, 92.97)	33.39 (27.01, 41.3)
White-throated Treecreeper *(Cormobates leucophaea)*	hr	142	342	53.36 (48.5, 58.77)	53.21 (41.66, 68)
Wompoo Fruit-Dove *(Ptilinopus magnificus)*	hr	222	556	68.81 (61.3, 77.19)	65.38 (52.93, 80.8)
Yellow Oriole *(Oriolus flavocinctus)*	hr	68	217	80.63 (64.7, 100.43)	16.8 (10.64, 26.5)
Yellow-breasted Boatbill *(Machaerirhynchus flaviventer)*	hr	162	305	35.94 (31.4, 41.09)	92.02 (72.17, 117)
Yellow-spotted Honeyeater *(Meliphaga notata)*	hn	602	2130	52.9 (49.5, 56.6)	227.52 (198.98, 260)
Yellow-throated Scrubwren *(Sericornis citreogularis)*	hr	151	285	15.27 (12.5, 18.65)	222.14 (163.25, 302.26)



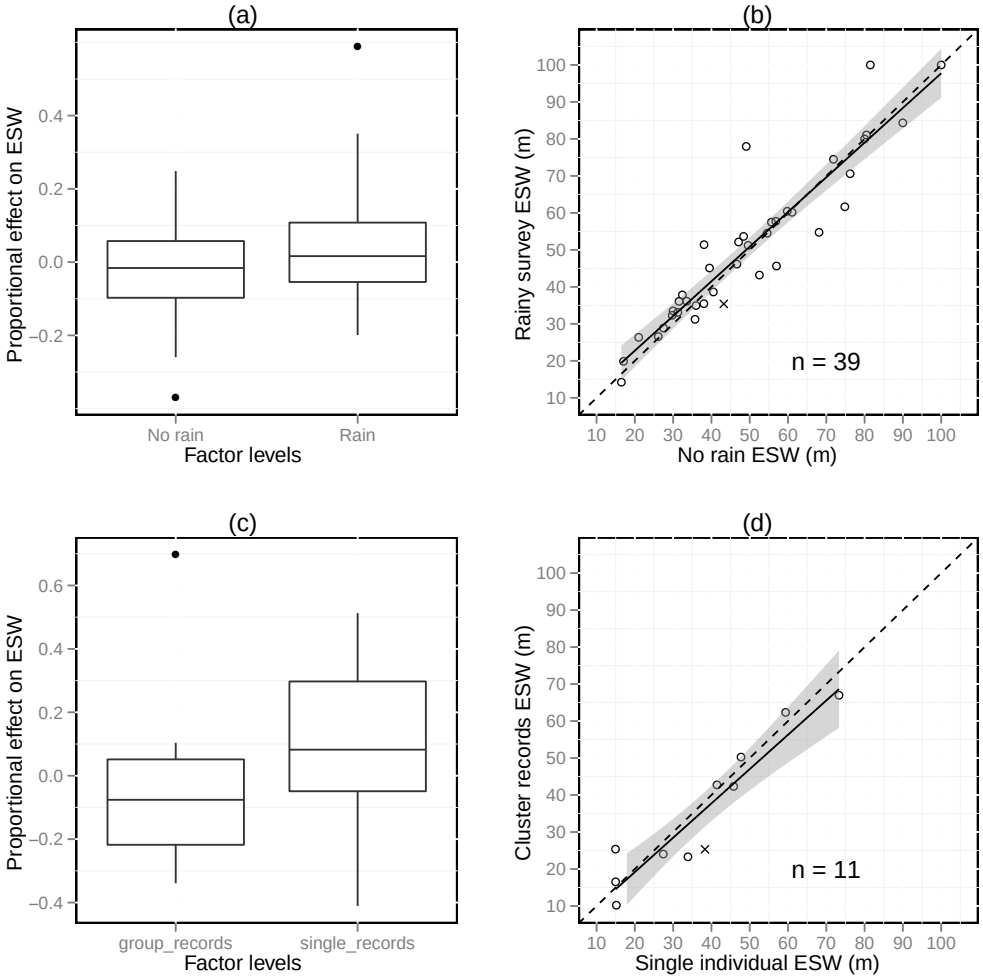
Appendix Figure 3.1. *Left column: A comparison of the relative effect of elevation, temperature and route covariates on Effective Strip Width (ESW). Horizontal bars represent the median, boxes the 25th quantile, and whiskers the 75th quantile of the range of ESW relative differences between treatments, expressed as the proportion of each species' total ESW. Right column: Biplots of covariate effects on each treatment, showing the distribution of shifts in ESW associated with each factor covariate treatment. Species with non-overlapping 95% confidence intervals are marked with an "x". N values refer to the number of species for which sufficient samples were available (see text). Dashed diagonal lines indicate zero difference, and the solid line is a simple linear regression of the relationship indicating the trend relative to the line of zero difference. Shaded areas delimit the upper and lower 95% confidence intervals for the regression.*



Appendix Figure 3.2. *Left column: A comparison of the relative effect of survey bird diversity, bird abundance and habitat complexity on Effective Strip Width (ESW). Horizontal bars represent the median, boxes the 25th quantile, and whiskers the 75th quantile of the range of ESW relative differences between treatments, expressed as the proportion of each species' total ESW. Right column: Biplots of covariate effects on each treatment, showing the distribution of shifts in ESW associated with each factor covariate treatment. Species with non-overlapping 95% confidence intervals are marked with an "x". N values refer to the number of species for which sufficient samples were available (see text). Dashed diagonal lines indicate zero difference, and the solid line is a simple linear regression of the relationship indicating the trend relative to the line of zero difference. Shaded areas delimit the upper and lower 95% confidence intervals for the regression.*



Appendix Figure 3.3. *Left column: A comparison of the relative effect of survey wind, noise and rain covariates on Effective Strip Width (ESW). Horizontal bars represent the median, boxes the 25th quantile, and whiskers the 75th quantile of the range of ESW relative differences between treatments, expressed as the proportion of each species' total ESW. Right column: Biplots of covariate effects on each treatment, showing the distribution of shifts in ESW associated with each factor covariate treatment. Species with non-overlapping 95% confidence intervals are marked with an "x". N values refer to the number of species for which sufficient samples were available (see text). Dashed diagonal lines indicate zero difference, and the solid line is a simple linear regression of the relationship indicating the trend relative to the line of zero difference. Shaded areas delimit the upper and lower 95% confidence intervals for the regression.*



Appendix Figure 3.4. *Left column: A comparison of the relative effect of rain and cluster size covariates on Effective Strip Width (ESW). Horizontal bars represent the median, boxes the 25th quantile, and whiskers the 75th quantile of the range of ESW relative differences between treatments, expressed as the proportion of each species' total ESW. Right column: Biplots of covariate effects on each treatment, showing the distribution of shifts in ESW associated with each factor covariate treatment. Species with non-overlapping 95% confidence intervals are marked with an "x". N values refer to the number of species for which sufficient samples were available (see text). Dashed diagonal lines indicate zero difference, and the solid line is a simple linear regression of the relationship indicating the trend relative to the line of zero difference. Shaded areas delimit the upper and lower 95% confidence intervals for the regression.*

Appendix 4

Appendix Table 4.1. *Estimates of ESW (Effective Strip Width) by species from Distance sampling and analysis in Central Queensland Coast. AICc refers to AIC values corrected for small sample size. Density values refer to an estimate per hectare based on the mean counts across all surveys. Model abbreviations are as follows: hn = Half-normal, hr = Hazard rate, uni = Uniform, (see methods, and Thomas et al. (2010) for a detailed description).*

Species	Model	n	AICc	ESW	Density
Australian King Parrot *(Alisterus scapularis)*	hr	35	89	79.77 (65.02, 97.87)	0.03 (0.02, 0.05)
Brown Cuckoo-Dove *(Macropygia amboinensis)*	uni	35	116	80 (80, 80)	0.03 (0.02, 0.04)
Brown Gerygone *(Gerygone mouki)*	hr	124	235	43.88 (41.4, 46.5)	0.18 (0.14, 0.23)
Brown Thornbill *(Acanthiza pusilla)*	hr	123	320	28.03 (24.99, 31.43)	0.28 (0.22, 0.37)
Eastern Whipbird *(Psophodes olivaceus)*	hn	43	162	70.23 (52.5, 93.95)	0.04 (0.02, 0.06)
Eastern Yellow Robin *(Eopsaltria australis)*	hn	77	171	14.53 (11.09, 19.05)	0.34 (0.24, 0.48)
Eungella Honeyeater *(Lichenostomus hindwoodi)*	uni	61	199	42.14 (32.9, 53.98)	0.09 (0.06, 0.15)
Golden Whistler *(Pachycephala pectoralis)*	hn	54	128	38.35 (31.25, 47.07)	0.09 (0.05, 0.15)
Grey Fantail *(Rhipidura albiscapa)*	uni	124	397	41.15 (34.77, 48.7)	0.19 (0.15, 0.25)
Large-billed Scrubwren *(Sericornis magnirostra)*	hr	160	467	32.34 (28.87, 36.24)	0.32 (0.25, 0.4)
Lewin's Honeyeater *(Meliphaga lewinii)*	hr	206	525	59.04 (54.02, 64.52)	0.22 (0.19, 0.27)
Little Shrike-Thrush *(Colluricincla megarhyncha)*	uni	128	338	50.09 (47.57, 52.74)	0.16 (0.13, 0.2)
Mistletoebird *(Dicaeum hirundinaceum)*	hn	53	124	37.72 (30.68, 46.37)	0.09 (0.06, 0.13)
Noisy Pitta *(Pitta versicolor)*	hn	41	125	61.21 (46.31, 80.9)	0.04 (0.03, 0.07)
Rainbow Bee-eater *(Merops ornatus)*	uni	135	224	24.52 (18.69, 32.17)	0.35 (0.25, 0.5)
Rose-crowned Fruit-Dove *(Ptilinopus regina)*	hr	55	170	73.75 (59.98, 90.68)	0.05 (0.03, 0.08)
Silvereye *(Zosterops lateralis)*	hr	188	615	43.2 (39.59, 47.14)	0.28 (0.22, 0.35)
Spectacled Monarch *(Symposiarchus trivirgatus)*	hn	100	214	27.08 (23.45, 31.27)	0.24 (0.18, 0.31)
Sulphur-crested Cockatoo *(Cacatua galerita)*	hr	48	41	67.86 (60.62, 75.95)	0.05 (0.03, 0.07)
Superb Fruit-Dove *(Ptilinopus superbus)*	hn	63	240	77.57 (60.34, 99.73)	0.05 (0.03, 0.08)

Species	Model	n	AICc	ESW	Density
Topknot Pigeon *(Lopholaimus antarcticus)*	uni	50	116	50.55 (34.64, 73.75)	0.06 (0.03, 0.14)
White-browed Scrubwren *(Sericornis frontalis)*	hn	135	222	24.83 (20.85, 29.57)	0.35 (0.26, 0.47)
White-throated Treecreeper *(Cormobates leucophaea)*	hr	110	317	67.47 (59.1, 77.01)	0.1 (0.08, 0.14)
Wompoo Fruit-Dove *(Ptilinopus magnificus)*	hr	123	292	81.4 (67.9, 97.57)	0.1 (0.07, 0.13)

Appendix Table 4.2*. Estimates of ESW (Effective Strip Width) by species from Distance sampling and analysis in Cape York Peninsula. AICc refers to AIC values corrected for small sample size. Density values refer to an estimate per hectare based on the mean counts across all surveys. Model abbreviations are as follows: hn = Half-normal, hr = Hazard rate, uni = Uniform, (see methods, and Thomas et al. (2010) for a detailed description).*

Species	Model	n	AICc	ESW	Density
Beccari's (Tropical) Scrubwren *(Sericornis beccarii)*	hn	172	421	22.11 (20.19, 24.21)	0.36 (0.29, 0.45)
Black Butcherbird *(Cracticus quoyi)*	hr	50	163	90.35 (81.55, 100.11)	0.03 (0.02, 0.03)
Black-winged Monarch *(Monarcha frater)*	hr	52	102	44.24 (40.32, 48.53)	0.05 (0.04, 0.08)
Dusky Honeyeater *(Myzomela obscura)*	hn	66	187	22.73 (19.9, 25.97)	0.13 (0.09, 0.2)
Eclectus Parrot *(Eclectus roratus)*	uni	63	132	100 (100, 100)	0.03 (0.02, 0.04)
Fairy Gerygone *(Gerygone palpebrosa)*	hn	104	338	32.94 (28.57, 37.97)	0.14 (0.11, 0.19)
Graceful Honeyeater *(Meliphaga gracilis)*	hn	236	677	38.34 (31.32, 46.93)	0.28 (0.22, 0.36)
Grey Whistler *(Pachycephala simplex)*	hr	71	147	39.77 (34.47, 45.88)	0.08 (0.06, 0.11)
Lewin's Honeyeater *(Meliphaga lewinii)*	hr	58	156	60.07 (50.3, 71.73)	0.04 (0.02, 0.08)
Little Shrike-Thrush *(Colluricincla megarhyncha)*	hr	323	790	40.22 (35.03, 46.18)	0.37 (0.31, 0.44)
Magnificent Riflebird *(Ptiloris magnificus)*	hr	143	168	66.47 (60.45, 73.08)	0.1 (0.08, 0.12)
Metallic Starling *(Aplornis metallica)*	hr	68	137	41.02 (37.11, 45.36)	0.08 (0.04, 0.14)
Mistletoebird *(Dicaeum hirundinaceum)*	hn	106	229	34.64 (30.01, 39.99)	0.14 (0.11, 0.18)
Noisy Pitta *(Pitta versicolor)*	hr	36	105	68.17 (56.34, 82.49)	0.02 (0.02, 0.04)
Orange-footed Scrubfowl *(Megapodius reinwardt)*	hn	47	165	59.55 (46.1, 76.93)	0.04 (0.02, 0.06)

Species	Model	n	AICc	ESW	Density
Red-cheeked Parrot *(Geoffroyus geoffroyi)*	uni	60	193	100 (100, 100)	0.03 (0.02, 0.04)
Rufous Fantail *(Rhipidura rufifrons)*	hn	65	168	27.34 (22.71, 32.92)	0.11 (0.08, 0.15)
Silvereye *(Zosterops lateralis)*	hn	91	301	33.58 (28.83, 39.11)	0.12 (0.09, 0.17)
Spangled Drongo *(Dicrurus bracteatus)*	uni	36	54	51.74 (28.27, 94.7)	0.03 (0.01, 0.07)
Spectacled Monarch *(Symposiarchus trivirgatus)*	hr	97	175	27.98 (24.16, 32.41)	0.16 (0.12, 0.21)
Spotted Catbird *(Ailuroedus melanotis)*	hn	44	117	34.95 (27.95, 43.71)	0.06 (0.04, 0.09)
Tawny-breasted Honeyeater *(Xanthotis flaviventer)*	hr	75	183	53.01 (46.31, 60.67)	0.06 (0.05, 0.08)
Trumpet manucode *(Phonygammus keraudrenii)*	uni	47	151	100 (100, 100)	0.02 (0.02, 0.03)
Varied Triller *(Lalage leucomela)*	hr	62	107	57.37 (48.45, 67.95)	0.05 (0.04, 0.07)
White-faced Robin *(Tregellasia leucops)*	hr	99	229	20.47 (16.79, 24.94)	0.22 (0.17, 0.3)
Wompoo Fruit-Dove *(Ptilinopus magnificus)*	hr	131	321	83.98 (70.08, 100.63)	0.07 (0.05, 0.09)
Yellow Oriole *(Oriolus flavocinctus)*	uni	76	240	68.98 (56, 84.97)	0.05 (0.03, 0.08)
Yellow-billed Kingfisher *(Syma torotoro)*	uni	45	79	52.85 (46.07, 60.62)	0.04 (0.03, 0.05)
Yellow-breasted Boatbill *(Machaerirhynchus flaviventer)*	hr	86	161	39.45 (33.11, 47.01)	0.1 (0.08, 0.13)
Yellow-spotted Honeyeater *(Meliphaga notata)*	hr	264	960	56.55 (51.64, 61.93)	0.21 (0.18, 0.25)

Appendix 5

Appendix Table 5.1. *Regression model summary for the rainforest bird energy-richness pathway in CYP and CQC.*

region	Dependent variable	Independent variable	N	coefficient	D.f.	F-statistic	adjusted r^2	p-value
CYP	Species richness	Mean annual NPP	7	0.227	5	1.901	0.131	0.227
CYP	Bird energy flux	Mean annual NPP	7	0.025	5	10.018	0.600	**0.025**
CYP	Bird density	Bird energy flux	7	0.000	5	102.790	0.944	**<0.001**
CYP	Bird density	Species richness	7	0.017	5	12.240	0.652	**0.017**
CQC	Species richness	Mean annual NPP	8	0.966	6	0.002	-0.166	0.966
CQC	Bird energy flux	Mean annual NPP	8	0.164	6	2.518	0.178	0.164
CQC	Bird density	Bird energy flux	8	0.037	6	7.102	0.466	**0.037**
CQC	Bird density	Species richness	8	0.527	6	0.450	-0.085	0.527

Appendix 6

Appendix Table 6.1. *AIC scores for competing models in a hierarchical Huissman-Olff-Frescoe (Huisman 1993) model selection analysis amongst elevational density responses across the 77 Australian Wet Tropics rainforest bird species with sufficient sampling in this study. Model selection was implemented using the approach implemented the R package "BiodiversityR" (Kindt 2011) (see methods in chapter 5 for details).*

		AIC scores						
	Species	**Model 1 (flat)**	**Model 2 (monotonic)**	**Model 3 (plateau)**	**Model 4 (gaussian)**	**Model 5 (skewed)**	**Top model**	**Top model ignoring skewness**
1	Australian Brush Turkey *(Alectura lathami)*	505.52	504.16	501.54	499.94	501.31	4	4
2	Atherton Scrubwren *(Sericornis keri)*	1677.05	1081.35	1036.95	1037.38	1036.99	3	3
3	Azure Kingfisher *(Ceyx azureus)*	356.66	298.21	297.53	295.10	264.85	5	4
4	Bassian Thrush *(Zoothera lunulata)*	900.11	826.98	750.22	774.48	752.20	3	3
5	Buff-breasted Paradise-Kingfisher *(Tanysiptera sylvia)*	174.61	148.45	150.44	150.44	150.23	2	2
6	Black Butcherbird *(Cracticus quoyi)*	211.72	141.46	140.01	143.46	141.10	3	3
7	Barred Cuckoo-Shrike *(Coracina lineata)*	514.55	499.88	457.73	465.71	459.44	3	3
8	Brush Cuckoo *(Cacomantis variolosus)*	503.08	469.72	417.02	456.97	414.00	5	3
9	Black-faced Monarch *(Monarcha melanopsis)*	1150.70	1150.61	1045.55	1013.66	989.56	5	4
10	Blue-faced Parrot-Finch *(Erythrura trichroa)*	666.00	667.27	590.39	538.15	453.23	5	4
11	Brown Gerygone *(Gerygone mouki)*	1299.02	1289.28	1076.49	884.67	853.18	5	4
12	Bridled Honeyeater *(Lichenostomus frenatus)*	806.58	704.32	669.44	668.08	666.80	5	4
13	Brown Cuckoo-Dove *(Macropygia amboinensis)*	319.75	321.75	310.66	302.21	303.75	4	4
14	Bowers Shrike-Thrush *(Colluricincla boweri)*	698.04	655.03	563.65	521.44	521.09	5	4
15	Southern Cassowary *(Casuarius casuarius)*	2.00	4.00	6.00	6.00	8.00	1	1
16	Spotted Catbird *(Ailuroedus melanotis)*	657.96	652.40	601.72	571.55	570.94	5	4
17	Chowchilla *(Orthonyx spaldingii)*	439.86	434.83	391.83	361.39	363.11	4	4
18	Cicadabird *(Coracina tenuirostris)*	25.49	23.02	22.36	20.30	21.90	4	4
19	Crimson Rosella *(Platycercus elegans)*	551.10	446.05	428.59	430.84	430.54	3	3
20	Pied Currawong *(Strepera graculina)*	267.89	216.26	199.66	195.77	192.63	5	4

AIC scores

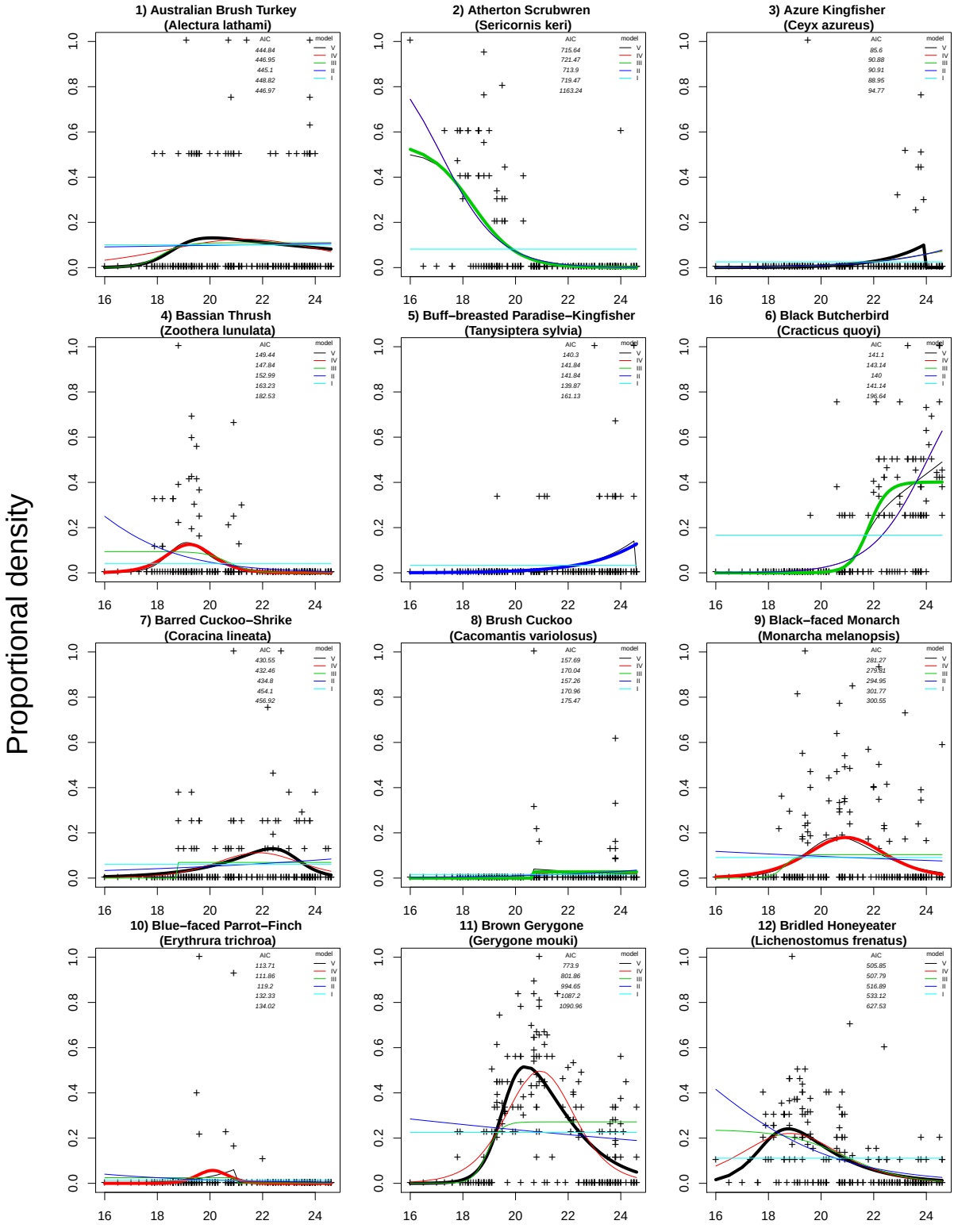
	Species	Model 1 (flat)	Model 2 (monotonic)	Model 3 (plateau)	Model 4 (gaussian)	Model 5 (skewed)	Top model	Top model ignoring skewness
21	Double-eyed Fig-Parrot *(Cyclopsitta diophthalma)*	504.61	397.44	399.38	399.42	398.51	2	2
22	Dusky Honeyeater *(Myzomela obscura)*	738.49	539.13	510.49	533.96	508.68	5	3
23	Emerald Dove *(Chalcophaps indica)*	138.30	123.80	115.09	125.24	117.08	3	3
24	Eastern Spinebill *(Acanthorhynchus tenuirostris)*	659.35	511.10	483.86	499.24	469.55	5	3
25	Eastern Whipbird *(Psophodes olivaceus)*	470.90	465.98	444.92	439.77	441.53	4	4
26	Fairy Gerygone *(Gerygone palpebrosa)*	587.91	346.36	330.40	344.26	317.22	5	3
27	Figbird *(Sphecotheres vieilloti)*	452.02	322.40	298.55	295.75	296.57	4	4
28	Fan-tailed Cuckoo *(Cacomantis flabelliformis)*	259.19	245.69	235.38	238.68	236.71	3	3
29	Fernwren *(Oreoscopus gutturalis)*	802.13	707.56	657.94	668.73	658.57	3	3
30	Grey Fantail *(Rhipidura albiscapa)*	874.79	868.09	828.27	761.19	751.49	5	4
31	Graceful Honeyeater *(Meliphaga gracilis)*	974.78	521.60	478.00	491.57	478.24	3	3
32	Grey-headed Robin *(Heteromyias cinereifrons)*	618.40	547.63	546.48	549.63	547.94	3	3
33	Golden Bowerbird *(Amblyornis newtonianus)*	755.69	495.05	442.02	441.33	441.92	4	4
34	Golden Whistler *(Pachycephala pectoralis)*	759.78	697.36	588.17	562.15	558.70	5	4
35	Grey Whistler *(Pachycephala simplex)*	476.49	286.29	281.08	283.32	281.35	3	3
36	Helmeted Friarbird *(Philemon buceroides)*	73.58	58.20	60.20	60.20	62.20	2	2
37	Australian King Parrot *(Alisterus scapularis)*	294.54	275.78	264.80	270.55	266.11	3	3
38	Little Bronze-Cuckoo *(Chalcites minutillus)*	167.20	158.57	159.09	158.99	160.96	2	2
39	Large-billed Scrubwren *(Sericornis magnirostra)*	1310.62	1268.48	1269.50	1269.56	1271.45	2	2
40	Lewin's Honeyeater *(Meliphaga lewinii)*	565.89	548.39	422.88	361.31	347.95	5	4
41	Little Shrike-Thrush *(Colluricincla megarhyncha)*	816.64	482.92	433.64	447.11	435.34	3	3
42	Macleay's Honeyeater *(Xanthotis macleayanus)*	481.14	357.87	335.08	346.62	332.91	5	3
43	Metallic Starling *(Aplornis metallica)*	851.67	435.83	437.83	437.83	439.83	2	2
44	Mistletoebird *(Dicaeum hirundinaceum)*	626.29	551.96	548.11	549.22	550.07	3	3
45	Mountain Thornbill *(Acanthiza katherina)*	1774.69	1157.98	894.41	861.59	853.01	5	4
46	Noisy Pitta *(Pitta versicolor)*	315.62	258.20	248.20	255.77	250.00	3	3
47	Orange-footed Scrubfowl *(Megapodius reinwardt)*	386.33	292.88	294.80	294.88	282.26	5	2

AIC scores

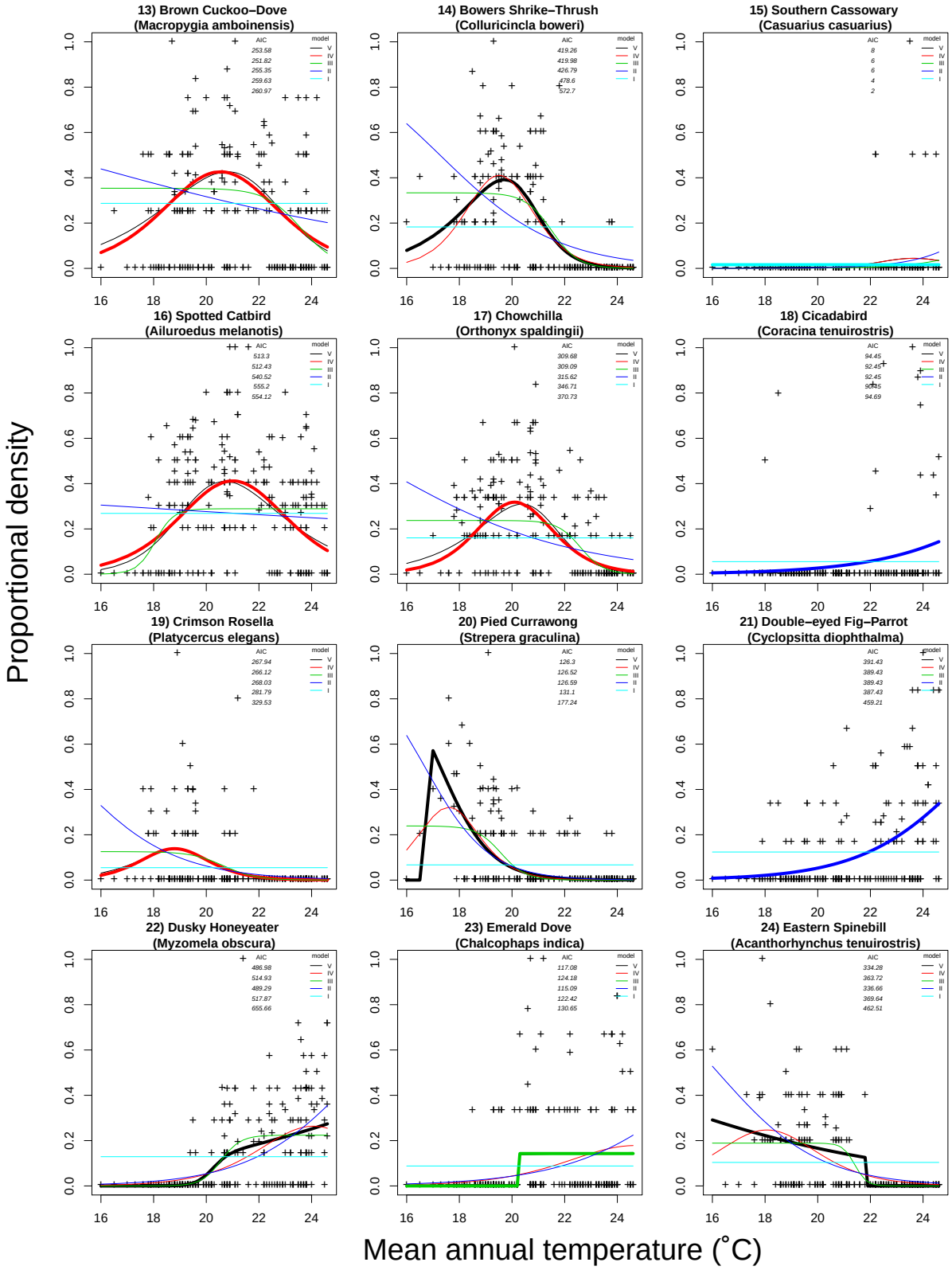
	Species	Model 1 (flat)	Model 2 (monotonic)	Model 3 (plateau)	Model 4 (gaussian)	Model 5 (skewed)	Top model	Top model ignoring skewness
48	Pacific Baza *(Aviceda subcristata)*	98.21	97.61	94.28	96.19	96.24	3	3
49	Pied Imperial Pigeon *(Ducula bicolor)*	369.48	294.09	295.64	295.50	287.52	5	2
50	Pied Monarch *(Arses kaupi)*	533.45	516.87	492.30	510.41	494.29	3	3
51	Pale-yellow Robin *(Tregellasia capito)*	1074.22	939.10	875.96	901.36	877.15	3	3
52	Rainbow Bee-eater *(Merops ornatus)*	348.02	320.61	302.86	299.19	300.39	4	4
53	Rose-crowned Fruit-Dove *(Ptilinopus regina)*	141.78	122.51	124.51	124.51	126.51	2	2
54	Rufous Fantail *(Rhipidura rufifrons)*	537.14	490.09	492.09	492.09	494.09	2	2
55	Rainbow Lorikeet *(Trichoglossus haematodus)*	365.20	366.84	352.84	357.80	352.67	5	3
56	Red-necked Crake *(Rallina tricolor)*	76.47	71.91	73.22	72.81	73.39	2	2
57	Russet-tailed Thrush *(Zoothera heinei)*	54.31	56.27	53.10	55.24	46.07	5	3
58	Satin Bowerbird *(Ptilonorhynchus violaceus)*	461.63	363.58	359.85	360.52	358.53	5	3
59	Shining Bronze-Cuckoo (Golden) *(Chalcites lucidus)*	296.29	293.93	260.00	234.06	235.54	4	4
60	Scaly-breasted Lorikeet *(Trichoglossus chlorolepidotus)*	814.01	789.97	763.19	741.74	743.59	4	4
61	Scarlet Honeyeater *(Myzomela sanguinolenta)*	231.10	226.44	206.05	211.89	206.73	3	3
62	Sulphur-crested Cockatoo *(Cacatua galerita)*	363.45	361.78	341.91	340.56	337.77	5	4
63	Spangled Drongo *(Dicrurus bracteatus)*	201.34	187.55	189.55	189.55	191.55	2	2
64	Silvereye *(Zosterops lateralis)*	1081.42	928.12	839.95	861.44	839.67	5	3
65	Superb Fruit-Dove *(Ptilinopus superbus)*	381.86	371.91	363.09	367.77	364.90	3	3
66	Spectacled Monarch *(Symposiarchus trivirgatus)*	1048.86	878.41	860.42	864.94	839.60	5	3
67	Tooth-billed Bowerbird *(Scenopoeetes dentirostris)*	505.96	481.08	410.82	387.74	388.26	4	4
68	Topknot Pigeon *(Lopholaimus antarcticus)*	814.42	810.43	779.15	777.95	756.95	5	4
69	Victoria's Riflebird *(Ptiloris victoriae)*	340.39	332.97	307.91	298.88	300.03	4	4
70	Varied Triller *(Lalage leucomela)*	392.47	252.11	246.51	248.17	248.47	3	3
71	White-browed Robin *(Poecilodryas superciliosa)*	74.94	60.10	51.34	37.71	39.71	4	4
72	White-eared Monarch *(Carternornis leucotis)*	231.14	216.17	208.10	205.58	206.92	4	4
73	White-headed Pigeon *(Columba leucomela)*	263.75	265.71	267.71	267.71	269.71	1	1

AIC scores

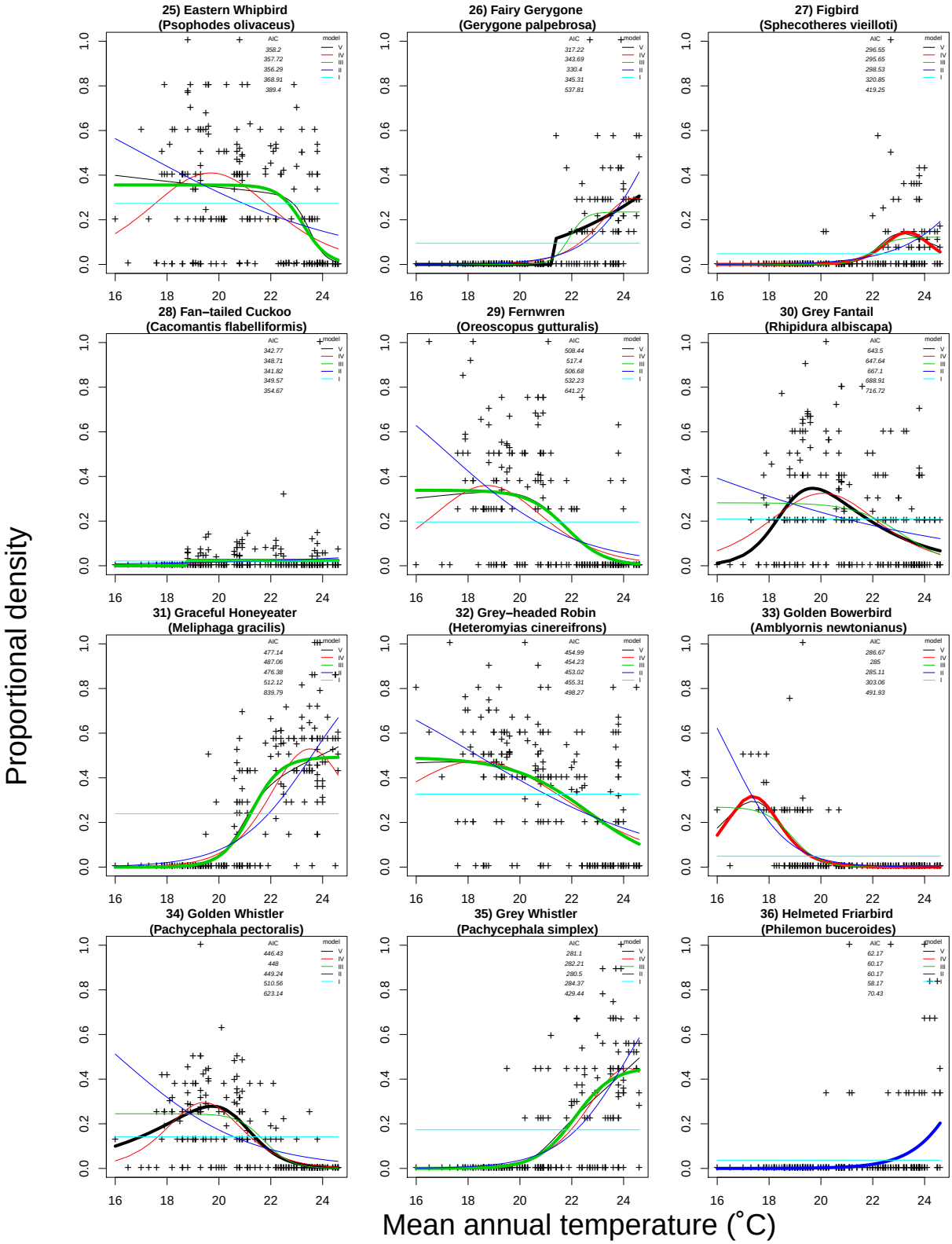
	Species	Model 1 (flat)	Model 2 (monotonic)	Model 3 (plateau)	Model 4 (gaussian)	Model 5 (skewed)	Top model	Top model ignoring skewness
74	Wompoo Fruit-Dove *(Ptilinopus magnificus)*	394.75	364.19	331.49	347.26	333.17	3	3
75	White-throated Treecreeper *(Cormobates leucophaea)*	544.17	483.21	410.42	420.08	403.07	5	3
76	Yellow-breasted Boatbill *(Machaerirhynchus flaviventer)*	588.79	505.34	471.01	472.58	470.05	5	3
77	Yellow-bellied Sunbird *(Nectarinia jugularis)*	283.86	191.88	176.69	190.92	178.67	3	3
78	Yellow Oriole *(Oriolus flavocinctus)*	157.99	129.87	112.64	114.24	105.19	5	3
79	Yellow-spotted Honeyeater *(Meliphaga notata)*	880.81	402.78	382.83	398.83	380.85	5	3
80	Yellow-throated Scrubwren *(Sericornis citreogularis)*	1710.21	1556.34	1356.82	1308.89	1293.38	5	4



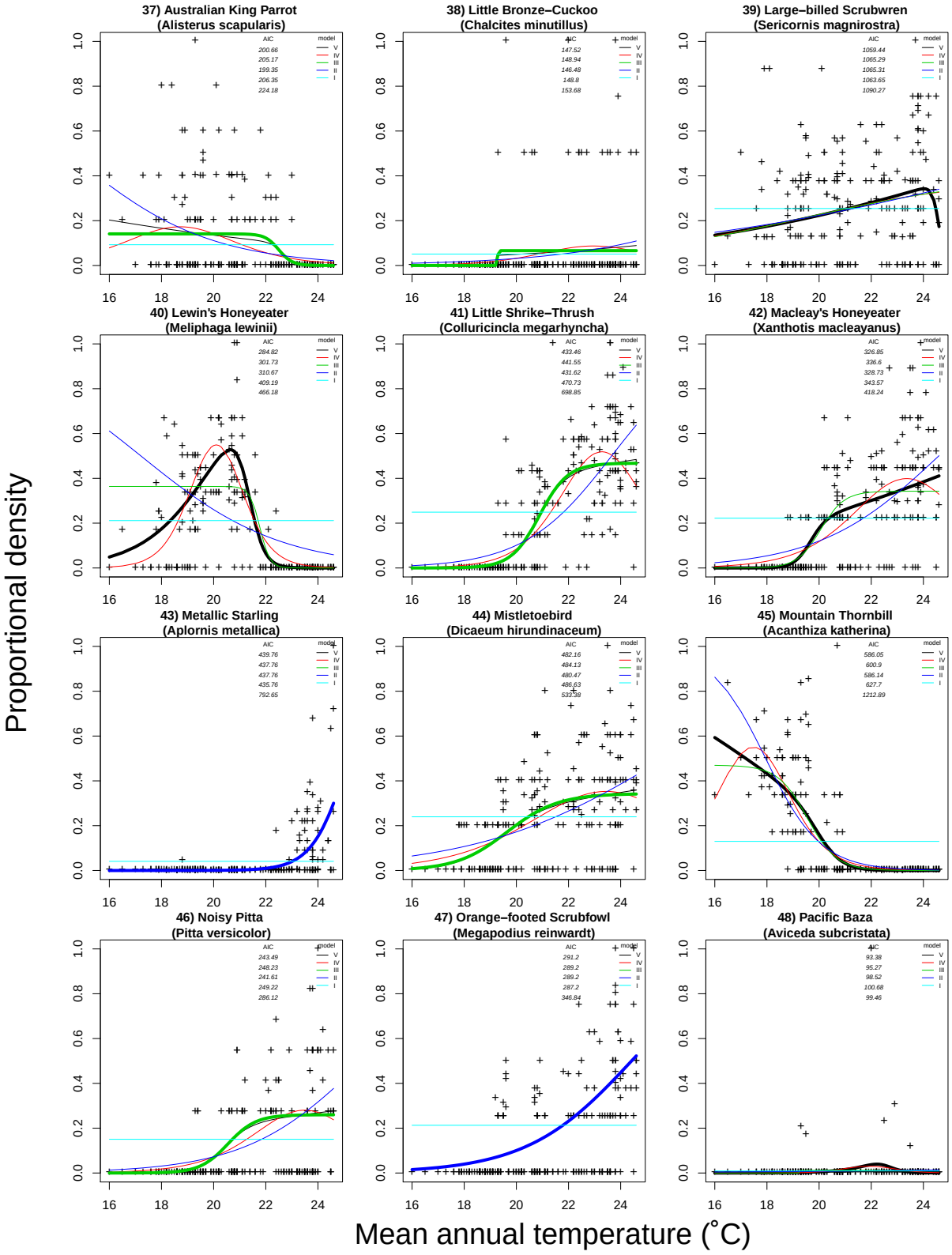
Appendix Figure 6.1. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



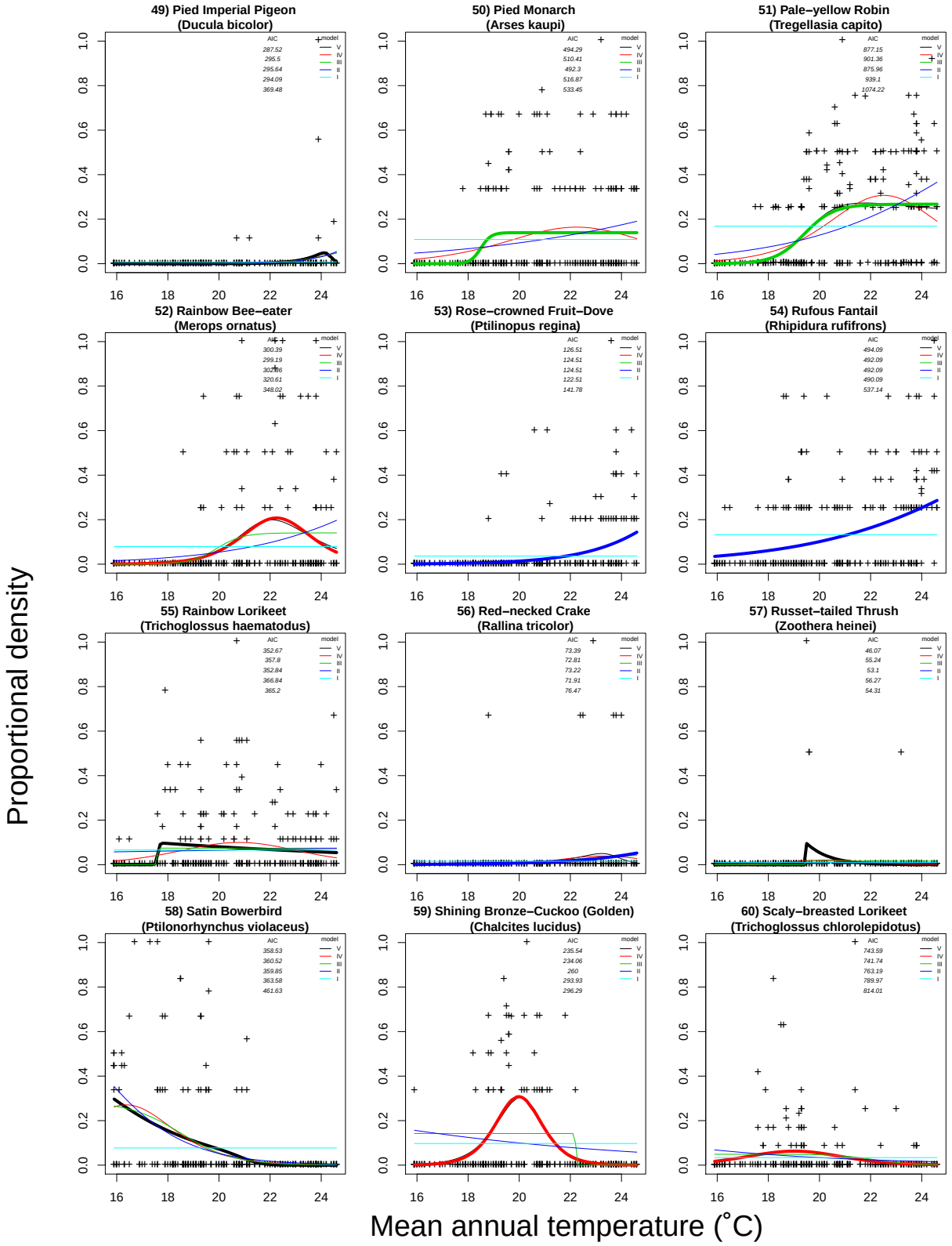
Appendix Figure 6.1. CONTINUED. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



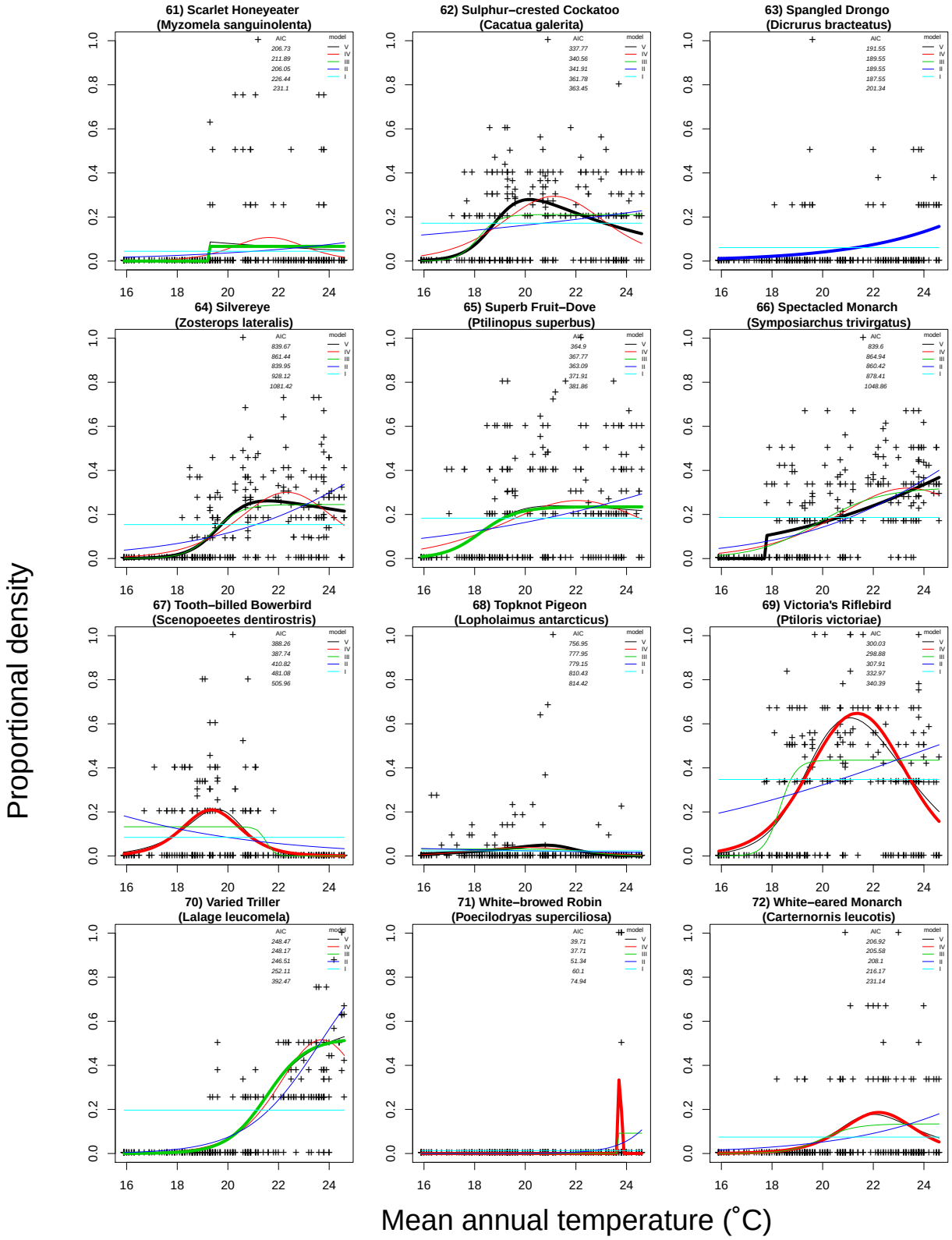
Appendix Figure 6.1. CONTINUED. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



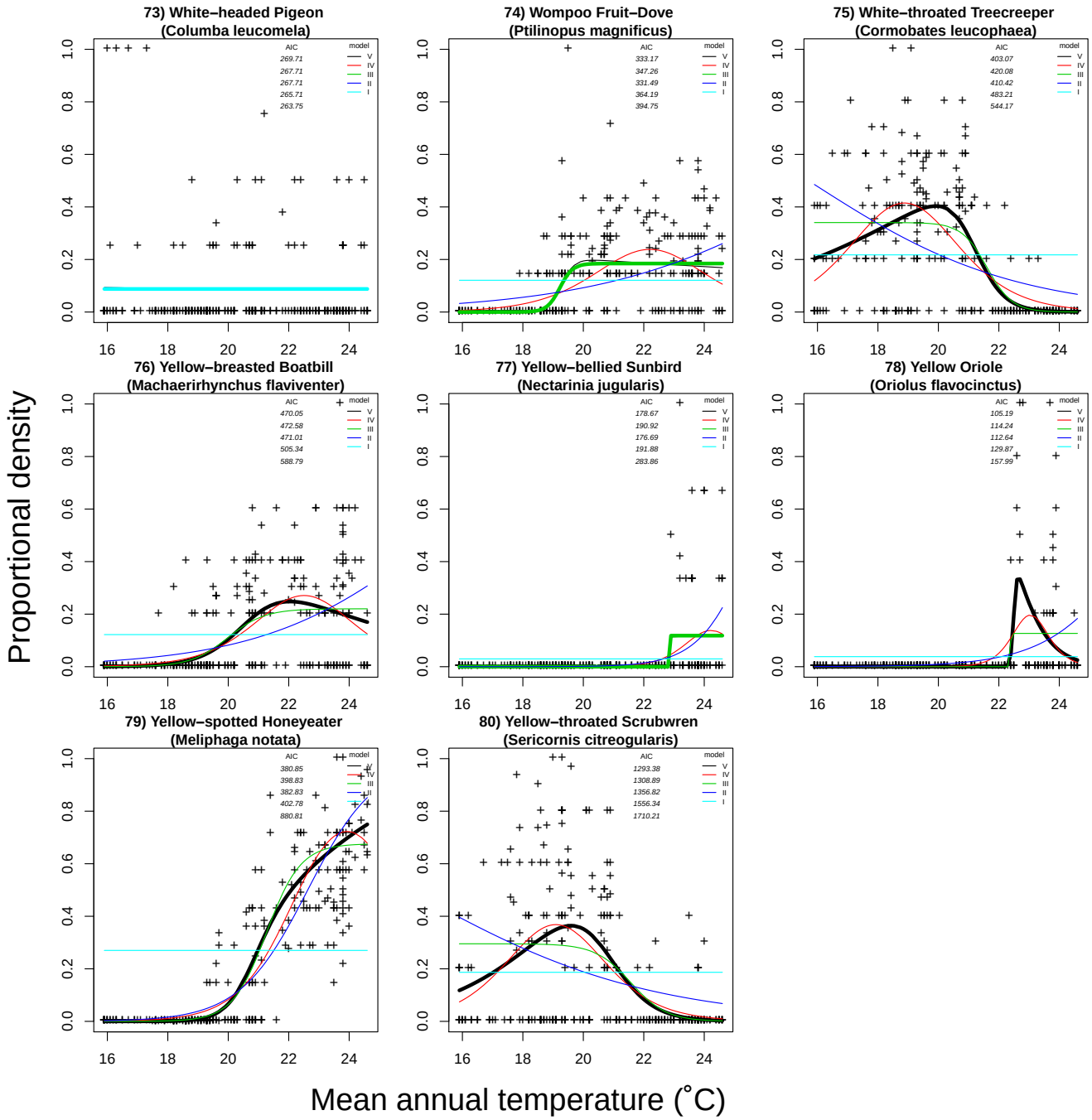
Appendix Figure 6.1 CONTINUED. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



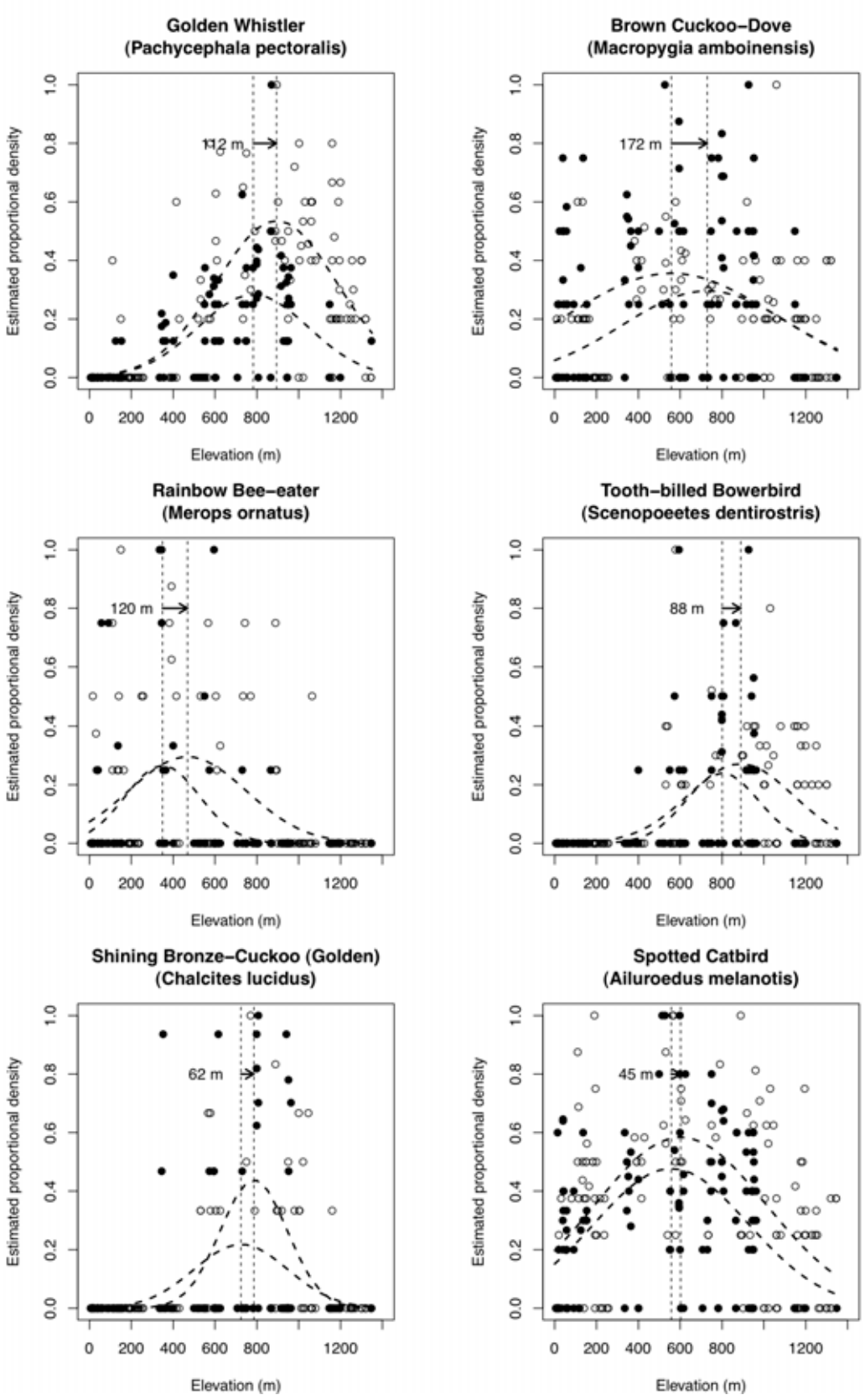
Appendix Figure 6.1 CONTINUED. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



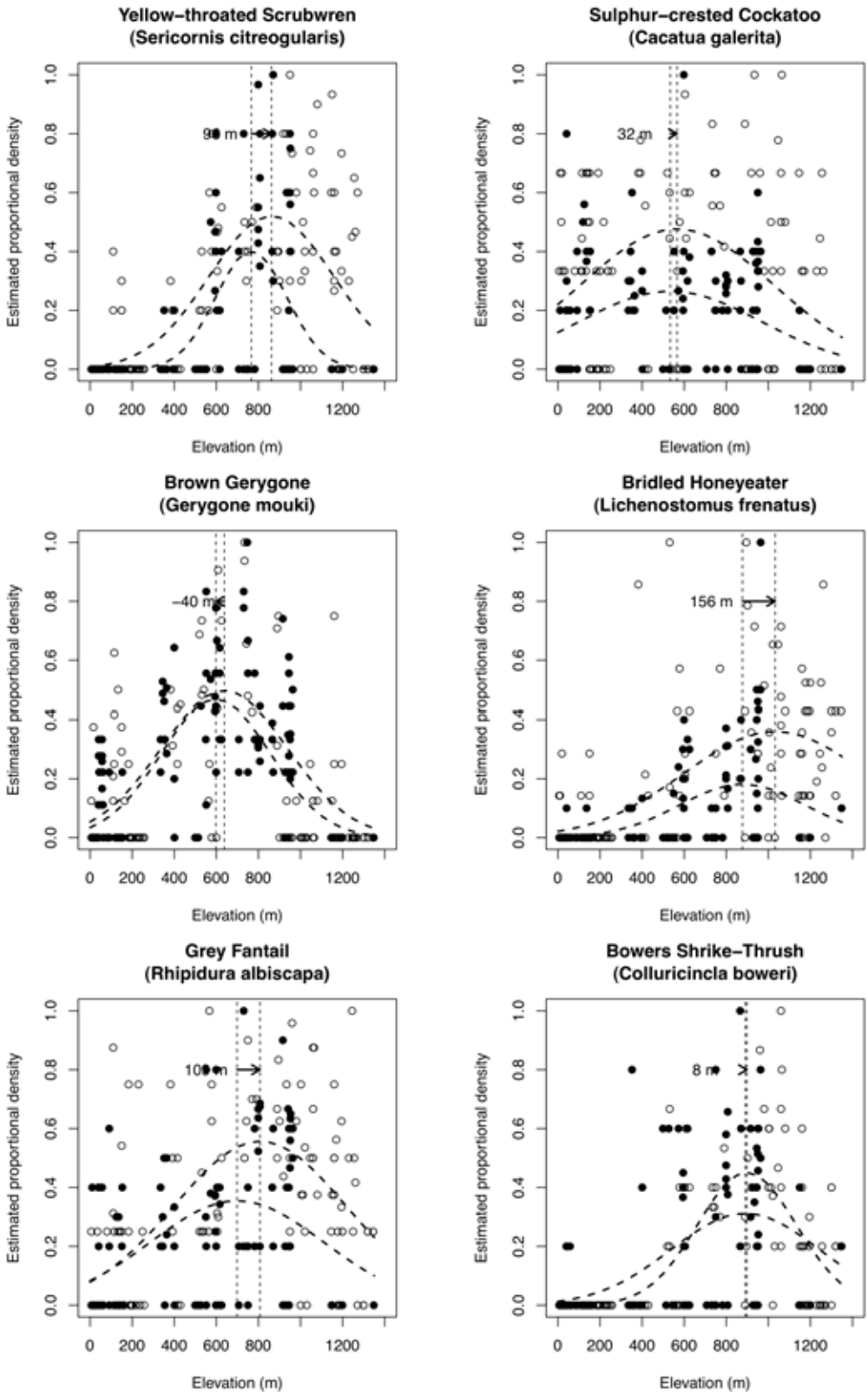
Appendix Figure 6.1 CONTINUED. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



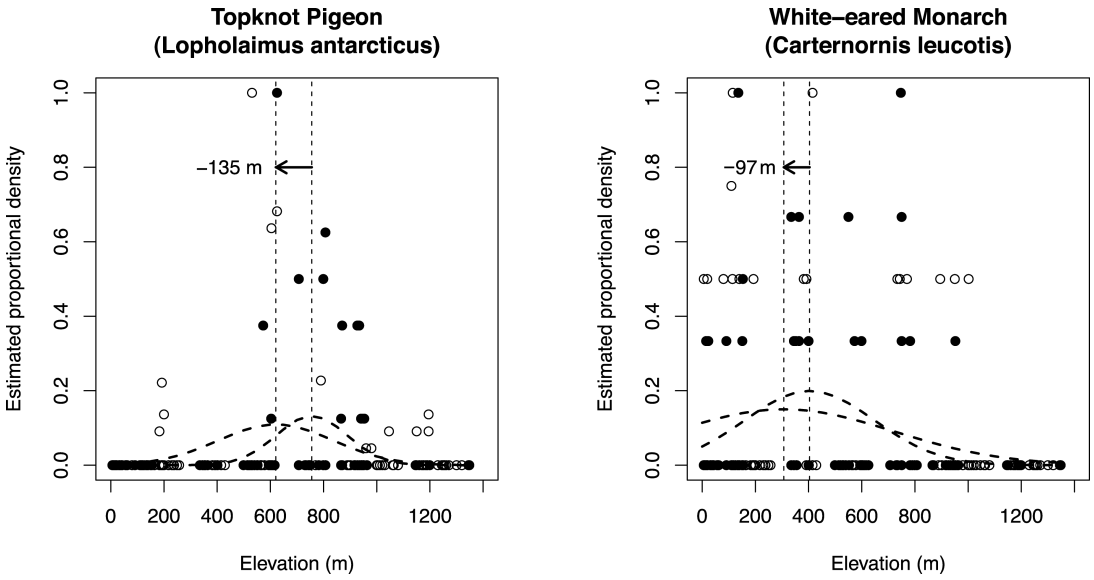
Appendix Figure 6.1 CONTINUED. *Results of the Huisman-Olff-Frescoe (HOF) hierarchical model fitting process for rainforest bird density responses across the temperature gradient in the study region. Models tested were flat (light blue), plateau (green), monotonic (dark blue), unimodal (Gaussian) (red) and skewed (black). AIC values (upper right of each plot) were used to select the most appropriate model in each case (curve shown in bold in each case).*



Appendix Figure 6.2. *Example fitted Gaussian curves (dashed lines) to the elevational density profiles for species that showed a significant elevational difference in their estimated density optima between southern AWT (unfilled circles) and northern AWT (filled circles). Data are the estimated densities calculated with Distance analysis at each sampling point across the elevational gradient. The arrows indicate direction of the elevational difference, the magnitude of which is indicated.*



Appendix Figure 6.2. CONTINUED *Example fitted Gaussian curves (dashed lines) to the elevational density profiles for species that showed a significant elevational difference in their estimated density optima between southern AWT (unfilled circles) and northern AWT (filled circles). Data are the estimated densities calculated with Distance analysis at each sampling point across the elevational gradient. The arrows indicate direction of the elevational difference, the magnitude of which is indicated.*



Appendix Figure 6.2. CONTINUED *Example fitted Gaussian curves (dashed lines) to the elevational density profiles for species that showed a significant elevational difference in their estimated density optima between southern AWT (unfilled circles) and northern AWT (filled circles). Data are the estimated densities calculated with Distance analysis at each sampling point across the elevational gradient. The arrows indicate direction of the elevational difference, the magnitude of which is indicated.*

Appendix 7

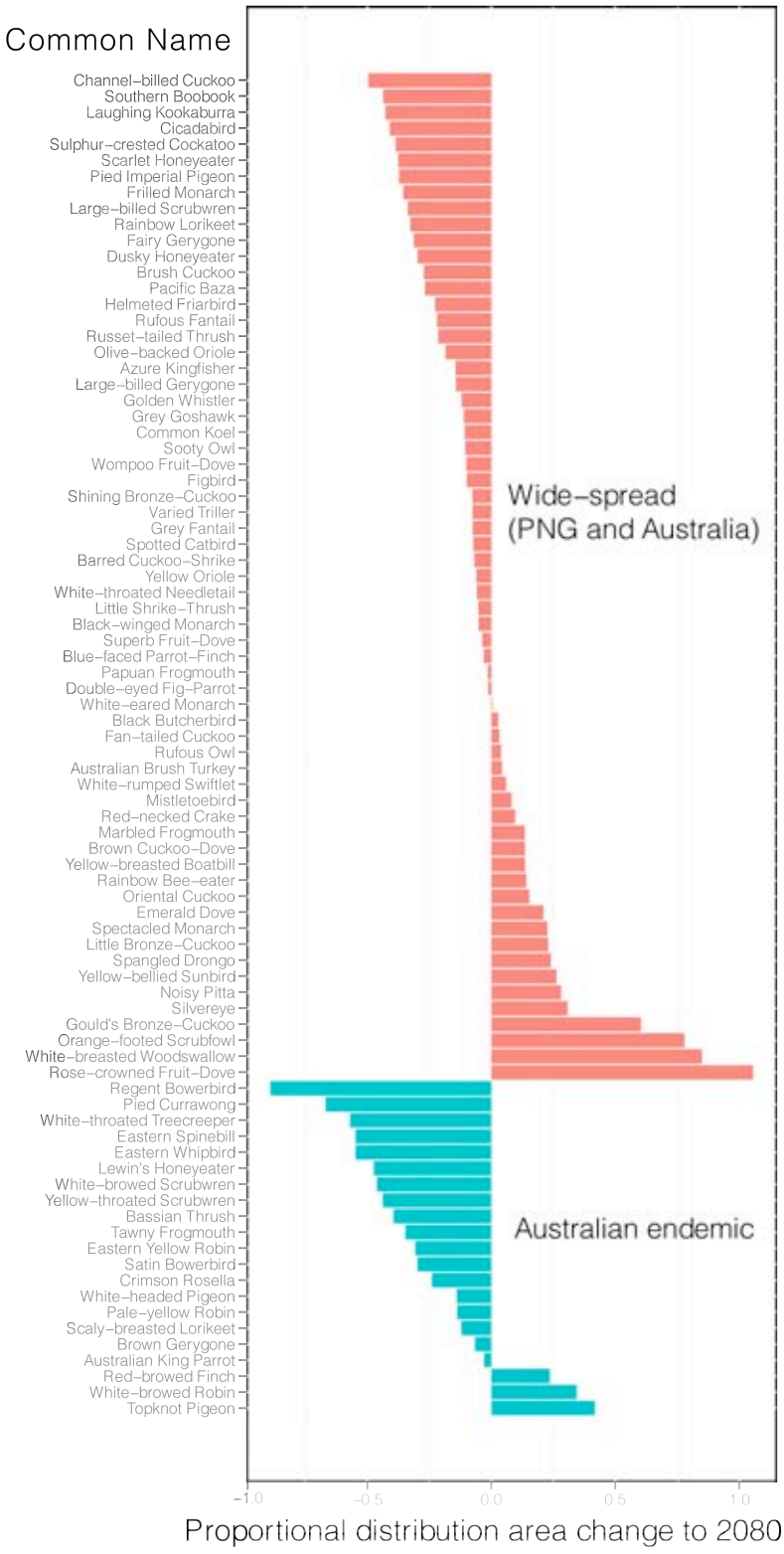
Appendix Table 7.1. *Samples sizes, Training AUC scores and BIOCLIM variable contributions for MAXENT modeled species. Species with less than 30 occurrence records are indicated in bold text*

Species	Training samples	Training AUC	BIOCLIM variables										
			1	2	3	4	5	6	7	9	12	14	15
Atherton Scrubwren *(Sericornis keri)*	157	1.00	0.12	1.15	2.80	1.38	0.19	0.46	0.98	0.32	14.95	53.58	0.25
Australian Brush Turkey *(Alectura lathami)*	785	0.96	0.84	52.67	2.61	0.29	1.88	0.24	3.84	1.14	15.85	16.44	2.72
Australian King Parrot *(Alisterus scapularis)*	469	0.99	0.27	0.87	0.35	0.74	2.13	0.32	0.38	0.09	6.11	79.90	1.64
Azure Kingfisher *(Ceyx azureus)*	129	0.95	1.76	26.91	0.90	1.34	2.32	2.00	2.64	0.70	29.37	23.16	6.10
Barred Cuckoo-Shrike *(Coracina lineata)*	331	0.99	1.63	3.59	0.73	0.99	5.89	0.34	3.18	0.73	14.54	62.67	2.78
Bassian Thrush *(Zoothera lunulata)*	78	1.00	0.00	0.66	0.21	0.12	5.55	0.02	2.37	0.16	2.91	54.22	0.89
Tropical Scrubwren *(Sericornis beccarii)*	53	0.99	0.26	0.48	3.32	26.19	0.00	19.43	11.51	4.62	19.11	14.15	0.92
Black Butcherbird *(Cracticus quoyi)*	749	0.98	1.49	6.22	2.77	0.23	3.48	0.49	5.64	0.60	61.50	15.08	1.31
Black-faced Monarch *(Monarcha melanopsis)*	444	0.98	1.17	10.72	0.16	0.14	7.51	0.94	2.10	0.32	11.44	62.92	1.25
Black-winged Monarch *(Monarcha frater)*	31	1.00	0.05	4.51	17.94	3.91	0.21	2.94	39.81	2.55	16.11	11.30	0.42
Blue-faced Parrot-Finch *(Erythrura trichroa)*	33	1.00	0.02	0.47	6.45	0.80	46.30	0.00	1.33	7.89	9.19	22.66	0.23
Bowers Shrike-Thrush *(Colluricincla boweri)*	436	1.00	1.07	0.45	0.28	2.25	0.82	0.25	1.19	0.41	11.84	72.63	0.39
Bridled Honeyeater *(Lichenostomus frenatus)*	577	1.00	0.90	1.16	1.71	1.67	2.68	0.16	5.18	0.48	11.27	69.61	0.26
Brown Cuckoo-Dove *(Macropygia amboinensis)*	906	0.99	0.23	3.35	1.81	0.83	5.32	0.78	0.60	0.18	29.58	55.49	0.96
Brown Gerygone *(Gerygone mouki)*	711	0.99	0.63	2.61	0.23	0.40	7.56	0.61	1.61	0.38	5.75	72.59	3.11
Brush Cuckoo *(Cacomantis variolosus)*	677	0.94	1.49	2.71	3.13	5.09	5.49	0.41	50.02	1.19	18.12	2.68	4.61
Buff-breasted Paradise-Kingfisher *(Tanysiptera sylvia)*	151	0.99	0.03	8.44	7.37	0.89	1.22	0.14	7.57	1.42	37.13	32.15	2.13
Channel-billed Cuckoo *(Scythrops novaehollandiae)*	407	0.89	1.36	44.60	1.35	4.13	8.91	2.02	2.05	5.05	3.08	15.21	3.73
Chestnut-breasted Cuckoo *(Cacomantis castaneiventris)*	68	0.99	0.06	20.20	10.62	3.59	0.25	0.60	21.35	2.11	30.15	8.59	1.17
Chowchilla *(Orthonyx spaldingii)*	490	1.00	0.41	1.02	0.77	3.97	1.43	0.28	0.62	0.34	6.06	79.40	0.11
Cicadabird *(Coracina tenuirostris)*	385	0.95	1.66	25.23	1.98	0.82	2.56	0.09	3.10	1.70	36.70	17.89	2.09
Common Koel *(Eudynamys orientalis)*	161	0.93	3.57	31.08	0.65	3.16	3.35	1.10	4.02	4.57	31.87	10.87	2.38
Crimson Rosella *(Platycercus elegans)*	235	1.00	1.30	0.95	0.40	0.06	0.96	0.33	0.71	0.19	2.16	62.68	0.77
Double-eyed Fig-Parrot *(Cyclopsitta diophthalma)*	454	0.99	0.05	6.28	4.76	0.88	1.06	0.45	0.68	0.66	35.93	45.55	1.04
Dusky Honeyeater *(Myzomela obscura)*	1137	0.96	0.17	51.42	0.50	0.09	2.43	0.80	1.25	0.08	29.55	8.80	2.38
Eastern Spinebill *(Acanthorhynchus tenuirostris)*	374	1.00	1.76	1.52	0.02	0.28	2.14	0.14	0.50	0.27	2.29	62.19	0.69
Eastern Whipbird *(Psophodes olivaceus)*	813	0.99	0.72	0.46	0.25	0.16	2.35	0.25	1.05	0.09	5.97	83.71	1.30

Species	Training samples	Training AUC	BIOCLIM variables 1	2	3	4	5	6	7	9	12	14	15
Eastern Yellow Robin *(Eopsaltria australis)*	313	0.99	5.2	2.2	0.1	0.3	5.8	0.7	2.2	0.5	5.4	71.6	1.7
Eclectus Parrot *(Eclectus roratus)*	78	1.00	0.2	13.2	24.4	1.3	0.0	13.3	7.5	0.1	20.3	17.6	1.7
Emerald Dove *(Chalcophaps indica)*	510	0.98	2.6	6.4	1.0	1.1	3.9	0.7	5.4	1.9	29.9	46.6	0.3
Eungella Honeyeater *(Lichenostomus hindwoodi)*	38	1.00	40.7	0.4	4.6	4.2	1.2	1.3	0.0	0.1	4.2	41.2	0.0
Fairy Gerygone *(Gerygone palpebrosa)*	659	0.95	1.7	33.1	1.4	0.3	3.1	1.1	5.3	1.2	42.9	6.3	2.5
Fan-tailed Cuckoo *(Cacomantis flabelliformis)*	425	0.97	1.5	29.5	0.1	0.1	5.2	0.1	0.4	4.1	0.8	51.7	4.3
Fernwren *(Oreoscopus gutturalis)*	364	1.00	1.3	0.6	0.6	1.2	1.6	0.4	2.3	0.0	7.1	75.2	0.3
Figbird *(Sphecotheres vieilloti)*	1259	0.96	1.5	66.5	0.8	1.1	1.6	1.1	2.6	0.8	0.6	18.9	2.9
Frilled Monarch *(Arses lorealis)*	37	1.00	0.0	0.3	23.1	2.0	0.5	9.4	39.3	1.2	2.2	17.9	3.6
Golden Bowerbird *(Amblyornis newtonianus)*	166	1.00	1.9	1.7	0.1	0.4	1.3	0.2	1.5	0.6	1.2	56.6	0.5
Golden Whistler *(Pachycephala pectoralis)*	768	0.99	0.3	0.6	0.4	0.1	1.6	0.1	0.3	0.1	6.8	80.9	1.6
Gould's Bronze-Cuckoo *(Chalcites minutillus)*	49	0.98	1.1	18.3	0.3	2.0	0.9	3.3	1.0	2.4	45.9	20.1	3.8
Graceful Honeyeater *(Meliphaga gracilis)*	1021	0.98	0.3	2.4	2.4	1.4	1.6	0.5	3.6	0.8	69.9	13.2	1.9
Green-backed Honeyeater *(Glycichaera fallax)*	24	1.00	0.5	0.0	15.4	1.2	0.0	7.5	0.0	11.7	37.0	26.6	0.0
Grey Fantail *(Rhipidura albiscapa)*	1586	0.92	3.6	6.9	0.4	2.4	17.4	0.2	3.4	5.7	1.6	49.7	7.0
Grey Goshawk *(Accipiter novaehollandiae)*	151	0.97	0.7	25.2	1.5	0.7	5.0	0.4	2.3	0.9	16.2	38.1	4.7
Grey Whistler *(Pachycephala simplex)*	399	0.98	1.5	4.9	4.2	1.8	0.8	0.2	2.1	1.0	58.3	22.9	2.0
Grey-headed Robin *(Heteromyias cinereifrons)*	714	1.00	1.8	0.9	0.5	4.5	4.3	0.1	0.7	0.4	5.6	76.6	0.9
Helmeted Friarbird *(Philemon buceroides)*	789	0.97	0.1	74.1	1.2	1.4	1.1	1.8	4.9	0.3	0.3	7.1	4.1
Large-billed Gerygone *(Gerygone magnirostris)*	269	0.96	1.9	3.7	1.8	1.6	2.2	3.3	42.3	1.6	21.1	11.5	3.5
Large-billed Scrubwren *(Sericornis magnirostra)*	756	0.99	1.2	0.9	0.5	1.2	2.0	0.5	0.5	0.5	13.0	78.0	1.2
Laughing Kookaburra *(Dacelo novaeguineae)*	1270	0.90	2.7	4.8	2.2	3.4	48.9	1.1	2.2	2.4	9.2	9.1	3.6
Lewin's Honeyeater *(Meliphaga lewinii)*	1145	0.98	2.5	7.9	0.5	0.0	16.5	0.0	0.6	1.4	0.2	66.8	2.0
Little Bronze-Cuckoo *(Chalcites minutillus)*	291	0.95	1.7	68.2	2.7	1.5	3.0	2.6	0.6	2.9	7.0	4.3	3.0
Little Kingfisher *(Ceyx pusilla)*	87	0.98	0.1	45.5	0.4	0.0	0.2	0.4	8.3	1.8	1.9	31.0	5.2
Little Shrike-Thrush *(Colluricincla megarhyncha)*	1341	0.97	1.4	65.8	2.3	0.4	0.7	0.3	0.9	0.7	7.4	15.7	2.9
Lovely Fairy-wren *(Malurus amabilis)*	224	0.98	1.6	5.8	3.9	0.2	0.7	7.5	3.0	1.9	62.4	6.3	4.5
Macleay's Honeyeater *(Xanthotis macleayanus)*	579	0.99	1.6	2.0	1.1	6.4	0.6	0.1	1.3	0.0	15.0	69.3	0.4
Magnificent Riflebird *(Ptiloris magnificus)*	168	0.99	1.1	2.1	11.5	21.1	0.2	0.4	36.2	1.0	10.8	9.6	3.8
Marbled Frogmouth *(Podargus ocellatus)*	18	0.99	0.5	1.7	15.8	0.0	0.0	0.0	18.2	10.6	35.3	17.8	0.0
Metallic Starling *(Aplornis metallica)*	148	0.99	2.4	0.3	3.0	3.5	0.9	1.1	2.6	5.0	33.1	46.4	1.6

Species	Training samples	Training AUC	BIOCLIM variables										
			1	2	3	4	5	6	7	9	12	14	15
Mistletoebird *(Dicaeum hirundinaceum)*	1536	0.89	0.3	52.8	2.8	4.7	5.6	0.6	2.9	1.1	9.4	11.7	5.4
Mountain Thornbill *(Acanthiza katherina)*	150	1.00	3.0	0.9	0.6	0.6	0.5	0.1	1.3	0.5	3.9	56.1	0.5
Noisy Pitta *(Pitta versicolor)*	296	0.98	4.2	42.9	1.8	0.2	1.2	2.4	3.3	1.6	10.1	28.2	3.6
Northern Scrub Robin *(Drymodes superciliaris)*	23	1.00	0.0	0.3	9.7	3.4	0.0	1.2	39.7	11.7	12.2	21.5	0.2
Olive-backed Oriole *(Oriolus sagittatus)*	561	0.86	4.3	47.1	1.3	6.7	1.8	2.4	8.5	5.9	1.8	10.8	5.5
Orange-footed Scrubfowl *(Megapodius reinwardt)*	581	0.98	1.1	8.4	1.7	0.2	2.5	1.1	2.2	0.6	58.5	21.0	1.2
Oriental Cuckoo *(Cuculus optatus)*	43	0.97	0.2	59.8	6.6	0.0	1.1	0.0	8.4	0.7	0.0	12.9	7.4
Pacific Baza *(Aviceda subcristata)*	225	0.92	0.7	42.3	4.4	3.3	6.7	0.0	4.8	3.7	4.1	23.5	6.0
Pale-yellow Robin *(Tregellasia capito)*	324	0.99	0.4	2.3	1.0	4.9	1.2	0.4	2.0	1.9	13.0	69.6	3.0
Palm Cockatoo *(Probosciger aterrimus)*	126	0.99	1.9	1.2	7.1	53.6	0.6	20.1	0.0	1.2	2.2	7.4	2.3
Papuan Frogmouth *(Podargus papuensis)*	119	0.97	0.1	4.1	4.1	6.2	4.5	0.7	27.4	0.9	37.1	3.8	5.1
Pied Currawong *(Strepera graculina)*	996	0.94	2.1	1.7	1.1	0.1	51.2	0.5	1.4	0.9	0.5	29.2	6.4
Pied Imperial Pigeon *(Ducula bicolor)*	900	0.97	0.3	25.3	2.5	0.6	0.6	2.7	21.4	1.6	33.4	4.3	1.0
Pied Monarch *(Arses kaupi)*	139	0.99	0.2	3.1	1.6	5.1	0.2	0.1	1.1	0.1	14.5	66.6	4.4
Rainbow Bee-eater *(Merops ornatus)*	1865	0.87	1.6	66.7	1.3	5.5	2.3	3.7	2.2	2.8	1.5	2.0	6.8
Rainbow Lorikeet *(Trichoglossus haematodus)*	2535	0.88	0.8	31.0	0.8	2.4	15.0	0.9	31.9	0.3	4.0	5.5	3.8
Red-bellied Pitta *(Pitta erythrogaster)*	8	1.00	0.0	0.0	4.3	0.0	0.8	0.0	73.3	9.3	3.9	1.2	7.2
Red-browed Finch *(Neochmia temporalis)*	513	0.97	2.5	27.2	1.7	0.5	8.0	0.1	0.2	1.4	26.6	25.5	3.0
Red-cheeked Parrot *(Geoffroyus geoffroyi)*	39	1.00	0.5	0.7	14.3	0.2	0.0	20.3	0.0	4.7	27.5	31.6	0.1
Red-necked Crake *(Rallina tricolor)*	34	0.99	0.0	2.9	2.9	4.6	0.3	4.3	2.1	0.2	21.0	57.8	3.8
Regent Bowerbird *(Sericulus chrysocephalus)*	27	1.00	71.7	0.1	0.3	4.3	8.2	2.2	0.0	0.0	2.1	11.0	0.2
Rose-crowned Fruit-Dove *(Ptilinopus regina)*	256	0.98	0.7	9.3	2.4	0.0	0.7	1.2	2.2	1.1	60.5	17.9	0.5
Rufous Fantail *(Rhipidura rufifrons)*	549	0.97	0.8	52.3	0.6	0.7	3.0	0.2	3.3	2.6	1.0	31.1	4.4
Rufous Owl *(Ninox rufa)*	30	0.96	0.5	47.3	3.9	3.0	0.0	0.0	6.3	0.0	12.1	17.7	4.7
Russet-tailed Thrush *(Zoothera heinei)*	25	0.99	15.4	1.5	0.2	0.0	6.4	3.1	0.2	0.5	11.3	59.3	1.0
Satin Bowerbird *(Ptilonorhynchus violaceus)*	103	1.00	1.1	0.9	1.2	0.6	2.6	0.1	1.3	2.1	1.4	65.8	2.4
Scaly-breasted Lorikeet *(Trichoglossus chlorolepidotus)*	547	0.98	0.8	16.5	2.6	2.8	41.6	0.1	4.2	2.9	2.9	19.8	4.0
Scarlet Honeyeater *(Myzomela sanguinolenta)*	456	0.97	1.5	13.6	0.4	1.1	35.9	0.3	3.3	6.6	3.4	28.2	5.5
Shining Bronze-Cuckoo *(Chalcites lucidus)*	225	0.97	1.8	16.7	1.1	1.0	5.5	0.4	2.4	2.3	3.9	55.0	5.2
Silvereye *(Zosterops lateralis)*	526	0.98	0.7	4.5	2.5	0.3	0.2	0.5	1.2	0.8	19.0	67.1	2.7
Sooty Owl *(Tyto tenebricosa)*	103	0.99	2.0	3.8	0.1	4.6	0.5	0.5	3.9	1.0	11.3	61.8	1.4

Species	Training samples	Training AUC	BIOCLIM variables										
			1	2	3	4	5	6	7	9	12	14	15
Southern Boobook *(Ninox novaeseelandiae)*	421	0.84	7.5	5.2	1.5	1.8	41.9	1.6	5.8	1.4	5.7	14.3	6.5
Southern Cassowary *(Casuarius casuarius)*	644	0.99	0.3	2.4	0.9	1.4	0.2	0.9	0.0	1.6	3.5	82.9	2.8
Spangled Drongo *(Dicrurus bracteatus)*	1445	0.94	2.0	38.2	1.1	1.7	1.4	0.3	34.6	2.1	6.4	6.3	3.8
Spectacled Monarch *(Symposiarchus trivirgatus)*	740	0.98	0.2	36.3	0.4	0.2	0.6	0.9	3.4	0.1	19.5	35.0	2.1
Spotted Catbird *(Ailuroedus melanotis)*	765	0.99	0.0	1.8	1.5	4.7	3.7	0.1	1.7	1.1	19.4	64.7	0.4
Sulphur-crested Cockatoo *(Cacatua galerita)*	1890	0.89	1.3	52.2	2.0	2.4	9.6	0.6	2.3	0.7	5.6	15.9	3.6
Superb Fruit-Dove *(Ptilinopus superbus)*	264	0.98	0.3	6.3	3.0	1.0	3.9	1.0	4.9	0.3	34.8	39.4	1.6
Tawny Frogmouth *(Podargus strigoides)*	173	1.00	0.0	1.5	0.6	1.0	14.1	0.0	1.1	0.2	1.2	55.9	0.6
Tawny-breasted Honeyeater *(Xanthotis flaviventer)*	120	0.99	3.4	1.1	9.9	51.3	1.0	2.0	4.6	0.5	20.3	4.7	0.7
Tooth-billed Bowerbird *(Scenopoeetes dentirostris)*	270	0.81	11.4	13.8	2.4	1.8	26.1	0.4	5.5	2.0	7.1	14.7	6.3
Topknot Pigeon *(Lopholaimus antarcticus)*	229	0.99	1.0	12.5	1.3	0.3	2.9	1.0	1.0	0.8	7.0	66.8	3.1
Trumpet manucode *(Phonygammus keraudrenii)*	12	0.99	0.2	2.4	2.1	23.6	0.8	16.5	3.9	26.3	11.3	4.8	8.2
Varied Triller *(Lalage leucomela)*	989	0.97	1.2	66.1	1.9	0.2	1.9	1.6	8.5	1.2	1.2	12.0	3.4
Victoria's Riflebird *(Ptiloris victoriae)*	305	0.99	0.0	2.8	0.8	2.8	0.6	0.2	1.5	0.8	10.9	72.5	3.1
White-breasted Woodswallow *(Artamus leucorynchus)*	829	0.95	2.4	51.9	3.1	1.1	2.9	0.5	5.9	3.3	1.0	20.0	3.2
White-browed Robin *(Poecilodryas superciliosa)*	136	0.98	0.2	42.7	3.7	0.6	2.2	0.7	0.9	2.0	13.7	22.1	6.9
White-browed Scrubwren *(Sericornis frontalis)*	184	0.99	3.2	0.3	0.3	1.3	2.2	2.6	2.3	1.1	8.7	66.3	2.2
White-eared Monarch *(Carternornis leucotis)*	39	0.98	0.1	32.7	0.0	0.0	0.1	1.1	2.2	1.6	12.5	48.5	0.7
White-faced Robin *(Tregellasia leucops)*	40	1.00	0.3	0.1	19.0	0.5	0.0	13.9	6.4	2.0	37.4	19.4	1.1
White-headed Pigeon *(Columba leucomela)*	85	0.99	3.3	0.9	0.7	0.7	4.6	0.1	1.6	0.3	5.9	76.5	0.7
White-rumped Swiftlet *(Aerodramus terraereginae)*	164	0.99	3.4	6.2	0.9	4.1	1.6	0.7	3.2	1.5	14.0	56.5	6.5
White-throated Needletail *(Hirundapus caudacutus)*	79	0.95	6.1	62.0	2.0	0.5	3.6	0.2	1.5	0.3	0.6	16.9	4.7
White-throated Treecreeper *(Cormobates leucophaea)*	301	0.99	1.2	1.5	0.4	0.5	2.2	0.5	0.8	0.1	0.4	68.5	1.2
Wompoo Fruit-Dove *(Ptilinopus magnificus)*	507	0.98	2.9	4.9	1.6	0.4	0.0	0.8	3.7	0.6	53.5	26.6	1.7
Yellow Oriole *(Oriolus flavocinctus)*	657	0.97	1.2	5.4	2.8	1.1	1.3	21.1	23.4	0.6	30.9	4.9	2.8
Yellow-bellied Sunbird *(Nectarinia jugularis)*	957	0.98	0.5	49.6	0.9	1.8	0.4	3.5	25.5	2.7	0.8	9.0	1.4
Yellow-billed Kingfisher *(Syma torotoro)*	69	0.99	0.5	0.9	6.5	49.4	0.0	5.4	0.1	2.3	17.8	14.8	2.2
Yellow-breasted Boatbill *(Machaerirhynchus flaviventer)*	232	0.99	1.0	5.0	3.7	0.9	1.9	0.1	2.3	0.9	48.0	32.5	2.1
Yellow-legged Flycatcher *(Microeca griseoceps)*	16	1.00	0.0	2.4	14.1	0.1	0.2	3.9	38.6	6.0	16.1	18.7	0.0
Yellow-spotted Honeyeater *(Meliphaga notata)*	994	0.98	1.4	39.1	1.3	3.0	1.0	0.7	6.5	0.0	38.9	5.2	1.4
Yellow-throated Scrubwren *(Sericornis citreogularis)*	174	1.00	2.4	0.4	0.6	0.5	2.7	0.1	3.3	0.1	0.3	68.4	0.9



Appendix Figure 7.1*. The change in predicted potential distributional area in km between the present and the year 2080 (assuming global warming scenario A1B and no dispersal) for non-endemic species. The difference is expressed as a proportion of current distribution, and both positive and negative values are shown, right and left of zero on the x axis. The region to which species are endemic is indicated by colour. Actual values for each species are shown in Appendix Table 7.2*

***Appendix Table 7.2.**: Summary of predicted distributional changes for rainforest bird species in north-eastern Australia between the present and 2080. Values are calculated assuming no dispersal, so that expansion estimates may be conservative. Species, or those with distinct populations or subspecies predicted to experience a greater than 50% reduction are indicated in red, those predicted to experience a greater than 40% reduction in orange, and a greater than 30% reduction in blue.*

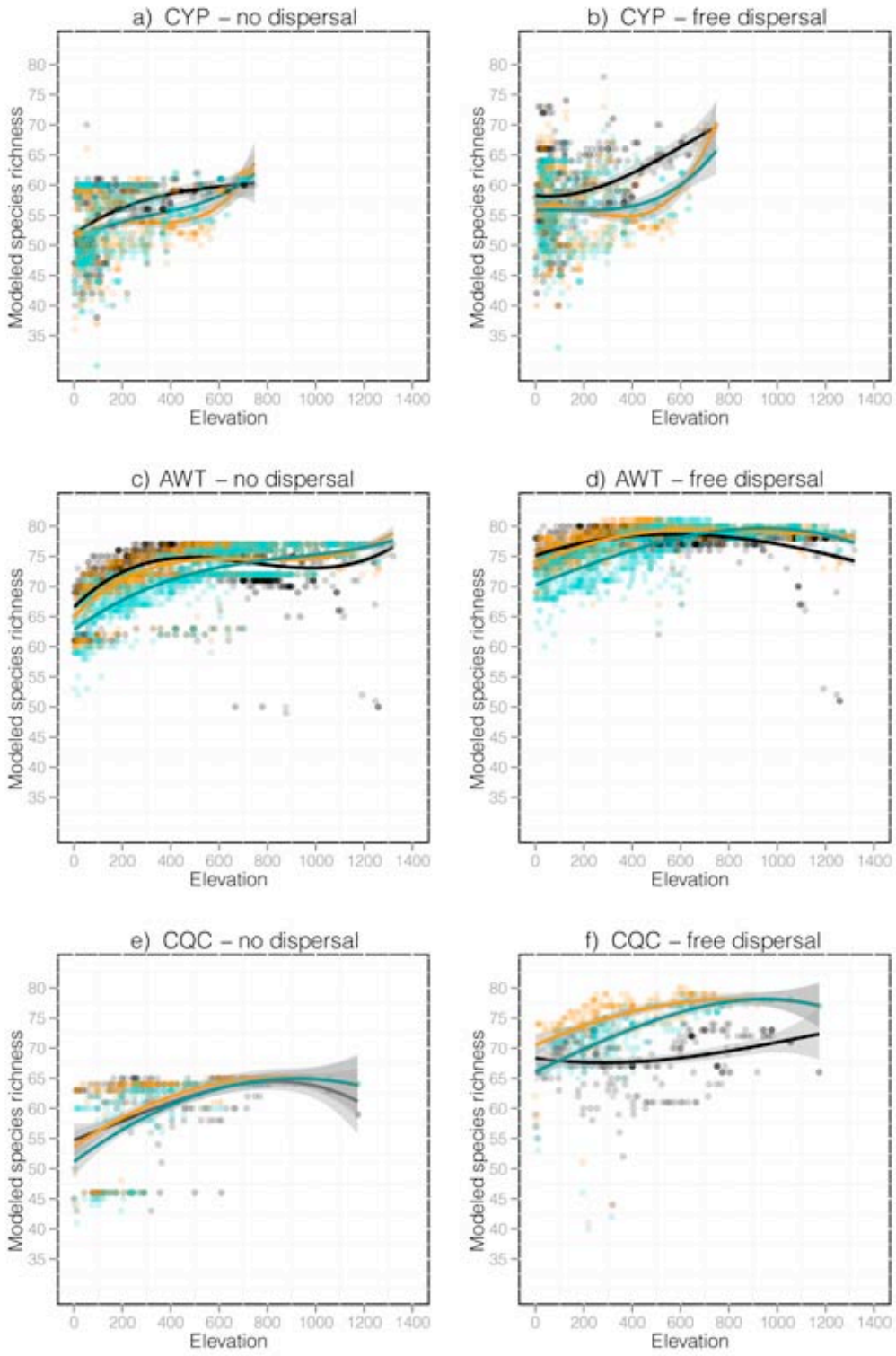
Species	Endemicity	Subregional endemicity	Current area (km^2)	2040 area (km^2)	2080 area (km^2)	Proportional 2040 area	Proportional 2080 area
Australian King Parrot *(Alisterus scapularis)*	Australian endemic	Australian endemic	29348	30154	28492	1.03	0.97
Bassian Thrush *(Zoothera lunulata)*	Australian endemic	Australian endemic	8831	8626	5344	0.98	0.61
Brown Gerygone *(Gerygone mouki)*	Australian endemic	Australian endemic	35041	34772	32743	0.99	0.93
Crimson Rosella *(Platycercus elegans)*	Australian endemic	Australian endemic	25699	26168	19531	1.02	0.76
Eastern Spinebill *(Acanthorhynchus tenuirostris)*	Australian endemic	Australian endemic	27265	21905	12323	0.80	0.45
Eastern Whipbird *(Psophodes olivaceus)*	Australian endemic	Australian endemic	25941	21745	11728	0.84	0.45
Eastern Yellow Robin *(Eopsaltria australis)*	Australian endemic	Australian endemic	45257	38556	31388	0.85	0.69
Lewin's Honeyeater *(Meliphaga lewinii)*	Australian endemic	Australian endemic	62196	49040	32724	0.79	0.53
Pale-yellow Robin *(Tregellasia capito)*	Australian endemic	Australian endemic	18051	17332	15564	0.96	0.86
Pied Currawong *(Strepera graculina)*	Australian endemic	Australian endemic	269937	172742	89518	0.64	0.33
Red-browed Finch *(Neochmia temporalis)*	Australian endemic	Australian endemic	119317	159169	147527	1.33	1.24
Regent Bowerbird *(Sericulus chrysocephalus)*	Australian endemic	Australian endemic	2637	1024	287	0.39	0.11
Satin Bowerbird *(Ptilonorhynchus violaceus)*	Australian endemic	Australian endemic	9170	9567	6438	1.04	0.70
Scaly-breasted Lorikeet *(Trichoglossus chlorolepidotus)*	Australian endemic	Australian endemic	112347	103800	98699	0.92	0.88
Tawny Frogmouth *(Podargus strigoides)*	Australian endemic	Australian endemic	8810	7648	5326	0.87	0.60
Topknot Pigeon *(Lopholaimus antarcticus)*	Australian endemic	Australian endemic	31984	41664	45338	1.30	1.42
White-browed Robin *(Poecilodryas superciliosa)*	Australian endemic	Australian endemic	56025	68662	75315	1.23	1.34
White-browed Scrubwren *(Sericornis frontalis)*	Australian endemic	Australian endemic	53263	40075	28667	0.75	0.54
White-headed Pigeon *(Columba leucomela)*	Australian endemic	Australian endemic	20661	24784	17775	1.20	0.86
White-throated Treecreeper *(Cormobates leucophaea)*	Australian endemic	Australian endemic	16966	12333	7301	0.73	0.43
Yellow-throated Scrubwren *(Sericornis citreogularis)*	Australian endemic	Australian endemic	10804	8927	6072	0.83	0.56
Atherton Scrubwren *(Sericornis keri)*	Northeast QLD endemic	AWT endemic	7674	4041	1777	0.53	0.23
Bowers Shrike-Thrush *(Colluricincla boweri)*	Northeast QLD endemic	AWT endemic	13105	10836	7333	0.83	0.56

Species	Endemicity	Subregional endemicity	Current area (km^2)	2040 area (km^2)	2080 area (km^2)	Proportional 2040 area	Proportional 2080 area
Bridled Honeyeater *(Lichenostomus frenatus)*	Northeast QLD endemic	AWT endemic	19660	17196	12863	0.87	0.65
Chowchilla *(Orthonyx spaldingii)*	Northeast QLD endemic	AWT endemic	14319	11505	7925	0.80	0.55
Fernwren *(Oreoscopus gutturalis)*	Northeast QLD endemic	AWT endemic	11314	8902	6079	0.79	0.54
Golden Bowerbird *(Amblyornis newtonianus)*	Northeast QLD endemic	AWT endemic	5835	5061	3123	0.87	0.54
Grey-headed Robin *(Heteromyias cinereifrons)*	Northeast QLD endemic	AWT endemic	18025	17028	13261	0.94	0.74
Macleay's Honeyeater *(Xanthotis macleayanus)*	Northeast QLD endemic	AWT endemic	22820	18904	17813	0.83	0.78
Mountain Thornbill *(Acanthiza katherina)*	Northeast QLD endemic	AWT endemic	7089	6176	4386	0.87	0.62
Pied Monarch *(Arses kaupi)*	Northeast QLD endemic	AWT endemic	17465	17498	17297	1.00	0.99
Tooth-billed Bowerbird *(Scenopoeetes dentirostris)*	Northeast QLD endemic	AWT endemic	407111	339977	265919	0.84	0.65
Victoria's Riflebird *(Ptiloris victoriae)*	Northeast QLD endemic	AWT endemic	16926	16558	14672	0.98	0.87
Eungella Honeyeater *(Lichenostomus hindwoodi)*	Northeast QLD endemic	CQC endemic	7013	4969	2995	0.71	0.43
Lovely Fairy-wren *(Malurus amabilis)*	Northeast QLD endemic	CYP and Northeast QLD endemic	86829	115427	115581	1.33	1.33
Yellow-spotted Honeyeater *(Meliphaga notata)*	Northeast QLD endemic	CYP and Northeast QLD endemic	80095	75120	35936	0.94	0.45
Tropical Scrubwren *(Sericornis beccarii)*	PNG and Northeast QLD	PNG and CYP only	31550	54615	56832	1.73	1.80
Eclectus Parrot *(Eclectus roratus)*	PNG and Northeast QLD	PNG and CYP only	8469	10353	10181	1.22	1.20
Green-backed Honeyeater *(Glycichaera fallax)*	PNG and Northeast QLD	PNG and CYP only	4150	7440	10048	1.79	2.42
Magnificent Riflebird *(Ptiloris magnificus)*	PNG and Northeast QLD	PNG and CYP only	32020	33838	34465	1.06	1.08
Northern Scrub Robin *(Drymodes superciliaris)*	PNG and Northeast QLD	PNG and CYP only	4473	15982	18817	3.57	4.21
Palm Cockatoo *(Probosciger aterrimus)*	PNG and Northeast QLD	PNG and CYP only	51613	72659	72689	1.41	1.41
Red-bellied Pitta *(Pitta erythrogaster)*	PNG and Northeast QLD	PNG and CYP only	8830	17327	18881	1.96	2.14
Red-cheeked Parrot *(Geoffroyus geoffroyi)*	PNG and Northeast QLD	PNG and CYP only	3863	16892	19088	4.37	4.94
Tawny-breasted Honeyeater *(Xanthotis flaviventer)*	PNG and Northeast QLD	PNG and CYP only	38269	71626	73293	1.87	1.92
Trumpet manucode *(Phonygammus keraudrenii)*	PNG and Northeast QLD	PNG and CYP only	26316	49792	54306	1.89	2.06
White-faced Robin *(Tregellasia leucops)*	PNG and Northeast QLD	PNG and CYP only	17341	25925	23146	1.50	1.33
Yellow-billed Kingfisher *(Syma torotoro)*	PNG and Northeast QLD	PNG and CYP only	28336	38461	39398	1.36	1.39
Yellow-legged Flycatcher *(Microeca griseoceps)*	PNG and Northeast QLD	PNG and CYP only	8766	10051	12420	1.15	1.42
Black-faced Monarch *(Monarcha melanopsis)*	PNG and Northeast QLD	PNG and Northeast QLD	46188	49411	50408	1.07	1.09

Species	Endemicity	Subregional endemicity	Current area (km^2)	2040 area (km^2)	2080 area (km^2)	Proportional 2040 area	Proportional 2080 area
Buff-breasted Paradise-Kingfisher *(Tanysiptera sylvia)*	PNG and Northeast QLD	PNG and Northeast QLD	30181	32026	30024	1.06	0.99
Chestnut-breasted Cuckoo *(Cacomantis castaneiventris)*	PNG and Northeast QLD	PNG and Northeast QLD	41816	43252	39063	1.03	0.93
Graceful Honeyeater *(Meliphaga gracilis)*	PNG and Northeast QLD	PNG and Northeast QLD	76616	100063	80649	1.31	1.05
Grey Whistler *(Pachycephala simplex)*	PNG and Northeast QLD	PNG and Northeast QLD	73472	99374	100220	1.35	1.36
Little Kingfisher *(Ceyx pusilla)*	PNG and Northeast QLD	PNG and Northeast QLD	92867	120490	126684	1.30	1.36
Metallic Starling *(Aplornis metallica)*	PNG and Northeast QLD	PNG and Northeast QLD	38923	44702	48439	1.15	1.24
Southern Cassowary *(Casuarius casuarius)*	PNG and Northeast QLD	PNG and Northeast QLD	18568	18907	18842	1.02	1.01
Frilled Monarch *(Arses lorealis)*	Wide-spread (PNG and Aust.)	CYP endemic	9724	6632	6270	0.68	0.64
Australian Brush Turkey *(Alectura lathami)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	160700	181506	167576	1.13	1.04
Azure Kingfisher *(Ceyx azureus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	142624	143672	122000	1.01	0.86
Barred Cuckoo-Shrike *(Coracina lineata)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	49557	47819	46139	0.96	0.93
Black Butcherbird *(Cracticus quoyi)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	105847	118401	108792	1.12	1.03
Black-winged Monarch *(Monarcha frater)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	25029	23924	23731	0.96	0.95
Blue-faced Parrot-Finch *(Erythrura trichroa)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	7642	7645	7407	1.00	0.97
Brown Cuckoo-Dove *(Macropygia amboinensis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	48330	53945	54907	1.12	1.14
Brush Cuckoo *(Cacomantis variolosus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	205643	231949	149596	1.13	0.73
Channel-billed Cuckoo *(Scythrops novaehollandiae)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	356736	251642	179764	0.71	0.50
Cicadabird *(Coracina tenuirostris)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	206510	205703	121836	1.00	0.59
Common Koel *(Eudynamys orientalis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	244528	222958	218211	0.91	0.89
Double-eyed Fig-Parrot *(Cyclopsitta diophthalma)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	24627	23732	24314	0.96	0.99
Dusky Honeyeater *(Myzomela obscura)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	140847	142544	98964	1.01	0.70
Emerald Dove *(Chalcophaps indica)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	46483	52907	56260	1.14	1.21
Fairy Gerygone *(Gerygone palpebrosa)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	174375	172195	119783	0.99	0.69
Fan-tailed Cuckoo *(Cacomantis flabelliformis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	120549	137682	124448	1.14	1.03
Figbird *(Sphecotheres vieilloti)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	188107	219901	169515	1.17	0.90
Golden Whistler *(Pachycephala pectoralis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	36004	34239	31676	0.95	0.88
Gould's Bronze-Cuckoo *(Chalcites minutillus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	78963	119851	126605	1.52	1.60
Grey Fantail *(Rhipidura albiscapa)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	352157	426476	325640	1.21	0.92

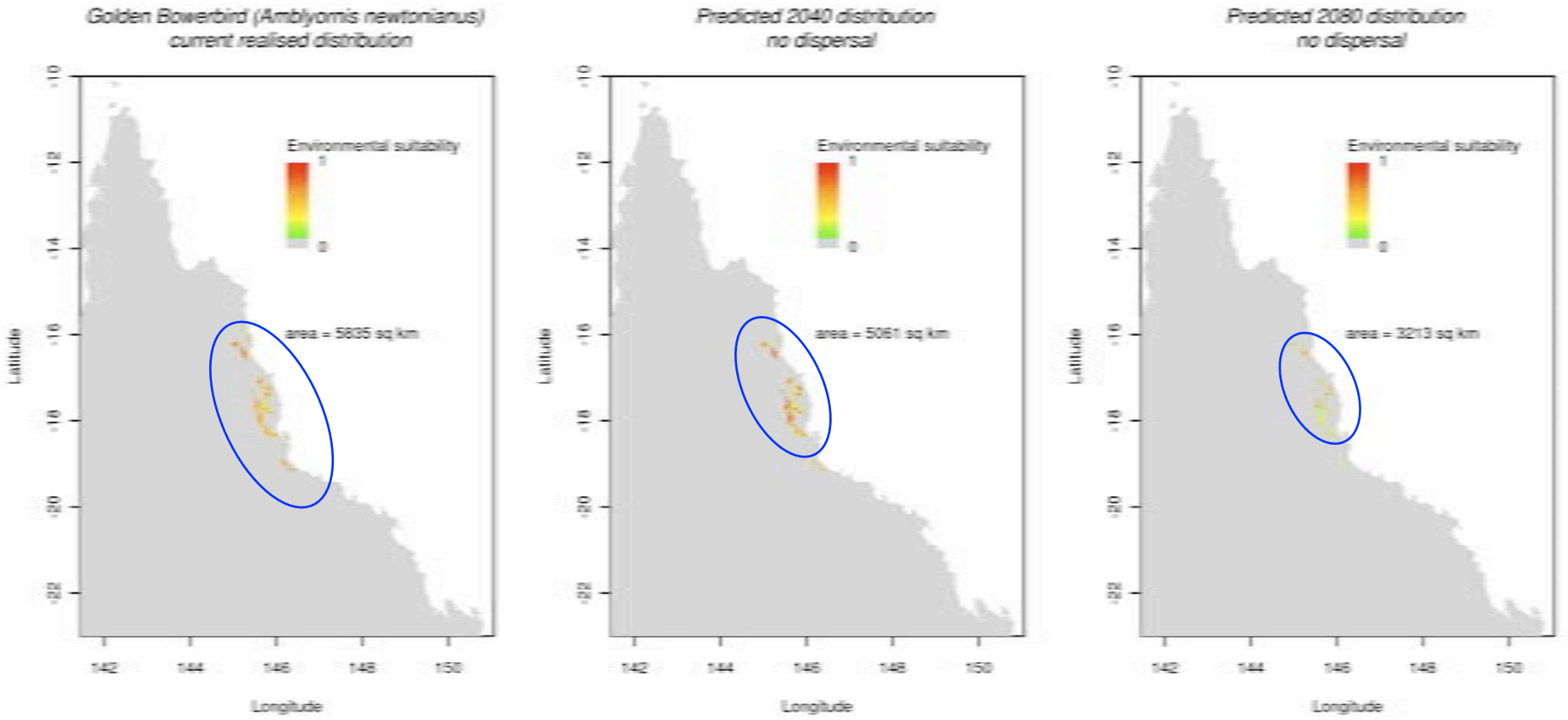
Species	Endemicity	Subregional endemicity	Current area (km^2)	2040 area (km^2)	2080 area (km^2)	Proportional 2040 area	Proportional 2080 area
Grey Goshawk *(Accipiter novaehollandiae)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	52797	43904	46936	0.83	0.89
Helmeted Friarbird *(Philemon buceroides)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	129242	118058	99873	0.91	0.77
Large-billed Gerygone *(Gerygone magnirostris)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	131692	129347	112864	0.98	0.86
Large-billed Scrubwren *(Sericornis magnirostra)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	28112	26690	18633	0.95	0.66
Laughing Kookaburra *(Dacelo novaeguineae)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	322936	218639	184873	0.68	0.57
Little Bronze-Cuckoo *(Chalcites minutillus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	191226	247362	235108	1.29	1.23
Little Shrike-Thrush *(Colluricincla megarhyncha)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	128642	144354	121913	1.12	0.95
Marbled Frogmouth *(Podargus ocellatus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	62110	70452	70512	1.13	1.14
Mistletoebird *(Dicaeum hirundinaceum)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	484276	521620	523670	1.08	1.08
Noisy Pitta *(Pitta versicolor)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	46543	57414	59626	1.23	1.28
Olive-backed Oriole *(Oriolus sagittatus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	403392	417626	328682	1.04	0.81
Orange-footed Scrubfowl *(Megapodius reinwardt)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	64806	113099	115256	1.75	1.78
Oriental Cuckoo *(Cuculus optatus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	85062	98032	98076	1.15	1.15
Pacific Baza *(Aviceda subcristata)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	257765	231378	188774	0.90	0.73
Papuan Frogmouth *(Podargus papuensis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	94870	95782	93493	1.01	0.99
Pied Imperial Pigeon *(Ducula bicolor)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	104488	107505	65557	1.03	0.63
Rainbow Bee-eater *(Merops ornatus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	479870	542215	547650	1.13	1.14
Rainbow Lorikeet *(Trichoglossus haematodus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	402248	356287	270637	0.89	0.67
Red-necked Crake *(Rallina tricolor)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	15438	16023	16924	1.04	1.10
Rose-crowned Fruit-Dove *(Ptilinopus regina)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	61209	131218	125786	2.14	2.04
Rufous Fantail *(Rhipidura rufifrons)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	146938	127465	114706	0.87	0.78
Rufous Owl *(Ninox rufa)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	86853	89135	90270	1.03	1.04
Russet-tailed Thrush *(Zoothera heinei)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	13196	13107	10368	0.99	0.79
Scarlet Honeyeater *(Myzomela sanguinolenta)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	154284	121076	96342	0.78	0.62
Shining Bronze-Cuckoo *(Chalcites lucidus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	128503	143772	118700	1.12	0.92
Silvereye *(Zosterops lateralis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	99565	1305657	130187	13.11	1.31
Sooty Owl *(Tyto tenebricosa)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	11911	12674	10659	1.06	0.89
Southern Boobook *(Ninox novaeseelandiae)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	423556	30557	238856	0.07	0.56

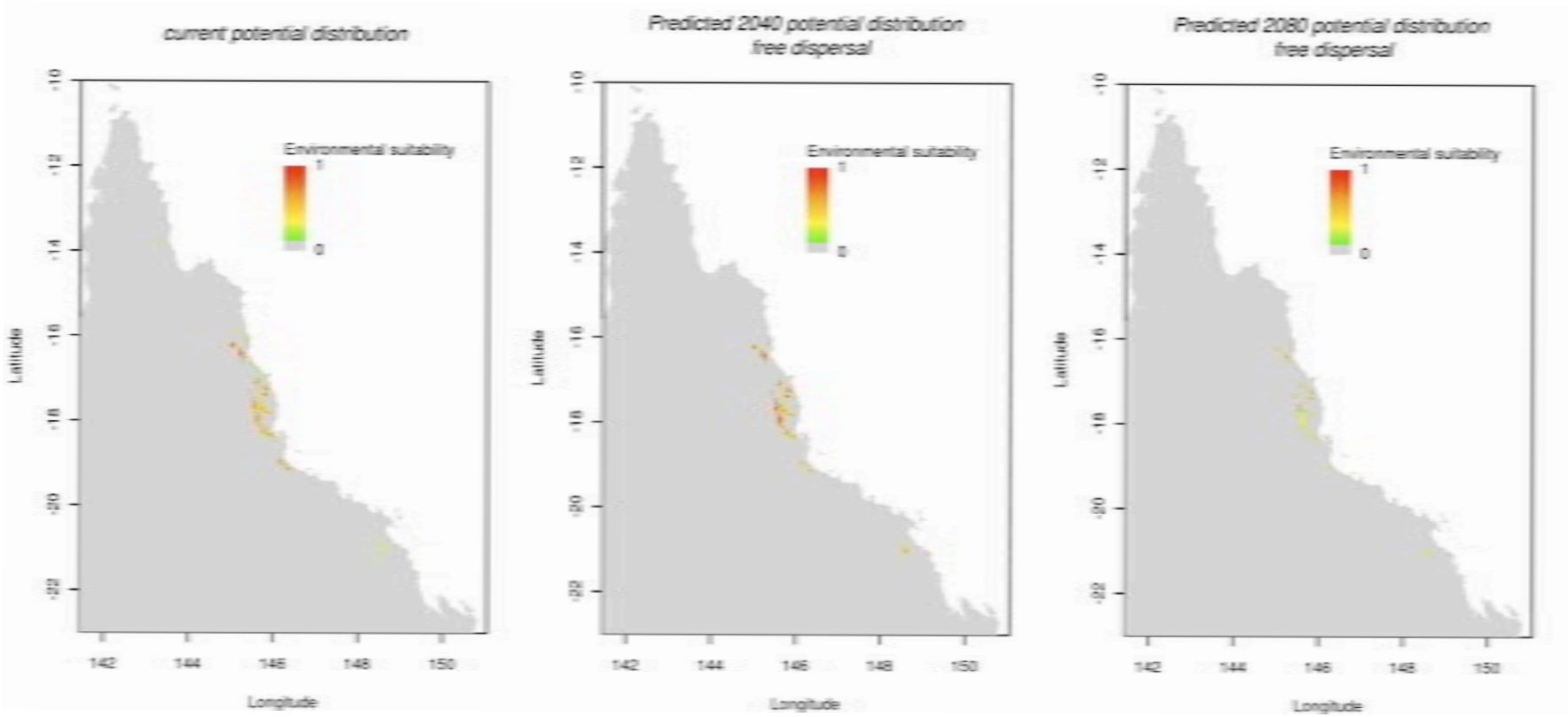
Species	Endemicity	Subregional endemicity	Current area (km^2)	2040 area (km^2)	2080 area (km^2)	Proportional 2040 area	Proportional 2080 area
Spangled Drongo *(Dicrurus bracteatus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	217245	300509	269339	1.38	1.24
Spectacled Monarch *(Symposiarchus trivirgatus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	65820	80141	80698	1.22	1.23
Spotted Catbird *(Ailuroedus melanotis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	25649	24977	23783	0.97	0.93
Sulphur-crested Cockatoo *(Cacatua galerita)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	416899	352537	256087	0.85	0.61
Superb Fruit-Dove *(Ptilinopus superbus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	45631	47220	43955	1.03	0.96
Varied Triller *(Lalage leucomela)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	147348	174834	136222	1.19	0.92
White-breasted Woodswallow *(Artamus leucorynchus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	254677	450226	470941	1.77	1.85
White-eared Monarch *(Carternornis leucotis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	30177	30719	30288	1.02	1.00
White-rumped Swiftlet *(Aerodramus terraereginae)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	36526	41543	38696	1.14	1.06
White-throated Needletail *(Hirundapus caudacutus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	118161	125921	111212	1.07	0.94
Wompoo Fruit-Dove *(Ptilinopus magnificus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	56003	50727	50340	0.91	0.90
Yellow Oriole *(Oriolus flavocinctus)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	132497	154232	124520	1.16	0.94
Yellow-bellied Sunbird *(Nectarinia jugularis)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	114103	149737	144111	1.31	1.26
Yellow-breasted Boatbill *(Machaerirhynchus flaviventer)*	Wide-spread (PNG and Aust.)	Wide-spread (PNG and Aust.)	35448	35475	40274	1.00	1.14



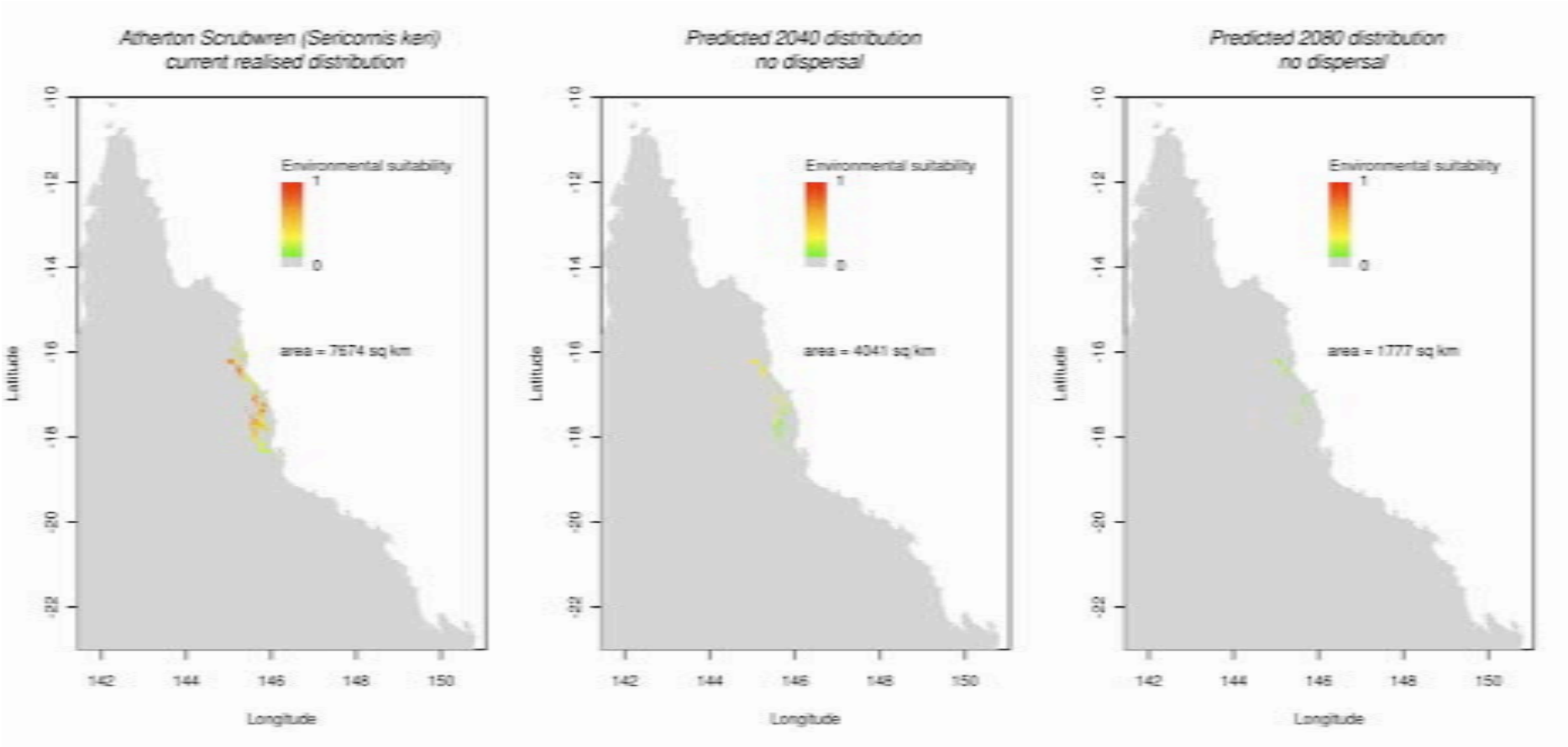
Appendix Figure 7.2. *Patterns of change in non-endemic species richness across elevation in CYP, AWT and CQC under climate change, showing the effect of unconstrained dispersal on predicted lowland biotic attrition in the AWT and CQC. Species richness layers were summed from binary species distribution models for all endemic species in each region, randomly sub-sampled from a regular grid of points in rainforest. Black points are estimated from current species distributions, orange points are estimated from 2040 predictions and blue points from 2080. The curves are 3rd order quadratic polynomials.*

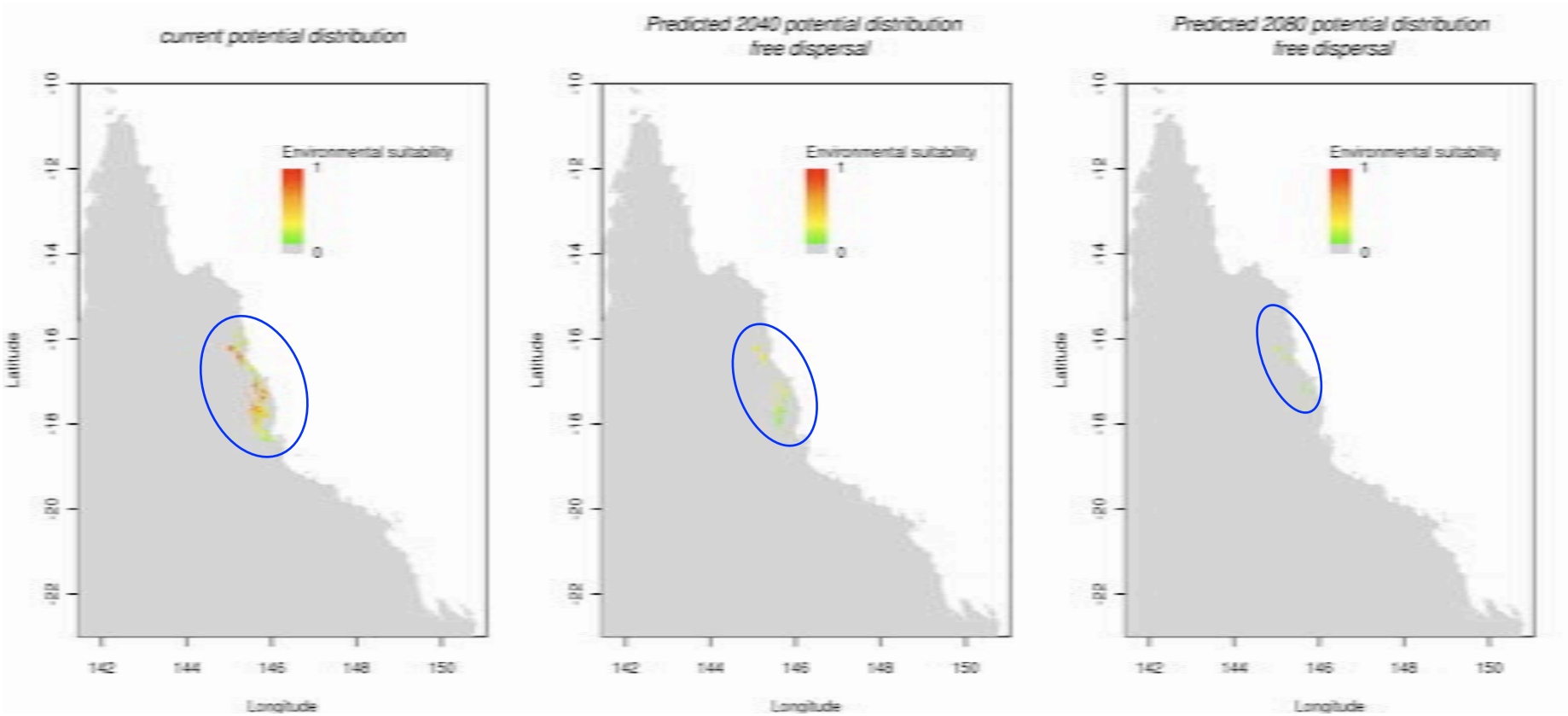
Figures 7.3 - 7.14. *Maps of the predicted distribution of suitable environmental area for selected species under under contrasting scenarios of no dispersal and free dispersal, showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Golden Bowerbird (Amblyornis newtonianus)
current realised distribution
Environmental suitability
1
0
area = 5835 sq km
Latitude
Longitude
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 5061 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 3213 sq km
Latitude
Longitude

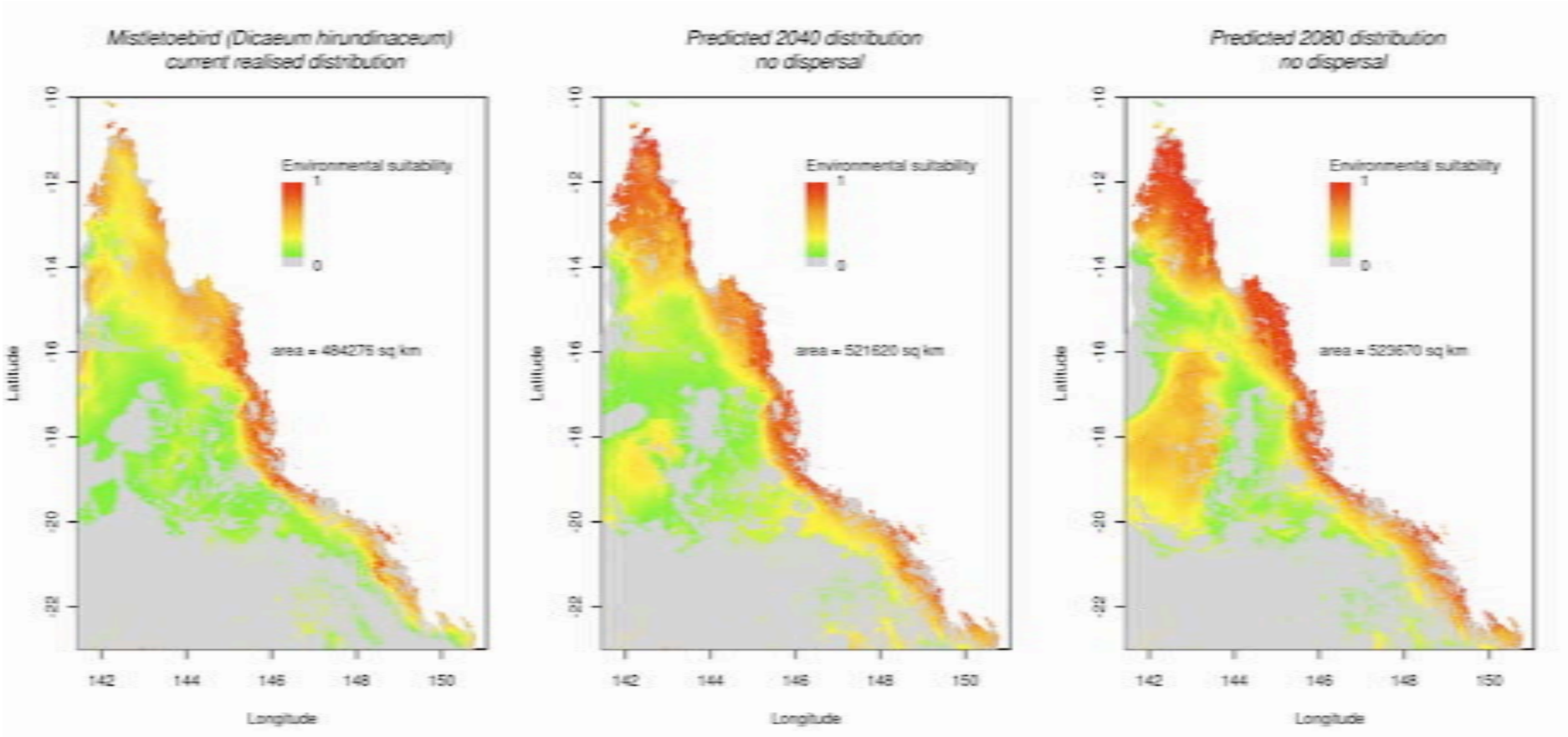


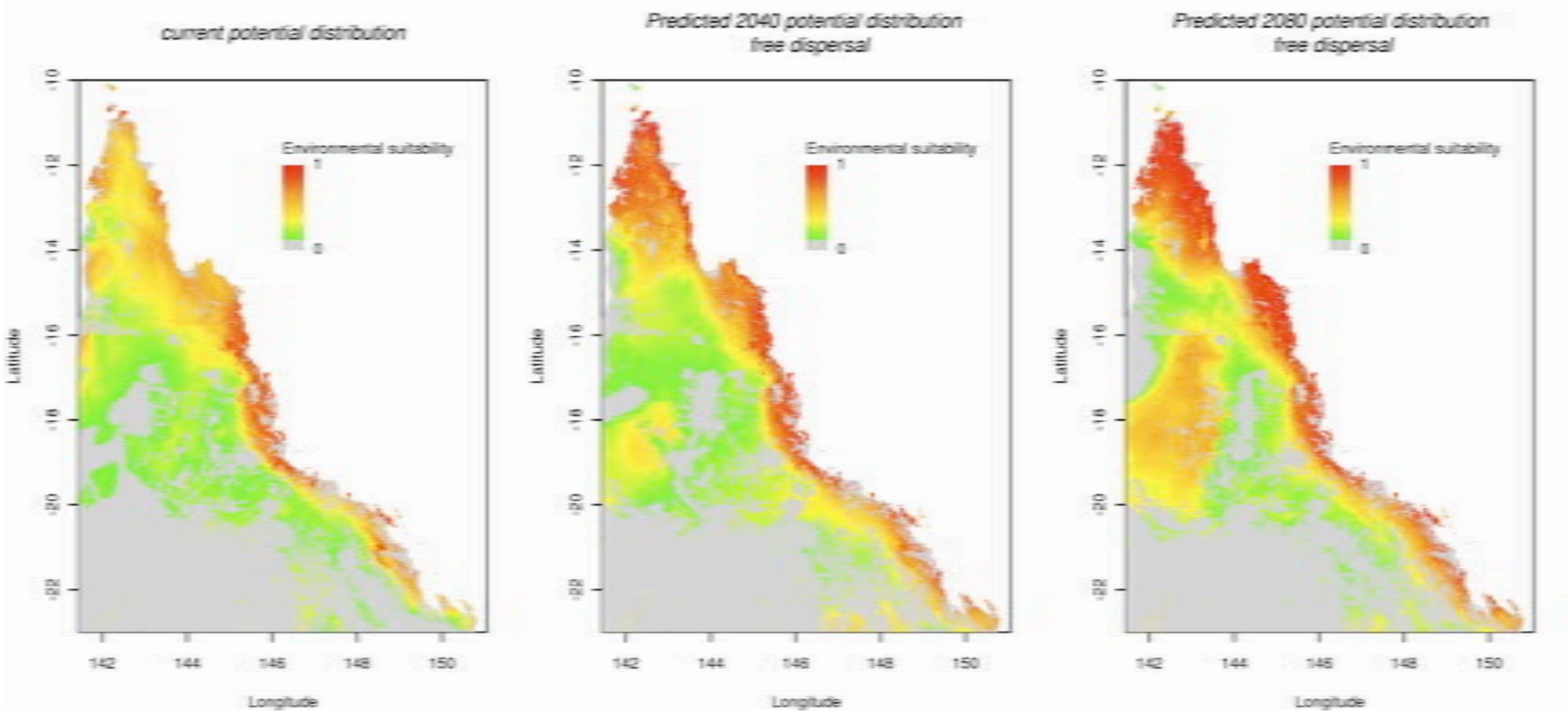
Appendix Figure 7.3. *Maps of the predicted distribution of suitable environmental area for Golden Bowerbird (*Amblyornis newtonianus*) under under contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Atherton Scrubwren (Sericornis keri)
current realised distribution
Environmental suitability
1
0
area = 7574 sq km
Latitude
Longitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 4041 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 1777 sq km
Latitude
Longitude

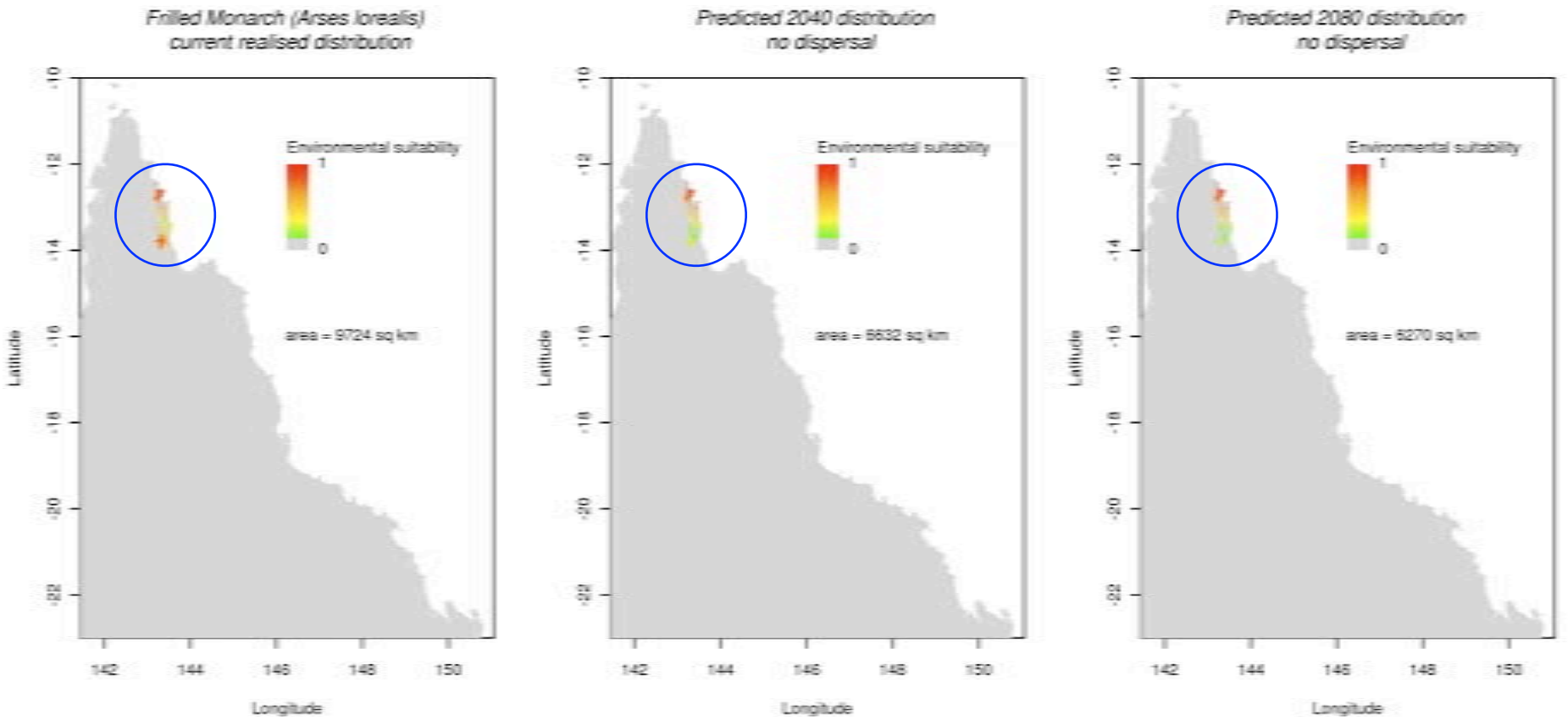


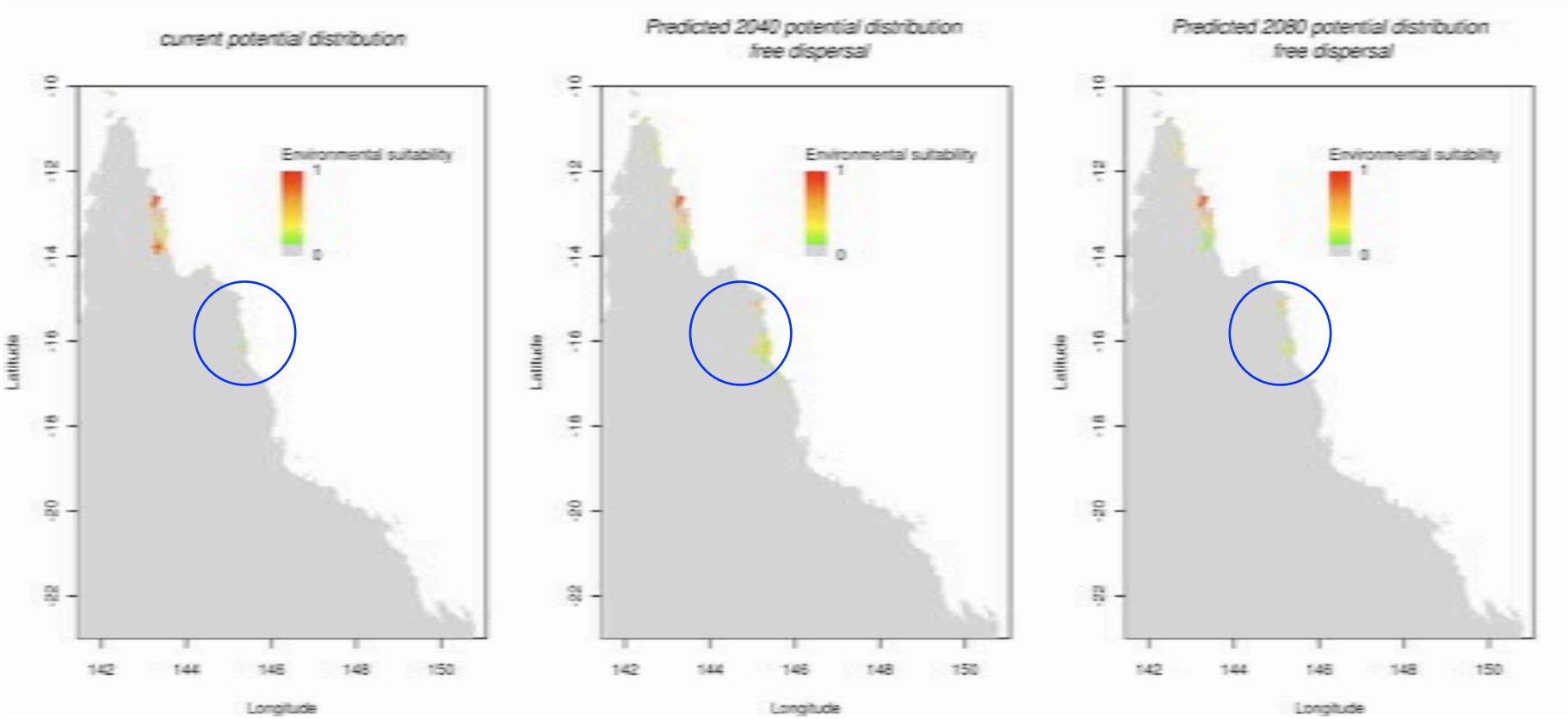
Appendix Figure 7.4. *Maps of the predicted distribution of suitable environmental area for Atherton Scrubwren (*Sericornis keri*) under under contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Mistletoebird (Dicaeum hirundinaceum)
current realised distribution
Environmental suitability
1
0
area = 484276 sq km
Latitude
Longitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 521820 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 523670 sq km
Latitude
Longitude

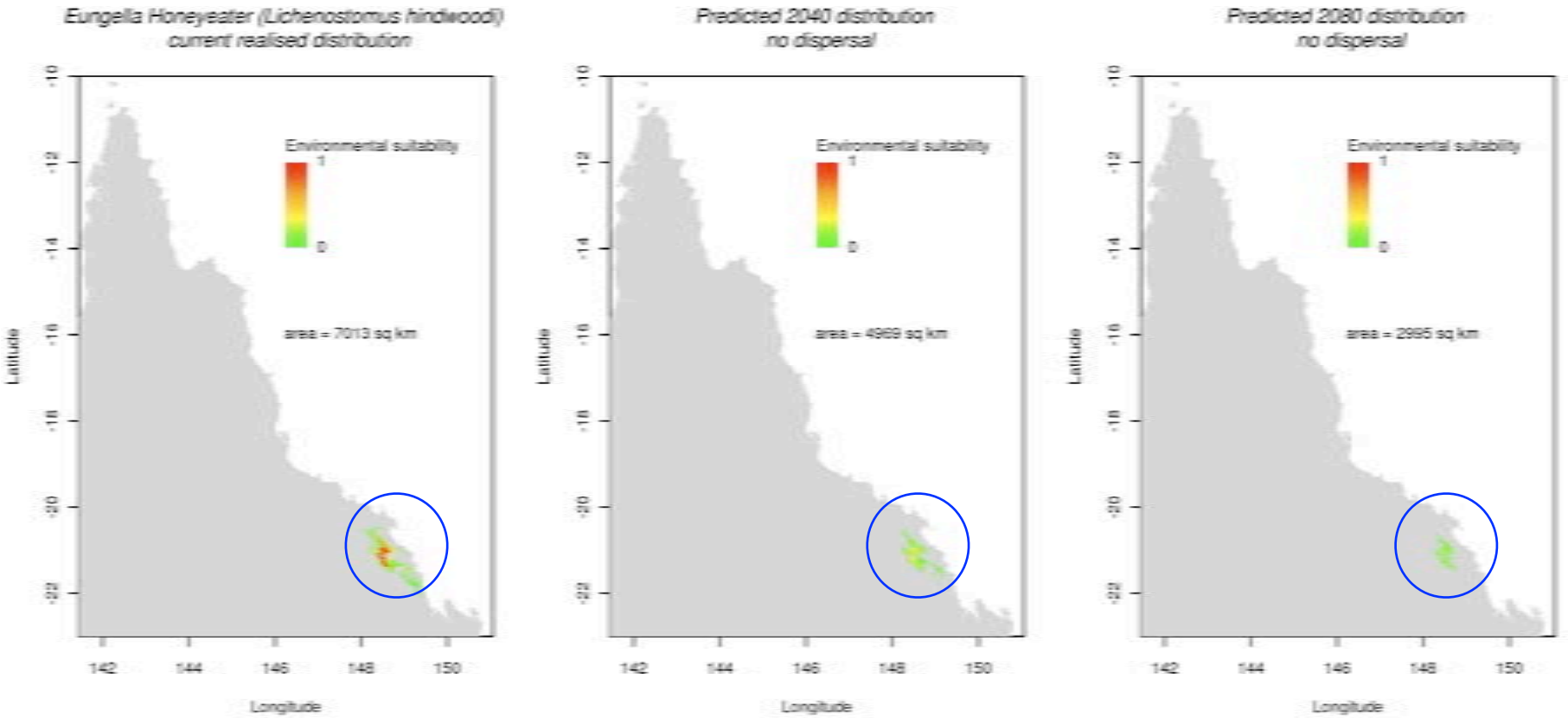


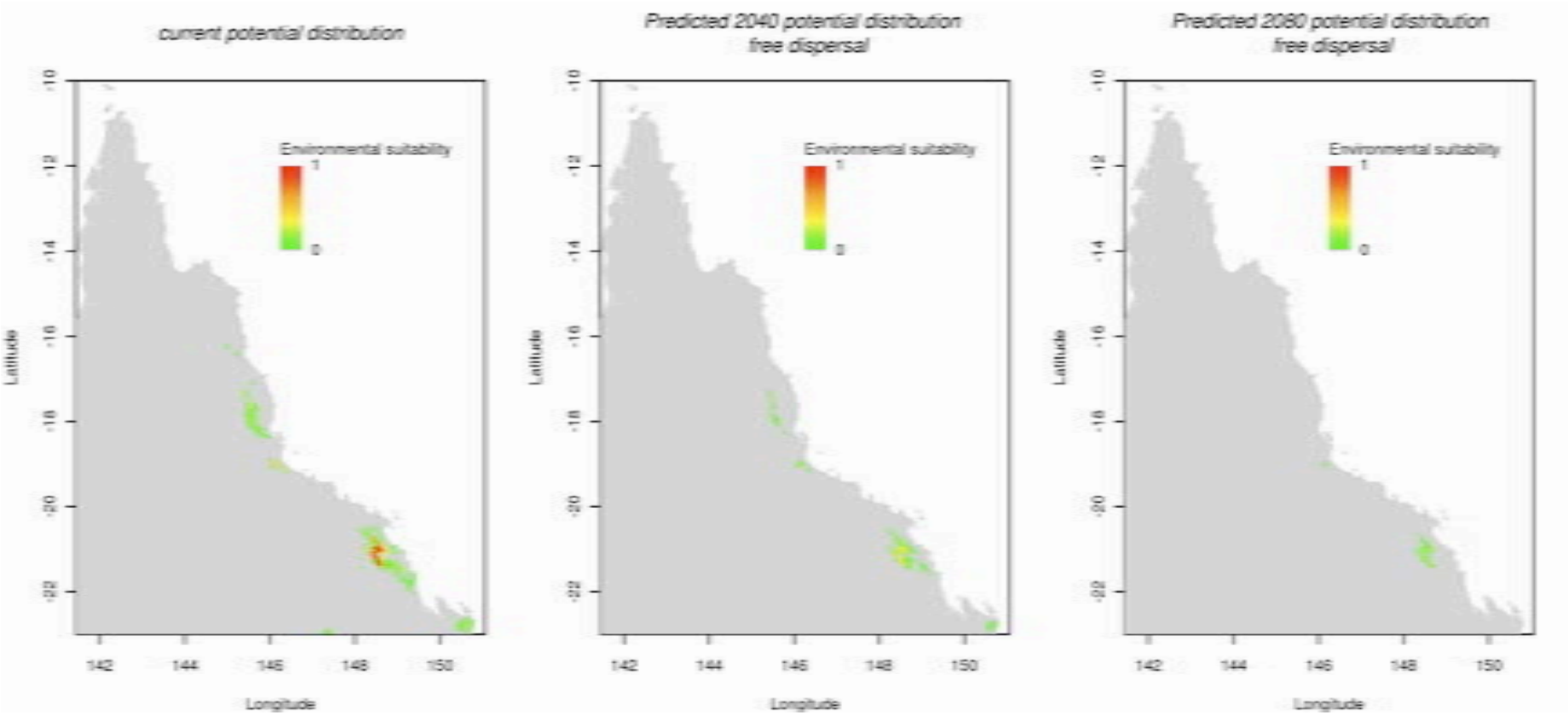
Appendix Figure 7.5. *Maps of the predicted distribution of suitable environmental area for Mistletoebird (*Dicaeum hirundinaceum)) under under *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Frilled Monarch (Arses lorealis)
current realised distribution
Environmental suitability
1
0
area = 9724 sq km
Latitude
Longitude
-10
-12
-14
-16
-20
-22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 6632 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 5270 sq km
Latitude
Longitude

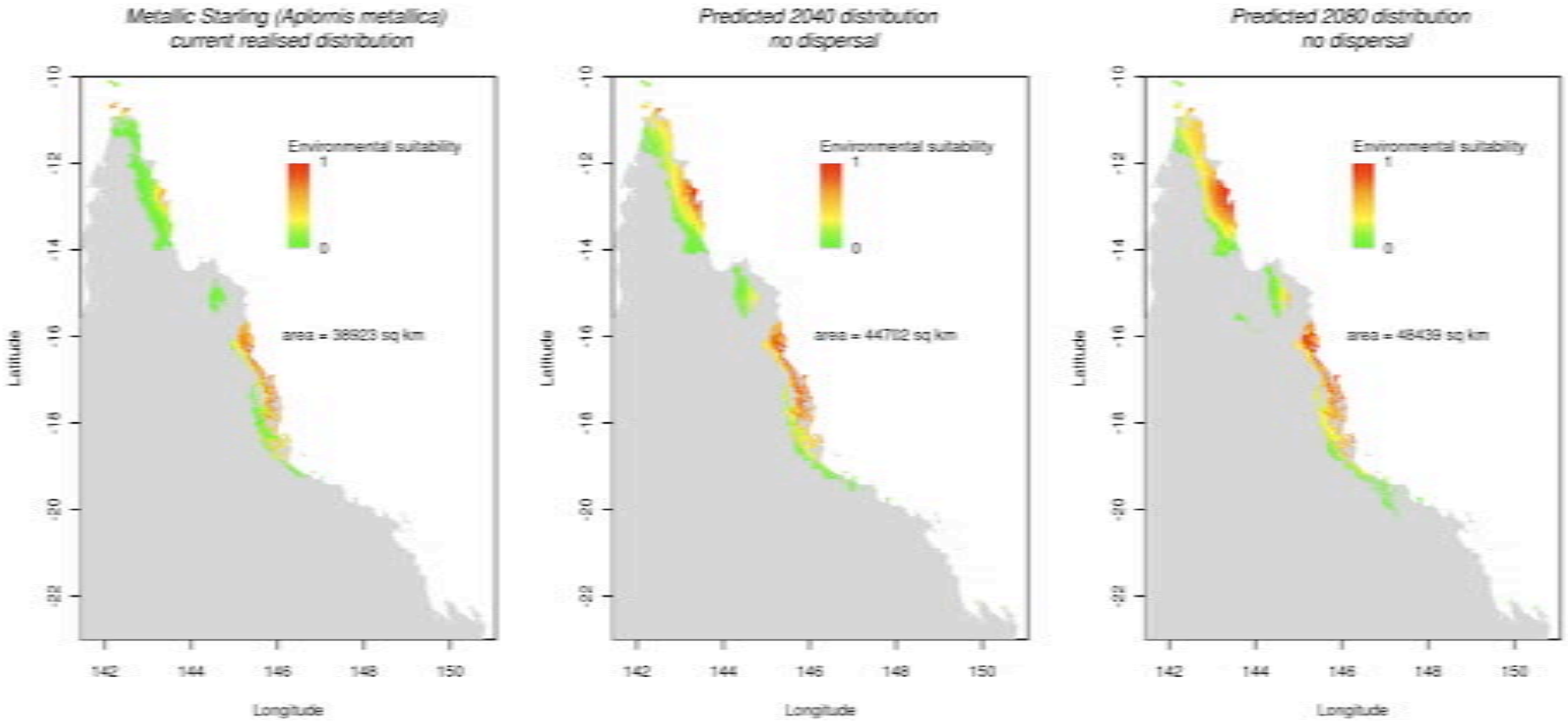


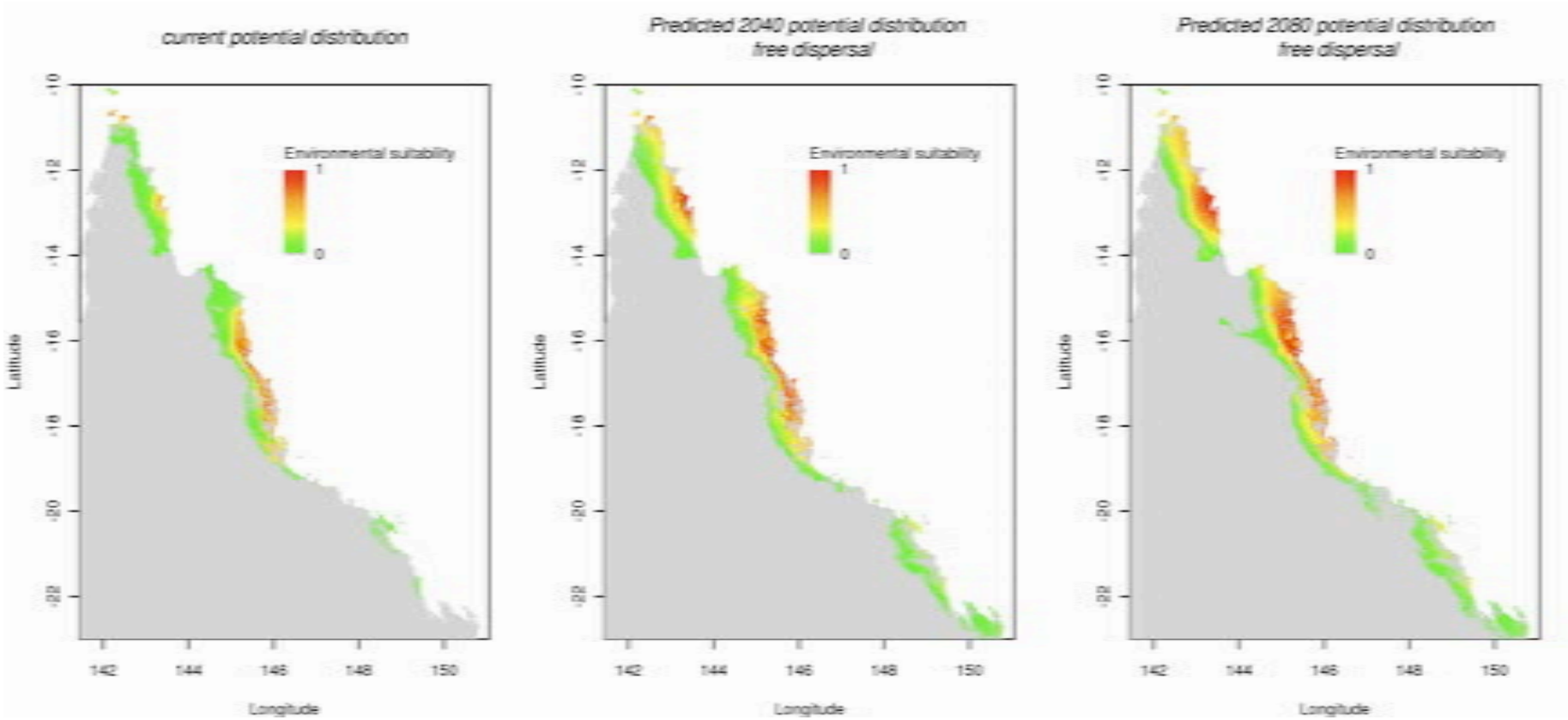
Appendix Figure 7.6. *Maps of the predicted distribution of suitable environmental area for Frilled Monarch (*Arses lorealis*) contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables. The area of change mentioned in the text is circled in blue.*


Eungella Honeyeater (Lichenostomus hindwoodi)
current realised distribution
Environmental suitability
1
0
area = 7013 sq km
Latitude
Longitude
10
12
14
16
18
20
22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 4969 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 2995 sq km
Latitude
Longitude

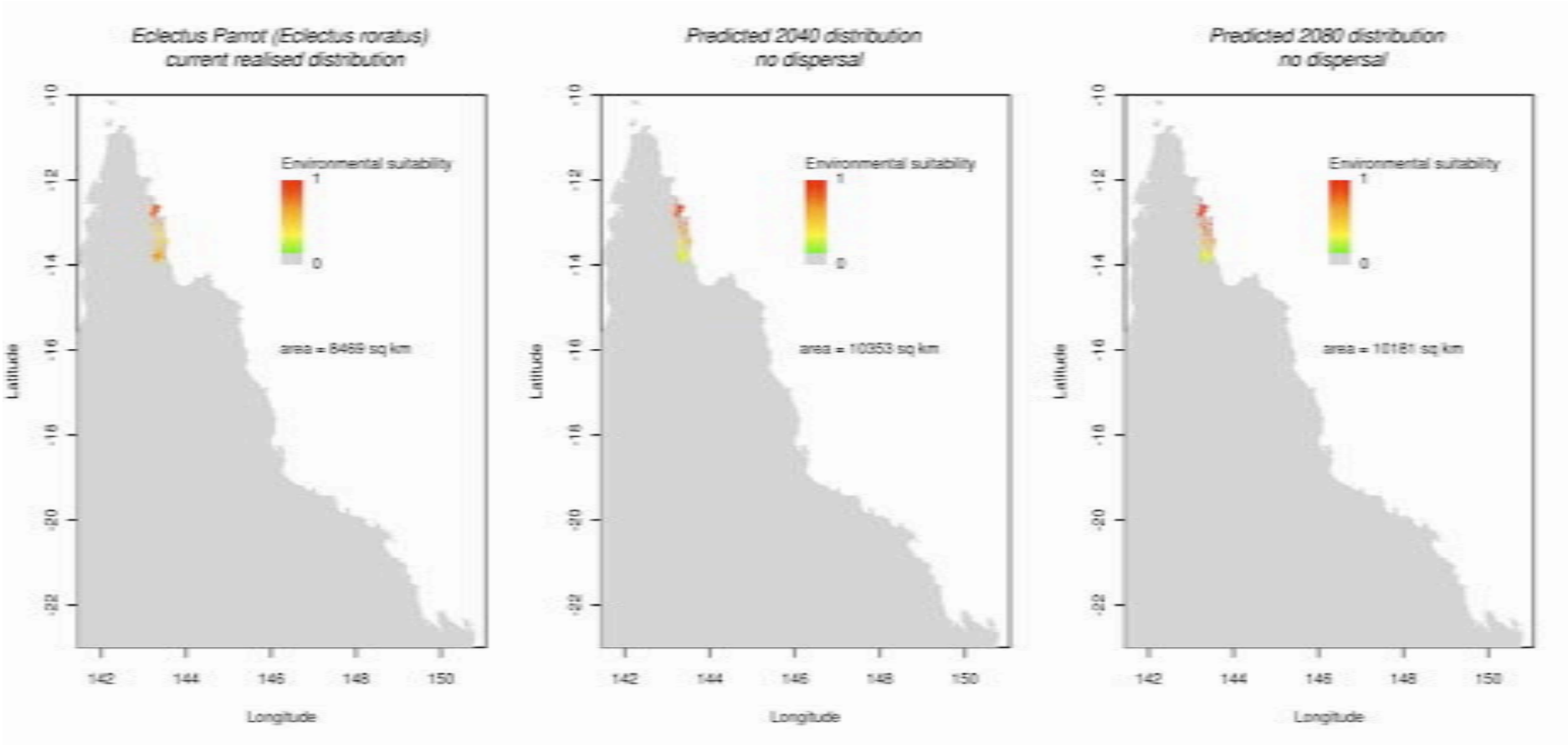


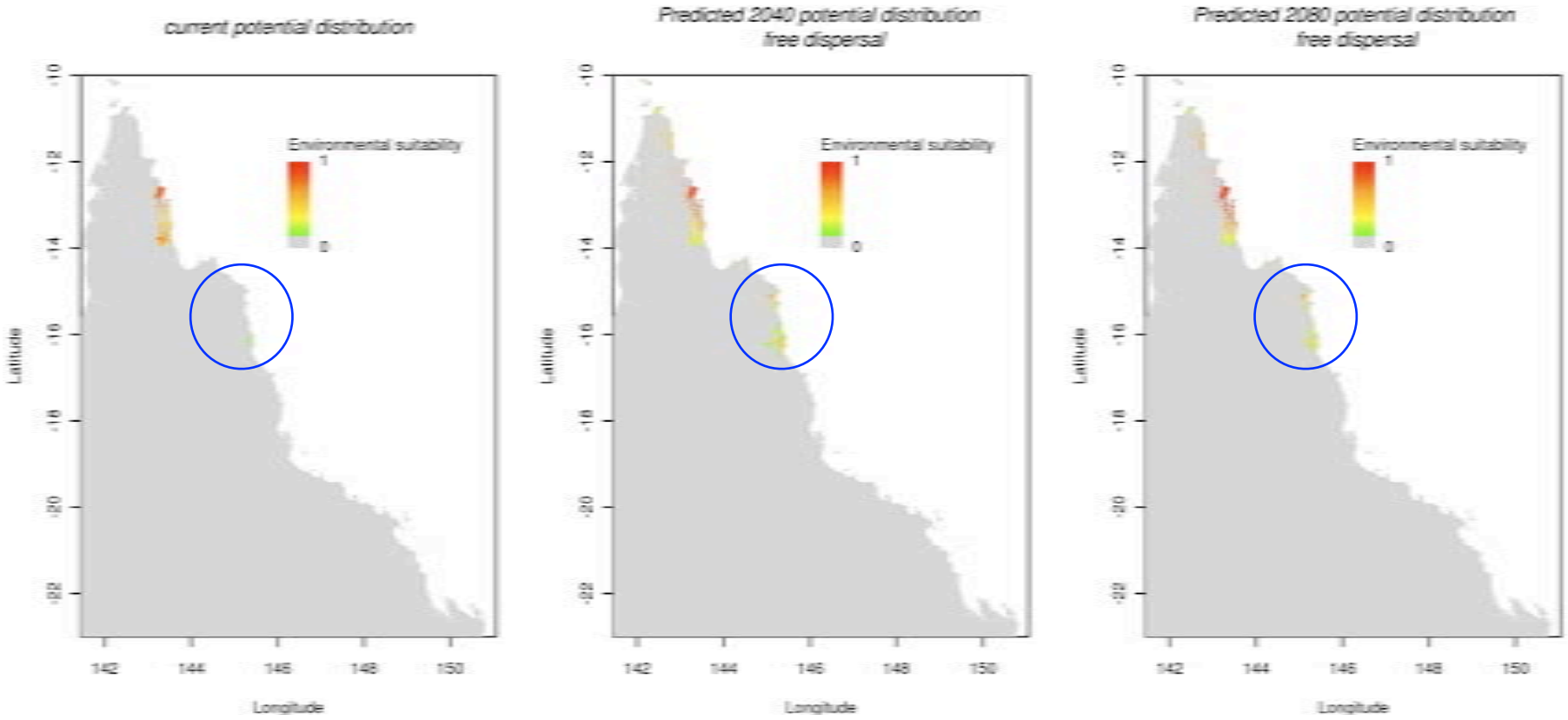
Appendix Figure 7.7. *Maps of the predicted distribution of suitable environmental area for Eungella Honeyeater* (Lichenostomus hindwoodi) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Metallic Starling (Aplomis metallica)
current realised distribution
Environmental suitability
1
0
area = 38823 sq km
Latitude
Longitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 44702 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 48439 sq km
Latitude
Longitude

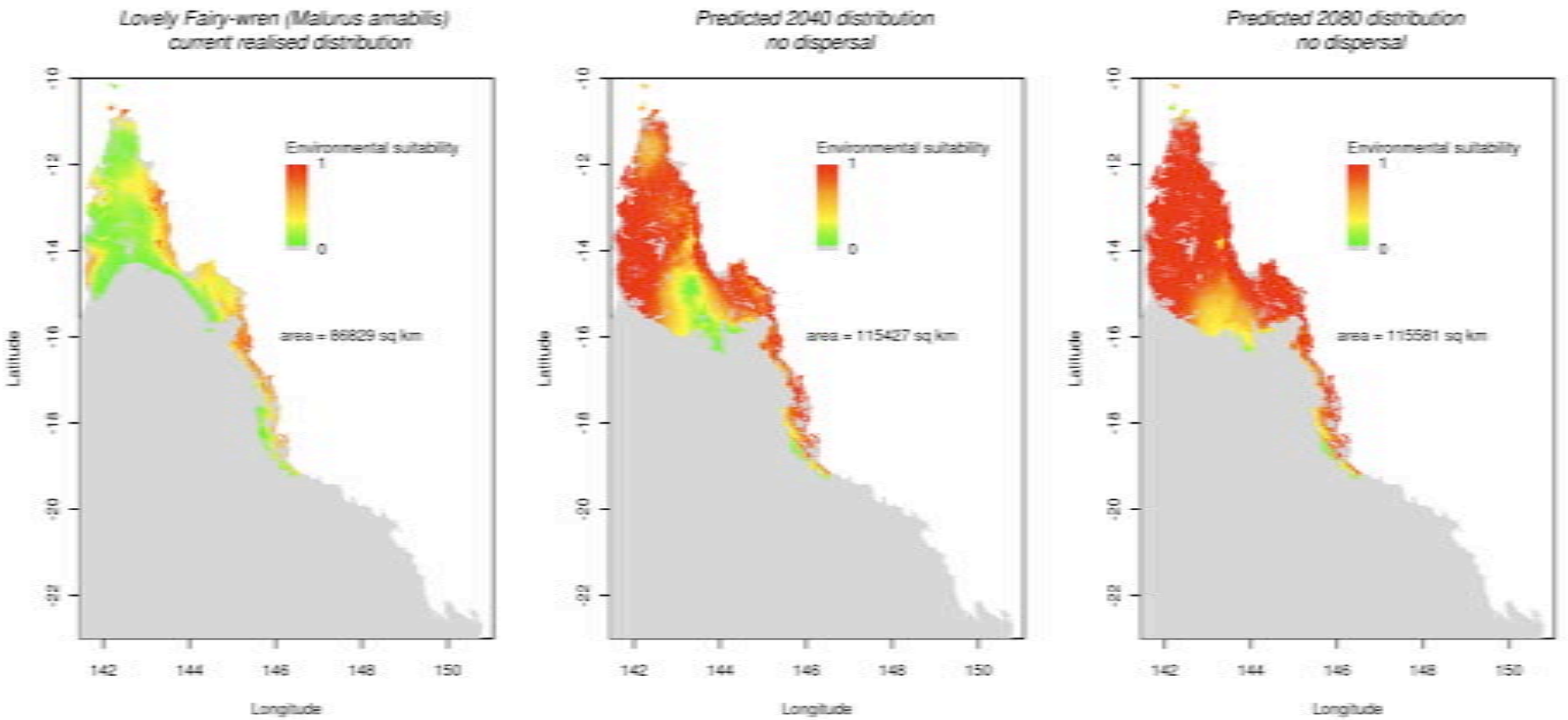


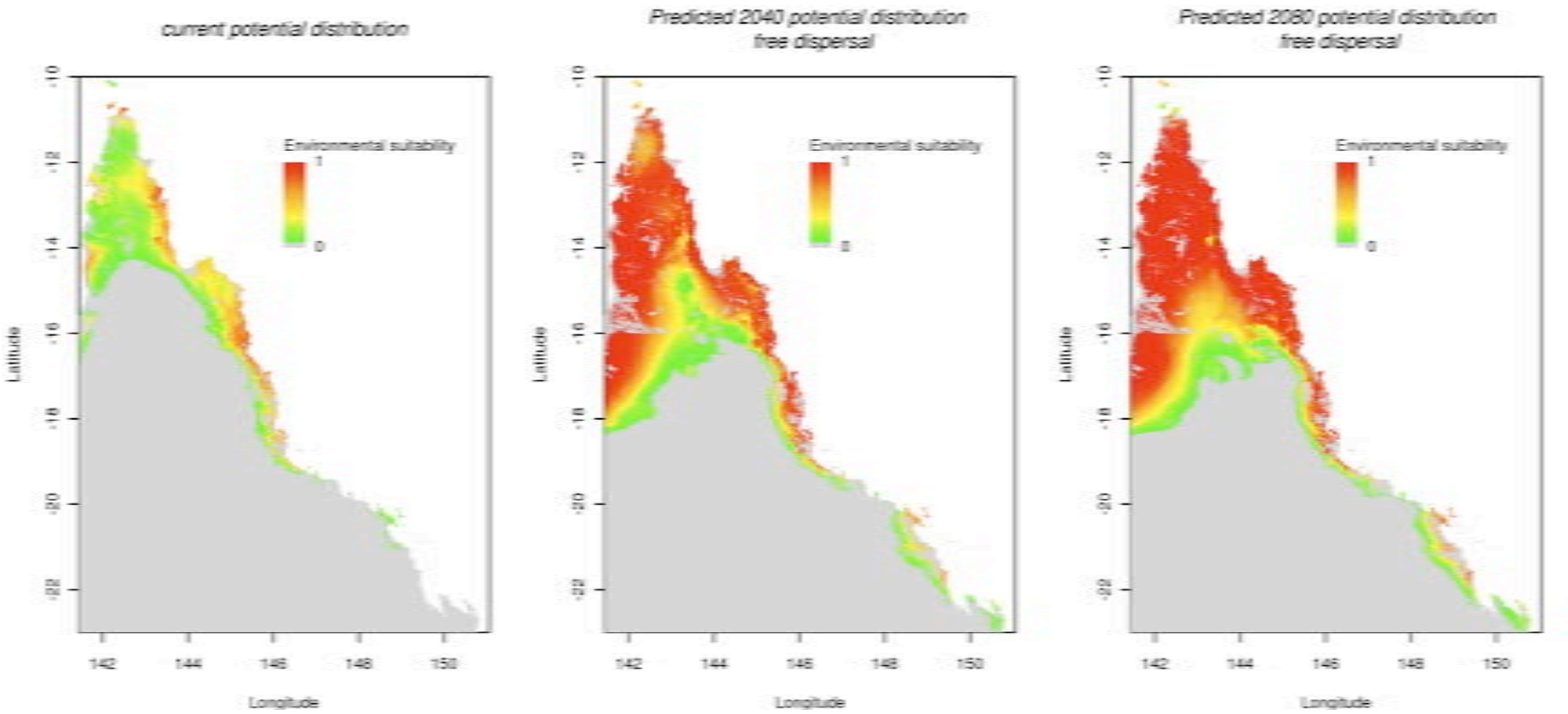
Appendix Figure 7.8. *Maps of the predicted distribution of suitable environmental area for Metallic Starling* (Aplornis metallica) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Eclectus Parrot (Eclectus roratus)
current realised distribution
Environmental suitability
1
0
area = 8469 sq km
Latitude
Longitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 10353 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 10181 sq km
Latitude
Longitude

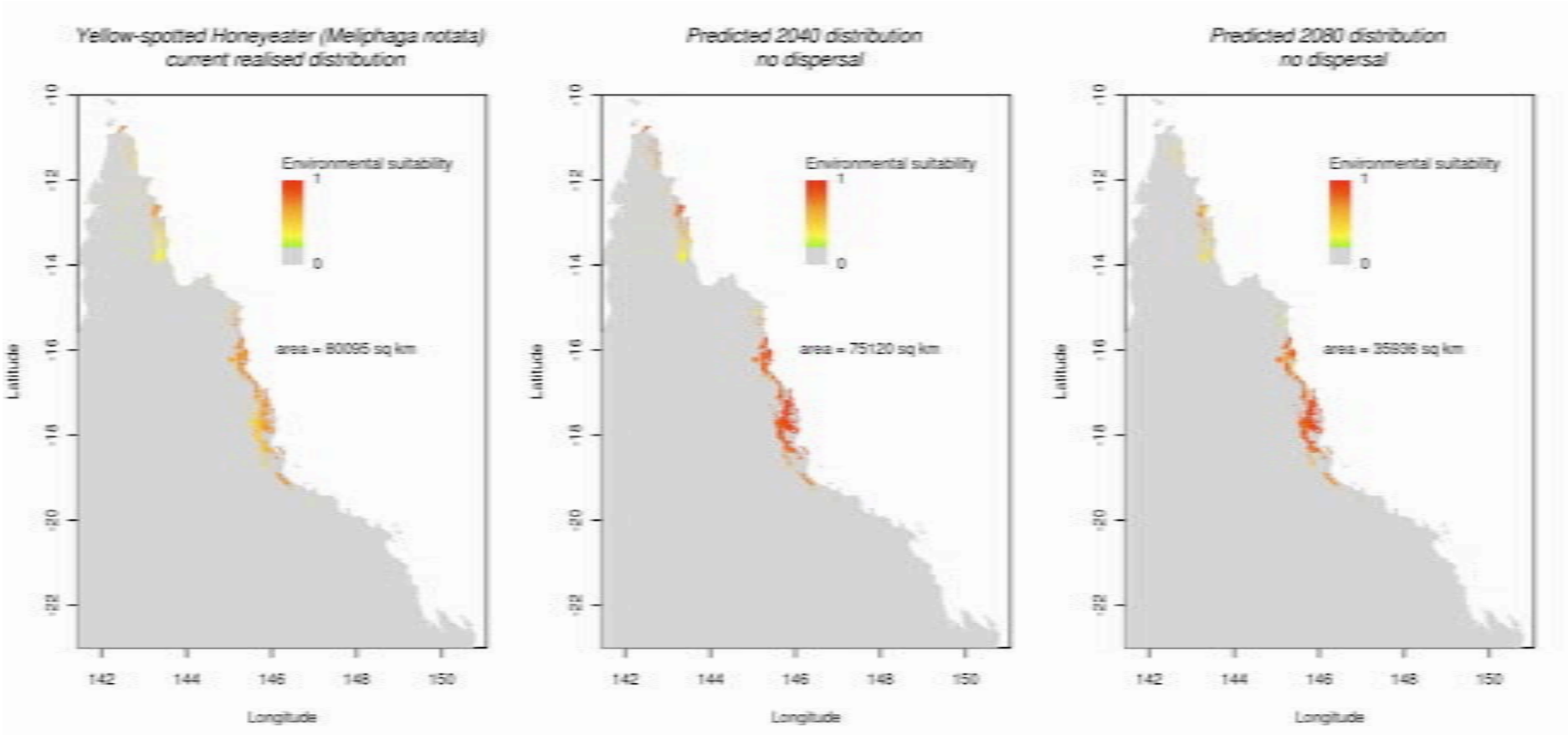


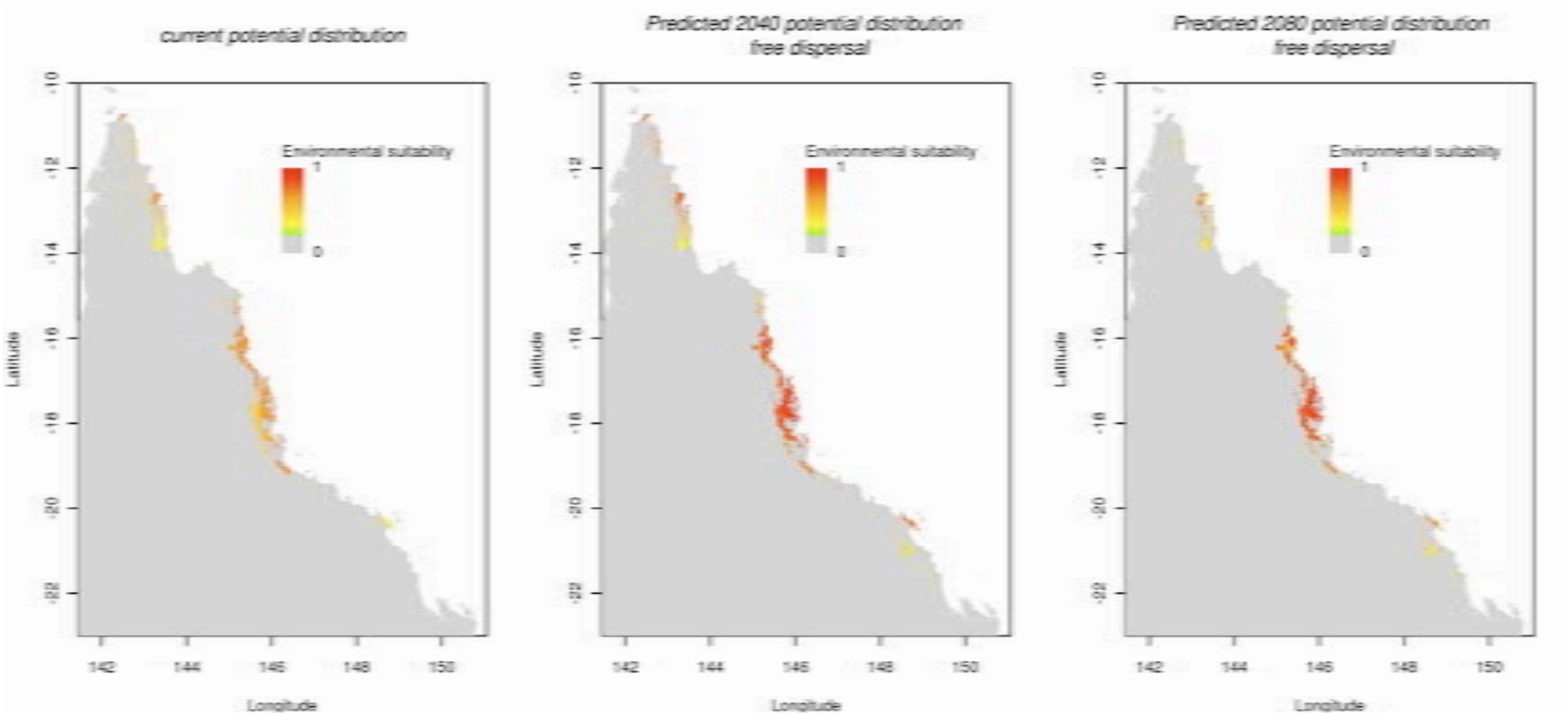
Appendix Figure 7.9. *Maps of the predicted distribution of suitable environmental area for Eclectus parrot (Eclectus roratus) under under contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Lovely Fairy-wren (Malurus amabilis)
current realised distribution
Environmental suitability
1
0
area = 88829 sq km
Latitude
Longitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 115427 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 115581 sq km
Latitude
Longitude

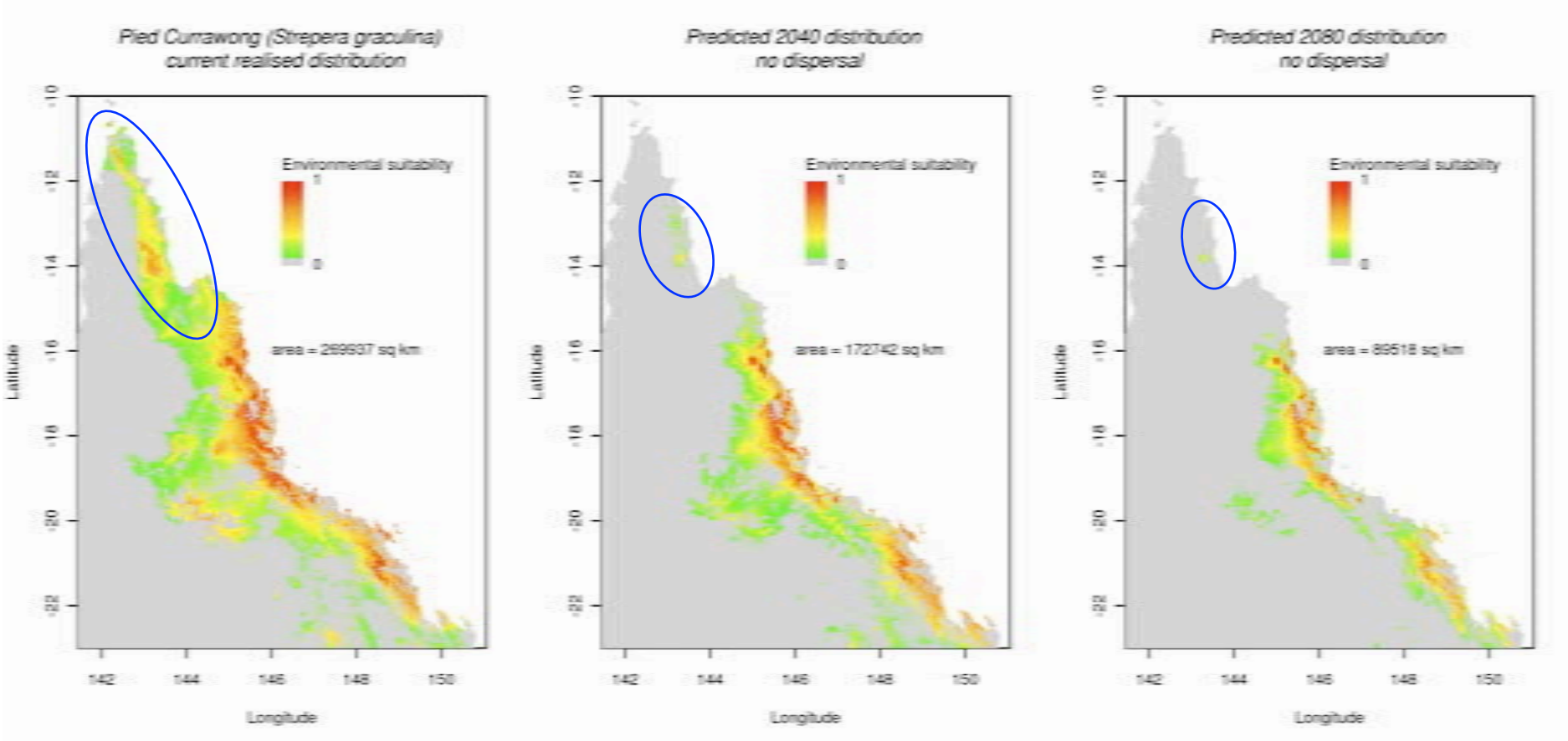


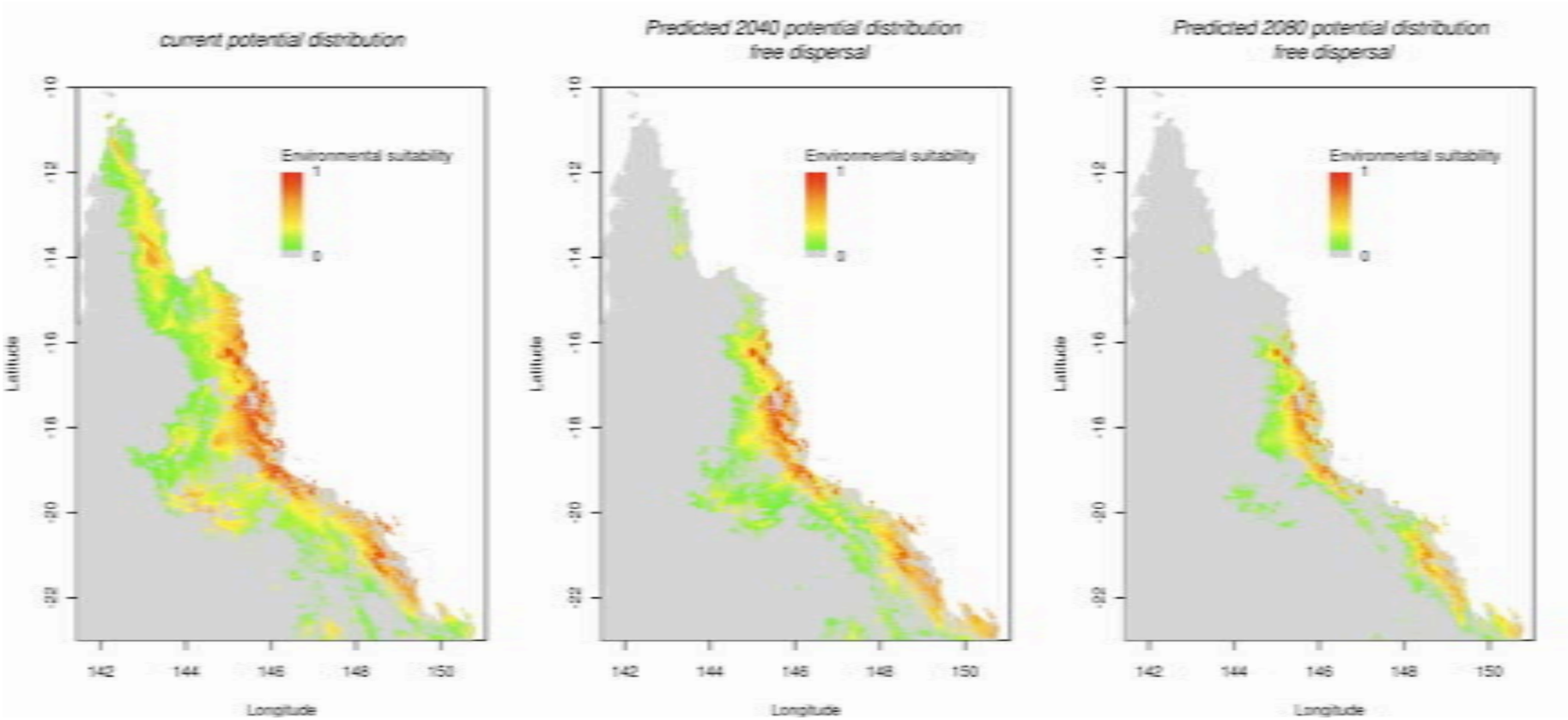
Appendix Figure 7.10. *Maps of the predicted distribution of suitable environmental area for Lovely Fairy-wren* (Malurus amabilis) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Yellow-spotted Honeyeater (Meliphaga notata)
current realised distribution
Environmental suitability
1
0
area = 80095 sq km
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 75120 sq km
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 35936 sq km
Latitude
Longitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150

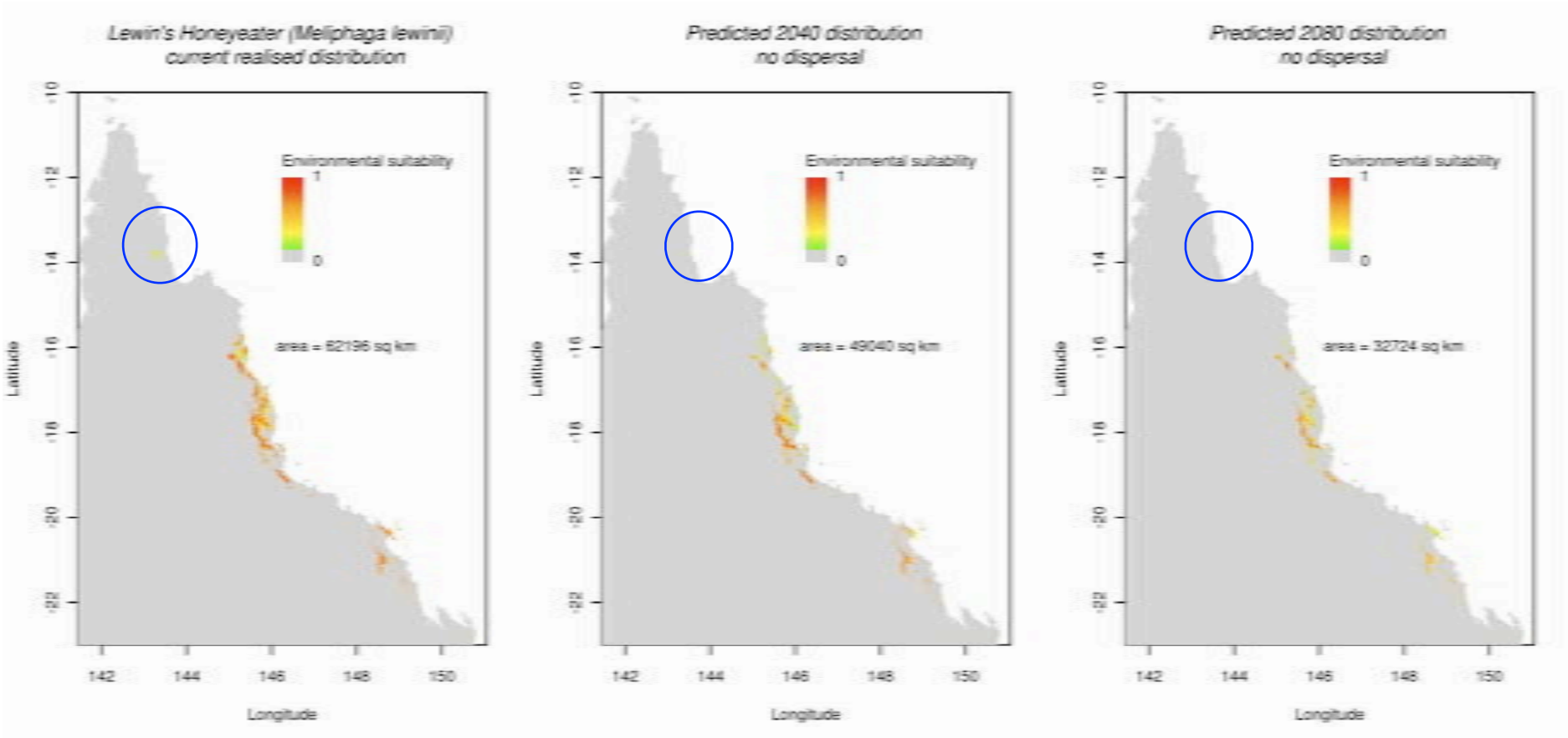


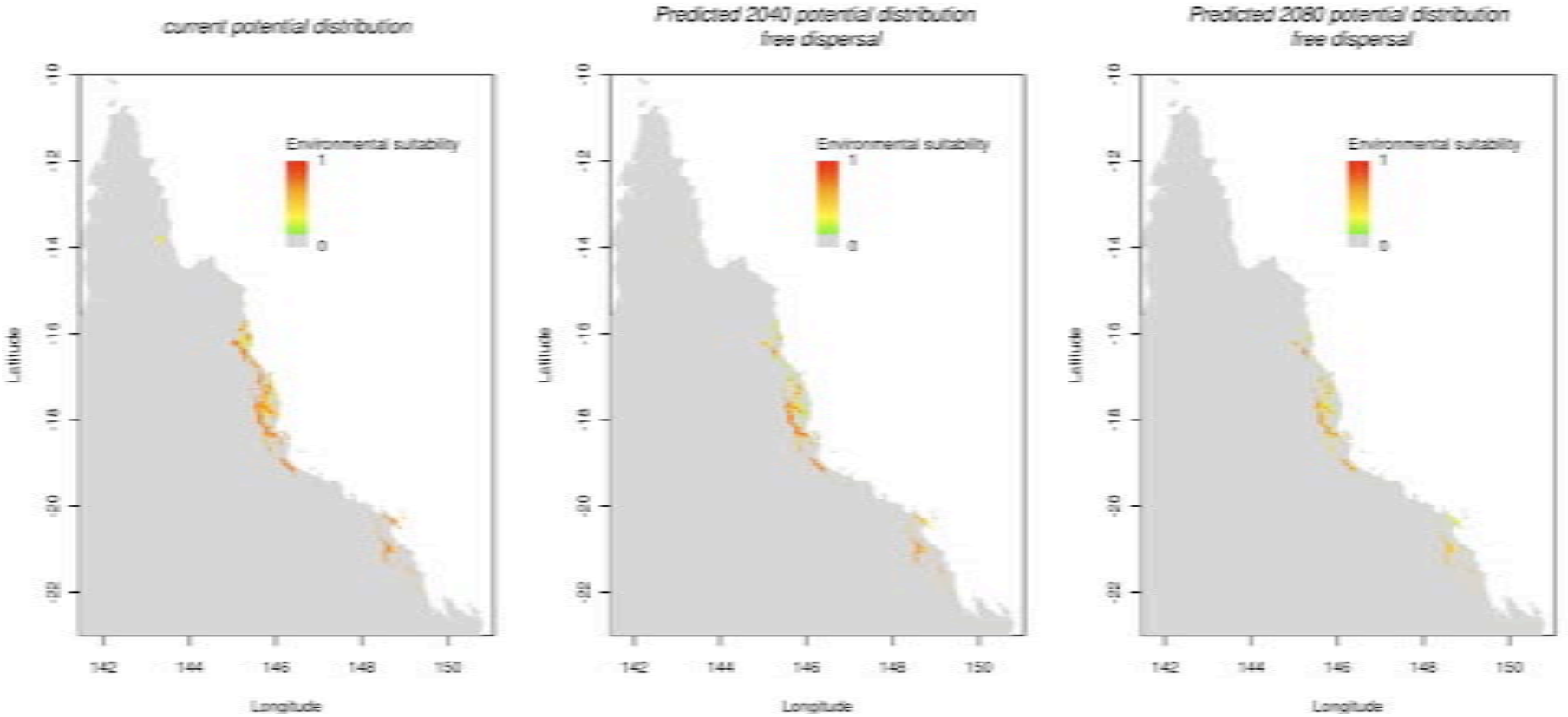
Appendix Figure 7.11. *Maps of the predicted distribution of suitable environmental area for Yellow-spotted Honeyeater* (Meliphaga notata) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables*


Pied Currawong (Strepera graculina)
current realised distribution
Environmental suitability
1
0
area = 269937 sq km
Latitude
Longitude
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 172742 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 89518 sq km
Latitude
Longitude

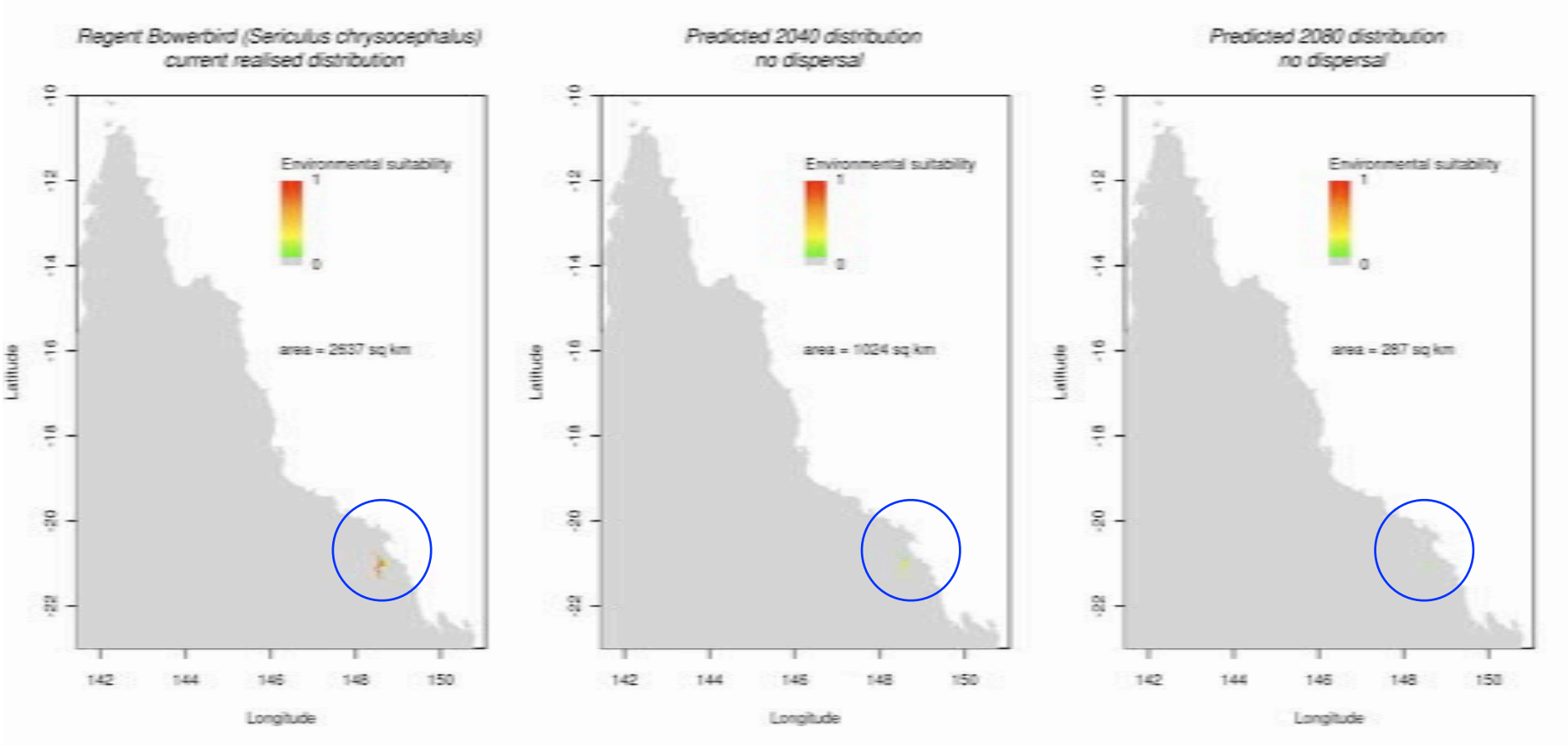


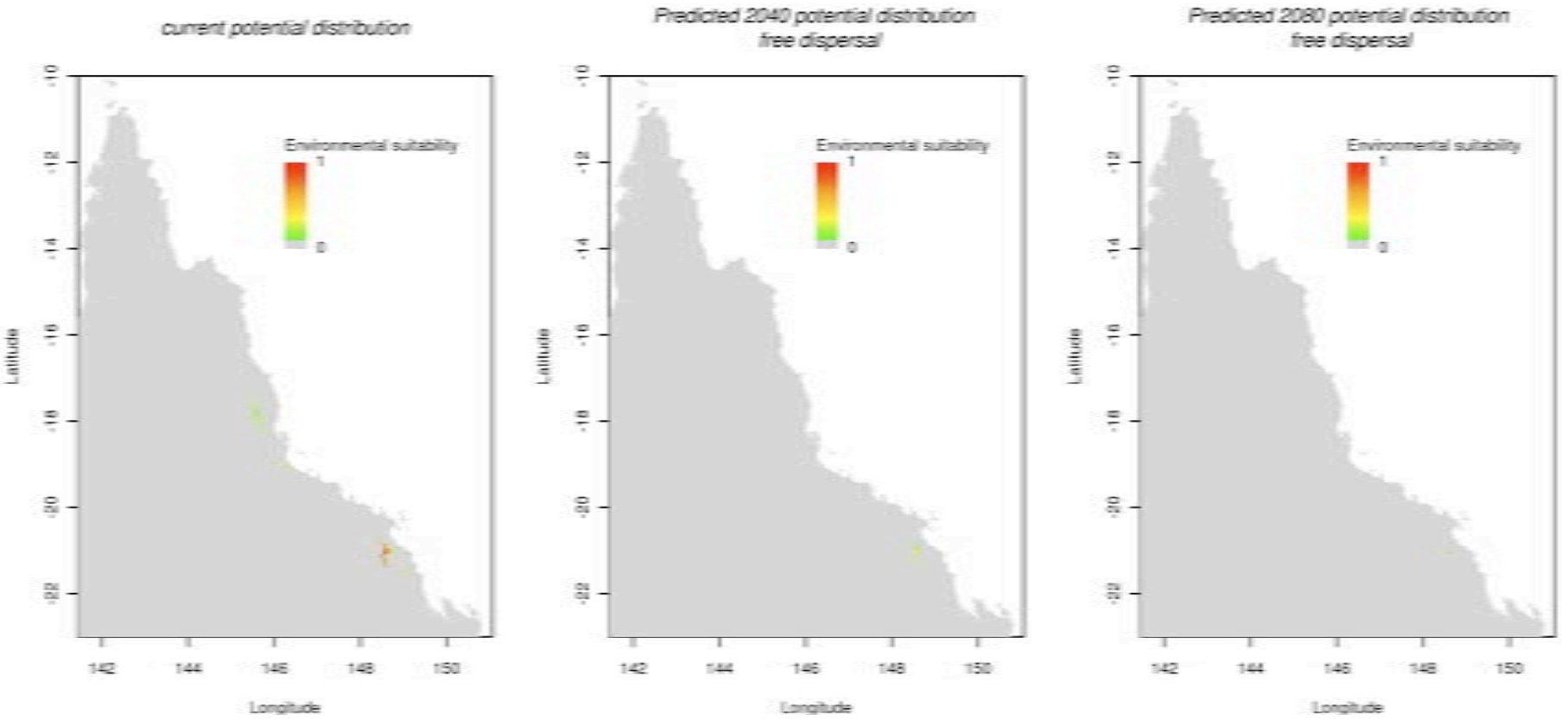
Appendix Figure 7.12. *Maps of the predicted distribution of suitable environmental area for Pied Currawong* (Strepera graculina) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables. The area of change mentioned in the text is circled in blue.*


Lewin's Honeyeater (Meliphaga lewinii)
current realised distribution
Environmental suitability
1
0
area = 82196 sq km
Latitude
Longitude
10
12
14
16
18
20
22
142
144
146
148
150
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 49040 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 32724 sq km
Latitude
Longitude



Appendix Figure 7.13. *Maps of the predicted distribution of suitable environmental area for Lewins Honeyeater* (Meliphaga lewinii) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables. The area of change of mentioned in the text is circled in blue.*


Regent Bowerbird (Sericulus chrysocephalus)
current realised distribution
Environmental suitability
1
0
area = 2637 sq km
Latitude
-10
-12
-14
-16
-18
-20
-22
142
144
146
148
150
Longitude
Predicted 2040 distribution
no dispersal
Environmental suitability
1
0
area = 1024 sq km
Latitude
Longitude
Predicted 2080 distribution
no dispersal
Environmental suitability
1
0
area = 287 sq km
Latitude
Longitude



Appendix Figure 7.14. *Maps of the predicted distribution of suitable environmental area for the isolated northern population Regent bowerbird* (Sericulus chrysocephalus) *contrasting scenarios of no dispersal (facing page) and free dispersal (above), showing the potential for expansion beyond the current limits of the species distribution as defined by climate variables. The area of change of interest is circled in blue.*